Examining the role of area closures for the protection and conservation of an over-exploited coastal shark species

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Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

University of Tasmania

October 2014

Declarations

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. All research was conducted with approval from the University of Tasmania Animal Ethics Committee (#A0011882) and the Department of Primary Industries and Water (Permit #11055).

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Statement of Co-authorship

Chapters 2-5 of this thesis have been prepared as scientific manuscripts and are currently in review with the journals as identified on the title page of each chapter. In all cases experimental design, field and laboratory work, data analysis and interpretation, and manuscript preparation were the primary responsibility of the candidate. However, these studies were carried out in collaboration with supervisors and co-authors. Contributions of co-authors are outlined below:

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Jayson Semmens and Adam Barnett provided advice on experimental design, assisted with fieldwork, and provided advice on manuscript preparation. Jeremy Lyle provided advice on manuscript preparation. Jayson Semmens was responsible for sourcing most of the funding for this study.

Chapter 3

Jayson Semmens and Adam Barnett provided advice on experimental design, assisted with fieldwork, and provided advice on manuscript preparation. Jeremy Lyle provided advice on manuscript preparation. Jayson Semmens was responsible for sourcing most of the funding for this study.

Chapter 4

Jayson Semmens and Adam Barnett provided advice on experimental design, assisted with fieldwork, and provided advice on manuscript preparation.

Chapter 5

Jayson Semmens and Adam Barnett provided advice on experimental design, assisted with fieldwork, and provided advice on manuscript preparation. Kátya Abrantes provided advice on stable isotope analysis and manuscript preparation. Jayson Semmens was responsible for sourcing most of the funding for this study.

We the undersigned agree with the above stated proportion of work undertaken for each of the above submitted peer-reviewed manuscripts contributing to this thesis:

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Abstract

Area closures have become increasingly popular in the management of marine resources and in helping to rebuild overexploited species, yet their effectiveness rely on a sound understanding of key animal behaviours such as movement and residency, which for many highly mobile species remains largely unknown. The nursery areas of school shark (*Galeorhinus galeus*) have been protected throughout southern Australia since the 1960s in an effort to re-build severely overfished stocks. Only recently have there been signs of recovery in the population, however, a limited understanding of how and when *G. galeus* utilise protected nurseries makes it difficult to evaluate the role and effectiveness of these areas in current stock re-building and management strategies. Throughout this thesis, acoustic telemetry and stable isotope analysis together with more traditional catch rate surveys are used in a series of studies to address these limitations in our current understanding of *G. galeus* early life history, by examining the population dynamics and ecology of this overfished species and several other chondrichthyan species in a protected nursery area in southeast Tasmania.

The first seasonal longline fishing surveys since the 1990s revealed young-of-the-year (YOY) and juvenile *G. galeus* continue to occupy protected nursery areas during summer and autumn, as was the case in the 1990s. However, longline catch rates indicated that abundances of YOY *G. galeus* may have increased or at least have remained stable since sampling in 1991-97, but are likely still below those of historic handline catches in 1947-52. A re-analysis of historic research survey data indicated that variations in YOY abundance in this nursery reflected modelled stock declines through the history of the fishery, suggesting that continued monitoring of YOY abundances may provide an alternative to fishery dependent tools for monitoring trends in overall stock recovery.

Acoustic telemetry was used to better understand ontogenetic differences in site fidelity, habitat preferences and seasonal use of protected nursery areas by YOY and juvenile (1+) *G. galeus*. Both age classes showed a distinct seasonal pattern of occurrence in the refuge area with most departing the area during winter and only some YOY returning

the following spring. Whilst nursery areas continue to function and provide important habitat for the offspring of *G. galeus*, evidence of YOY and juveniles emigrating from these areas within their first 1-2 years and the fact that few YOY (33%) return suggest these areas may only afford protection for a more limited amount of time than previously thought. These results suggest that adopting a multi-facet management approach incorporating conventional fisheries management (e.g. catch limits) with area closures is critical to ensuring long-term conservation outcomes and recovery for this species.

Integration of acoustic telemetry with a novel application of stable isotope analysis was used to determine movement behaviours and the separation of parturition sites within a nursery area. YOY captured from an estuary historically considered an important pupping site for *G. galeus* had enriched $\delta^{13}C$ and $\delta^{15}N$ and were distinctly separated from those captured in an adjoining coastal embayment suggesting that individuals were born at either site and remained within their birth sites for an extended period. This conclusion was supported by acoustic tracking which showed that YOY *G. galeus* remained in the estuary for 3-4 months after parturition before migrating to the coastal embayment.

Stable isotope analysis and acoustic telemetry were also integrated with traditional catch rate surveys to examine how various chondrichthyan species (three sharks, three rays and one chimera) and a common teleost coexist in an important pupping area for *G. galeus* with limited predation risk. Dietary partitioning was evident between species which had high spatial overlap. In contrast species which were competing for similar dietary requirements often foraged in different habitats. These results demonstrate that resource partitioning strategies play an important role in shaping the dynamics of shark nursery areas, ecological mechanisms that must be maintained in developing strategies to enhance the recovery of *G. galeus*.

Together these studies provide a greater understanding of how nursery areas are utilised by *G. galeus* and chondrichthyans in general. This study demonstrates the value of integrating multiple sampling methodologies to improve the resolution and understanding of key animal behaviours needed to evaluate and refine the effectiveness

of current area closures and enhance our efforts to conserve and promote the recovery of overexploited marine resources.

School shark (*Galeorhinus galeus*). Copyright Fisheries Research and Development Corporation (FRDC).

Acknowledgements

Firstly thanks must go to my supervisors, Jayson Semmens and Jeremy Lyle for all their support, guidance and inspiration throughout the PhD. Jayson for giving me the opportunity to take on this project, the endless hours discussing ideas and direction of the project, and for teaching me the intricacies of surgery techniques for acoustic tagging of animals. Jeremy for encouraging me to take on a PhD and for providing valuable guidance in the writing and structuring of the thesis. Also thanks must go to Colin Buxton for support and guidance during the initial phases of my study.

A special mention to Adam Barnett who provided much of the inspiration for my work and for all the field assistance. Your advice, knowledge, guidance, and friendship have been a significant driver for the success and completion of this thesis. Thanks also to Kátya Abrantes for your guidance and help with stable isotope analysis; you truly are the isotope guru.

By far some of the greatest appreciation and thanks must go to all the staff and students at IMAS who have assisted and supported me throughout this study. In particular, to Edward Forbes, Dane Jones, Dave Faloon, Luisa Forbes, Cynthia Awruch, Andrew Pender, Justin Hulls, Mike Porteus, Kilian Stehfest, and Rob French for their friendship, and fantastic field and laboratory assistance. I suspect the baked morning teas provided much of the incentive for your help on all those freezing mornings retrieving longlines and acoustic receivers, but either way much of this study would never have happened without you, so thank you all very much. To all the remaining staff at IMAS, whether it was helping pour concrete when building all those acoustic receiver moorings or just asking how things were travelling with the PhD in passing, thanks also for making me feel part of the team at IMAS Taroona.

Thanks to the generosity of the Winifred Violet Scott Foundation, Save Our Seas Foundation, and Holsworth Wildlife Research Endowment. They have provided the funding for the project which would not have been the success it was without their

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General Introduction

1.1 Area closures as a management tool

Overfishing has resulted in widespread decline and collapse of many global fisheries (Pauly *et al.*, 1998; Hutchings, 2000; Myers and Worm, 2003). In response, conventional fisheries management techniques such as catch and effort restrictions are often used to limit overfishing, however, spatial management in the form of area closures are being increasingly used to supplement these strategies (Roberts *et al.*, 2001; Dinmore *et al.*, 2003; Gell and Roberts, 2003; Gaylord *et al.*, 2005; Thorpe *et al.*, 2011). Area closures are regions where the extraction of resources, primarily by fisheries, and access to vulnerable habitats is restricted either temporarily, seasonally or permanently (Botsford *et al.*, 2003; Sobel and Dahlgren, 2004; Gaines *et al.*, 2010). In their simplest form they provide refuges where populations of exploited species can recover and habitats modified by anthropogenic disturbance can regenerate (Gell and Roberts, 2003). Surrounding areas and subsequent fisheries may then benefit from spillover of juveniles and adults, and export of eggs and larvae outside the closed area boundaries (Roberts *et al.*, 2001; Gell and Roberts, 2003; Hilborn *et al.*, 2004b; Russ *et al.*, 2004; Roberts *et al.*, 2005; Roberts, 2012).

Perhaps the most recognised use of area closures are the implementation of Marine Protected Areas (MPAs) (Gubbay, 1995b; Agardy, 1997; Edgar *et al.*, 2007; Thorpe *et al.*, 2011). MPAs are funadmentaly designed to enahnce biodiversity by providing a

safe haven for marine life and their habitats (Gubbay, 1995a; Dahlgren *et al.*, 2006). However, MPAs are probably one of the more contencious strategies used in marine resource management and there is still considerable debate surrounding their conservation merits (Agardy *et al.*, 2003; Halpern, 2003; Hilborn *et al.*, 2004b; Jones, 2007; Kearney *et al.*, 2012; Kearney *et al.*, 2013). Much of the uncertainty surrounding MPAs, and area closures in general, stems from a limited understanding of how key species utilise these areas and how these systems function (Agardy, 2000). Prior to establishing an area closure it is crucial to understand key animal behaviours such as movement and species interactions to properly evaluate and appreciate the benefits that areas closures will derive. However, due to the urgent need to protect vulnerable species already suffering from over-exploitation many area closures are implemented withouout any firm knowledge of these behaviours, thus limiting our understanding of how closed areas will function and benefit those species that they are designed to protect (Roberts, 2000; Agardy *et al.*, 2003; Heupel and Simpfendorfer, 2005b; Lucifora *et al.*, 2011).

Until recently, the difficulties of obtaining data on key behaviours for aquatic organisms, particulalry those that are highly mobile, has been a major reason for the paucity of information available when developing spatial management options. Traditionally researchers have relied on sampling techniques such as abundance surveys and tag-recapture experiments to examine behaviours such as movement, habitat selection and species interactions (McFarlane *et al.*, 1990; Nichols, 1992; Kohler and Turner, 2001). Whilst these techniques are still valuable in providing some understanding of these key behaviours and for comparing with historical records, they generally lack the resoultion needed to design effective area closures (Sibert and Nielsen, 2001; Nielsen *et al.*, 2009). For example traditional tag-recapture data provide only two points in an animals life history, the point of tagging and release and the point of re-capture; it does not provide any detail of behaviours that occur in between tagging and re-capture. However, advancements in modern electronic tracking tools such as acoustic telemetry and trophic-analytical methods such as stable isotope analysis, are rapidly overcoming these limitations to advance our undertanding of animal behaviour, movements and ecosystem dynamics, needed to understand the effectiveness of spatial area closures (e.g. DeAngelis *et al.*, 2008; Kinney *et al.*, 2011; Speed *et al.*, 2011).

Whilst understanding key animal behaviours is essential to establishing area closures, of equal importance is a need to monitor closed areas over time in order to evaluate their perfomance and continued ability to function as designed (Alder *et al.*, 2002; Pomeroy *et al.*, 2004; Gerber *et al.*, 2005; Pomeroy *et al.*, 2005). Simply restricting access to an area does not guarantee it will be immune from environmental and anthropogenic disturbances and there is growing evidence that these disturbances are altering the function and conservation benefits afforded by many area closures (Rogers and Beets, 2001; Jones *et al.*, 2004; Williamson *et al.*, 2014). Urban development, alteration of catchments, and sewage and waste disposal, are emerging as some of the greatest anthropogenic threats to coastal areas, including those managed by area closures (Kappel, 2005; Halpern *et al.*, 2007). Monitoring is therefore critical to assess the effectiveness of area closures and allow prompt adjustment of management strategies to maintain their functional role (Gerber *et al.*, 2005).

1.2 Shark nursery area closures

In the marine realm, one of the broad criticisms of area closures is that they typically only provide the greatest benefits to species which have high site fidelity and remain within the closed area, such as reef fishes (Gell and Roberts, 2003; Gerber *et al.*, 2003; Hilborn *et al.*, 2004b). For more mobile and highly migratory species it is generally considered that in order to protect these species using area closures, vast areas of coastline would need to be protected in order to afford effective protection, making conservation unfeasible (Kramer and Chapman, 1999a; Roberts, 2000; Baum *et al.*, 2003; Gell and Roberts, 2003; Shipp, 2003; Heupel and Simpfendorfer, 2005b; Heupel *et al.*, 2007; Kinney and Simpfendorfer, 2009; Grüss *et al.*, 2011). Therefore spatial management of mobile marine species has mostly concentrated on protecting more targeted, discrete areas and habitats used during early life history, such as nursery areas (Roberts, 2000; Heupel and Simpfendorfer, 2005b).

Sharks are among some of the more highly mobile species in our oceans, however, many species utilise shallow coastal embayments and estuaries as nursery areas where their offspring spend the first few months to years of their lives (Castro, 1993; Bethea *et*

al., 2007; Heupel *et al.*, 2007; Skomal, 2007b). Protection of nursery areas has therefore been a common strategy that has been employed to protect the early life stages of sharks (see Shotton, 1999) as they are generally thought to be essential for the long term sustainability of shark populations (Lack and Group, 2004; Fowler *et al.*, 2005; Bethea *et al.*, 2007). However, because of their high mobility, it is recognised that nursery closures may have little benefit in the absence of conventional fisheries management strategies that protect sharks at vulnerable life stages and limit fishing mortality outside of closed areas (Kinney and Simpfendorfer, 2009). Nevertheless, careful placement of small area closures has been demonstrated to benefit some mobile species such as teleosts (Kerwath *et al.*, 2009; Claudet *et al.*, 2010) and there is emerging evidence that they may benefit some shark species (Knip *et al.*, 2012). Therefore studies are required to test the role and effectiveness of nursery areas in the overall management of shark populations based on understanding how and when sharks utilise such protected areas (Heupel and Simpfendorfer, 2005b).

Shark nursery areas serve many functions, such as providing important habitats for reproduction (Castro, 1993), foraging (Bethea *et al.*, 2004; Barnett and Semmens, 2012), and refuge from predation (Heupel and Hueter, 2002; Heupel and Simpfendorfer, 2005a; Wetherbee *et al.*, 2007). Therefore compiling a sound understanding of an animals ecology, movement and habitat is essential for optimising the placment and effectiveness of closed nursery areas for mobile species (Kramer and Chapman, 1999b; Grüss *et al.*, 2011). However, like many area closures the implementation of shark nursery protection is often done with little ecological understanding of these functions and are often based on the capture of only a few juveniles (Heupel *et al.*, 2007). Heupel *et al.* (2007) recommends that a shark nursery area should demonstrate that newborn or juvenile sharks (1) are more abundant than in other areas where the species is found, (2) remain within the area for extended periods (i.e. weeks or months) and (3) repeatedly used as a pupping area across years. Yet only recently have studies begun to gather empirical data needed to understand the functional role of nurseries prior to their establishment as protected areas (e.g. Barnett *et al.*, 2012). Nevertheless, gathering these data after establishment can still provide management with useful guidance on how best to manipulate current designs to improve area closure effectiveness, particularly as sampling techniques advance and improve our understanding of key

animal behaviours. Without these data the effectiveness of nursery closures will be severely compromised if they fail to encompass a large part of a sharks home range or functional habitat that is important for the survival of that species' (Heupel *et al.*, 2007). Understanding these behaviours also enables nurseries to be re-defined in accordance with more appropriate criteria, such as proposed by Heupel *et al.* (2007), which will assist management in prioritising conservation efforts directed towards protecting areas of greatest importance.

Shark nurseries can host multiple shark species and are often characterised as being shallow, coastal areas where young sharks have access to ample food resources and are less vulnerable to predation (Springer, 1967; Castro, 1987; 1993; Morrissey and Gruber, 1993; Simpfendorfer and Milward, 1993). However, evidence of slow growth and high mortality among juvenile sharks in nurseries, partly attributed to limited food resources and high rates of predation (Bush and Holland, 2002; Heupel and Simpfendorfer, 2002; Duncan and Holland, 2006), indicate that traditional nursery area paradigms may no longer be applicable in all situations (Heupel *et al.*, 2007). Similarly, several studies have demonstrated that dietary (e.g. Bethea *et al.*, 2004; Vaudo and Heithaus, 2011) and habitat partitioning (e.g. White and Potter, 2004; DeAngelis *et al.*, 2008) play a critical role in enabling multiple species to coexist in nursery areas with a view that these behaviours may be adaption's in response to limited resources (Bethea *et al.*, 2004; Kinney *et al.*, 2011). However, most of these studies have examined dietary and habitat partitioning in isolation, and there is limited published evidence of these behaviours occurring in unison (e.g. Speed *et al.*, 2012), as a response to predation risk (e.g. Papastamatiou *et al.*, 2006), or between other competitor species, including teleosts (e.g. Kinney *et al.*, 2011). Knowledge of how multiple species interact and respond to competition and predation is essential to understanding how ecosystems are structured and function (Holt, 1977; Sih *et al.*, 1985; Cherrett and Bradshaw, 1989). An understanding of these ecosystem dynamics can then be used to make more informed decisions regarding the development and implementation of effective ecosystem-based management strategies and for assessing how animals may respond to anthropogenic disturbance and disrupted ecosystem balance (Walters and Kitchell, 2001; Dill *et al.*, 2003; Baskett *et al.*, 2006).

1.3 Main study species: school shark (*Galeorhinus galeus*)

School shark (*Galeorhinus galeus*) are members of the family Triakidae, commonly referred to as 'houndsharks'. *Galeorhinus galeus* are widely distributed throughout temperate waters of the world and are generally found in small schools of predominantly the one sex and size class (Last and Stevens, 2009). *Galeorhinus galeus* can reach up to 195 cm in length and live for up to 60 years with maturity typically occurring at about four years for males and eight years for females (Last and Stevens, 2009). During the summer and autumn months pregnant females migrate into shallow coastal embayment's where they give birth to litters of around 30 pups every three years after a gestation period of 12-months (Olsen, 1984; Last and Stevens, 2009).

Galeorhinus galeus have been exploited throughout their distribution since the 1920s and once formed the bulk of the market for shark meat, more commonly known as 'flake', however, intense fishing pressure has resulted in significant stock declines, particularly in Australia (Walker *et al.*, 2006). In Australia the *G. galeus* comprised the bulk of the Southern and Eastern Scalefish and Shark Fishery (SESSF) up until the early 1950s when the fishery experienced significant catch declines (Olsen, 1959) (Fig. 1.1; see Table 1.1 for a historical summary of the SESSF). In response to declining stocks eleven bays and estuaries around Tasmania (Fig. 1.2) identified as nurseries for the species were proclaimed as Shark Refuge Areas (SRAs) in 1962, and the taking of sharks from these areas prohibited to reduce fishing mortality on juvenile and pregnant *G. galeus*, in an attempt to rebuild the population (Walker, 1999; Kinney and Simpfendorfer, 2009). Recreational and limited commercial fishing were still permitted in SRAs, however, sharks were not to be targeted or retained; regulations which remain current today (DPIPWE, 2013). Furthermore, several Victorian estuaries also identified as nurseries have been protected through the closure in 1988 of Victorian coastal waters, offshore to three nautical miles, to commercial shark fishing (Walker, 1999).
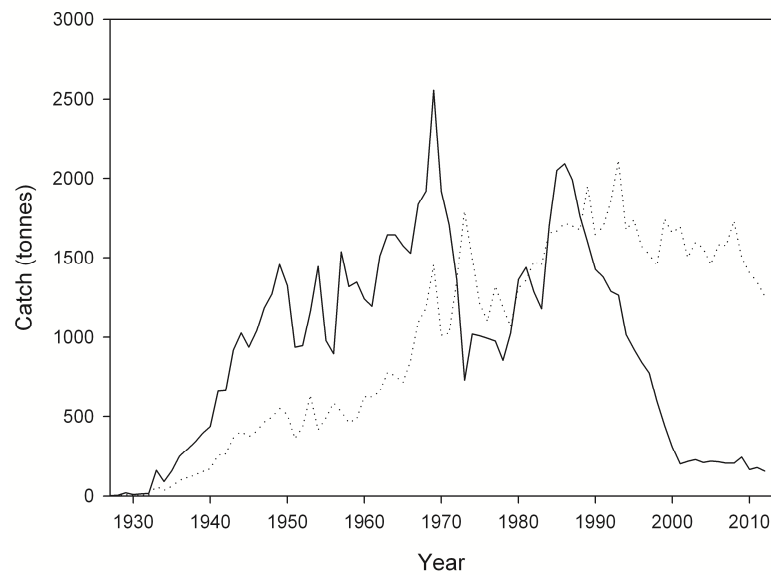
Figure 1.1 Total catch of *G. galeus* (solid line) and gummy shark (*Mustelius antarcticus*) (dotted line) from 1927 to 2013 in the Southern and Eastern Shark Fishery. (Source: Australian Fisheries Management Authority)

Despite protection of nurseries and closure of fishing grounds, the fishery had showed no signs of recovery and juvenile *G. galeus* were either absent from or occurred in significantly lower numbers in many of these protected areas in the late 1990s compared with the 1950s (CSIRO, 1993; Stevens and West, 1997). Continued overfishing and a limited reduction in fishing effort throughout the 1970s and 1980s was considered the main reason for the population collapse and failed recovery, however, it has been suggested that habitat degradation, particularly the loss of seagrass meadows in Victorian nursery areas and a reduction in the abundance of YOY *G. galeus* occurring in these areas may have also contributed to these declines (Stevens and West, 1997; AFMA, 2009). Therefore the functional role of some of these nurseries has been fundamentally questioned (McLoughlin, 2008; AFMA, 2009), in particular do known nursery areas continue to be significant to the population or has there been a shift in the functionality and relative importance of particular nurseries as a result of environmental and fishing pressures? However, interpreting the nature of these potential changes in nursery area function is difficult without an understanding of current population dynamics within nursery areas and the animal behaviours which contribute to their use and how they may compare historically.
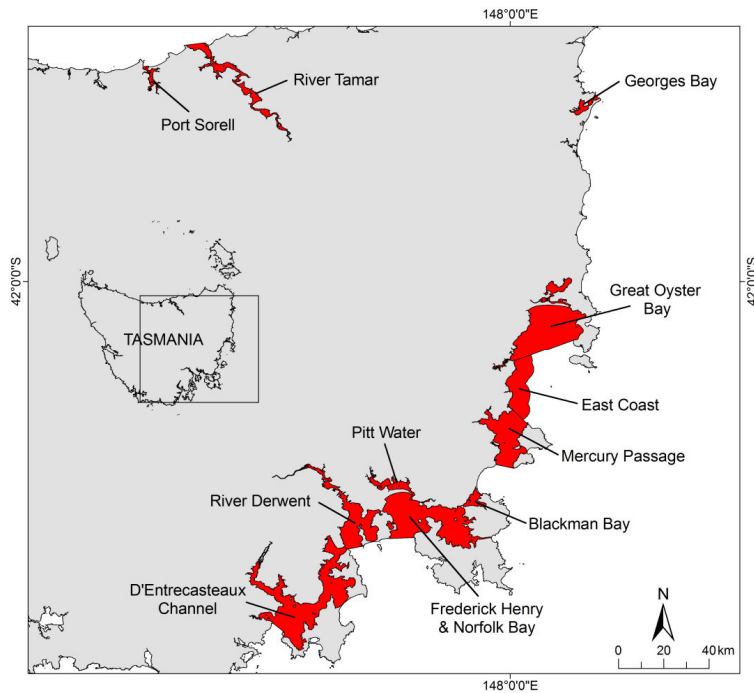
Figure 1.2 Location of Shark Refuge Areas (SRAs) in Tasmania. Map reproduced with permission of the Department of Primary Industries Parks Water and Environment, Tasmania.

Since the early 2000s further fishing restrictions, gear modifications and fishing ground closures have been implemented in an effort to reduce fishery captures (McLoughlin, 2008) and a School Shark Rebuilding Strategy (SSRS) has been in place since 2008 to help promote stock recovery (AFMA, 2009) (see Table 1.1 for a summary of management changes). Recent stock assessments indicate that *G. galeus* populations in southern Australia may have stabilised at around 9-14% of virgin biomass and there is anecdotal evidence that suggest they are becoming increasingly common in fishery catches as a non-target species in the SESSF (AFMA, 2009; SharkRAG, 2010). Whilst it is unclear as to the extent that the protection of nurseries have contributed to this stabilisation, identifying the full extent of other areas used as nursery areas that may not currently be identified and continuing to protect established nurseries by reducing pressures such as environmental degradation, has been recognised as the first stage in the SSRS (AFMA, 2009). Yet, there have been no formal assessments of SRAs since the 1990s to address questions regarding their current functionality as nursery habitat for *G. galeus* or if the functionality of particular nurseries has altered in response to the degradation and deterioration of some nurseries such as those in Victoria. A paucity of

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this information makes it difficult to evaluate the current role of nursery area closures in the overall management and conservation of *G. galeus*.

Moreover, despite the high importance placed on shark refuge areas for the protection of *G. galeus* these areas also support a diversity of chondrichthyan and teleost species (Stevens and West, 1997). However, much of this earlier work on shark nursery areas in southeast Australia were based mainly on research fishing to determine indices of abundance and conventional tagging surveys to determine movement (Olsen, 1954; Stevens and West, 1997) providing limited understanding of how *G. galeus* and other chondrichthyans utilise and interact within these nurseries. Recent studies have demonstrated that the dominant apex predator, the broadnose sevengill shark (*Notorynchus cepedianus*) have complex predator-prey interactions with mesopredators (i.e. mid-level predators) including *G. galeus* in these areas and may be largely responsible for determining nursery area dynamics (Barnett *et al.*, 2010a; Barnett *et al.*, 2010b; Barnett *et al.*, 2010c; Barnett *et al.*, 2011; Barnett and Semmens, 2012). Yet these studies also conclude by emphasising the need to better understand the role mesopredators play in these systems particularly in areas historically important to *G. galeus*, by better understanding their abundance and behaviour.

Table 1.1 Historical summary of major fishery and management events relating to *G. galeus* in the Southern and Eastern Shark Fishery (Walker, 1999; Stobutzki *et al.*, 2010; Huveneers *et al.*, 2013).

Year	Description
1927	Shark fishing first recorded in southern Australia.
1940s	Fishery expands due to demand for shark liver oil (fishery targets mainly pregnant adults and juveniles found in inshore areas such as Port Phillip Bay, Victoria). Introduction of first minimum legal size limits.
1950s	Fishery plateaus as demand for shark liver oil declines. Fishery shifts from inshore to offshore waters as catches decline in inshore areas by up to 50%. Nursery areas are identified (Olsen, 1954) and concerns rise over declining *G. galeus* CPUE in the fishery. Seasonal closures are introduced to protect migrating pregnant females.
1954	Closure of Tasmanian inshore waters to commercial shark fishing (becoming formally recognised as Shark Refuge Areas in 1962).
1960s	Demand for shark meat increases which coincides with the introduction of gillnets into the fishery. Fishery catches peak at 2556 tonnes in 1969.
1970s	Concern over high mercury levels in shark see the banning of large *G. galeus* from sale from 1972 to 1985. Fishery shifts to targeting predominantly *M. antarcticus* and a minimum legal gillnet mesh size of 150 mm is introduced in 1975.
1977	First *G. galeus* stock assessment conducted.
1980s	Fishery assessed as overfished. Fishery remains open access until 1984, after which a fishing boat licence endorsement was required to access the fishery. Mercury ban lifted and catches reach 2090 tonnes in 1986.
1988	*Southern Shark Fishery management plan* (1988) introduced creating a limited entry gillnet fishery, in an attempt to reduce fishing effort. Targeted shark fishing in all Victorian coastal waters out to 3 nm is banned to protect *G. galeus* pupping grounds.
1990s	Stevens and West (1997) re-visit nursery areas examined by Olsen (1954) to discover neonate and juvenile *G. galeus* were either absent from or found in significantly lower abundances.
1990 to 1993	Fishery assessed as overfished and in danger of collapse. Fishing effort is reduced by decreasing net units from 6000 m to 4200 m.
1997	An upper mesh size limit of 165 mm was introduced to reduce capture of large adult *G. galeus*.
2000 to 2001	Responsibility of management of *G. galeus* is transferred from States to the Commonwealth. Introduction of Individual Transferable Quotas (ITQs) effectively stopping the targeted fishing for *G. galeus*. A Total Allowable Catch (TAC) limit is set at 434 tonnes.
2007	*Galeorhinus galeus* stock size estimated at between 9-14 % of original pup production levels (McLoughlin, 2008). Regional area closures implemented to prevent fishing for sharks in areas deeper than 130-183 m.
2008	The School Shark Rebuilding Strategy introduced with the objective of rebuilding stocks to between 20% and 40% within biologically reasonable timeframes.
2009	*Galeorhinus galeus* listed as conservation dependant under the *Environment Protection and Biodiversity Conservation Act 1999*.
2012	*Galeorhinus galeus* TAC set at 150 tonnes.

1.4 Thesis objectives and structure

The overall aim of this study was to better understand how *G. galeus* and other chondrichthyans utilise designated SRAs. The study has two major objectives which are 1) to determine the historical changes in the population structure and abundance of *G. galeus* occurring in shark refuge areas, and 2) to determine the spatial and temporal use of shark refuge areas by *G. galeus* and co-occurring chondrichthyans. Through an improved understanding of chondrichthyan movement behaviours it is anticipated that the role of SRAs will be better understood and refined where necessary to enhance their effectiveness in the recovery and conservation of *G. galeus*. Furthermore, by establishing spatial and temporal movement behaviours, habitat use and feeding ecology, this study will further our understanding of chondrichthyans and their role in driving the ecosystem dynamics of these inshore areas. To achieve these objectives a combination of conventional and modern survey techniques have been applied in four major studies and corresponding data chapters, with an overall discussion linking Chapters 2-5 together (Chapter 6). Chapters have been prepared as standalone manuscripts for publication, all of which are currently under peer-review.

Determining the abundance and dynamics of ecological communities following periods of anthropogenic and environmental change is critical to assessing and improving the effectiveness of conservation and management strategies such as area closures. Chapter (2) re-examines the abundance and population structure of *G. galeus* in a shark refuge area using baited longline fishing to determine if these areas still host *G. galeus* populations. Recent (2012-14) young-of-the-year (YOY) longline catches are compared with similar surveys conducted in years 1991-97 to determine changes in relative abundance of *G. galeus*. This chapter also compares historical (1947-53, 1991-97 and 2012-14) YOY *G. galeus* catches in nursery areas with modelled stock productivity during these same time periods to determine the suitability of adopting fishery independent catch rate surveys to monitor stock recovery.

Understanding how animals use particular areas and the habitats within is essential to evaluating the effectiveness of current area closures. Chapter 3 examines the movement

behaviours of YOY and juvenile *G. galeus* to better understand how they are utilising these areas based on residency times. Acoustic telemetry is used to examine the spatial and temporal movement behaviours of *G. galeus* and determine the utilisation and importance of different habitats within the SRA. These data provide empirical evidence needed to assess if present area closure management strategies are providing adequate protection for *G. galeus* during early life history.

Stable isotope analysis has emerged as a viable tool for delineating the previous movement behaviours of animals by examining assimilated material in their tissues to trace back to where they may have foraged. Integrating stable isotope analysis with acoustic telemetry in Chapter 4 provides a greater understanding of the past foraging behaviours and subsequent movements of YOY *G. galeus* within a shark nursery. Together with dietary data these movement behaviours are then used to further understand the functional role of these nursery areas by inferring the distribution of birthing sites for *G. galeus*.

Competition and predation play a significant role in determining the structure and function of ecosystems. In Chapter 5, these behaviours were examined using a combination of stable isotope analysis to determine dietary overlap and acoustic telemetry to examine spatial overlap of chondrichthyans and a dominant teleost that occupy an important birthing site identified for *G. galeus* (Chapter 4). It examines the role of resource partitioning between chondrichthyans to enable multiple species to coexist in similar areas and how this may influence the recovery in *G. galeus* populations.

The thesis concludes with a general discussion (Chapter 6) which provides an overall summary of findings and discusses implications for fisheries management. It discusses the importance of shark nurseries for the recovery of *G. galeus* and outlines how the findings of this study can be used to make more informed and robust management decisions in the application of area closures for the conservation of sharks.

2

Re-examining the abundance of an over exploited fisheries species in a nursery area closure to monitor population recovery

2.1 Abstract

Determining the abundance and dynamics of ecological communities following periods of anthropogenic and environmental change is critical to assessing and improving the effectiveness of conservation and management strategies. Several coastal waters of south-east Tasmania have been proclaimed as shark refuge areas (SRAs) after significant overfishing and catch declines of school shark (*Galeorhinus galeus*) in Australia since the 1940s. These areas have provided protection for juvenile *G. galeus* in conjunction with fisheries management changes. This study compared recent (2012-2014) research longline catch data with historical research catch records (1947-1952 and 1991-1997) to determine whether young-of-the year (YOY) and juvenile *G. galeus* continue to utilise these nursery areas and whether changes in abundance reflected modelled stock production through time. Longline catch rates indicated that abundances of YOY *G. galeus* may have increased or at least have remained stable since sampling in 1991-97, but are likely still below those of historic handline catches in 1947-52. Catch records from 1947-52 were significantly correlated with modelled declines in stocks at the time, however, recent longline catch rates showed weak correlation with the model possibly due to depleted stock levels or a period of stock re-building and stabilisation. In the absence of reliable fishery dependant catch data, given the initially promising correlations with modelled stock size, ongoing YOY catch sampling in these areas may provide a viable fishery independent tool for measuring the recovery of over exploited species.

2.2 Introduction

Overfishing has been identified as the single greatest cause of ecological change in marine communities, resulting in widespread collapse of many global fisheries (Jackson *et al.*, 2001). Fisheries management strategies such as catch and effort restrictions and in more recent years, area closures, are typically implemented to reduce overfishing and help rebuild overfished stocks (Botsford *et al.*, 1997; Hilborn *et al.*, 2004a; Worm *et al.*, 2009). Therefore knowledge of how stocks respond to these strategies is essential for evaluating and refining their effectiveness and achieving conservation outcomes (Hilborn *et al.*, 1993; Walters and Maguire, 1996; Punt and Hilborn, 1997).

Monitoring fishery catch and effort data is typically used as an indicator of stock size (Maunder and Punt, 2004), however, long-term data sets are often incomplete (Mesnil *et al.*, 2009) and their reliability is variable due to changes in fisher behaviour and fishing techniques (Hilborn and Walters, 1992; Chen *et al.*, 2009). Although complex catch standardisations can account for these variations (Bishop, 2006), indices of stock size should ideally be based on fishery independent data (Maunder and Punt, 2004). Furthermore, collecting fishery independent data from areas closed to extractive fishing may also contribute to a better understanding of stock size because it provides a control baseline against which exploited populations can be compared (Hilborn *et al.*, 2004b).

School shark (*Galeorhinus galeus*) are widespread throughout the temperate waters of the world and historical overfishing has resulted in significant stock declines, particularly in Australia during the 1940s (Walker, 1999). In response to these declines, techniques including fishing gear restrictions and catch quotas have been implemented progressively and nursery areas proclaimed as Shark Refuge Areas (SRAs), where the taking of sharks was prohibited. Yet by the 1990s follow up surveys of several SRAs established that newborn *G. galeus* were either absent or present in significantly lower numbers in some SRAs when compared to the 1940s (Stevens and West, 1997). Continued overfishing of the adult stock was considered the most likely cause, although degradation of nursery habitats, possibly from coastal development and pollution, may have also contributed to the declines, particularly in Victorian waters (AFMA, 2009). Further gear restrictions and catch quotas were implemented and recent stock

assessment modelling suggests there has been some stabilization in stocks (AFMA, 2009). Along with managing catches, maintenance of SRAs is considered essential to ongoing stock rebuilding strategies for *G. galeus* (AFMA, 2009). There have been no repeat surveys of these SRAs since the 1990's to assess whether these areas are still being utilised by *G. galeus* and remain functional as nursery areas.

Galeorhinus galeus are currently managed as incidental bycatch in the Australian Southern and Eastern Scalefish and Shark Fishery (SESSF) with a total allowable catch (TAC) of between 200 – 225 tonnes/annum, with current fishing effort directed predominantly at gummy shark (*Mustelius antarcticus*) (AFMA, 2009). As a consequence, the use of fishery catch per unit effort (CPUE) is no longer considered appropriate as an indicator for *G. galeus* stock assessment modelling which has lead to several questions about the suitability of the model (Huveneers *et al.*, 2013). Similarly, the relationship between *G. galeus* young-of-the-year (YOY) abundance in SRAs as an indicator of stock production (or abundance) remain largely unknown. Fishery independent data such as the relative abundance of newborn *G. galeus* in SRAs may provide a proxy for monitoring trends in adult stock abundance. The objectives of this study were to 1) determine the temporal and spatial patterns of abundance and size structure of *G. galeus* to assess the current functionality of a historically important shark nursery area, and 2) assess the viability of using YOY abundances in nurseries as an indicator of *G. galeus* stock abundance.

2.3 Materials and methods

2.3.1 Study site

This study was conducted in Upper Pitt Water (UPW) and Frederick Henry Bay (FHB) in south east Tasmania, Australia (Fig. 2.1). UPW is a shallow (~4 m average depth) estuary, comprised of mostly intertidal sand flats and a deep central channel (~8 m) with a surface area of approximately 20.7 km2 (Fig. 2.1). UPW receives freshwater input from the Coal River after which it drains into Lower Pitt Water (LPW) via a manmade road causeway where it eventually enters into the deeper waters (10 – 30 m) of Frederick Henry and Storm Bay. Pitt Water and FHB (FHB) are managed by the

Tasmanian State Government as SRAs, which prohibits retention of any chondrichthyan species, apart from a limited take of elephant fish (*Callorhinchus milii*).
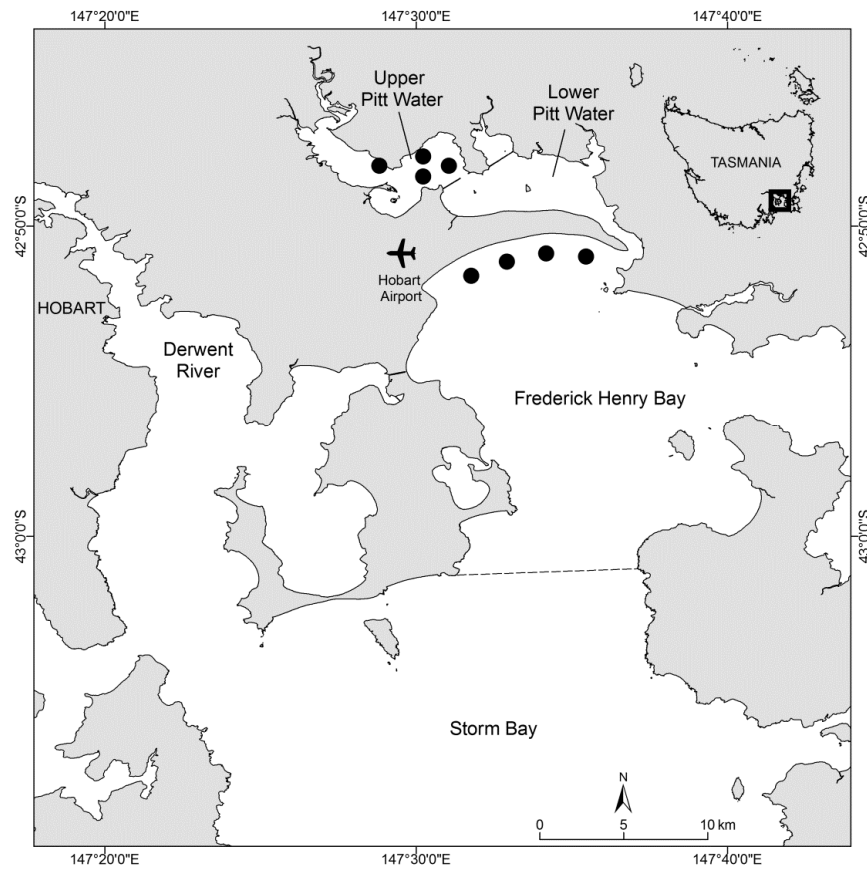
Figure 2.1 Map of study area in south east Tasmania showing the longline sampling sites (●). Dashed line represents the boundary of the shark refuge area.

2.3.2 2012 – 2014 animal collection

Sampling was undertaken seasonally between January 2012 and April 2014 using bottom set baited longlines (n = 28 shots). Longlines consisted of a 210 m, 6 mm lead core rope to which 50 stainless steel wire snoods with hooks (7x7 stainless steel wire, 160 lb breaking strain, Mustard #8260 size 5/0 hook) were attached at 4 m intervals using 100 mm swivel shark snap clips. Hooks were baited with squid. Longlines were set at four fixed locations in both UPW and FHB (Fig. 2.1) between 0700 and 0730 hours and were hauled between 0800 and 1000 hours. Lines were typically deployed for 1 – 2 hours. Captured sharks were identified, measured for total length (TL) to the nearest cm, sexed and released.

2.3.3 Historical and additional fishery data

Comparison of relative abundance between recent (i.e. 2012-2014) and historical periods was undertaken using available historical raw catch data collected by CSIRO between 1947 and 1956, and 1991 and 1997. Data collected during the 1947-56 period consisted of daily handline catches of *G. galeus* in upper and lower Pitt Water recorded during an intensive tagging programme of shark nurseries around Tasmania which have been published elsewhere (Olsen, 1954; Olsen, 1984). Shark nursery areas in southern Australia, including Pitt Water, were re-sampled between 1991 and 1997 to investigate changes in the abundance of *G. galeus* and M. antarcticus (see Stevens and West, 1997). Sampling was based on seasonal longline fishing in UPW (except winter and spring) (n = 77 shots) at sites nearby to those sampled in 2012-2014. Longlines were of the similar configuration to those used in the current study (i.e. bottom set using 50 hooks), the main differences were the snoods which were made from 27 kg breaking strain monofilament line, and lines were deployed overnight with soak times ranging between 10-18 hours.

To determine if there was any relationship between *G. galeus* YOY abundance in the shark refuges and estimated stock pup production based on the population assessment model (Punt *et al.*, 2000a; Thompson and Punt, 2008; Thompson, 2012), catches from 2012-14 and historical catch records from the 1947-56 and 1991-97 sampling periods were compared with pup production data for the same periods. Pup production is used as a proxy for spawning biomass in the model (i.e. recruitment into the fishery) (Huveneers *et al.*, 2013). The number of pups modelled is dependent on the estimated number of mature animals, the proportion of pregnant adult females and the average fecundity of pregnant individuals (see Punt *et al.*, 2000a; Punt *et al.*, 2000b; Thompson and Punt, 2008) for detailed explanation of model and parameters). Data is presented as pup depletion (pup production divided by pristine pup production in the year 1927) (Thompson, 2012). Beyond the year 2008, the model no longer incorporates fishery CPUE data therefore pup production has been projected up until 2014 using a total catch of 225 t to reflect an average *G. galeus* bycatch TAC set at 215 t for the fishery since 2008. Size composition and modal progression data from the study area suggest that *G. galeus* >500 mm TL caught during summer months (December – February) are

typically juveniles (1+) (Stevens and West, 1997). For the purposes of this study individuals <500 mm TL were defined as YOY (or pups) (0+).

2.3.4 Data analysis

Recent and historical shark abundance data were pooled into their respective areas (UPW and FHB), and comparisons made between the catch per unit effort (CPUE), defined as the number of sharks captured per hook hour for longlining, while handline catch data for years 1948-53 was analysed as the number of sharks captured per fishing day. Each longline site within an area was treated as a replicate for analysis. Data collected in 1991-97 and 2012-14 were analysed separately to examine the effects of year, season and area on CPUE within each sampling period. Data for each period were, however, pooled for between period comparisons. Comparisons between 1991-97 and 2012-14 longline data have been performed using both standardised (sharks × hook hr-1) and non-standardised longline data, defined as the number of sharks captured per line of 50 hooks, to account for the influence of soak times that differed between periods (i.e. 1-2 vs. 10-18 hours) on the magnitude of variation in catches between periods. Since longline fishing was not undertaken in FHB during 1991-97, between-period comparisons are limited to UPW.

Kruskal-Wallis non parametric tests were used to determine the effects of year, season and site on CPUE between and within sampling periods. Analysis of variance (ANOVA) was used to compare size distributions between sites. Generalised linear models (GLM) were used to examine relationships between estimated CPUE of *G. galeus* YOY captured in Pitt Water and modelled pup depletion.

2.4 Results

2.4.1 UPW vs. FHB catch rates

Standardised CPUE (sharks × hook hr^{-1}) for YOY and juvenile *G. galeus* was nine times higher in 2012-14 compared to 1991-97 in UPW (Table 2.1; Fig. 2.2). Similarly, non-standardised CPUE (sharks × 50 hooks^{-1}) was significantly higher for juveniles, however, only 0.44 times higher but not significantly different (Kruskal-Wallis, $\chi^2 =$

5.12, d.f. = 1, p = 0.02) for YOY in 2012-14 (Table 2.1; Fig. 2.2). There were no significant differences in CPUE between years within each of the two sampling periods, including the peak seasons (summer/autumn), for both size classes, with CPUE being highly variable between years (Table 2.2; Fig. 2.2). There were no seasonal differences in CPUE in 1991-97 (data for summer and autumn only), however, there were significant differences between seasons in 2012-14 for YOY and juveniles in UPW which was mostly attributed to nil catches during winter and spring (Table 2.2; Fig. 2.2).

In FHB there were no significant differences in annual catch rates for YOY or juveniles between 2012 and 2014 (Kruskal-Wallis, χ^2 = 1.29 and 1.66, d.f. = 2, p = 0.52 and 0.43, respectively) (Fig. 2.2). There were no significant seasonal differences in YOY CPUE (Kruskal-Wallis, χ^2 = 8.27, $d.f.$ = 3, p = 0.05), however, juvenile CPUE varied seasonally (Kruskal-Wallis, χ^2 = 11.97, d.f. = 3, p < 0.01), mainly influenced by low catch rates during autumn. No YOY or juveniles were captured during winter and spring (Fig. 2.2).

In 2012-14 catch rates of YOY were significantly higher in UPW compared to FHB whereas the catch rates for juveniles were comparable between areas (Table 2.1; Fig. 2.2).

Table 2.1 Kruskal-Wallis test results (χ^2) for YOY and juvenile *G. galeus* captured in UPW comparing CPUE for the combined overall (i.e. all seasons) and peak time of occurrence (i.e. summer and autumn) between sampling periods. Both calculation methods for CPUE are included. CV = coefficient of variation. Significant differences are denoted by bold *p*-values.

Method	Size	Period	CPUE (± s.e.)	CV	Overall			Peak		
					d.f.	χ^2	*p*	d.f.	χ^2	*p*
Shark × hook hr^{-1}	YOY	1991-97	0.004 (<0.001)	1.31	1	17.77	**<0.01**	1	38.69	**<0.01**
		2012-14	0.041 (<0.01)	1.25						
	Juvenile	1991-97	0.000075 (<0.001)	5.47	1	10.32	**<0.01**	1	14.36	**<0.01**
		2012-14	0.0052 (<0.01)	1.99						
Shark × 50 hooks^{-1}	YOY	1991-97	3.01 (0.02)	1.34	1	0.73	0.39	1	5.12	**0.02**
		2012-14	4.35 (0.07)	0.99						
	Juvenile	1991-97	0.05 (0.001)	5.31	1	9.71	**<0.01**	1	13.55	13.55
		2012-14	0.43 (0.12)	1.73						
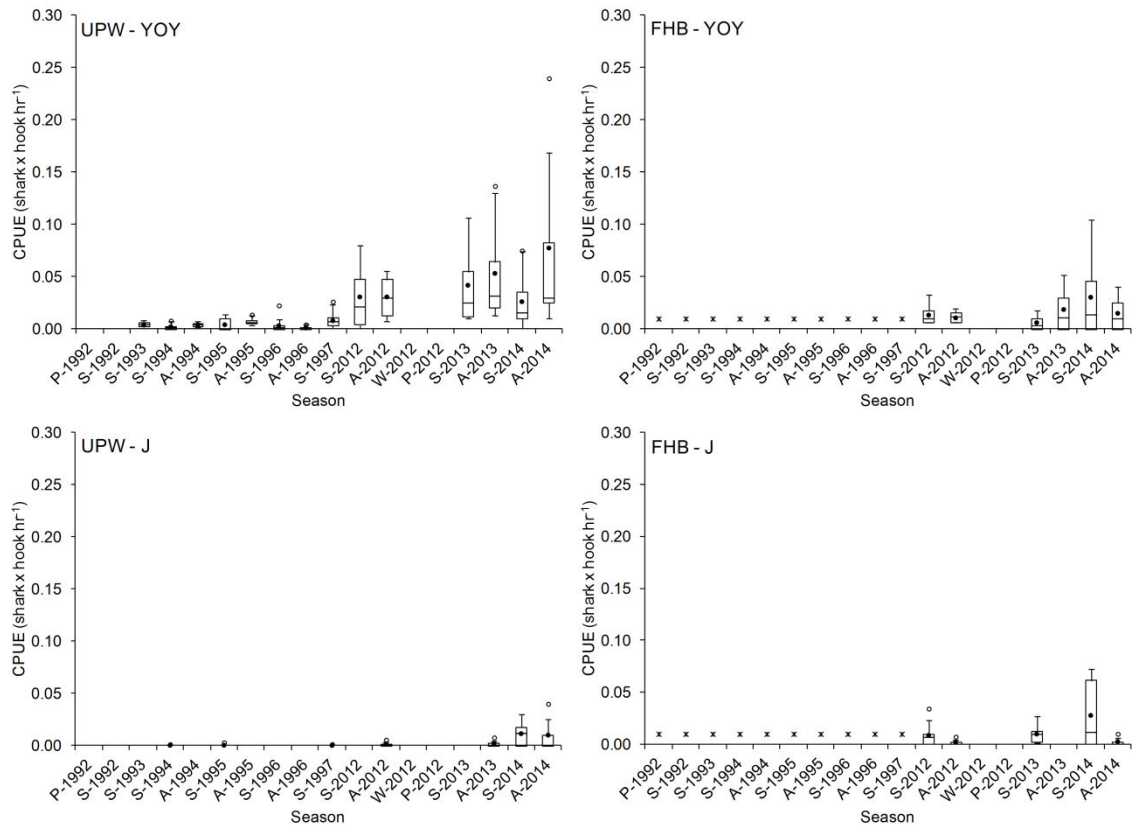
Figure 2.2 Seasonal CPUE (individuals per hook hour) of YOY and juvenile (J) *G. galeus* for UPW and FHB. Box plots show the median (line within boxes), interquartile ranges (boxes), 10th and 90th percentiles (whiskers), outliers (○), and mean (●) CPUE for each season. * not sampled. P = spring; S = summer; A = autumn; W = winter.

Table 2.2 Kruskal-Wallis test results (χ^2) for YOY and juvenile *G. galeus* 1) captured in UPW comparing CPUE (shark × hook hr^{-1}) between years and seasons within each time period, and 2) overall differences in catch rates between the two sites in 2012-14. Significant differences are denoted by bold *p*-values.

Size	Period	Years			Seasons			UPW v FHB 2012-14		
		d.f.	χ^2	p	d.f.	χ^2	p	d.f.	χ^2	p
YOY	1991-97	5	12.91	0.02	2	1.15	0.56	1	5.57	**<0.01**
	2012-14	2	7.74	0.02	3	23.92	**<0.01**			
Juvenile	1991-97	5	2.88	0.72	2	0.73	0.69	1	1.65	0.19
	2012-14	2	7.69	0.02	3	14.09	**<0.01**			

2.4.2 Size distribution

The size distributions of *G. galeus* were typically skewed towards smaller individuals in UPW, representing mostly YOY, whereas FHB distributions were bi-modal and skewed

towards juveniles (Fig. 2.3). Overall *G. galeus* were significantly larger in FHB (mean TL = 491 ± 19.2 mm) compared to UPW (mean TL = 396 ± 2.1 mm) (ANOVA: $F_{1, 609}$ = 109.99, *p* < 0.01). There was a distinct modal progression from summer to autumn in both regions, with increased proportions of neonatal size classes and fewer juveniles occurring in FHB during autumn (Fig. 2.3).
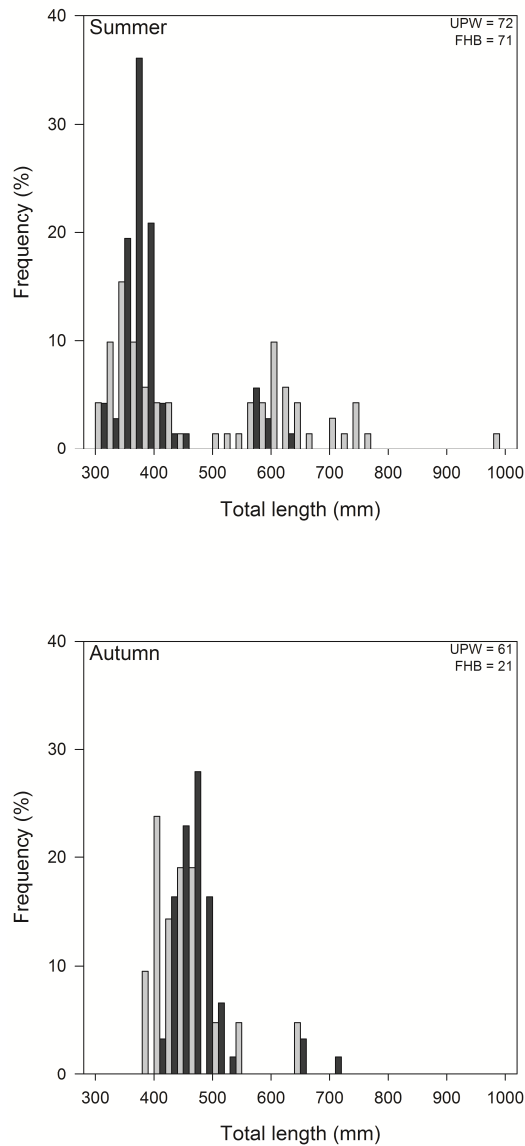
Figure 2.3 Size frequency of *G. galeus* captured by longline in Upper Pitt Water (UPW) (black) and Frederick Henry Bay (FHB) (grey) in summer and autumn during 2012-14 sampling. Sample sizes are also given.

2.4.3 Historical pup production

Modelled pup production declined between the 1950s and late 1990s to less than 20% of pre-fishing levels, but is predicted to have stabilised by 2014 and is projected to increase slowly at current harvest levels (i.e. 200-225 t) beyond 2014 (Fig. 2.4d). YOY handline catch rates in Pitt Water between 1948 and 1953 were significantly correlated with a 9% decline in pup production (Depletion = 0.83 to 0.75) during that period ($F_{1,4}$ = 45.69, p < 0.01) (Fig. 2.4a). By contrast, in UPW there was no significant relationship between pup production and YOY longline catches between 1993 and 1997 (24% decline; 0.18 to 0.14: $F_{1,4}$ = 1.08, p = 0.38) (Fig. 2.4b) or between 2012 and 2014 (0.6% decline; 0.122 to 0.121: $F_{1,4}$ = 7.73, p = 0.23) (Fig. 2.4c).
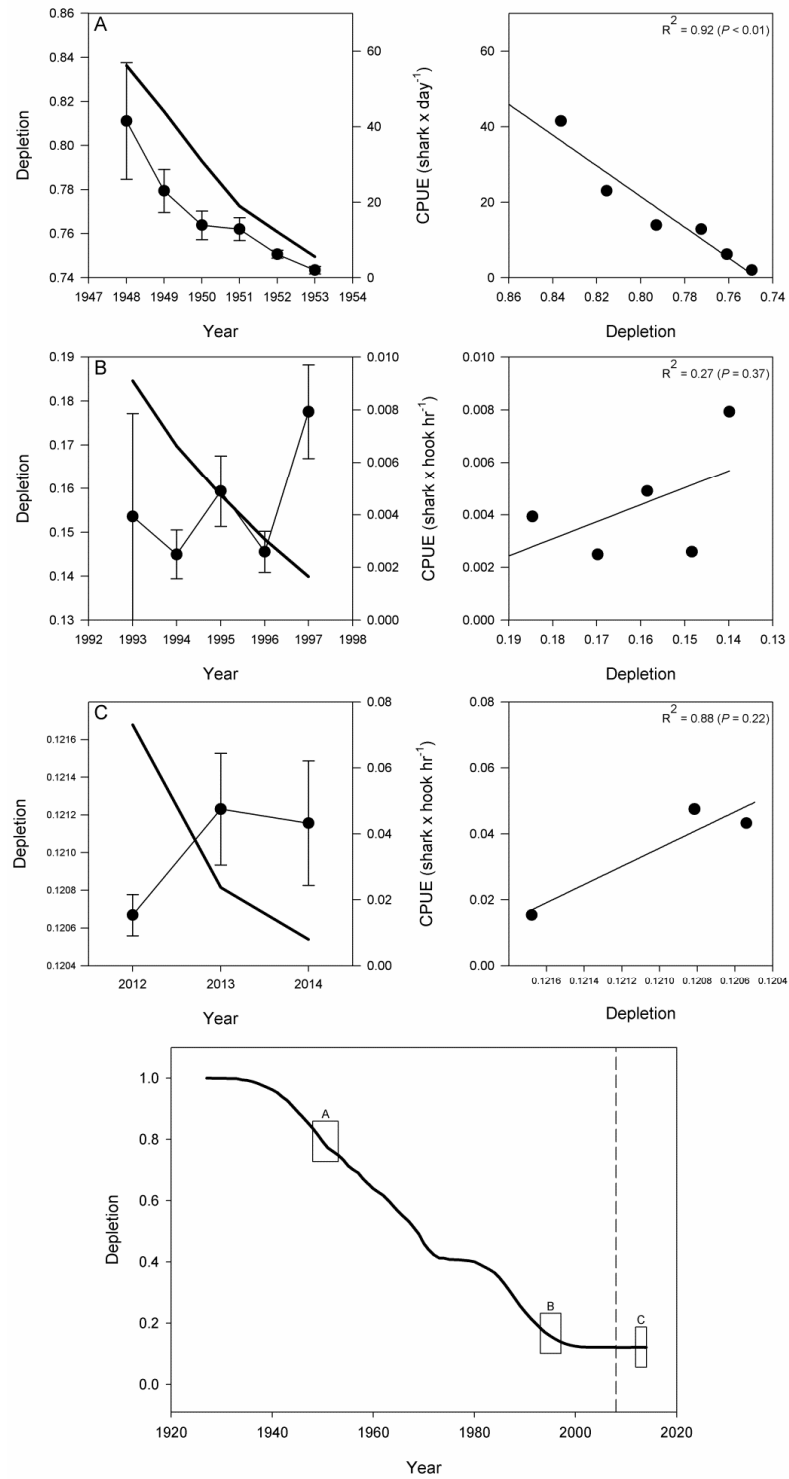
Figure 2.4 Relationship between pup depletion (pup production divided by pristine pup production) (solid line) and YOY *G. galeus* CPUE (mean ± s.e.) for (A) handline fishing in LPW in the period 1948-53, and seasonal longline fishing in UPW in the period (B) 1993-97 and (C) 2012-14. Model predicted pup depletion for the Tier 1 2009 base case assessment model for the period 1927-2008 and projected future depletions are shown for future catch scenarios of 200 t (solid line) and 225 t (dashed line) beyond 2008 (D). Note the differences in *y*-axis.

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2.5 Discussion

2.5.1 Seasonal G. galeus abundance in nursery areas

After almost 80 years of fishing pressure, this study shows that YOY and juvenile *G. galeus* still occur in the shallow, protected embayment's of Pitt Water and Frederick Henry Bay with evidence that their abundance may have increased or at least stabilised after decades of significant stock declines. This study has confirmed findings of Olsen (1954; 1984) and Stevens and West (1997) that YOY and juvenile *G. galeus* are present predominantly in Pitt Water and FHB during summer and autumn. The progressive shift of smaller animals from UPW to FHB, and disappearance of juveniles from FHB during autumn also conforms to previous migratory patterns observed in these areas (Olsen, 1954; Stevens and West, 1997). The higher catch rates of YOY *G. galeus* in UPW compared to FHB are also consistent with those of Stevens and West (1997), providing further evidence to support suggestions that UPW is an important pupping area for this species (Olsen, 1954) and that these areas are likely to still function as nursery areas for *G. galeus*.

Upper Pitt Water has consistently produced the highest catch rates of newly pupped *G. galeus* of all the known pupping areas monitored since Olsen's (1954) sampling in the 1940s (Stevens and West, 1997). Although re-sampling of other nurseries is needed to confirm the comparative importance of UPW, catch results from 2012-14 provide strong evidence of an increased abundance of YOY *G. galeus* in UPW since the last assessment was conducted in 1991-97. Whilst it is difficult to assess whether newborn *G. galeus* abundances are similar to those reported by Olsen (1954; 1984) in the 1940s, as direct comparisons are complicated by the different gear types used (handline vs. longline), the higher catch rates in 2012-14 suggest there may have been some recovery in the *G. galeus* breeding population.

Alternatively, the increased abundances of YOY in UPW may represent a behavioural change in the utilisation of the area. For instance, an uncoupling of the link between the overall stock and degraded nurseries such as those in Victoria, and a reliance on fewer nurseries like UPW. Links among nursery areas and the broader population are rapidly uncoupled when degradation of essential habitats occur such as spawning sites (Roberts

and Hawkins, 1999). For example, degradation of the nursery habitats for flatfish in the Eastern Channel (Western Europe) is thought to have contributed to an increased dependence on fewer nurseries for recruitment into the fishery (Rochette *et al.*, 2010). Therefore re-visiting other recognised nursery areas may be required to determine if increased abundances of YOY *G. galeus* are specific to UPW or are more widespread and indicative of the trend in the breeding population.

Standardisation of catch rates is often performed in order to make reliable comparisons between catch rates where variations in fishing techniques have occurred (Maunder and Punt, 2004). Longlining is typically characterised by rising catches to a maximum followed by a decline in catch rates with increasing soak times (Løkkeborg and Pina, 1997) which is partly due to loss of bait efficiency (i.e. loss of odour), rising proportions of broken snoods and hooked animals falling off, or animals being removed by predators (Murphy, 1960; Ward *et al.*, 2004). Consequently catch data from longlines can underestimate abundance when long soak times occur (Ward *et al.*, 2004). Therefore, the nine-fold increase in YOY *G. galeus* abundance in 2012-14 revealed using standardised catch rates should be interpreted with caution given the longer soak times (i.e. 1-2 hours vs. 10-18 hours) and snood construction (monofilament vs. stainless steel wire) in 1991-97 compared to 2012-14. Indeed comparing non-standardised catch rates (i.e. shark $\times$ 50 hooks^{-1}) revealed a 44% increase in abundance during 2012-14 suggesting the actual magnitude of increase probably fits somewhere in between estimates derived using standardised or non-standardised data. Despite this both scenarios indicate that YOY catch rates have increased or at very least remained stable suggesting that the *G. galeus* spawning population has probably not deteriorated any further since 1991-97. Validating short (1-2 hours) vs. long soak times (10-18 hours) and monofilament vs. stainless steel snoods could help resolve the rate of increase using longline catch data but this was not possible in this study due to logistic and ethical/permit constraints.

2.5.2 CPUE as a stock abundance indicator

Comparing the relationship between YOY *G. galeus* catch rates in Pitt Water and modelled pup recruitment over time indicated that there may be some merit in monitoring YOY abundance in nursery areas (based on catch rates) as a proxy for trends

in overall stock size. This is particularly evident during the years 1948 to 1953 when there was a strong correlation between declines in both handline catch rates in Pitt Water and predicted stock size. Conversely, the relationship is unclear for data from 1993 to 1997 and 2012 to 2014 showing a weak but positive correlation between YOY catches and productivity. This may be due to the fact that the fishing method (handline vs. longline), site (LPW and UPW), and sampling duration (six, five and three years) differ between the 1940/50s and 1991-97 and 2012-14 sampling periods.

Stock-recruitment relationships are inherently difficult to demonstrate appropriately and are influenced by diverse biological and inter-annual variations in environmental conditions (Walters and Ludwig, 1981; Fogarty *et al.*, 1991; Myers, 2001). One possible explanation for the mismatch in YOY abundance and modelled production for data between 1991-97 and 2012-14 is that the stock assessment model contains no recent or reliable catch data. The model no longer uses commercial catch rates (or any other indices of abundance) beyond 1997, because industry were forced to no longer target *G. galeus* (Thompson and Sporcic, 2013). Anecdotal reports from industry suggest the incidental capture of *G. galeus* have increased in recent years suggesting that the modelled productivity may be underestimated and that greater population recovery then predicted by the model has occurred (R. Thompson pers. comm.). Developing a time series of YOY abundances from UPW may therefore provide a fishery independent measure that validates the trend in stock productivity.

Shark recruitment is also strongly related to the size of the breeding population (Kinney and Simpfendorfer, 2009), and recruitment variability in fisheries generally increases when population abundances of reproductive stocks are low (Myers and Barrowman, 1996; Myers, 2001). *Galeorhinus galeus* recruitment also appears to follow a similar pattern, with low variability around YOY catches during the 1940s compared to the later sampling periods where the stock was much lower and had declined to between 9-14% of virgin biomass (Punt *et al.*, 2005; McLoughlin, 2008). Subsequently the strong relationship between YOY catch rates from 1948-53 with production may be due to the higher stock sizes and low variability around recruitment during this period compared to the later sampling periods. Therefore the value of using YOY catch rates to monitor

stock size may be more beneficial at a point in time where the stock is at a size that causes minimal inter-annual recruitment variability.

Perhaps the weakest aspect of using YOY catch rates to determine trends in stock size is the direct connectivity of YOY *G. galeus* between nursery areas and the broader population. Previous movement studies of conventionally tagged YOY and juveniles in UPW and FHB found they widely migrate to waters where much of the fishery is based in southern Australia (Olsen, 1954; 1959; Stevens and West, 1997). However, the relative contribution of YOY from UPW or FHB, and indeed remaining nursery areas remains largely unknown. Determining the level of population mixing using modern genetic techniques to examine kinship (Palsbøll *et al.*, 2010), coupled with further yearly monitoring of newborn *G. galeus* catch rates is therefore needed to provide a better understanding of the relative contribution and importance of YOY recruitment from Pitt Water to the wider stock before adopting the stock-recruitment index as proposed. Understanding these connections would not only give greater confidence in using YOY abundances for monitoring stock size but would also provide management with a framework around which to base more focussed management of the most essential nursery areas.

Another important caveat in using recruitment indices from Pitt Water is that natural mortality in YOY *G. galeus* soon after birth may also need to be considered in estimating absolute pup recruitment. High rates of natural mortality can sometimes occur in sharks soon after birth (Heupel and Simpfendorfer, 2002) which may therefore limit the number of YOY sharks available to capture during recruitment monitoring studies if significant numbers are dying prior to sampling. Although this study attempted to capture YOY *G. galeus* at the earliest possible stage after birth, the extent to which natural mortality affects the availability of YOY to sampling remains unclear and it is therefore impossible to account for these in estimating recruitment without conducting further research to estimate neonatal mortality rates.

Despite these limitations, using longline catch rates to monitor YOY abundances does have the advantage of being less destructive compared to other fishing methods such as gillnets. Mortality associated with hook and line fishing can be variable but is generally considered low (Hoffmayer and Parsons, 2001; Gurshin and Szedlmayer, 2004) with

recent studies demonstrating that gummy shark (*Mustelus antarcticus*), in the same family as *G. galeus*, have significantly higher survival rates when captured by longlines compared to gillnets (Frick *et al.*, 2010). Similarly, Stevens and West (1997) noted that survival of *G. galeus* captured on longlines during their sampling was 69% compared to 29% in gillnets. Less-destructive research techniques are becoming increasingly desirable in fisheries management particularly for vulnerable and threatened species such as sharks (Heupel and Simpfendorfer, 2010; Hammerschlag and Sulikowski, 2011). Moreover, collecting reliable information for overfished and recovering species in fisheries where they are no longer the primary target of that fishery is critical to their effective management and conservation (Bonfil, 2004). Given the current conservation status of *G. galeus* and absence of reliable fishery dependant data to monitor stock sizes, adopting a precautionary approach to monitoring stock size such as YOY longline catch rates in nurseries may be the most appropriate management tool at the present time, an approach which could have broad applicability to managing the recovery of other overfished species elsewhere.

3

Examining the functional role of current area closures used for the conservation of an overexploited and highly mobile fishery species

3.1 Abstract

Protecting essential habitats through the implementation of area closures has been recognised as a useful management tool for rebuilding overfished populations and minimising habitat degradation. School shark (*Galeorhinus galeus*) have suffered significant stock declines in Australia, however, recent stock assessments suggest the population may have stabilised and the protection of closed nursery areas has been identified as a key management strategy to rebuilding their numbers. Young-of-the-year (YOY) and juvenile *G. galeus* were acoustically tagged and monitored to determine ontogenetic differences in residency and seasonal use of an important protected nursery area (Shark Refuge Area or SRA) in south-eastern Tasmania. Both YOY and juvenile *G. galeus* showed a distinct seasonal pattern of occurrence in the SRA with most departing the area during winter and only a small proportion of YOY (33%) and no juveniles returning the following spring, suggesting areas outside the SRA may also be important during these early life history stages. Whilst these behaviours confirm SRAs continue to function as essential habitat during *G. galeus* early life history, evidence of YOY and juveniles emigrating from these areas within their first 1-2 years and the fact that few YOY return suggest these areas may only afford protection for a more limited amount of time than previously thought. Determining the importance of neighbouring coastal waters and maintaining the use of traditional fisheries management tools are therefore required to ensure effective conservation of *G. galeus* during early life history.

3.2 **Introduction**

Anthropogenic impacts on marine life such as overfishing, pollution and coastal development have resulted in widespread collapse of many global fisheries and degradation of marine habitats (Pauly *et al.*, 1998; Hutchings, 2000; Myers and Worm, 2005). Management tools such as catch quotas and fishing gear restrictions have traditionally been used to curb over-fishing, however, in more recent times area closures and implementation of marine reserves have gained popularity as a supplementary management strategy for enhancing stock recovery whilst at the same time protecting important marine habitats (Roberts *et al.*, 2001; Gell and Roberts, 2003; Hilborn *et al.*, 2004b; Gaylord *et al.*, 2005; Thorpe *et al.*, 2011).

Area closures typically involve protecting areas regularly used by key species for feeding, predator avoidance, or reproduction by restricting access to activities such as fishing, mining or other human disturbances (Gell and Roberts, 2003). Area closures are considered most beneficial to species such as invertebrates and reef fishes that are relatively sedentary and spend a significant proportion of their time within the protected area (Gell and Roberts, 2003; Gerber *et al.*, 2003; Hilborn *et al.*, 2004b). However, for more highly migratory species such as sharks and pelagic fishes, the protection afforded by area closures may be limited given the difficulties of protecting expansive areas that cover their large-scale migrations and movement patterns (Kramer and Chapman, 1999a; Shipp, 2003; Heupel *et al.*, 2007; Kinney and Simpfendorfer, 2009).

Spatial closures for sharks have typically focussed on protecting areas used during vulnerable stages such as mating, pupping and early life history stages when their movements are often confined to discrete areas (Heupel *et al.*, 2007). Although some shark nursery areas have been protected, many of these have been protected with very little prior understanding of how and when sharks use such areas (Heupel and Simpfendorfer, 2005b; Heupel *et al.*, 2007). There is also a view that protecting nursery areas may have limited value to shark populations if more traditional fishery management is not used to protect juveniles and adults outside the closed area (Kinney and Simpfendorfer, 2009). Therefore determining the movement behaviours of juvenile sharks and the nature of their association with particular areas during early life history is

crucial for implementing more effective area closures or evaluating their effectiveness for protecting these life history stages (Speed *et al.*, 2010).

The school shark (*Galeorhinus galeus*) is found circumglobally in temperate waters and has been subject to intense fishing pressure resulting in significant stock declines, particularly in Australia (Walker *et al.*, 2006). As a strategy to aid rebuilding the population, recognised nursery grounds around Tasmania and Victoria were declared as Shark Refuge Areas (SRAs) as early as 1954. In such areas the taking of any species of shark is prohibited (Walker, 1999). However, despite 40 years of protection, surveys of SRAs conducted during the 1990s found that young-of-the-year (YOY) and juveniles were either absent from or occurred in very low numbers in many of these refuges (Stevens and West, 1997; Walker, 1999). Overfishing is considered the main reason for the population collapse (Walker, 1999), however, it has also been suggested that habitat degradation, particularly the loss of seagrass meadows in Victorian nursery areas may have contributed to this decline (AFMA, 2009). Subsequently further fishing restrictions, gear modifications and fishing ground closures have been implemented in an effort to reduce fishery captures (McLoughlin, 2008) and a School Shark Rebuilding Strategy (SSRS) has been in place since 2008 to promote stock recovery (AFMA, 2009). Recent stock assessments estimate *G. galeus* populations in southern Australia are at 9-14% of virgin biomass, although, modelling indicates the population may have stabilised (AFMA, 2009; SharkRAG, 2010). Furthermore, recent research fishing in southern Tasmanian SRAs has recorded significantly higher catches of YOY and juvenile *G. galeus* than reported in similar surveys conducted in the 1990s (authors unpublished data). Whilst the relative contributions of the various management measures to this stabilisation are unclear, identifying additional nurseries and protecting current nursery areas has been recognised as the first priority in the SSRS (SharkRAG, 2010).

Despite the high importance placed on SRAs as a management measure, little is known about the role they play in supporting *G. galeus* during the early life history phases, with much of the previous research on SRAs in south-east Australia assessing patterns in relative abundance and movement based on conventional tag-recapture methods (Olsen, 1954; Stevens and West, 1997). Knowledge of how *G. galeus* utilise these

areas in space and time is required to evaluate the effectiveness of the SRAs in the overall conservation of this species. Furthermore, understanding how *G. galeus* use these areas may also provide greater insight into this species' functional role in these areas, particularly in relation to predator-prey dynamics (Barnett and Semmens, 2012). In this study acoustic telemetry was applied to describe spatial and temporal movement behaviours, including seasonality of residency of YOY and juvenile *G. galeus*, within a long-established nursery ground off south-eastern Tasmania. Duration of residency and patterns of emigration from the protected area are also examined to inform an assessment of the effectiveness of the protected area in the management and conservation of this species.

3.3 Material and methods

3.3.1 Study site

The main study area was located in a SRA in south-east Tasmania, Australia (42° 53.710'S 147° 34.228'E) that incorporates Pitt Water (PW), Frederick Henry Bay (FHB) and Norfolk Bay (NB) (Fig. 3.1). Pitt Water is a shallow estuary (average depth 4 m; maximum depth 9 m) originating from the Coal River and is comprised of mostly intertidal sand flats and a narrow tidal entrance that connects to the deeper waters of Frederick Henry and Norfolk Bay (average depth 15 m; maximum depth 44 m).

Fifty-eight acoustic receivers (VEMCO Ltd, Halifax, Canada) were deployed either as standalone units (FHB1-20) or in a line with overlapping detection ranges (E and H) so as to form a gate or curtain through which a tagged animal would need to pass to confirm it had entered a given area (Heupel *et al.*, 2006) (Fig. 3.1). In PW receivers were deployed in a Vemco Positioning System (VPS) array (Fig. 3.1) to examine fine-scale movements and behaviour of *G. galeus* (authors unpublished data), and as standalone units located throughout the area but in particular in a main channel. Previous range testing in Norfolk Bay (42° 59.943'S 147° 47.153'E), which adjoins FHB (curtain E; Fig. 3.1), using the same transmitters as in this study had determined that 100% of tag transmissions could be detected at a range of 400–500 m (Barnett *et al.*, 2011). Therefore curtain receivers were deployed at a maximum distance of 800 m

apart. The entire array was deployed on 6 January 2012 and recorded data until 22 May 2013.

In addition to the main study area, an array of 66 acoustic receivers was also deployed off the east coast of Tasmania by the Australian Animal Tagging and Monitoring System (AATAMS) and Ocean Tracking Network (OTN) forming two curtains which extended from mainland Tasmania to Maria Island and then to the continental shelf break (MARIA – 27 receivers) (42° 40.874'S 148° 15.101'E), and from the most easterly point of Cape Barren Island to the continental shelf break (CAPE BARREN – 39 receivers (Fig. 3.1) (40° 28.901'S 148° 39.189'E).
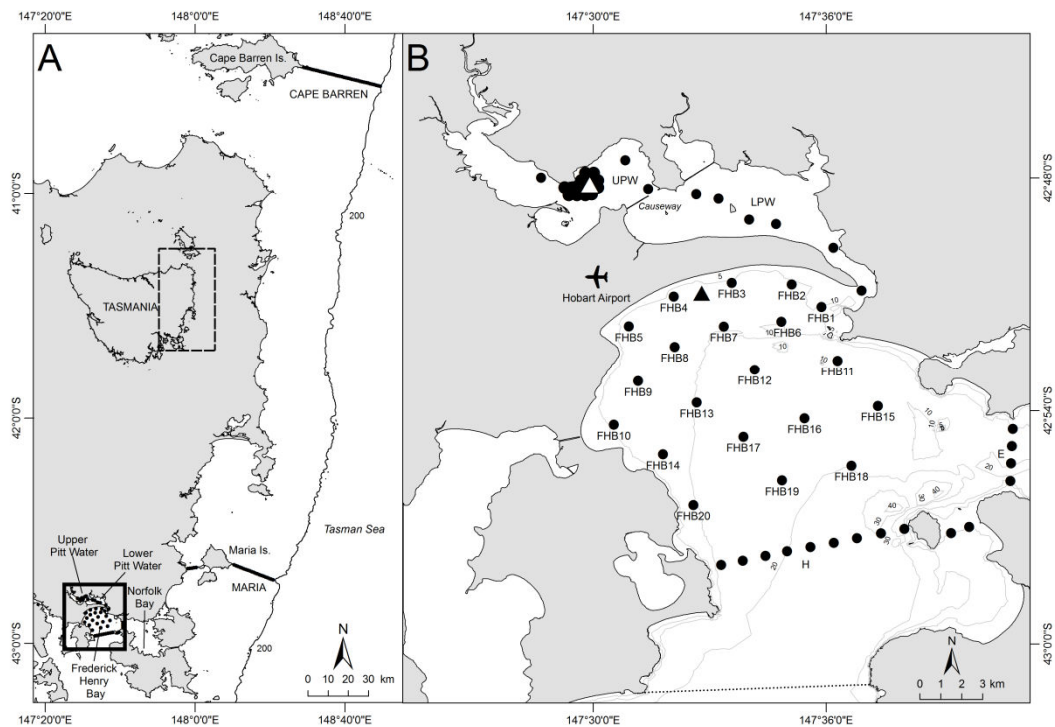
Figure 3.1 Map of main study area showing position of acoustic receivers (filled circles) in southern Tasmania (A and B). Note that receivers without a unique identification have been pooled to form a resource (UPW and LPW) or curtain (E and H). Dotted line represents Shark Refuge Area boundary and grey lines are the 5 m then 10 m depth contours. Triangles represent the approximate capture and tagging sites in UPW and FHB. Map (A) shows the receiver curtains MARIA and CAPE BARREN extending to the continental shelf break (200 m).

3.3.2 Acoustic tagging

Sharks were captured using bottom set baited longlines and were measured from the snout to the tip of the tail to the nearest mm (total length or TL mm) and their sex

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recorded. Sharks were categorised as either YOY (<500 mm TL) or juveniles (>500 mm but typically >600 mm TL and <1000 mm TL) in January and February 2012 (austral summer). Previous seasonal sampling from the same area suggests that during summer individuals larger than 500 mm TL are typically 1+ years of age, with most YOY (0+) typically 350 to 450 mm TL (Stevens and West, 1997).

YOY were fitted with either VEMCO V9 2L (n = 6) or V13 1L (n = 26) coded acoustic transmitters (transmission off times: random between 120-180 s; predicted battery life: 2 and 5 years, respectively). Also, one YOY and seven juveniles were implanted with V13P 1L acoustic-sensor tags (transmission off times: random between 60-180 s; predicted battery life: 5 years) (VEMCO Ltd., Halifax, Canada) (Table 3.1). Sharks were held ventral side up on a piece of foam with running sea water pumped over the gills. The acoustic tag was surgically inserted in the peritoneal cavity by making a 1-2 cm incision in the abdominal wall, and closing the incision using surgical sutures (Braun Safil® HS26s). Aseptic techniques were used during all stages of the surgery, taking no longer than 2-5 minutes to complete, after which the animal was released back into the water. Animals were held in the water boat side until they could swim unassisted prior to being released. Sharks were tagged in PW (32 YOY and one juvenile) and FHB (seven juveniles) between January 2012 and May 2012 (Fig. 3.1). In PW sharks were captured and released near the VPS array, and between receivers FHB3 and FHB4 in FHB (Fig. 3.1).

3.3.3 Data analysis

3.3.3.1 Seasonal residency and use of SRA

Seasonal use of the SRA (% of time animals spent within the SRA) was determined by examining a visual plot of daily detections and by dividing the total number of days an individual was detected in the SRA by the total number of days that animal had been at liberty since tagging. An animal was considered present in the SRA if it was detected by any receiver within PW or FHB more than once per day. FHB comprised receivers FHB1-20, and curtains E and H. An animal was considered to have departed the SRA if it was detected on the H-curtain, and subsequently went undetected by any receiver in the SRA for >1 day.

3.3.3.2 Seasonal distribution within SRA

Receivers were grouped into five locations and the number of days an animal was detected at each location used to compare the seasonal distribution of YOY and juveniles throughout the SRA. The five locations were: Upper Pitt Water (UPW) (receivers to the north of the causeway), Lower Pitt Water (LPW) (receivers to the south of causeway), FHB (receivers FHB1-20), and curtains E and H (Fig. 3.1). The number of sharks detected per day for each location for each month was analysed using circular statistics (Oriana 4 software, Kovach Computing Services). Rao's Spacing Test was used to test for uniformity in detections over a year. For this purpose, a 12-month subsample of the data was used, collected between January-December 2012.

3.3.3.3 Fine-scale ontogenetic utilisation and spatial overlap within SRA

Fine-scale utilisation of the SRA by YOY and juveniles was determined by examining the total number of hours each animal was detected at geographical location of standalone receivers (FHB1-20) or groups of receivers (UPW, LPW, E and H) in a given day. If an animal was detected at least once in a given hour for that day then it was considered as being present during that hour. Using the standalone and grouped receivers, spatial overlap between YOY and juveniles was then compared using niche overlap analysis in the EcoSimR package (Gotelli and Ellison, 2013) with R statistics software (R Development Core Team, 2013). Pianka's index (O) was selected and permutated 1000 times using the RA3 algorithm (Meyer et $al.$, 2009). The degree of overlap is presented by values between 0 and 1, where 0 = no overlap and 1 = 100% overlap. In addition a log-likelihood test (χ^2) was performed using the adehabitatHS package (Calenge, 2006) in R statistics software to test for individual selection (w_i) for particular receivers. Selection ratios >1 indicate a preference for a particular receiver whereas values <1 indicate avoidance (Manly et $al.$, 2002). Kernel Utilisation Densities (KUD) were also used to visually estimate the preference for each receiver and approximate area used, the 95% fixed kernel representing the overall use of available receivers and the 50% fixed kernel the receivers most often used. KUDs were estimated using the Hawth's Analysis Tools for ArcGIS 9.3. Minimum movement paths between each possible combination of two standalone and/or grouped receivers made by each animal were also summed and mapped to show approximate travel paths.

Receivers at E, H and FHB were also assigned a depth zone based on the average depth covered by the receiver (<10, 10-15, 15-20 or >20 m) to calculate selection (w_i) and overlap in the use of particular depths between YOY and juveniles in these locations. Circular statistics were also used to determine the diel use of each depth zone.

3.3.3.4 Long-distance movement patterns

Additional acoustic detection data from the MARIA and CAPE BARREN curtain, and the recapture of an acoustically tagged individual was also mapped to describe the long-distance movement patterns of *G. galeus* once leaving the shark refuge area.

3.4 Results

Of the 40 sharks that were tagged, one YOY went undetected and was excluded from the analysis. Therefore a total of 31 YOY and 8 juvenile sharks were monitored for seasonal occurrence in the SRA over the duration of the study. On average individual YOY and juveniles were detected for 91 (S.E. ± 16) and 93 (S.E. ± 32) days, representing 19% and 21% of their time at liberty, respectively (Table 3.1).

3.4.1 Seasonal residency and use of SRA

Overall, 19 (62%) YOY remained within the SRA for the duration of the study, three (9%) departed the SRA and were not detected again in the SRA, and nine (29%) periodically departed and returned to the SRA between May and September 2012. The general trend was for YOY (and the single juvenile) tagged in UPW to spend the summer months (December – February) in UPW and progressively migrate to LPW in autumn (March – May) and then into FHB. YOY then either remained within FHB or departed the SRA (i.e. past the H-curtain) in late autumn (May – June) returning at a later date (Figs. 3.2 and 3.3). This latter group was typically absent from the SRA for most of winter (July – September), and not detected in FHB again until mid-spring (October) (Figs. 3.2 and 3.3).

On average, YOY were present in the SRA for 392 days representing 80% (range: 22-100% days) of their time at liberty (Table 3.1). Eighteen YOY (58%) remained in PW, whereas the others (42%) moved out of the estuary towards the end of May 2012 (Fig.

3.2). Of the YOY that remained in PW, one was exclusively detected moving throughout UPW for the entire study duration and 16 were detected moving for up to 47 days (average = 15 days) after being released but then went undetected thereafter. Of the 14 YOY that departed PW, only two returned to UPW, one remaining there for the rest of the study (Fig. 3.2). All but one of these 14 YOY departed the SRA around late autumn 2012 after moving from UPW, of which nine returned to FHB around spring 2012, one remaining there for the rest of the study, the others departing the SRA again soon after or in winter the following year (Fig. 3.2).

All tagged juveniles departed the SRA (Fig. 3.2). On average juveniles were present in the SRA for 81 days representing 18% (range: 3-100% present) of their time at liberty (Table 3.1). The juvenile tagged in UPW moved to FHB in early autumn (i.e. March 2012), passed the H-curtain in late autumn (i.e. May 2012) and was not detected again (Figs 2 and 3). None of the juveniles tagged in FHB entered PW and all remained in FHB up until April 2012 (autumn), after which they all moved out of the SRA with only one individual returning in spring before departing again in late autumn the following year (i.e. May 2013) (Fig. 3.2).

Table 3.1 Details of YOY (N) and juvenile (J) *G. galeus* fitted with acoustic or sensor (P) tags. Date is the day animal was tagged. TL is total length in mm. Predicted battery life is the estimated number of days the tag was expected to transmit. Days detected are the number of days an individual was detected by the acoustic array; % detected represents the percentage of days detected from the date of tagging until the end of the study (i.e. 22/5/2013); Days present represents the number of days the animal was considered inside the SRA (i.e. had not passed the H-curtain); % present represents the percentage of days the animal was considered inside the SRA during its time at liberty. The symbols in the Return column indicate whether an animal departed the SRA and did not return (*), departed and returned to FHB (**) or departed and returned to UPW (***). † Detected by MARIA curtain. ‡ Detected by CAPE BARREN curtain.

ID	Location	Tagging date	Sex	TL	Age	Tag type	Predicted battery life	Last detection date	Days detected	% detected	Days present	% present	Return
4061	UPW	1/02/2012	M	385	N	V9-2L	633	19/03/2012	45	9	477	100	
4062	UPW	1/02/2012	M	390	N	V9-2L	633	16/02/2012	16	3	477	100	
4063	UPW	11/01/2012	F	350	N	V9-2L	633	14/01/2012	4	1	498	100	
4064	UPW	11/01/2012	F	355	N	V9-2L	633	15/01/2012	5	1	498	100	
4067	UPW	4/02/2012	M	395	N	V9-2L	633	16/02/2012	13	3	474	100	
4069	UPW	1/02/2012	F	380	N	V9-2L	633	15/02/2012	15	3	477	100	
14714	UPW	11/03/2012	M	460	N	V13P-1L	879	24/07/2012	75	17	135	31	**
31159	UPW	15/01/2012	F	365	N	V13-1L	1336	11/04/2013	247	50	452	91	***
31160	UPW	15/01/2012	M	370	N	V13-1L	1336	15/06/2012	131	27	152	31	*‡†
31161	UPW	15/01/2012	F	355	N	V13-1L	1336	12/02/2012	26	5	494	100	
31162	UPW	15/01/2012	M	333	N	V13-1L	1336	9/02/2012	18	4	494	100	
31163	UPW	11/01/2012	F	370	N	V13-1L	1336	5/02/2012	12	2	498	100	
31164	UPW	15/01/2012	M	370	N	V13-1L	1336	6/07/2012	156	32	494	100	
31165	UPW	15/01/2012	M	388	N	V13-1L	1336	6/02/2012	14	3	494	100	
31166	UPW	15/01/2012	M	340	N	V13-1L	1336	15/11/2012	127	26	305	62	**
31167	UPW	15/01/2012	F	358	N	V13-1L	1336	10/04/2013	304	62	451	91	**
31169	UPW	18/01/2012	M	405	N	V13-1L	1336	21/06/2012	159	32	155	32	*†
31170	UPW	18/01/2012	F	400	N	V13-1L	1336	8/02/2012	15	3	491	100	

Table 3.1 (continued)

31171	UPW	18/01/2012	M	350	N	V13-1L	1336	20/01/2012	3	1	491	100	
31172	UPW	18/01/2012	F	385	N	V13-1L	1336	19/04/2013	320	65	457	93	**†
31173	UPW	15/01/2012	F	442	N	V13-1L	1336	10/07/2012	156	32	177	36	**
31174	UPW	1/02/2012	M	395	N	V13-1L	1336	12/02/2012	8	2	477	100	
31175	UPW	27/01/2012	F	385	N	V13-1L	1336	21/07/2012	144	30	176	37	**†
31176	UPW	20/01/2012	M	395	N	V13-1L	1336	27/05/2012	124	25	489	100	
31178	UPW	18/01/2012	M	370	N	V13-1L	1336	7/02/2012	9	2	491	100	
31181	UPW	1/02/2012	F	405	N	V13-1L	1336	21/06/2012	114	24	141	30	**†
31183	UPW	1/02/2012	M	380	N	V13-1L	1336	14/05/2012	104	22	103	22	*
31184	UPW	1/02/2012	F	392	N	V13-1L	1336	7/06/2012	106	22	127	27	**
31194	UPW	11/01/2012	F	365	N	V13-1L	1336	Not detected					
31196	UPW	11/01/2012	F	360	N	V13-1L	1336	17/01/2012	7	1	498	100	
31197	UPW	11/01/2012	F	365	N	V13-1L	1336	15/05/2013	181	36	498	100	
31198	UPW	11/01/2012	F	370	N	V13-1L	1336	9/02/2012	24	5	498	100	
14727	UPW	19/01/2012	M	675	J	V13P-1L	879	18/04/2012	91	19	90	18	*
14713	FHB	29/02/2012	M	510	J	V13P-1L	879	21/04/2013	286	64	417	93	**
14718	FHB	29/02/2012	F	680	J	V13P-1L	879	12/03/2012	13	3	12	3	*
14722	FHB	28/02/2012	M	730	J	V13P-1L	879	12/03/2012	14	3	13	3	*
14723	FHB	28/02/2012	F	745	J	V13P-1L	879	12/03/2012	13	3	13	3	*
14728	FHB	29/02/2012	F	630	J	V13P-1L	879	13/04/2012	45	10	44	10	*
14729	FHB	29/02/2012	F	710	J	V13P-1L	879	11/04/2012	38	8	42	9	**
14733	FHB	29/02/2012	F	685	J	V13P-1L	879	13/03/2012	11	2	13	3	**
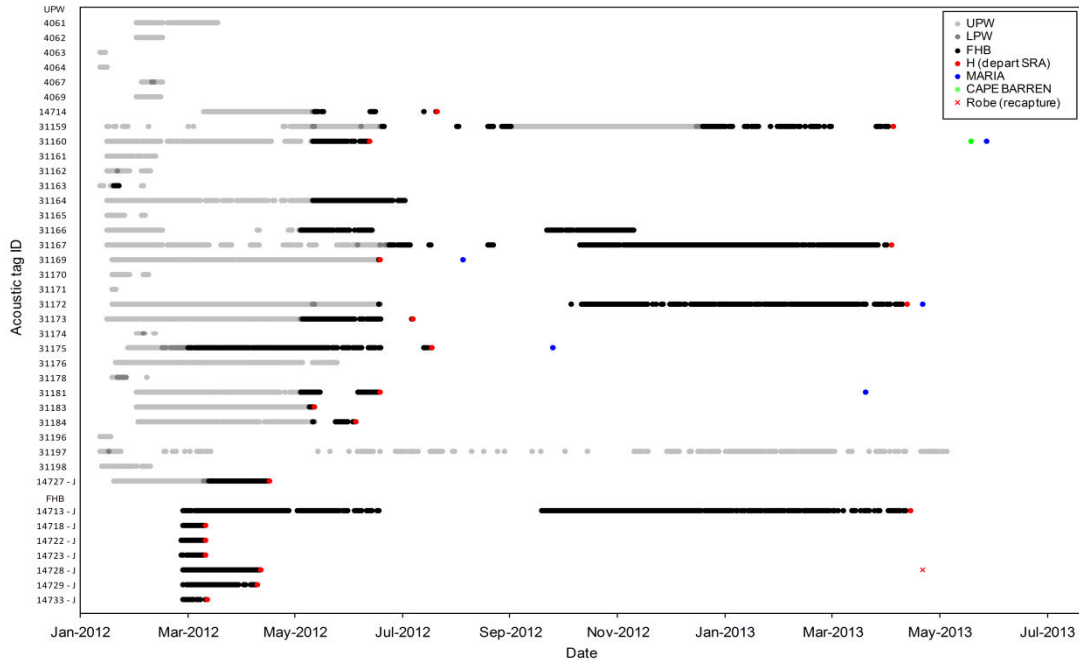
Figure 3.2 Abacus plot showing the detection dates for YOY and juvenile (J) *G. galeus* tagged in Upper Pitt Water (UPW) and Frederick Henry Bay (FHB) between January 2012 and May 2013. Each line represents an individual shark.

3.4.2 Fine-scale movements and spatial overlap within the SRA

Overall, YOY tagged in UPW were detected by UPW receivers for 88% of their time at liberty and were detected at most receivers in LPW and FHB upon leaving UPW (Fig. 3.3). Given juveniles were not detected in PW spatial overlap with YOY was only compared in FHB. Overall there was a significant overlap in the use of receivers in FHB between YOY and juveniles ($O = 0.8$, $p < 0.01$), however, YOY tended to utilise a larger proportion of FHB ($KUD_{95} = 132.76$ km^2), compared to juveniles ($KUD_{95} = 90.95$ km^2) (Fig. 3.4). . Selectivity analysis revealed a strong preference for YOY to remain near the entrance to PW and select receivers FHB1, FHB4-5, E and H once leaving UPW ($\chi^2 = 75712.7$, d.f. = 205, $p < 0.01$) (Fig. 3.4). In contrast juveniles selected receivers in the middle of FHB (FHB4, 5, 7, 12, 17) ($\chi^2 = 12583.1$, d.f. = 93, $p < 0.01$) and to a lesser extent receivers near shore (FHB1, 4, 5) (Figs. 3.4 and 3.5). YOY displayed more movements between receivers than juveniles and appeared to move mostly between receivers closer to land in contrast to juveniles which appeared to occupy and move mostly between receivers located in the middle of FHB (Fig. 3.5).

Receiver preference was also reflected in depth use with YOY preferring shallower areas (<10 m) in FHB ($\chi^2 = 11953$, d.f. = 37, $p < 0.01$) (Fig. 3.6). YOY used largely the

same depths over a 24-hour period, however, they had a slight preference for deeper waters >20 m at night (χ^2 = 5267.8, d.f. = 35, p < 0.01). In comparison juveniles showed a strong preference for depths 10-15 m during the day (χ^2 = 2591.2, d.f. = 27, p < 0.01) and the shallower areas < 10 m during the night (χ^2 = 3152.95, d.f. = 28, p < 0.01).
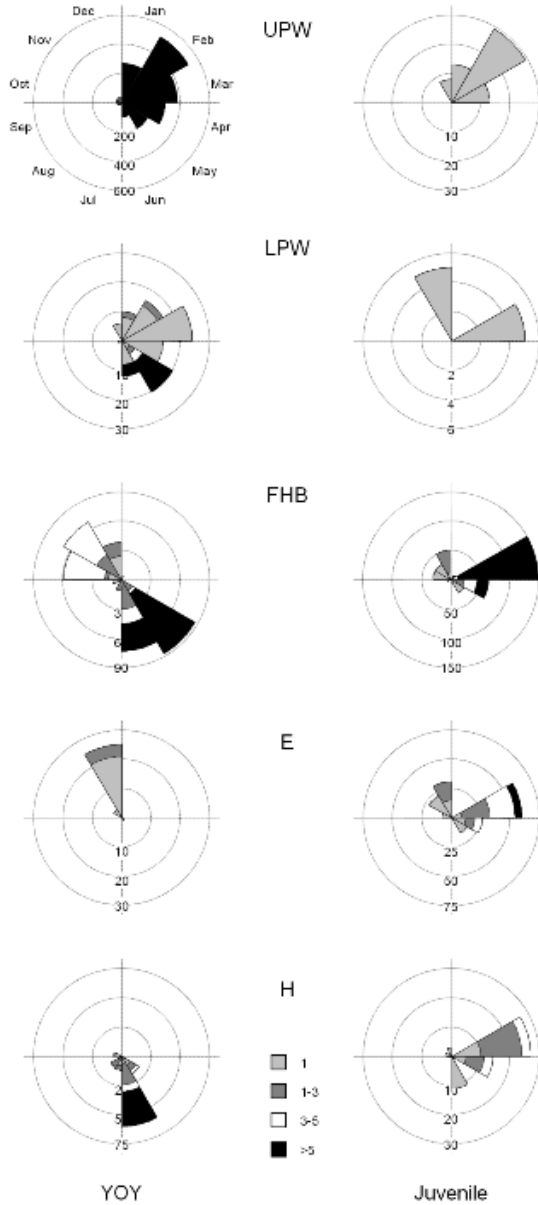
Figure 3.3 Circular plots showing the number of days YOY and juvenile *G. galeus* spent in each area for each month. Plots represent one year of data from January 2012 until December 2012. Note the number of days individuals were detected varies on the axis between YOY and juveniles, and between areas. Different greyscale colours represent the maximum number of individuals detected in a given day for that month.
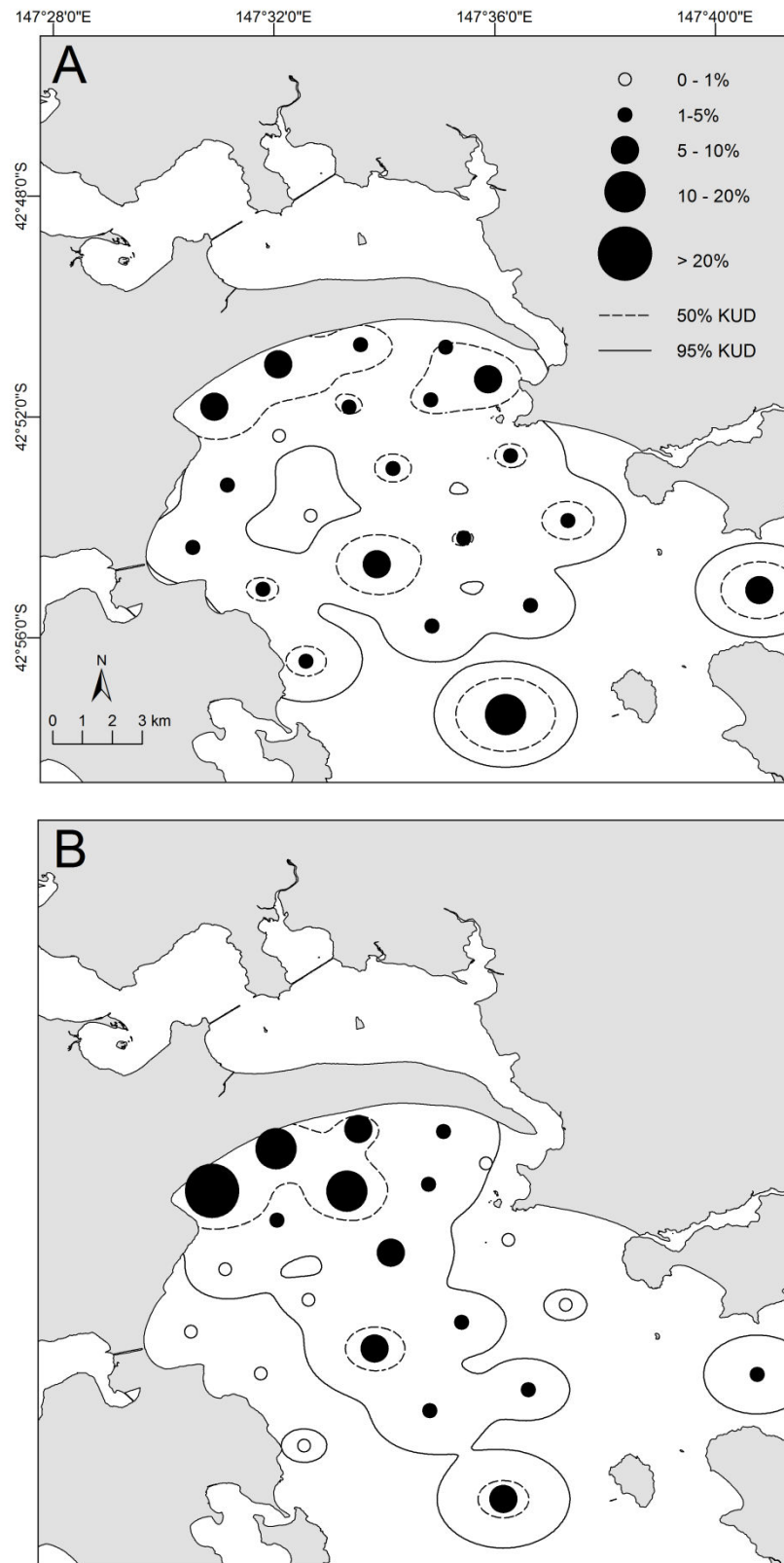
Figure 3.4 Spatial use of the Shark Refuge Area, excluding UPW, by YOY *G. galeus* tagged in Upper Pitt Water (A) and juveniles in Frederick Henry Bay (B). Size of circles indicate the percentage of total detections at each receiver. Dashed and solid line represents the overall 50 and 95% kernel utilisation distribution (KUD), respectively.
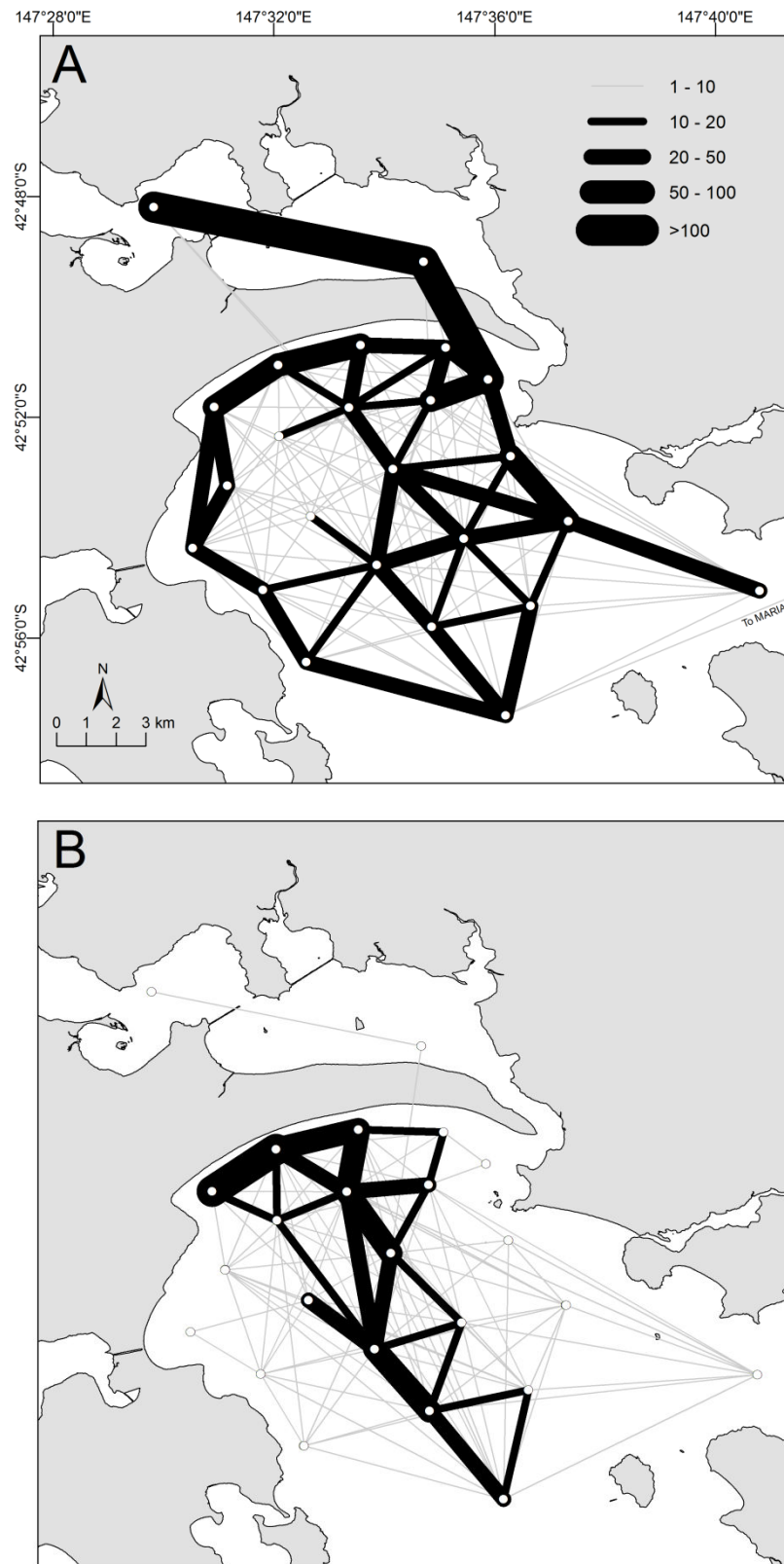
Figure 3.5 Movement patterns of YOY (A) and juvenile (B) *G. galeus* showing minimum transition paths between receivers. Thickness of line represents the number of times the transition was made. Circles represent position of acoustic receiver or midpoint of pooled receivers in UPW, LPW, E and H.
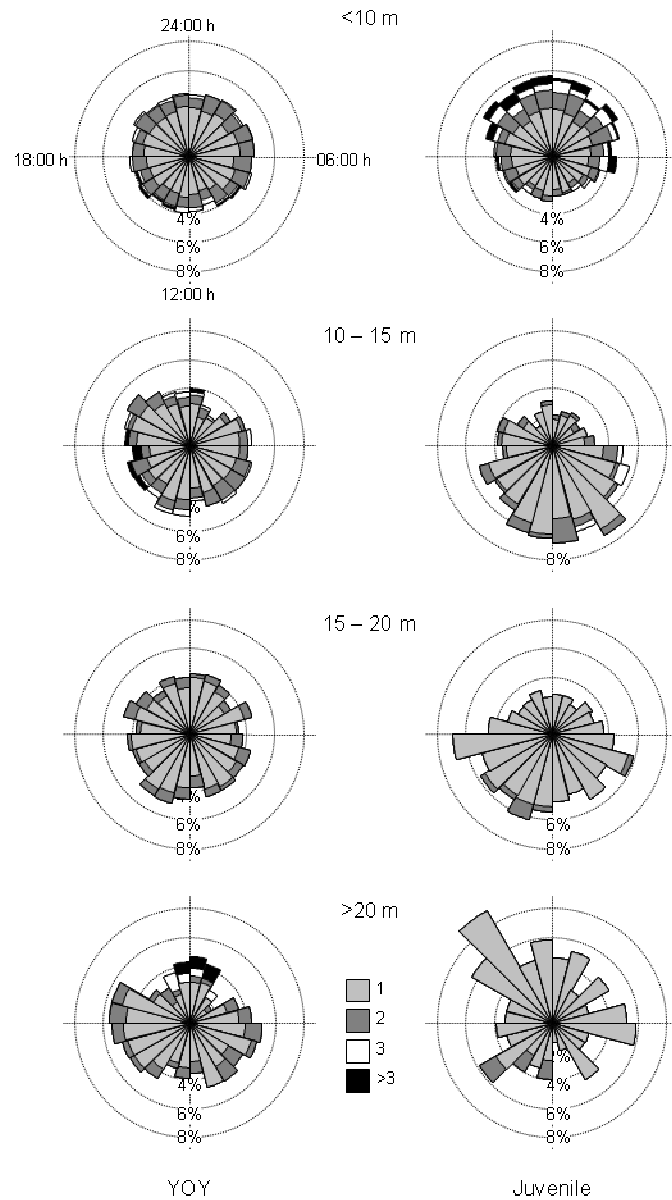
Figure 3.6 Circular plots showing the number of YOY and juvenile *G. galeus* detected at each hour of the day (% in total) at different depth contours in FHB. Different shading represents the number of sharks detected in a given hour.

3.4.3 Long-range movements

Five YOY were detected at the MARIA curtain (receiver depth: 88 – 113 m), which represents a minimum travel distance of 155 km, 10 to 358 days (mean = 154 ± 70 days) after leaving the SRA (Figs. 2 and 7). One YOY (Tag ID# 31160) was detected by the CAPE BARREN curtain (bottom depth: 105 m), representing a minimum travel distance of 280 km, 348 days after leaving the SRA and was then detected nine days

later at the MARIA curtain (Figs. 2 and 7). This animal was not detected at the MARIA curtain prior to the initial detection on the CAPE BARREN curtain. In addition one acoustic tagged juvenile was recaptured in waters near Robe, South Australia 383 days after leaving the SRA representing a minimum distance of 1200 km (Figs. 2 and 7).
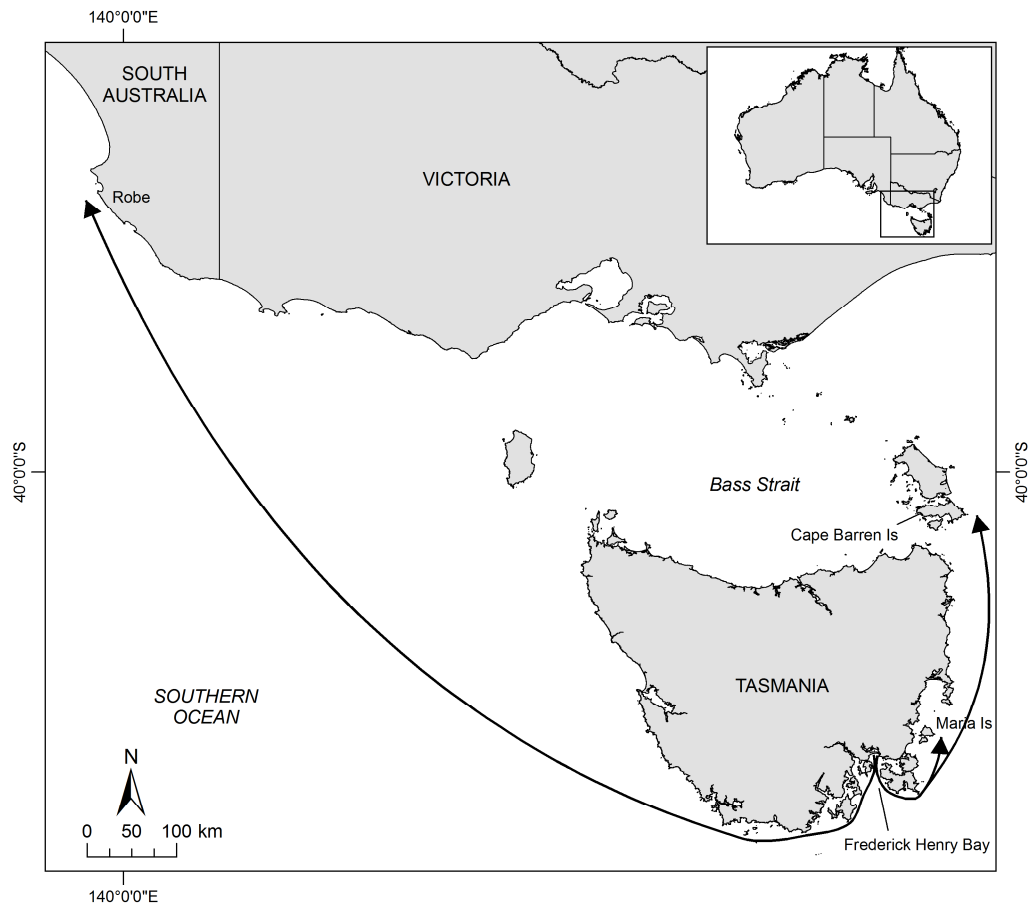
Figure 3.7 Long-distance movements and presumed travel paths of *G. galeus* detected at the MARIA and CAPE BARREN curtains, and recapture location of an acoustically tagged juvenile.

3.5 **Discussion**

3.5.1 Residency in the SRA

This study has confirmed that YOY and juvenile *G. galeus* seasonally use shark refuge areas in south-eastern Tasmania. However, evidence of YOY and juveniles emigrating from these areas within their first 1-2 years and the fact that few YOY (33%) and none of the juveniles returned suggests these areas may only afford protection for a limited amount of time, much less than the 3-4 years that was estimated from previous mark-

recapture results (Olsen, 1954; Stevens and West, 1997). Despite the high percentage of YOY that appeared to remain in the SRA (62%) for the duration of the study (80% of days spent in SRA), it is important to note that most of these animals (15 of 19) were detected for only a small percentage of their time at liberty (<5% of days) upon being released in UPW, and this needs to be considered in evaluating neonatal residency in the SRA. Whilst it is possible that these YOY were still present in the SRA but residing in areas of low receiver coverage, which seems unlikely given the number of receivers in UPW (n = 17) covering a relatively small area (approximately 20 km^2) and the positioning of several receivers in areas forming gates through which animals would need to pass, it is more likely these animals may have died outside receiver coverage. Given natural mortality rates tend to be comparatively high in juvenile sharks (Bush and Holland, 2002; Heupel and Simpfendorfer, 2002) then removing the likely deceased YOY from the analysis would imply that the relative proportion of surviving YOY leaving the protection of the SRA in their first year could be as high as 75%. However, further research may be required to validate these residency behaviours given that tag-induced mortality in large pelagic fishes including sharks can also be comparatively high (Skomal, 2007a) and may therefore have been responsible for mortality in this study.

Similarly, all juveniles that emigrated from the SRA within 12 months of being tagged were present in the SRA for only 18% of their time at liberty and only one individual returned to the SRA the following spring after leaving for winter. Considering these juveniles were most likely only >1+ based on size at the time of emigration (Stevens and West, 1997), they are spending considerable time in other areas outside the protection of the SRA at a young age. In fact three YOY were detected by acoustic receivers up to 280 km from the SRA and one juvenile was re-captured 1200 km away demonstrating that animals <2+ years are moving considerable distances outside the SRA during their early life development.

The northward movements of some YOY and juveniles is also consistent with previous mark-recapture studies demonstrating that juveniles typically moved from southern Tasmania nurseries to areas of Bass Strait and South Australia (Stevens and West, 1997). However, in contrast to these earlier findings our study indicates that YOY are

migrating much greater distances in their first few months of life than previously shown and could explain why there are fewer YOY returning to their natal areas. Whether these individuals are migrating to other known nursery areas around Tasmania such as Georges Bay (42° 19'0S 148° 14'0E) or utilising neighbouring waters of Storm Bay (Stevens and West, 1997) remains unclear. Our results would suggest that a proportion of YOY are moving long distances to locations such as Cape Barren Island (Bass Strait), which coincides with Bass Strait being a traditional hotspot for juvenile abundance (Olsen, 1954; Stevens and West, 1997; Walker *et al.*, 1999).

The movement of young *G. galeus* from the SRA within their first 1-2 years and the ability to migrate long distances suggest that once individuals find suitable habitats elsewhere there is little need to return to their natal origins. Similar observations have been made in other coastal elasmobranches such as gray smooth-hound sharks *Mustelus californicus*, leopard sharks *Triakis semifasciata* (Carlisle and Starr, 2009), and blacktip sharks *Carcharhinus limbatus* (Heupel and Simpfendorfer, 2005a). These studies reported that most young sharks spent their first 12 months in estuarine and inshore nursery areas before moving into adjacent coastal waters, with only a small portion of the population exhibiting philopatry to their natal origins. Therefore, determining where and how these additional areas are being used will be essential to ongoing recovery efforts for *G. galeus* as many of these areas remain un-protected from exploitation activities.

3.5.2 *Fine-scale movements and spatial overlap within the SRA*

YOY typically resided in the shallow estuary of Pitt Water for most of the summer months before emigrating to FHB during autumn. After entering FHB only two individuals returned to UPW, while none of the juveniles tagged in FHB were detected in UPW. This is somewhat contrary to previous work using conventional fisheries tags, which suggests that most YOY *G. galeus* are philopatric and return to their former estuarine nurseries (i.e. UPW) in the following spring (Olsen, 1954). Our data showed that having left UPW most individuals either then left the SRA entirely or only returned to FHB. Delayed tag induced mortality seems unlikely given that some YOY returned to FHB or were detected elsewhere outside the SRA at a later date. One possible explanation why YOY did not return to UPW is that there may have been some

behavioural changes in the utilisation of this area by *G. galeus* during later life stages given the habitat degradation that has occurred throughout the estuary such as the loss of seagrass meadows (Rees, 1993). Philopatry to nursery grounds is common among sharks yet habitat degradation is thought to have been responsible for the demise of this behaviour in many shark species (Hueter *et al.*, 2005). Continuing to monitor UPW and the remaining SRA with acoustic receivers may therefore be useful in determining if philopatric behaviour is still occurring but at a later stage in *G. galeus* life history.

YOY and juveniles showed a distinct ontogenetic disparity in their use of habitats in the SRA. YOY upon leaving UPW spent time in LPW before moving into and widely dispersing throughout mostly the shallower margins of FHB. In contrast juveniles were typically associated with habitats towards the middle of FHB. Ontogenetic resource partitioning by way of feeding on different prey or occupying different habitats is a common strategy among chondrichthyans that occupy similar spatial areas (Bethea *et al.*, 2004; Papastamatiou *et al.*, 2006; Taylor and Bennett, 2008; Grubbs, 2010). Crustaceans and cephalopods are important prey for YOY *G. galeus,* whereas teleosts become increasingly important in their diet with age (Stevens and West, 1997), suggesting that individuals may be selecting habitats based on the presence of their preferred prey. However, without data on the abundance and distribution of these prey types in the area it is not possible to ascertain whether this represents a key separation.

Juvenile use of deeper parts of FHB, particularly during the day, and expansion of their range and use of shallower areas at night may also represent a strategy to avoid predation. Juvenile *G. galeus* and gummy shark (*Mustelus antarcticus*) also preferred deeper waters of nearby Norfolk Bay (Fig. 3.1) (Barnett and Semmens 2012). Using the growing literature on behavioural responses of prey to the threat of predation and relevant theory as a guiding framework for interpretation (e.g. Wirsing & Ripple, 2011), Barnett and Semmens (2012) suggested that deeper water may enable a greater escape probability from, or allow easier detection of, the dominant predator in the area, the broadnose sevengill shark (*Notorynchus cepedianus*) in a relatively featureless environment (i.e. there is a lack of complex habitats in which to hide). Similarly, FHB is also a fairly featureless environment and suggests the use of deeper waters may be a common tactic used by juvenile *G. galeus* in these inshore waters to avoid predation

during the day. Conversely, juveniles may then use the cover of darkness to move into shallower, potentially riskier foraging areas, at night (Barnett and Semmens, 2012). In contrast YOY were less selective in their habitat choice during the day as evidenced by their exploratory behaviour and broad use of FHB, and may represent more naive behaviour as they have not yet learnt to move into deeper areas where they are potentially less vulnerable to predation. Previous studies on lemon sharks (*Negaprion brevirostris*) have shown that naive individuals become more efficient at foraging as they mature as they learn to feed when prey is easily targeted and predation risks are lower (Guttridge *et al.*, 2009; Guttridge *et al.*, 2013). In addition, *N. cepedianus* are rarely found in UPW compared to FHB and NB (Stevens and West, 1997; Barnett *et al.*, 2011; Barnett and Semmens, 2012), therefore, the higher fidelity and residency times that YOY spend in UPW may be an innate mechanism to avoid predation from *N. cepedianus*. Conversely, juveniles can trade-off the risk of predation in FHB for potentially increased resources (food, etc) because they are more adept at avoiding predators.

3.5.3 *Implications for conservation and management*

This study has demonstrated that south-east Tasmania SRAs continue to represent important nursery habitats for *G. galeus*, however, they may only play a temporary role in their overall conservation given YOY and juveniles spend a considerable time outside of the SRAs. In addition to the protection afforded by SRAs during the early life history phase, these regions also have a role in protecting pregnant females as they move in to the inshore areas to pup (Olsen, 1954; Walker, 1999). However, the protection of nursery areas such as with the implementation of SRAs alone are not sufficient to ensure rebuilding and sustainability of the populations (Kinney and Simpfendorfer, 2009). Of great importance are fisheries management measures such as minimum size limits that protect pre-recruits from fishing pressure when outside the protection of SRAs and total catch limits. In essence, a combination of SRAs and fisheries management has likely been key to stabilisation in *G. galeus* stocks providing a good example of how overfished populations can be stabilised using multiple management strategies. Therefore maintaining the function of SRAs and fisheries management measures will be essential for recovery of this species.

The strong affiliation of YOY with UPW and shallow areas of FHB in the SRA reinforces that continued protection of these areas is important. Although current management measures prevent the take of sharks in the SRA, recreational fishing practices such as gillnetting are still permitted in shallow waters of FHB (i.e. out to 200 m beyond the low tide mark). Given that YOY and to a lesser extent juveniles utilise a large proportion of these shallow habitats and the fact that gillnetting may cause significant incidental mortality of young *G. galeus* (Williams and Schaap, 1992; Lyle *et al.*, 2014), re-assessing the use of gillnets in these areas is warranted.

Fishery closed areas (in the absence of take) can provide an opportunity to monitor the recovery of over-exploited species by acting as control sites (Gell and Roberts, 2003; Hilborn *et al.*, 2004b). Given there are currently no fishery independent surveys or other appropriate means of monitoring *G. galeus* stock sizes as the fishery is now managed as incidental bycatch and fishers no longer target *G. galeus* (Huveneers *et al.*, 2013), examining the long-term use of closed areas by acoustically tagged animals in this study may therefore be helpful in monitoring the recovery of the *G. galeus* population. For example, acoustic monitoring of YOY *G. galeus* may provide estimates of natural mortality (Heupel and Simpfendorfer, 2002) which could be used to refine current recruitment and stock assessment modelling. Expansion of the acoustic array to cover areas outside of SRAs may also provide further insight to the importance of un-protected areas to *G. galeus* during early life history, providing critical empirical evidence needed to refine and enhance current management and conservation strategies such as closed area boundaries.

4

Delineating the movement behaviours and parturition sites of school shark (*Galeorhinus galeus*) in a shark refuge area using stable isotopes

4.1 Abstract

Determining the natal origin and birth site of highly mobile animals such as sharks is critical to understanding their ecology and in developing more focused management strategies which protect vulnerable early life stages. However, traditional catch sampling and tagging techniques often provide little useful information on the past movement and residency behaviours of animals to determine natal origins. Stable isotope analysis was used to determine if differences in isotope signatures were the result of young-of-the-year (YOY) school shark *Galeorhinus galeus* originating from separate pupping locations. YOY *G. galeus* were captured from an estuarine site which has historically been considered a pupping area, and δ^{13}C and δ^{15}N compared with those captured from a coastal embayment during the peak pupping season. YOY from the estuary had enriched δ^{13}C and were distinctly separated from those captured in the coastal embayment suggesting that individuals were born in either site and remained in those areas for extended periods. This was further supported by acoustic tracking which showed YOY *G. galeus* remained in the estuary for 3-4 months after parturition before migrating to the coastal embayment. These results demonstrate the value of using multiple methods to capture movement and residency patterns of animals, providing evidence that separate pupping areas exist in the shark nursery area.

4.2 Introduction

Identifying the natal origins or birth sites of animals has traditionally been regarded as an important component to their effective conservation since efforts can be more appropriately directed at protecting areas used during early life history when many species are most vulnerable (Hobson, 1999; Webster *et al.*, 2002; Webster *et al.*, 2005). However, there are emerging views that directing significant resources at protecting such areas may have little benefit in the overall conservation of a species in the absence of research and management outside these early life history areas (Kinney and Simpfendorfer, 2009). Again directing resources at protecting these areas may also have their limitations, thus a combination of management approaches may be more appropriate particularly in the case where the reproductive success of some species is limited by the quality and quantity of suitable birthing habitat (Baltz *et al.*, 2003). Therefore locating these areas should continue to form a component of the overall evaluation and management of a species population (Rowe and Hutchings, 2003). This is particularly important for commercially harvested species which may depend on particular birthing sites for the viability of harvested populations (Hobson *et al.*, 2009). Despite the importance of identifying these areas, birthing sites for many species remain largely unknown (Hobson *et al.*, 2009).

Stable isotopes, notably δ^{13}C and δ^{15}N, have been increasingly used as an alternative technique to track the historical (i.e. monthly – yearly) movements of animals by examining the assimilation and turnover of isotopically distinct food sources in their tissues (Hobson, 1999; Rubenstein and Hobson, 2004; Hobson *et al.*, 2008). This approach is based on differences in δ^{13}C and δ^{15}N occurring between regions having distinct baseline nutrient sources which are then assimilated in the tissues of animals that reside and forage in those areas over time. Stable isotopes therefore provide time integrated information on where an animal has been prior to capture and have been successfully used to define the movement patterns of animals and delineate natal origins (see Hobson 2009 for review). Combining stable isotope analysis with more traditional tagging techniques and advancements in modern tracking techniques such as electronic tags is also revealing more detailed movement behaviours and connectivity between

breeding and foraging sites of animals (e.g. Cerling *et al.*, 2006; Abrantes and Barnett, 2011; Van Wilgenburg and Hobson, 2011; Zbinden *et al.*, 2011).

Nursery areas are widely used by marine species to give birth to their offspring or to shelter juveniles, as they generally provide habitats which maximise the survival and development of young animals during their early life stages (Springer, 1967; Castro, 1993; Morrissey and Gruber, 1993; Heupel *et al.*, 2007). However, for many species, the specific function and importance of nurseries remains largely unknown, particularly the delineation of birthing sites which are often incorporated with nurseries (Castro, 1993; Parsons *et al.*, 2005). Nursery areas may play an important role in the viability of a species overall population (Beck *et al.*, 2001a; Gillanders *et al.*, 2003), therefore identifying birthing sites is important to developing more focused conservation strategies which protect habitats used during these vulnerable early life stages (Roberts, 2012).

Since 1954, eleven coastal embayment's and estuaries around Tasmania, Australia have been managed as no-take Shark Refuge Areas (SRAs), after being identified as important nursery areas for school shark (*Galeorhinus galeus*), in an effort to rebuild populations which have declined to 9-14% of virgin stock biomass as a result of overfishing (Olsen, 1959; Walker, 1999). During late spring and early summer pregnant *G. galeus* females are thought to migrate from offshore waters near the continental slope to these inshore areas where they give birth to their pups (Olsen, 1954; Walker *et al.*, 1999). Most of the pupping is thought to occur in the Upper Pitt Water estuary, in southeast Tasmania, where pups then disperse into the remaining areas of the nursery area over autumn and winter. However, pregnant females have been poorly represented in recent and historical catch surveys to infer pupping grounds, and high catches of neonates and young-of-the-year (YOY) sharks that fall within the appropriate length-at-age category (28 – 35 cm TL) in early summer in other areas of the refuge suggests that these regions may also provide important pupping grounds for *G. galeus* (Stevens and West, 1997). Whilst it has been demonstrated that the protection of nurseries alone has historically failed to stem the decline of the overfished *G. galeus* population (Kinney and Simpfendorfer, 2009), recent trends in the population suggest stocks may have stabilised as a result of implementing additional management changes

such as catch and effort restrictions (Huveneers *et al.*, 2013). Although the relative contribution of nursery area protection to these signs of recovery in the stock remains unclear, better understanding where and how these locations are used during early life history may provide important information that can be used to refine protection measures and potentially assist in the rebuilding of the overfished population.

The aim of this study was to identify the natal origins of *G. galeus* in a shark nursery area in southeast Tasmania. This was achieved by: (1) determining if there were differences in baseline isotope signatures between two areas where YOY *G. galeus* were captured; and (2) the use of stable isotopes together with acoustic tracking and stomach content data to determine differences in the movement and residency behaviours of YOY *G. galeus* captured from hypothesised pupping areas.

4.3 Methods

4.3.1 Study Site

This study was conducted at two main sites: Upper Pitt Water (UPW) (42° 48.1S 147° 30.4E) and Frederick Henry Bay (FHB) (42° 50.9S 147° 33.2E), located in southeast Tasmania, Australia (Fig. 4.1). UPW is a shallow, turbid estuary (~4 m average depth), comprised of mostly intertidal sand flats and river channels with a narrow entrance that connects to the deeper, coastal waters of FHB (~15 m average depth). FHB is an exposed coastal bay comprised mostly of beaches and sandy bottom habitats (Fig. 4.1). UPW receives freshwater input from regulated irrigation flows in the Coal River and also supports a number of oyster farming operations. Both UPW and FHB are managed as part of the Frederick Henry and Norfolk Bay Shark Refuge Area.
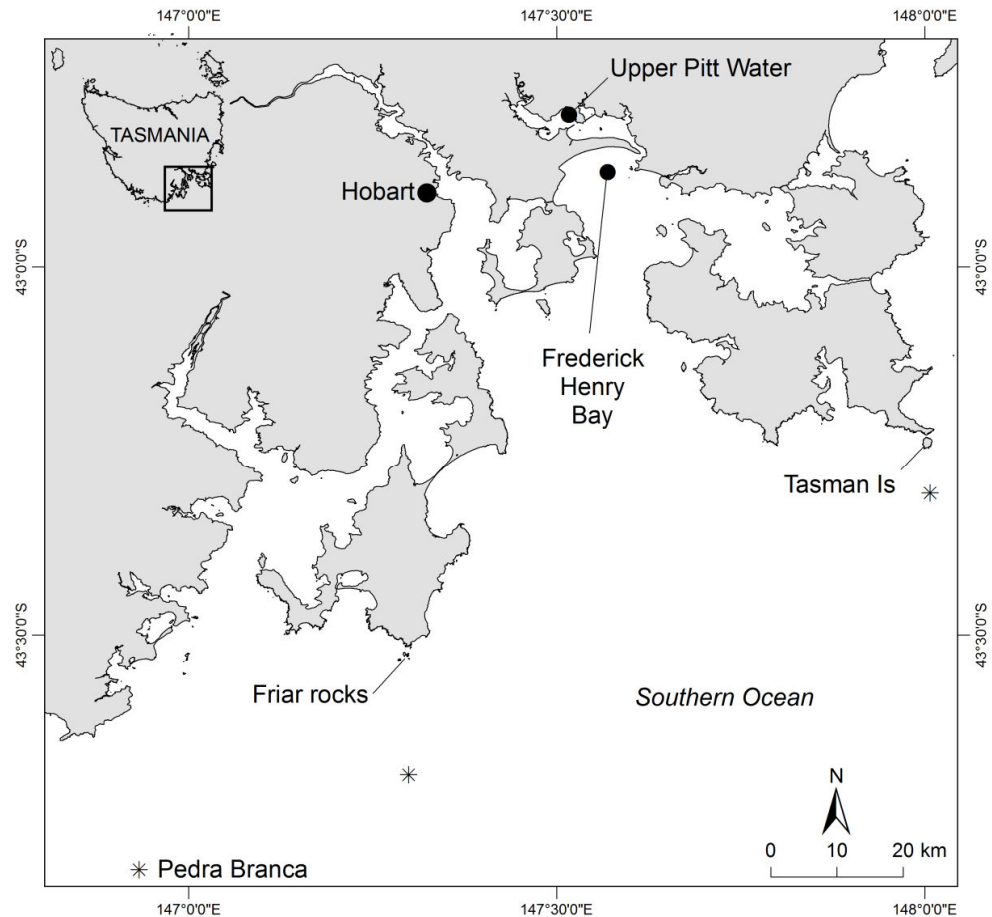
Figure 4.1 Sampling sites in Tasmania for stable isotope analysis of YOY and adult (asterisk) *G. galeus*.

4.3.2 *Stable isotope tissue collection and preparation*

Sharks were sampled from UPW and FHB between January and May 2012 using baited longlines. Because offspring are born with the maternal signature of their parent which is then diluted overtime as the tissue turns over and the young integrate their own diet isotope value (McMeans *et al.*, 2009; Olin *et al.*, 2011) adult *G. galeus* samples were also collected from commercial fishing operations at various offshore sites near the continental shelf break (~200 m depth) in southern Tasmania between Pedra Branca (43° 51.6S 146° 58.5E) and Tasman Island (43° 13.9S 148°E) (Fig. 4.1) to determine potential sources of error in isotope interpretation. YOY *G. galeus* were collected from UPW and FHB over two consecutive days during summer (February 27-28th) and autumn (May 4-5th). YOY *G. galeus* were defined as those individuals <500 mm TL. Previous seasonal length frequency studies in the same area have shown *G. galeus* >500 mm TL during summer are typically 1+ years of age (Stevens and West, 1997). Upon landing, sharks were measured for total length, sexed and a white muscle sample taken

from the dorsal flank using a 6 mm diameter biopsy punch and immediately placed on ice and later frozen at -30°C until analysis. All sharks were returned to the water alive after taking the tissue sample except for samples which were collected from commercial catch landings.

To determine an isotopic baseline at the main study sites (i.e. UPW and FHB) samples of seagrass (*Zosteraceae* family) and green algae (*Caulerpaceae* family) were collected from each site in February 2012. Three fresh plants from each family were collected, rinsed with deionised water, oven dried at 60°C to a constant weight, and ground to a fine powder for isotope analysis.

Because tissue lipids can affect its δ^{13}C (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979), lipid extraction of shark tissue was performed by sonicating samples in petroleum ether (PE) for 15 minutes, then in deionised water for a further 15 minutes following the method of Kim and Koch (2012). This procedure was repeated three times after which samples were dried to a constant weight at 60°C, and ground to a fine powder using a mortar and pestle. Prepared shark and algae samples were measured for δ^{13}C and δ^{15}N using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) by the University of California Davis Stable Isotope Facility,. Isotope abundances were expressed as per mille (‰) relative to international standards using the following equation:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000$$

where R equals either 13C/12C or 15N/14N. The standard reference materials used were Vienna PeeDee Belemnite and Air for carbon and nitrogen, respectively.

4.3.3 Seasonal use of study sites by YOY G. galeus

An array of 52 acoustic receivers were deployed in UPW and FHB between January 2012 and May 2013. The array was set up to detect the presence of acoustic tagged sharks in either UPW or FHB and to track their movements between the two areas. Sharks captured in UPW (size range: 33 – 44 cm TL) were fitted with eitherV9 2L (n = 6; Tag ID#4061 - 4069) or V13 1L (n = 22; Tag ID#31159 - 31198) acoustic-coded tags

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(29 and 36 mm length x 9 and 13 mm diameter; weight in water: 2.9 and 6 g; transmission off times: random between 120-180 s; predicted battery life: 2 and 5 years, respectively) between January and May 2012. The acoustic tag was surgically inserted in the peritoneal cavity of the animal by making a 1-2 cm incision in the abdominal wall, and the incision closed using surgical sutures (Braun Safil® HS26s). Aseptic techniques were used and running water was pumped over the animals gills during all stages of the surgery, taking no longer than 2-5 minutes to complete, after which the animal was released back into the water. Animals were held in the water boat side until they could swim unassisted prior to being released.

For analysis of acoustic tracking data, receivers were pooled into two regional groups, UPW (n = 17 receivers) and FHB (n = 35). Daily detection data was presented as a timeline of detections in each region and visually inspected to determine the residency patterns and times spent in either UPW or FHB. An individual was considered to have moved into either region if it was detected by a receiver in that region at least once in a given day.

4.3.4 Dietary analysis

To identify dominant prey groups and potential sources of isotope material that would be reflected in shark muscle tissue, available stomach sample data from YOY *G. galeus* captured in UPW (size range: 31 – 50 cm TL; n = 53) and FHB (size range: 32 – 50 cm; n = 64) between February 1991 and December 1992 by Stevens and West (1997) was examined. The frequency of occurrence (%F), percentage of numerical importance (%N), and percentage of weight (%W) dietary metrics were quantified and then used to determine the percentage Index of Relative Importance (%IRI) for each prey group (Hyslop, 1980). Prey were identified and grouped to at least family level and where possible to species.

4.3.5 Isotopic data analysis

Classification and regression tree analysis (CART) were used to determine the effects of site of collection, season, sex, and animal size on $\delta^{13}C$ and $\delta^{15}N$ for YOY *G. galeus*. CART analysis was performed on each isotope element separately using the 'rpart' package in R (Therneau *et al.*, 2010). The size of the tree was selected by using the 10-

fold cross validation and 1 – SE rule. Kruskal-wallis tests (χ^2) in R (R Core Devolpment Team, 2013) were then performed to test for significance difference in δ^{13}C and δ^{15}N which were identified from separation that occurred in the CART models (α = 0.01). The degree of isotopic overlap between regions and seasons was also determined by calculating the standard ellipse area (SEA$_B$) using a Bayesian approach known as SIBER (Stable Isotope Bayesian Ellipses in R) with the SIAR package in R following methods of Jackson *et al.* (2011). Differences in isotope composition between YOY and adult *G. galeus*, and between primary producers were determined using Kruskal-wallis tests (α = 0.01).

4.4 Results

4.4.1 Isotopic analysis

A total of 80 YOY and 25 adult *G. galeus* were used for stable isotope analysis (Table 4.1). Carbon (δ^{13}C) isotope compositions ranged from -17.0 to -18.1‰, and δ^{15}N from 14.9 to 16.5‰, and varied between YOY and adults, sites and season (Table 4.1).

Table 4.1 Number of YOY and adult G. galeus collected at each site and season, size range, δ^{13}C and δ^{15}N values and bulk C:N ratio (mean ± SD). FHB = Frederick Henry Bay; UPW = Upper Pitt Water; OS = Offshore; Su = summer; Au = autumn; F = female; M = male.

Site-Season	n	Size range (cm)	δ^{13}C	δ^{15}N	C:N ratio
YOY					
FHB-Su	28	33-43	-18.1 ± 0.3	14.9 ± 0.4	3.4 ± 0.1
UPW-Su	30	31-41	-17.5 ± 0.7	15.3 ± 0.5	3.3 ± 0.1
FHB-Au	11	39-49	-17.7 ± 0.3	15.3 ± 0.2	3.3 ± 0.1
UPW-Au	11	43-47	-17.0 ± 0.5	15.5 ± 0.6	3.3 ± 0.1
Adult					
OS-F	5	120-150	-18.0 ± 0.5	16.2 ± 0.6	3.3 ± 0.1
OS-M	20	130-150	-18.0 ± 0.2	16.5 ± 0.5	3.3 ± 0.1

4.4.2 YOY G. galeus

For δ^{13}C, the CART model (explaining 55% of the variability) revealed that YOY *G. galeus* δ^{13}C depends primarily on size with individuals larger than 43 cm total length (TL) having higher δ^{13}C (Fig. 4.2). For YOY *G. galeus* smaller than 43 cm TL a

second split separated animals by site with individuals captured in FHB having lower δ^{13}C than those from UPW (Fig. 4.2). There were no effects of sex or season on the δ^{13}C, as none of these variables were responsible for a branch separation in the CART (Fig. 4.2).
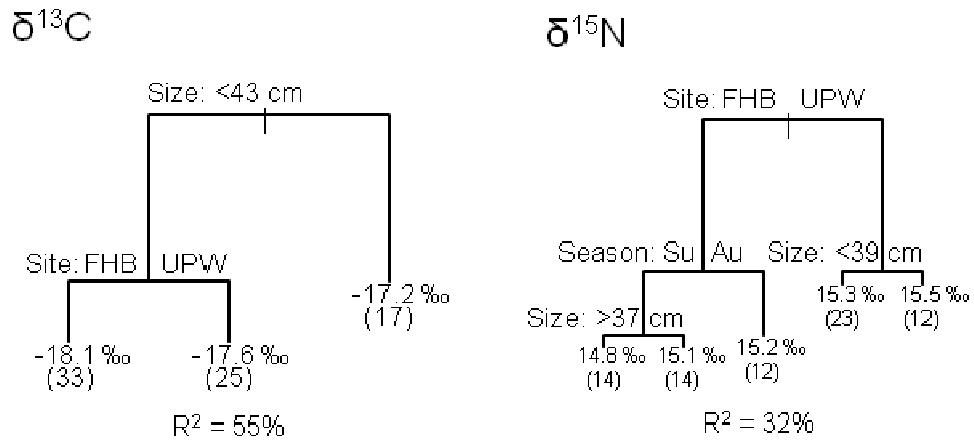
Figure 4.2 Classification and regression tree analyses of δ13C and δ15N for YOY *G. galeus* based on site of collection, sex, total length (TL), year, and season. Mean δ13C / δ15N and sample size (in parentheses) are provided at each terminal node. FHB = Frederick Henry Bay; UPW = Upper Pitt Water.

YOY *G. galeus* δ^{15}N depended primarily on capture site with individuals from FHB having lower δ^{15}N than those from UPW (Fig. 4.2). YOY *G. galeus* collected in FHB had higher δ^{15}N in autumn than those in summer, and for those collected in summer a further split separated individuals by size with individuals larger than 37 cm TL having lower δ^{15}N (Fig. 4.2). Of the YOY *G. galeus* collected in UPW, individuals less than 39 cm TL had lower δ^{15}N. Sex had no effect on δ^{15}N (Fig. 4.2).

For YOY *G. galeus* there was low overlap of standard ellipse area (SEA$_B$) between UPW and FHB during summer (Fig. 4.3), with individuals from FHB having significantly lower δ^{13}C and δ^{15}N than those from UPW (Tables 4.2 and 4.3). Similarly there was no overlap between sites during autumn, with individuals from FHB continuing to have significantly lower δ^{13}C than those from UPW (Table 4.2). Conversely, there was some overlap (SEA overlap = 0.11 ‰^{2}, corresponding to 50% and 92% in summer and autumn, respectively) and no significant difference in δ^{13}C and δ^{15}N between individuals caught in UPW during summer and those caught in FHB during autumn (Tables 4.2 and 4.3).

4.4.3 Adult G. galeus

There was overlap in SEA (0.27 ‰^{2}, corresponding to 23% and 96% of the total SEA of females and males, respectively) and no significant differences in δ^{13}C and δ^{15}N between adult male and female *G. galeus* captured offshore (Table 4.2 and 4.3) therefore sexes were pooled for comparisons with YOY. There was no overlap between SEA of adults and YOY and δ^{15}N was significantly higher in adults (Table 4.2 and 4.3). There were no significant differences in δ^{13}C between adults and YOY captured in FHB during summer but δ^{13}C was significantly lower than YOY from UPW captured in both summer and autumn and those from FHB captured during autumn (Table 4.2).
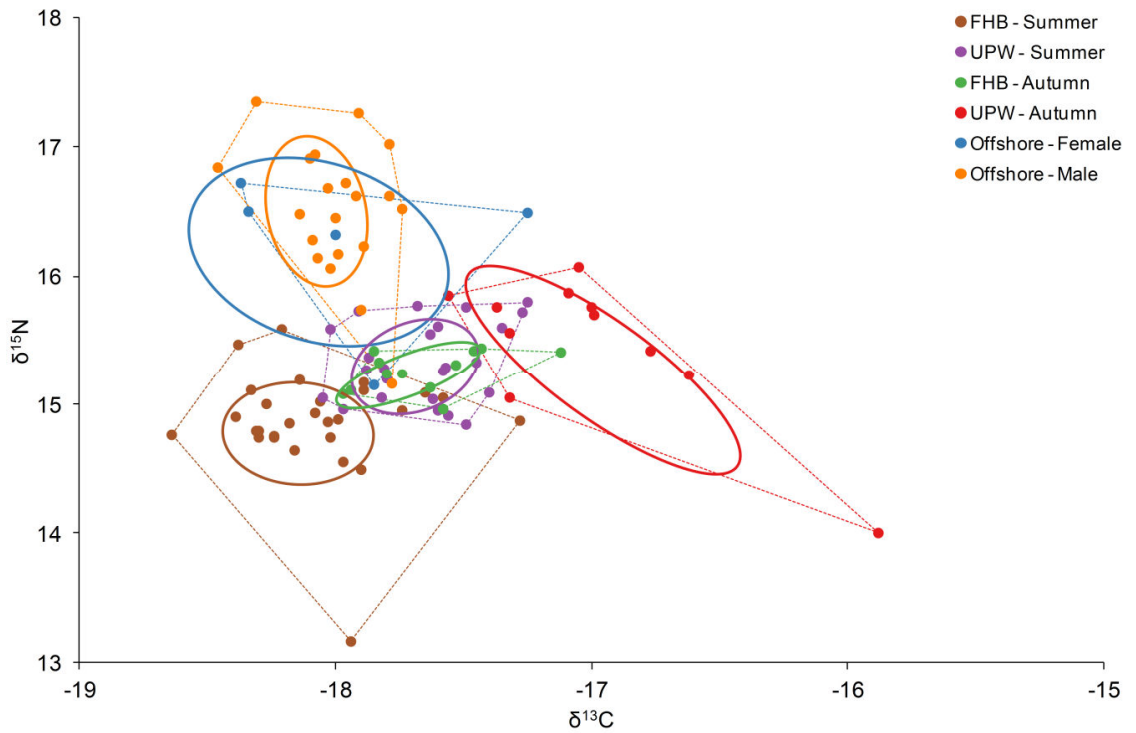
Figure 4.3 Stable isotope values for YOY G. galeus captured in Upper Pitt Water (UPW) and Frederick Henry Bay (FHB) during summer (Su) and Autumn (Au), and adult females (OSF) and males (OSM) from offshore waters. Bayesian standard ellipses (SEAB) (solid lines) used for comparing isotopic niche overlap between regions, seasons and life stages. Convex hulls (i.e. isotope extent) are also shown for each combination of above (dashed lines).

Table 4.2 Kruskal-wallis tests for differences in d13C between sites and seasons for YOY and adult G. galeus. . *p* < 0.01. FHB = Frederick Henry Bay; UPW = Upper Pitt Water; Su = summer; Au = autumn.

Site-Season	UPW-Su	FHB-Au	UPW-Au	Adult
FHB-Su	22.52*	14.73*	21.92*	1.83
UPW-Su	-	0.02	17.44*	17.4*
FHB-Au	-	-	13.19*	12.06*
UPW-Au	-	-	-	21.03*

Table 4.3 Kruskal-wallis tests for differences in d15N between sites and seasons for YOY and adult G. galeus. *p* < 0.01. FHB = Frederick Henry Bay; UPW = Upper Pitt Water; Su = summer; Au = autumn.

Site-Season	UPW-Su	FHB-Au	UPW-Au	Adult
FHB-Su	19.66*	13.84*	12.78*	37.14*
UPW-Su	-	0.66	2.91	28.09*
FHB-Au	-	-	4.13	18.91*
UPW-Au	-	-	-	15.19*

4.4.4 Primary producers

Seagrass and macroalgae from FHB were distinctly lower in δ^{13}C than those from UPW, which was then replicated in the mean δ^{13}C composition of sharks captured at each site during summer (Fig. 4.4). There were no obvious differences in δ^{15}N for primary producers between sites, however, δ^{15}N was on average two times greater in sharks than primary producers (Fig. 4.4).
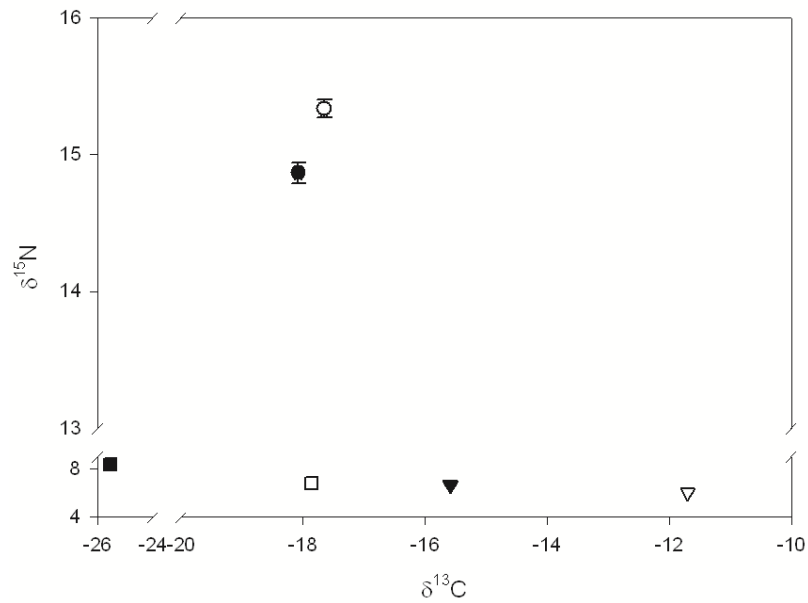
Figure 4.4 Isotope values of YOY *G. galeus* (○), and baseline isotope signatures of *Caulerpa* sp. (□), and *Zostera* sp. (▽) collected during summer 2012. Closed symbols denote samples collected in FHB and open symbols in UPW.

4.4.5 Seasonal use of study sites by YOY G. galeus

YOY *G. galeus* had strong fidelity to UPW between January and May 2012 (summer/autumn) with only one individual (ID# 31163) moving into FHB and returning to UPW during this period (Fig. 4.5). Twelve of the 28 tagged individuals departed UPW and were detected in FHB between May and July 2012, with all but one of the remaining animals which was constantly detected in UPW, going undetected for the remainder of the tracking period (Fig. 4.5). Of the individuals that moved into FHB, nine of 12 went undetected in FHB after July 2012, probably representing a movement out of FHB (Fig. 4.5). Four of the 12 individuals which presumably moved out of FHB were again detected in FHB around September/October 2012 with only one of these animals returning to UPW in October 2012 before re-entering FHB in January 2013 (Fig. 4.5).
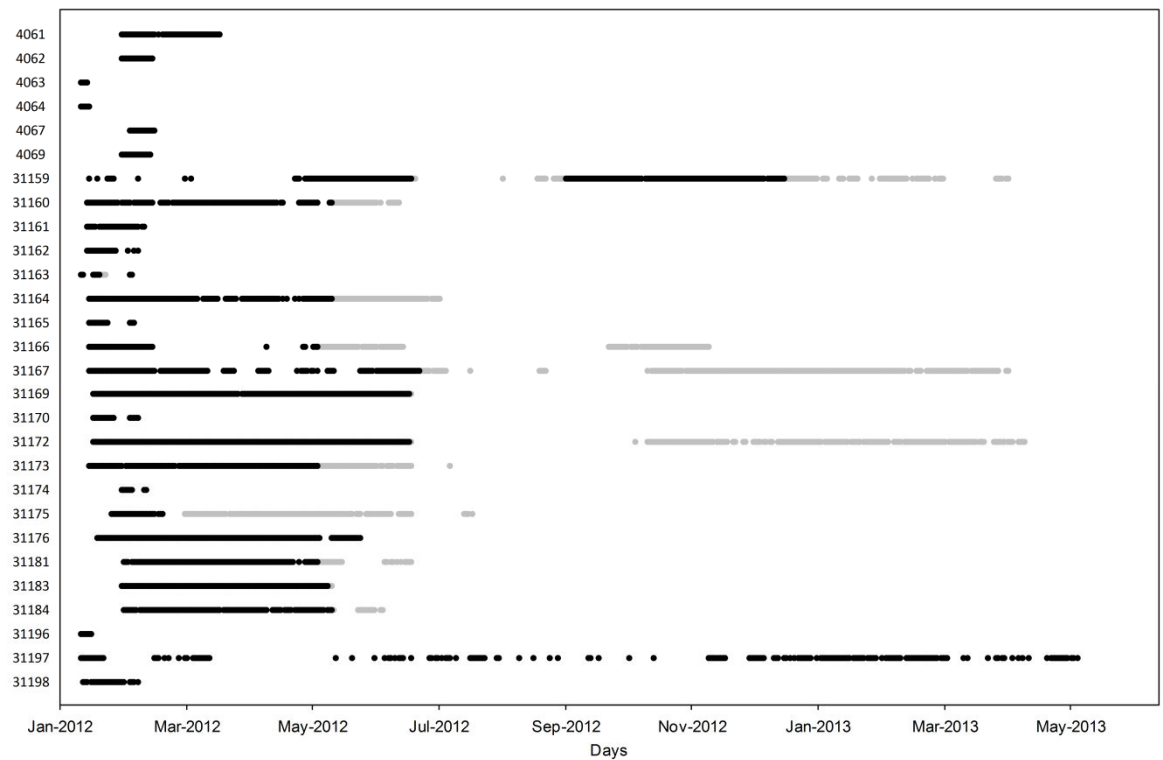
Figure 4.5 Abacus plot showing the daily detections for YOY *G. galeus* between January 2012 and May 2013. Each line represents an individual shark. Black represents detections by receivers in the UPW and grey represents detections in FHB.

4.4.6 YOY G. galeus dietary analysis

Data from a total of 117 YOY *G. galeus* stomach samples were re-analysed; 64 from FHB and 53 from UPW. Teleosts were the main prey at both sites (IRI = 81-84%) followed by cephalopods (12%), however crustaceans were slightly more important in UPW (7%) than FHB (4%) (Table 4.4).

Table 4.4 Dietary composition of YOY G. galeus sampled during summer 1991 – 1992. n = number of sharks containing prey, percentage of weight (%W), percentage of number counted (%N), frequency of occurrence (%FO), and index of relative importance (%IRI).

Prey	Upper Pitt Water (n = 53)				Frederick Henry Bay (n = 64)			
	%W	%N	%FO	%IRI	%W	%N	%FO	%IRI
Cephalopoda	**17.24**	**23.81**	**24.19**	**11.52**	**14.50**	**25.00**	**27.45**	**11.87**
Loliolus noctiluca	-	-	-	-	5.02	1.32	1.96	0.27
Unid cephalopod	17.24	23.81	24.19	24.33	9.48	23.68	25.49	18.06
Crustacea	**2.84**	**24.34**	**22.58**	**7.12**	**1.93**	**18.42**	**17.65**	**3.93**
Isopoda	-	-	-	-	0.01	1.32	1.96	0.06
Amphipoda	-	3.17	1.61	0.13	0.22	5.26	5.88	0.69
Unid crustacean	2.84	21.16	20.97	12.33	1.70	11.84	9.80	2.84
Teleostii	**79.92**	**51.85**	**53.23**	**81.36**	**83.57**	**56.58**	**54.90**	**84.20**
Arenigobius bifrenatus	20.25	17.99	14.52	13.60	-	-	-	-
Atherinidae	-	-	-	-	0.27	1.32	1.96	0.07
Atherinosoma microstoma	5.28	2.12	1.61	0.29	1.53	5.26	5.88	0.85
Engraulis australis	8.77	2.12	3.23	0.86	-	-	-	-
Platycephalidae	2.77	1.06	1.61	0.15	8.31	1.32	1.96	0.40
Rhombosolea tapirina	1.84	2.12	3.23	0.31	-	-	-	-
Silaginidae	-	-	-	-	29.29	6.58	5.88	4.51
Unid teleosts	41.02	26.46	29.03	48.00	44.18	42.11	39.22	72.27

4.5 Discussion

Differences in $\delta^{13}C$ and $\delta^{15}N$ between YOY *G. galeus* captured in Tasmanian estuarine and coastal waters supports our hypothesis of a potential separation of natal birth sites for this species in the shark refuge areas. In general, YOY from the coastal waters of FHB had lower $\delta^{13}C$ and $\delta^{15}N$ than those captured in UPW which was in agreement with baseline $\delta^{13}C$ signatures of macroalgae collected at each site. If all YOY *G. galeus* sampled were born in the same area, either UPW or FHB, and they were moving between sites, isotope signatures of their tissues should have been overlapping irrespective of where they were caught, particularly during the peak pupping season in summer. These results therefore confirm historical reports that pupping occurs in UPW (Olsen, 1954; Stevens and West, 1997), however, it also suggests that *G. galeus* pupping is probably more widely dispersed throughout other areas within the shark refuge area than previously thought.

Isotope turnover in shark tissue is relatively slow (up to 2-years) (Malpica-Cruz *et al.*, 2012), therefore as YOY *G. galeus* were collected on consecutive days in UPW and FHB it is unlikely that their tissue would have assimilated a new isotopic baseline if they had moved between sites. This may explain the lower $\delta^{13}C$ in YOY from FHB and suggests that newborn individuals rarely move into UPW if they are born in FHB. Previous studies have demonstrated that isotope signatures will strongly overlap when species regularly move between isotopic gradients. For example Atlantic salmon (*Salmo salar*) parr which made repeated forays between the Little Southwest Miramichi River and Otter Brook were shown to have an intermediate mean $\delta^{13}C$ signature in contrast to that of parr which had high site fidelity to each site and as a result isotope signatures consistent with being long-term residents in either system (Cunjak *et al.*, 2005). Acoustic tracking indicated that YOY *G. galeus* had strong fidelity to UPW (i.e. 3-4 months), suggesting they have small home ranges, do not move long-distances initially, and forage close to their birth site. If these characteristics are typical of newborn *G. galeus* elsewhere in the SRA then it is most likely that they do not move between sites but instead remain close to their birth site for an extended duration (i.e. first 3-6 months).

Enriched $\delta^{13}C$ is generally associated with inshore and estuarine waters which derive much of their nutrients and organic matter from benthic food-webs, in contrast to coastal and oceanic waters which have food-webs primarily based on plankton (Fry *et al.*, 1983; France, 1995). Similarly, seagrass and other aquatic macrophytes typically associated with inshore marine environments are generally higher in $\delta^{13}C$ than planktonic producers (Clementz and Koch, 2001) and $\delta^{15}N$ is typically more enriched in inshore waters close to urban areas due to pollutants and/or agricultural runoff (Costanzo *et al.*, 2003). UPW is characterised by areas of patchy seagrass (Mount *et al.*, 2005) and nutrient sources from sewage treatment plants and agricultural runoff (Davies *et al.*, 2002), most likely explains the enrichment of primary producer $\delta^{15}N$ compared to coastal waters of FHB. Studies have shown that lower order consumers such as invertebrates and small fish which feed and reside in these systems will generally reflect the isotopic enrichment of estuaries (Paterson and Whitfield, 1997; Leakey *et al.*, 2008). Historically the diet of *G. galeus* was similar between UPW and FHB, comprised almost exclusively of teleosts. Therefore, assuming diet hasn't significantly changed since the 1990s and there is little movement of prey species between UPW and FHB, it is unlikely that dietary differences are the reason for the lack of isotope overlap but rather different carbon sources and/or pollutants affecting $\delta^{15}N$ of primary producers between the two regions.

However, one caveat to low overlap in isotope signatures of YOY *G. galeus* between UPW and FHB is that there may have been some pre-capture movement between sites immediately after birth which isotope analysis would not detect as individuals would not have spent enough time in their birth site to accumulate that area's signature in their tissue. Given that acoustic tracking implied YOY *G. galeus* have small home ranges it seems unlikely that there would have been any major movement or dispersal behaviours prior to sampling. For example, acoustic tagged YOY blacktip sharks (*Carcharhinus limbatus*) demonstrated small home ranges in the weeks following parturition which was characterised by strong site fidelity and limited movement within a nursery area (Heupel *et al.*, 2004). The lack of migration into UPW from FHB is further supported by conventional tagging of YOY *G. galeus* in FHB during the years 1947-56 (n = 4) and 1991-92 (n = 152) which re-captured tagged animals close to their tagging site (i.e. FHB) but never in UPW (Olsen, 1954; Stevens and West, 1997).

Maternal meddling (i.e. the transfer of maternal reserves and subsequent isotope signatures between mother and young) may also influence the isotope signature of their offspring and interpretation of isotope data in young sharks (McMeans *et al.*, 2009; Olin *et al.*, 2011). Reproduction in *G. galeus* is via aplacental viviparity (i.e. embryos develop inside the uterus but all nutrition is provided via unfertilised ovum and each other, before they emerge as live young ca. 28-35 cm TL) (Ripley, 1946; Camhi *et al.*, 2009). In the few studies that have examined maternal meddling in neonate and YOY sharks most report enriched isotope signatures and a loss of that signature in YOY over time and increasing size (McMeans *et al.*, 2009; Olin *et al.*, 2011). For example YOY Atlantic sharpnose shark *Rhizoprionodon terraenovae* at birth are likely to have higher $\delta^{13}C$ and $\delta^{15}N$ values than their parents and older YOY whose postpartum feeding habits have restructured their isotope profiles to reflect their postembryonic diet (McMeans *et al.*, 2009). However, YOY *G. galeus* were significantly lower in $\delta^{13}C$ and $\delta^{15}N$ compared to adults therefore implying that YOY had already lost the majority of their paternal signature and were now incorporating the isotope signature of their respective inshore birth sites. If maternal meddling was occurring then the isotope signature of YOY should have been more enriched and similar to that of adults, and largely overlap between YOY from both sites. However, it must be noted that only a small number adult females were collected in this study (n = 5). Incorporating a larger sample size of females and from within the nursery area at the time of pupping may be more appropriate before discounting the maternal influence on YOY isotope signatures.

Effective protection of essential habitats such as birthing areas requires a sound understanding of their distribution so that more focused management strategies can be implemented (Hobson, 1999; Webster and Peter 2005). In this study, stable isotopes were used to identify a much broader distribution of pupping habitats in a historically important nursery area for *G. galeus* which are then used for an extended duration post-parturition. The use of stable isotope analysis for YOY captured elsewhere may therefore help in broadening our understanding of alternative pupping sites both within and outside the refuge area.

Given the anthropogenic degradation and loss of other historically important nursery habitats elsewhere such as in Port Phillip Bay, Victoria (McLoughlin, 2008) and the

subsequent declines in newborn *G. galeus*, nursery areas and their associated pupping grounds identified in this study may be critical to the viability of the greater *G. galeus* population. Although fisheries management strategies such as gear restrictions afford some protection to the pupping areas in UPW, different management approaches may be required to encompass and protect the broader distribution of pupping areas identified in FHB from anthropogenic disturbance. For example, expansion of finfish aquaculture farming in Norfolk Bay (DPIPWE, 2014) and irrigation schemes in the UPW catchment (Tasmanian Irrigation, 2013) both have the potential to influence the quality and quantity of available pupping habitats. Moreover permitted fishing practices such as gill netting in FHB may cause significant incidental mortality to pregnant *G. galeus* using these areas to give birth to their young (Williams and Schaap, 1992; Lyle *et al.*, 2014). The greater understanding of these important pupping habitats has therefore provided managers with greater empirical evidence that will help in their decision making for better conservation outcomes and the continued recovery of *G. galeus*.

5

The role of dietary and habitat partitioning in alleviating interspecific competition in shark nursery areas

5.1 Abstract

Determining interactions between animals such as how they shares resources and space is central to understanding ecosystem dynamics and is critical in the development of effective conservation strategies. Acoustic telemetry in conjunction with stable isotope analysis was used to examine how multiple chondrichthyans (i.e. sharks, rays and chimeras) and a common teleost utilise an important shark nursery area, and the mechanisms that enable multiple species to coexist in an environment with limited predation risk. Animals utilised largely the same overall area and were most often associated with deeper habitats, however, stable isotopes revealed possible dietary dissimilarities which suggest dietary partitioning facilitates habitat sharing between animals in the nursery area. In contrast, high dietary overlap between some species suggest that their prey species may not be limiting, however, acoustic tracking revealed that these species often foraged in different habitats resulting in reduced competition. These results demonstrate that resource partitioning strategies play an important role shaping the dynamics of shared environments used by multiple species, ecological mechanisms that must be maintained in developing strategies to enhance the recovery of overfished populations.

5.2 Introduction

Ecosystem structure is often determined by community interactions and the various ways in which organisms respond to competition and predation (Holt, 1977; Sih *et al.*, 1985; Cherrett and Bradshaw, 1989). For example, competition between animals with similar dietary niches can lead to animals occupying different habitats in a common environment in order to coexist, i.e. resource partitioning (Schoener, 1974). Similarly, risks imposed by predators may also cause prey to reside or forage in habitats where there are lower predation risks but potentially fewer resources (Glasser, 1979; Dupuch *et al.*, 2009; Wirsing *et al.*, 2010). Competition and predation can also occur in unison and it is thought that increased competition resulting from the re-distribution of prey avoiding areas of higher predation risk is a major driver of resource partitioning and coexistence between animals (Chase *et al.*, 2002; Werner and Peacor, 2003). Therefore determining trophic interactions between species and the ways in which animals move and share common environments is essential to understanding how competition and predation influence community dynamics.

Competition and predation may also play an important role in determining the effectiveness of ecosystem-based management decisions (Hixon and Jones, 2005). For example, the removal of large numbers of predatory fishes from a population is thought to be partly responsible for the slow recovery of some species which have suffered significant overfishing such as Newfoundland Atlantic cod (*Gadus morhua*) (Swain and Sinclair, 2000; Walters and Kitchell, 2001) and rock lobsters (*Jasus lalandii*) (Barkai and McQuaid, 1988) because of the increased competition between their juvenile offspring and the greater numbers of juveniles of other competing species resulting from the reduced predation pressures. Therefore, knowledge of how multiple species interact and respond to competition and predation is essential to understanding how ecosystems are structured and function in response to anthropogenic disturbance. This can be used to make informed decisions regarding the development and implementation of effective ecosystem-based management strategies (Walters and Kitchell, 2001; Dill *et al.*, 2003; Baskett *et al.*, 2006).

Many marine species use shallow coastal waters as nursery areas during early life stages as they are thought to provide ample food resources and protection from predation (Springer, 1967; Branstetter, 1990; Simpfendorfer and Milward, 1993; Beck *et al.*, 2001a; Beck *et al.*, 2001b). Therefore indentifying and protecting nursery areas has formed an essential component of shark (Bethea *et al.*, 2007; e.g. AFMA, 2009) and teleost (e.g. Benaka, 1999) recovery strategies. However there is emerging evidence that nursery areas are more resource limited than previously thought and competition likely plays an important role in structuring these communities, particularly those used by sharks (Bush and Holland, 2002; Baker and Sheaves, 2007; Heupel *et al.*, 2007). With the advent of modern electronic tracking tools such as acoustic telemetry and trophic analytical methods such as stable isotope analysis, there has been an increased effort to further improve our understanding of how competition, predation, and resource partitioning structure multi-species marine communities, including nursery areas (e.g. DeAngelis *et al.*, 2008; Kinney *et al.*, 2011; Speed *et al.*, 2011).

In Tasmania, Australia, a network of Shark Refuge Areas (SRAs) was established in the 1960s to protect the nursery grounds of school sharks (*Galeorhinus galeus*) in response to significant catch declines in the Southern and Eastern Scalefish and Shark Fishery (SESSF) (Kinney and Simpfendorfer, 2009). Recent stock assessments suggest the *G. galeus* population may have stabilised, although still at 9-14% of virgin biomass, and nurseries have been identified as important to stock rebuilding (AFMA, 2009). In addition to *G. galeus*, these areas also support multiple chondrichthyan (i.e. sharks, rays and chimeras) and teleost (i.e. bony fishes) species (Stevens and West, 1997; Barnett and Semmens, 2012). Given the diversity of chondrichthyans and teleosts found in these SRAs, it is likely that competition, predation, and resource sharing all play a role in structuring the dynamics of these areas. However there has been no examination of the fine-scale habitat use and foraging behaviours of the chondrichthyan and teleost assemblages in these areas to understand the interactions and mechanisms that enable species to partition resources and co-occur. Coexistence within communal chondrichthyan assemblages is often demonstrated by dietary (e.g. Bethea *et al.*, 2004; Papastamatiou *et al.*, 2006) and habitat partitioning (e.g. White and Potter, 2004; DeAngelis *et al.*, 2008) between species, however, there is limited evidence of these behaviours occurring in unison or between chondricthyans and teleosts (e.g. Kinney *et*

al., 2011).   This study used a multi-methods approach to investigate competitive interactions between young-of-the-year (YOY) *G. galeus*, six other chondrichthyans (two sharks, one chimaera and three batoids), and the sand flathead (*Platycephalus bassensis)*, a common predatory teleost in the area. Given the importance of SRAs in Tasmania for recovery of *G. galeus* and the possible competition and predation that occurs in these areas, this study elucidates the role of resource partitioning in shaping SRA dynamics and the impact this may have on the recovery of the *G. galeus* population.

5.3 Methods

5.3.1 Study site

Upper Pitt Water (UPW) is a shallow (~4 m average depth) estuary located in southeast Tasmania, Australia (42° 47.91′S, 147° 30.56′E; Fig. 5.1), and is comprised of mostly intertidal sand flats and a deep central channel (~8 m deep) (20 km^2). The main source of freshwater input is from the Coal River, after which UPW drains into Lower Pitt Water (LPW) through a manmade road causeway where it eventually enters into Frederick Henry Bay (FHB). UPW supports a number of oyster farms and is part of the Frederick Henry and Norfolk Bay Shark Refuge Area (SRA). Recreational fishing for teleosts and chimeras (i.e. elephant fish *Callorhinchus milii*) is allowed in the SRA however the removal of elasmobranchs (i.e. sharks and rays) is not permitted (DPIPWE, 2013).

A VEMCO Positioning System (VPS, Vemco Canada) was deployed to monitor the presence and movements of chondrichthyans and teleosts implanted with acoustic tags in UPW.   The VPS consisted of 14 acoustic receivers (VR2W, Vemco Canada) deployed in a grid of equilateral triangles such that the detection range of receivers overlapped (Fig. 5.1).   Range testing was conducted prior to deployment of receivers and acoustic transmitters, and determined an optimum distance between receivers of 350 m which allowed for simultaneous detections by three or more receivers. Receivers were deployed in depths of 3-9 m (~4 m average) and were secured to a concrete filled tyre and vertical steel pole which supported the receiver at 1.5 m from the seafloor. A

synchronising transmitter or "sync tag" with a nominal transmission delay of 600s was moored approximately 1 m above each receiver to synchronise the internal clocks of receivers. Three additional sync tags were deployed at fixed locations to help measure system performance (Fig. 5.1). This array ensured tag transmissions were detected by at least three receivers, the difference in the timing of arrival of an acoustic ping at each receiver being used to triangulate a tagged animal's position. The array covered an area of approximately 1.8 km^2 and was deployed on 6th January 2012 and recorded data until 22nd May 2013. The site of the VPS array in UPW (Fig. 5.1) was chosen based on previous information suggesting high occurrence of chondrichthyans (Stevens and West 1997; R Daley pers. comm.). Three additional acoustic receivers were placed in UPW to monitor tagged animals outside the VPS (Fig. 5.1).
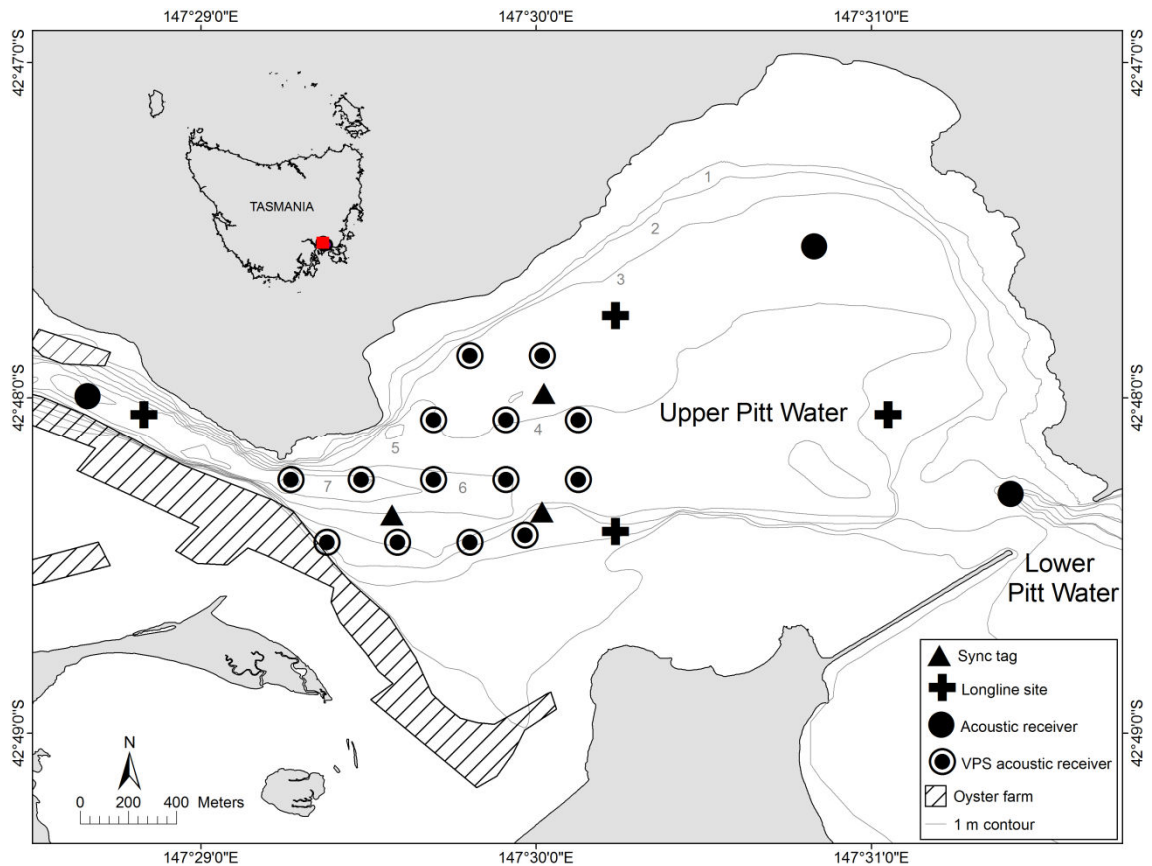
Figure 5.1 Map of study area showing VPS array in Upper Pitt Water (UPW) in south east Tasmania.

5.3.2 Animal collection and acoustic tagging

Chondrichthyans and *P. bassensis* were captured using bottom set baited longlines and internally fitted with individually coded acoustic tags (see Table 5.1 for tag details). Longlines consisted of a 210 m, 6 mm lead core rope to which 50 stainless steel wire snoods with hooks (7x7 stainless steel wire, 160 lb breaking strain, Mustard #8260 size 5/0 hook) were attached at 4 m intervals using 100 mm swivel shark snap clips. Hooks were baited with squid. Longlines were set at four fixed locations in UPW (Fig. 5.1) between 0700 and 0730 hours and were hauled between 0800 and 1000 hours. Lines were typically deployed for 1 – 2 hours.

In total 203 animals were acoustically tagged: 55 *G. galeus*, 24 gummy shark (*Mustelus antarcticus*), seven broadnose sevengill sharks (*Notorynchus cepedianus*) (sharks); 42 *C. milii* (chimera); 31 *P. bassensis* (teleost); seven Melbourne skate (*Spiniraja whitleyi*), 16 smooth stingray (*Dasyatis brevicaudata*), and 21 southern eagle ray (*Myliobatis tenuicaudatus*) (batoids). Based on mean size-at-birth ranges for each species (Last and Stevens, 2009), 95% of *G. galeus* were considered young-of-the-year (YOY) whereas for most other species, with the exception of one YOY *M. antarcticus,* individuals were classed as sub-adults or adults (Table 5.2). *Notorynchus cepedianus* represent the main predator the study system, with previous dietary analysis demonstrating they consume all the other species (Barnett *et al.*, 2010a).

Upon collection, total length (TL, cm) of all animals and disc width of batoids (DW, cm) was measured and the sex of chondrichthyans recorded. Prior to tag insertion surgery, chondrichthyans were either placed on a padded cradle or held by another person while running water was pumped over their gills, whereas *P. bassensis* were anaesthetised in a seawater bath of Aqui-S^{TM} (0.03 ml·L^{-1}). Acoustic tags were then internally inserted in the peritoneal cavity of the animal by making a 1-2 cm incision in the abdominal wall with a scalpel, and the incision closed using surgical sutures (Braun Safil$^®$ HS26s). Aseptic techniques were used during all stages of the surgery. Surgical procedures took no longer than 2-5 minutes to complete. Following surgery, chondrichthyans were held in the water on the side of the boat until they could swim unassisted whereas *P. bassensis* were held in an aerated container of seawater until they fully recovered from the anaesthetic, prior to being released back into the water in the

middle of the VPS array. Animals were tagged between January 2012 and May 2012, and again between December 2012 and April 2013.

5.3.3 Stable isotope tissue collection and preparation

Muscle samples for stable isotope analyses were collected between January 2012 and May 2012. Samples were taken from the dorsal flank with a 6 mm diameter biopsy punch and immediately placed on ice and later frozen at -30°C until analysis. Biopsy puncher wounds were treated with antiseptic cream (Betadine[®]) prior to the animal being returned to the water alive. Tissue samples were prepared and analysed for $\delta^{13}C$ and $\delta^{15}N$ following the same procedures detailed in Chapter 4.

5.3.4 Data analysis

VPS position fixes (latitude and longitude) were derived using Vemco VPS software (Vemco, Canada). Each position was given a horizontal position error (HPE) which is based on the error sensitivity of the receiver array, calibrated to the local environmental conditions. Only positions where HPE was <15 m at dawn and dusk were included in analyses. Dawn and dusk were defined as 1 hour before and 1 hour after the predicted sunrise and sunset times for a given day obtained from the Bureau of Meteorology, Australia (www.bom.gov.au). Animal positions were examined at dawn and dusk to observe spatial overlap between species at times when they were most likely to be feeding, as these are times when many animals show diel patterns of increased activity which are often associated with foraging (Conover, 2010) particularly in sharks (Carrier *et al.*, 2010). Animal positions were used to estimate Kernel Utilisation Densities (KUD) to determine spatial use of the VPS habitats, with the 95% fixed kernel representing the overall habitat use and the 50% fixed kernel the core use area. KUD were estimated using the bivariate normal density kernel in the adehabitatHR package (Home Range Estimation in R; Calenge, 2011) in R statistical computing package (R Development Core Team, 2013). The Utilisation Density Overlap Index (UDOI) was then calculated to determine the KUD overlap between species using the adehabitatHR package in R. The degree of overlap is generally represented by values between 0 (no overlap) and 1, (100% overlap), however UDOIs can be >1 when KUDs are non-uniformly distributed and have a high degree of overlap (Fieberg and Kochanny, 2005).

Individual VPS positions were also assigned a habitat category based on depth and location within UPW to test for habitat selection (w_i) (Fig. 5.1). The habitats ranged from the shallow sand flats (flats, 17% of area covered by the VPS), to the drop-off (edge; 10%) into the main basin (basin, 70%) and deepest part of UPW (channel; 3%). Selection for each habitat was determined using a log-likelihood test (χ^2) in the adehabitatHS package (Exploratory Analysis of the Habitat Selection by Wildlife in R; Calenge 2011) in R. Selection ratios >1 indicate a preference for a particular habitat whereas values <1 indicate avoidance.

Residency patterns and seasonal use of UPW was determined by visually examining a plot of daily detections for animals that were fitted with acoustic tags with a battery life >71 days and were detected by any receiver in UPW (including VPS receivers). Residency within the VPS area was determined for animals that were fitted with acoustic tags with a battery life >71 days and had at least one VPS position (i.e. simultaneously detected by >3 VPS receivers). Additional acoustic data from another related study in LPW and FHB was also included to examine if tagged animals had moved out of UPW (J. McAllister unpublished data). Mean site fidelity in UPW or within the VPS (% of time animals spent within UPW or the VPS array) was determined by dividing the total number of days an individual was detected in UPW or positioned within the VPS, by either the battery duration of the tag or the number of days that animal had been at liberty depending on which fell first, respectively. In addition, all seasonal longline catch data from UPW between 2012 and 2013 was pooled and Kruskal-Wallis non parametric tests ($\alpha = 0.01$) used to determine seasonal differences in catch per unit effort (CPUE) for all species. CPUE was defined as the number of sharks captured per hook hour.

To investigate dietary overlap, the isotopic niches of each species were quantified based on sample size corrected Bayesian standard ellipse areas (SEA$_C$; expressed in ‰^{2}) along with the degree of overlap in SEA$_C$. SEA$_C$ and overlap were calculated using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson *et al.*, 2011) of Stable Isotope Analysis in R (SIAR; Parnell *et al.*, 2008; Parnell *et al.*, 2010). SEAs are comparable to univariate standard deviations but are less affected by uneven sample

group sizes, therefore allowing for more reliable comparisons of isotopic niche between communities (Jackson *et al.*, 2011).

Due to capturing no *N. cepedianus*, *S. whitleyi* or *D. brevicaudata*, and insufficient *M. tenuicaudatus* (n = 1) from UPW for muscle samples, data was supplemented with stable isotope data collected for these species during a previous study in Norfolk Bay (42° 59.94′S, 147° 47.15′E), a sheltered embayment connected to Pitt Water through Frederick Henry Bay (FHB) (42° 55.4′S, 147° 36.5′E), during 2009 (Abrantes and Barnett, 2011). Sufficient data (i.e. >2 samples) was available to calculate SEA_C for *N. cepedianus* and *S. whitleyi* and include in overlap analysis, whereas *D. brevicaudata* and *M. tenuicaudatus* were used for qualitative analysis only (i.e. one sample each).

5.4 Results

5.4.1 Habitat use

Most animals were detected at multiple receivers in UPW for an average of 22% of their time at liberty (Table 5.1), however, four *C. milii* remained in a stationary position within the VPS array for the duration of the study. These animals most likely died and were therefore excluded from further analysis. Overall, there was a clear seasonal use of UPW and areas within the VPS array (Fig. 5.2). Typically animals were detected for most of summer/autumn (January to May) in UPW and the VPS before moving into FHB in winter (Fig. 5.2). However, species variations in this pattern were evident, particularly for *C. milii* and *M. antarcticus* which regularly moved between UPW to FHB during summer and autumn (Fig. 5.2). For all other species other than *G. galeus*, with the exception two *C. milii* and two *P. bassensis*, animals tagged in 2012 that left UPW during winter returned to UPW between spring 2012 and autumn 2013 (Fig. 5.2). For most *G. galeus* (43 of 45 tagged) however, no individuals returned to UPW after departing the estuary.

Seasonal occurrence in UPW was also reflected in seasonal longline catches, with *G. galeus*, *C. milii*, and *P. bassensis* showing significant seasonal differences in CPUE ($p < 0.01$). This was mostly attributed to higher catches during summer and autumn, nil catches in winter and lower catches during spring (Fig. 5.3). Catches did not vary

significantly between seasons for *M. antarcticus* (χ^2 = 8.7, d.f. = 3, *p* = 0.03), *N. cepedianus* (χ^2 = 9.8, d.f. = 3, *p* = 0.02), *S. whitleyi* (χ^2 = 6.2, d.f. = 3, *p* = 0.1), *D. brevicaudata* (χ^2 = 7.9, d.f. = 3, *p* = 0.05) or *M. tenuicaudatus* (χ^2 = 3.2, d.f. = 3, *p* = 0.4). *Galeorhinus galeus* and *P. bassensis* dominated catches in most seasons whereas *N. cepedianus*, *D. brevicaudata* and *S. whitelyi* had the lowest catch rates (CPUE <0.01 sharks × hook × hr^{-1}) of the remaining species in all seasons (Fig. 5.3).

A total of 57654 positions (<15 m HPE) were estimated using the VPS. Of the 203 animals tagged, more than five VPS positions were estimated for 34 *G. galeus*, 21 *C. milii*, four *M. antarcticus*, eight *P. bassensis*, four *N. cepedianus*, four *S. whitleyi*, seven *D. brevicaudata*, and five *M. tenuicaudatus* and were included in UDOI and depth selection analysis. Overall, animals were positioned in the VPS for an average of 9% their time at liberty (Table 5.1). In addition, these same animals were also detected at UPW receivers outside of the VPS array for 27% of their time at liberty (Table 5.1). Overall area use (i.e. 95% KUD) ranged between 0.8 – 1.6 km^2 and 1.0 – 3.71 km^2 at dawn and dusk, respectively. Average core habitat use (i.e. 50% KUD) area estimates ranged between 0.2 – 0.5 km^2 and 0.2 – 1.0 km^2 at dawn and dusk, respectively and mostly corresponded to the basin habitat (Fig. 5.4).

Table 5.1 Summary of tracking data for animals fitted with acoustic tags. In the acoustic tag type column, A, P, L and H indicate accelerometer sensors, pressure (depth) sensors, low signal output power and high signal output power, respectively. Nominal delay is the delay (seconds) between tag transmissions, and battery life is the predicted battery life of the tag. Size ranges represent total length (TL) for sharks, chimeras and teleosts, and disc width (DW) for batoids (cm). Overall UPW fidelity is the mean percentage of days all animals were detected in UPW (including the VPS) during their time at liberty. For animals that recorded VPS positions, tracking duration is the mean number of days an animal was positioned in the VPS array; site fidelity is the percentage of days an animal was positioned in the VPS array during its time at liberty, and; UPW fidelity is the percentage of days an animal was detected outside the VPS array in UPW during its time at liberty. Note sensor tags were removed from site fidelity analysis and calculations represent pooled data of the various tag types used for each species. (± s.e. in parenthesis).

Species	Acoustic tag type	Nominal delay (sec)	Battery life (d)	Number tagged	Size range (mean ± s.e.) (cm)	Sex	Overall UPW fidelity (% d)	VPS positions Tracking duration (d)	Site fidelity (% d)	UPW fidelity (%d)
G. galeus	V13 1L	120-180	1336	30						
	V13P 1L	120-180	879	2	33-68 (41±9)	30 F 25 M	20 (3)	32 (6)	9 (2)	22 (5)
	V9 2L	120-180	633	6						
	V9A 2L	120-180	35	17						
C. milii	V13 1L	120-180	1336	2						
	V13A 1L	120-180	71	5						
	V16 4L	120-180	3650	29	67-96 (81±13)	27 F 15 M	30 (5)	41 (11)	12 (2)	37 (7)
	V16 6L	120-180	3650	1						
	V9A 2L	120-180	35	5						
M. antarcticus	V13 1L	120-180	1336	8						
	V13A 1L	120-180	71	5	34-121 (94±47)	7 F 17 M	13 (2)	13 (4)	3 (1)	23 (7)
	V9A 2L	120-180	35	11						

Table 5.1 continued

P. bassensis	V9 2H	190-290	633	10	30-42 (34±12)	Unsexed	10 (2)	4 (1)	1	12 (4)
	V9A 2L	190-290	35	21						
N. cepedianus	V13 1L	120-180	1336	1						
	V13A 1L	60-120	68	2						
	V13A 1L	120-180	71	1	103-209 (133±14)	3 F 4 M	22 (6)	14 (4)	3 (1)	15 (8)
	V16 6L	60-120	3650	1						
	V16 6L	120-180	3650	1						
S. whitleyi	V16 6L	120-180	3650	7	62-119 (89±72)	4 F 3 M	58 (14)	20 (10)	22 (8)	75 (8)
D. brevicaudata	V16 4L	120-180	3650	1						
	V16 6L	120-180	3650	11	49-123 (79±46)	5 F 11 M	24 (3)	7 (2)	3 (1)	22 (5)
	V9 2L	120-180	633	4						
M. tenuicaudatus	V16 6L	120-180	3650	7						
	V13P 1L	120-180	879	7	52-105 (81±25)	4 F 17 M	27 (4)	20 (8)	4 (2)	36 (5)
	V9A 2L	190-290	35	7						
Total				203			22 (2)	27 (4)	9 (1)	28 (3)
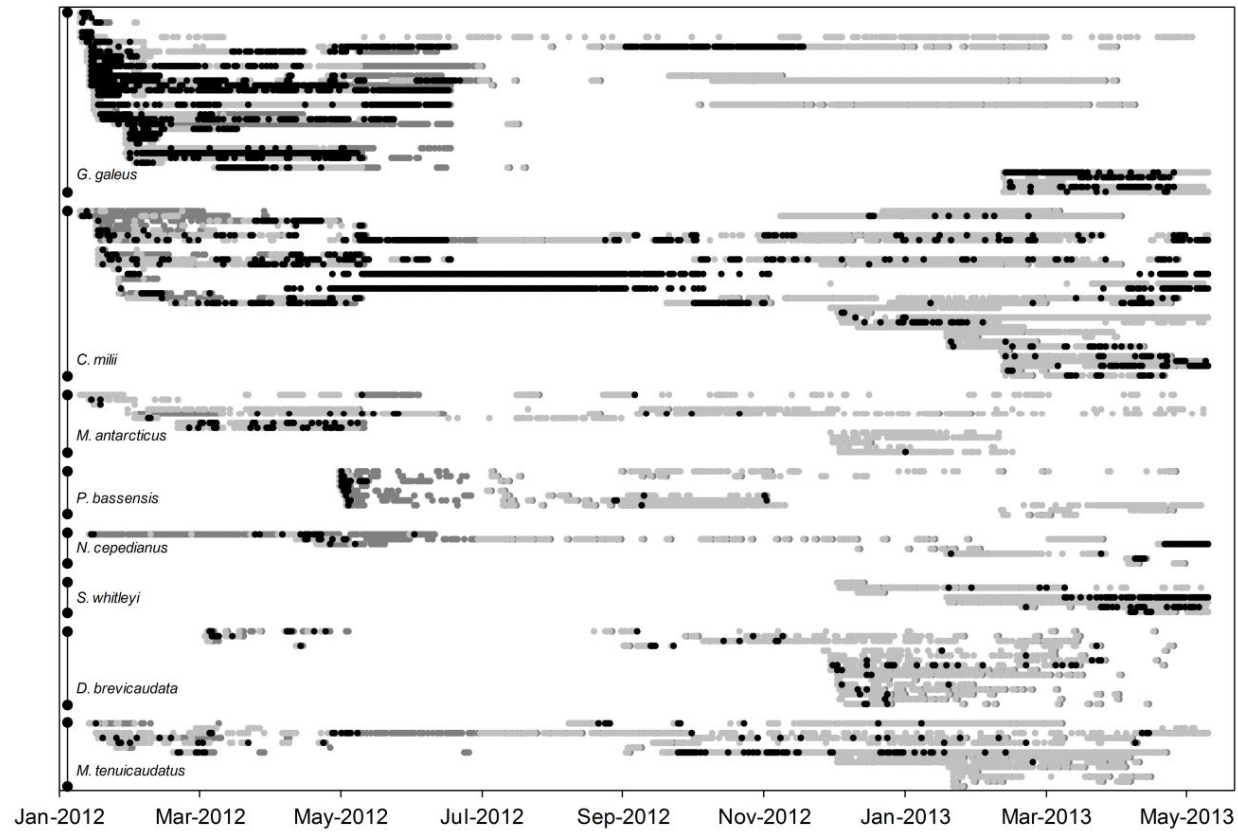
Figure 5.2 Abacus plot showing the daily detections for each individual of each species between January 2012 and May 2013. Each line represents an individual. Black dots represent positions in the VPS, light grey represents detections outside the VPS array in UPW, and dark grey are detections by receivers in LPW and FHB.
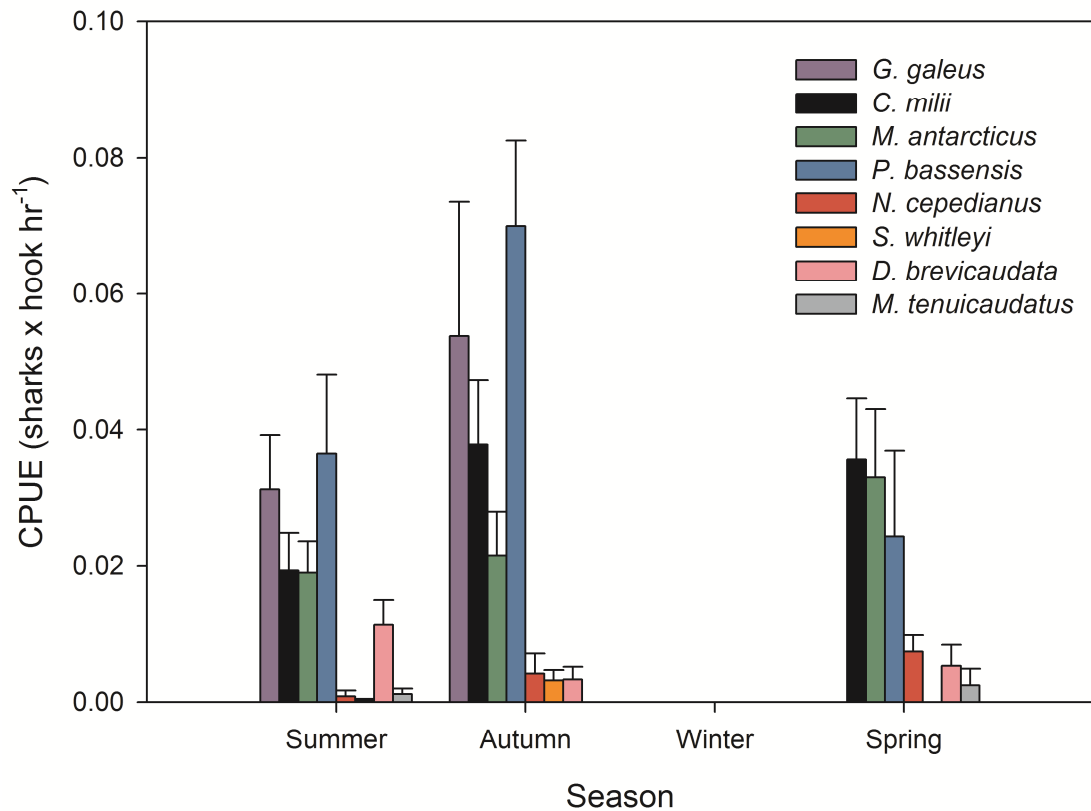
Figure 5.3 Seasonal catch per unit effort (mean CPUE ± s.e.) of chondrichthyans and *P. bassensis* caught from longlining in UPW.

Individuals of all species used largely the same overall area (i.e. 95% KUD) (Fig. 5.4) which was reflected in the strong overlap between species at dawn and dusk (mean UDOI = 0.72 ± 0.19 SD) (Table 5.2). Core area overlap (i.e. 50% KUD) was equally highest between *G. galeus* and *N. cepedianus* with all other species (mean UDOI = 0.16) (Table 5.2). *Platycephalus bassensis* and *M. tenuicaudatus* had the lowest core habitat overlap with all other species (mean UDOI = 0.05 – 0.09) (Table 5.2). There was generally very little overlap in the use of core areas compared to overall habitat use (UDOI < 0.2) (Table 5.2), with each species appearing to utilise their own discrete areas, particularly at dawn (Fig. 5.4).

The basin habitat was most commonly utilised by all species, however, sharks, *C. milii* and *P. bassensis* had the strongest (i.e. $w_i > 1$) selection for the channel habitat at both dawn ($\chi^2 = 438.8$, d.f. = 13, $p < 0.01$) and dusk ($\chi^2 = 936.1$, d.f. = 17, $p < 0.01$) (Fig. 5.5).

There was also a preference for the edge habitat at dawn by *S. whitleyi* and *P. bassensis* and at dusk by *M. antarcticus*, *D. brevicaudata*, and *M. tenuicaudatus* (Fig. 5.5).
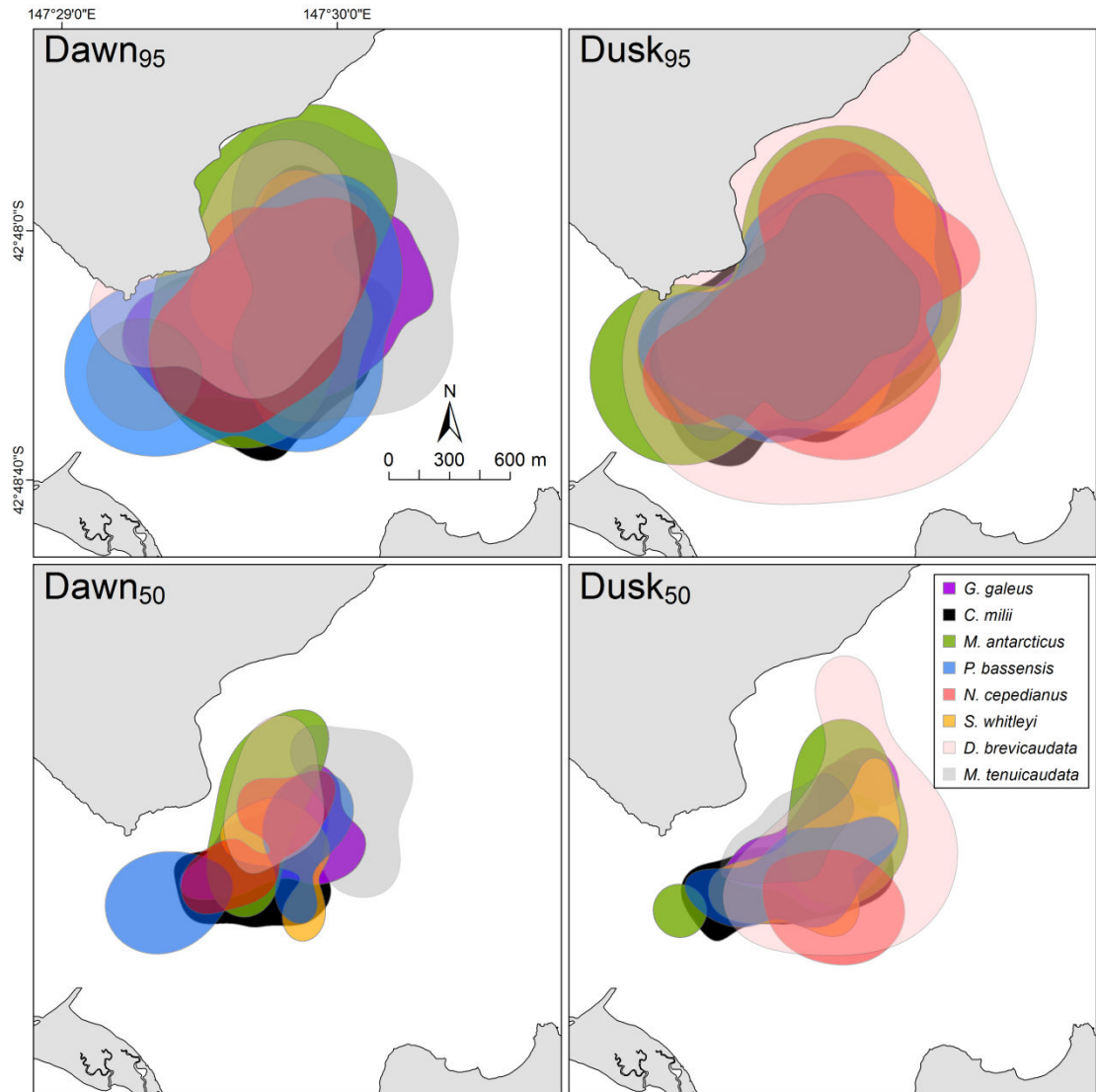
Figure 5.4 Kernel utilisation distributions (KUDs) showing the overall (95% contour) and core habitat (50%) overlap between each species tracked in UPW at dawn and dusk.

Table 5.2 Summary of Utilisation Density Overlap Indices (UDOI) for 50% (upper triangle) and 95% (lower triangle) kernel utilisation densities (KUD) at dawn and dusk. * denotes species where <5 animals were detected as required for UDOI to be calculated. Note species names have been abbreviated for columns.

Dawn	GG	CM	MA	PB	NC	SW	DB	MT
G. galeus (GG)		0.15	0.12	0.15	0.22	0.15	0.12	0.05
C. milii (CM)	0.91		0.10	0.11	0.16	0.10	0.04	0.00
M. antarcticus (MA)	0.62	0.75		0.05	0.18	0.09	0.24	0.02
P. bassensis (PB)	0.75	0.80	0.52		0.13	0.08	0.06	0.02
N. cepedianus (NC)	0.84	0.92	0.82	0.68		0.10	0.16	0.01
S. whitleyi (SW)	0.73	0.75	0.60	0.52	0.65		0.12	0
D. brevicaudata (DB)	0.64	0.57	0.91	0.49	0.72	0.62		0.01
M. tenuicaudatus (MT)	0.57	0.32	0.36	0.46	0.27	0.31	0.29	

Dusk	GG	CM	MA	PB	NC	SW	DB	MT
G. galeus (GG)		0.24	0.23	0.17	0.20	0.24	*	0.09
C. milii (CM)	0.88		0.17	0.10	0.26	0.27	*	0.12
M. antarcticus (MA)	0.90	0.89		0.09	0.12	0.16	*	0.06
P. bassensis (PB)	0.84	0.83	0.71		0.08	0.10	*	0.02
N. cepedianus (NC)	0.94	1	0.85	0.87		0.27	*	0.12
S. whitleyi (SW)	0.98	1	0.87	0.82	1		*	0.13
D. brevicaudata (DB)	*	*	*	*	*	*		
M. tenuicaudatus (MT)	0.83	0.86	0.82	0.53	0.91	0.94		
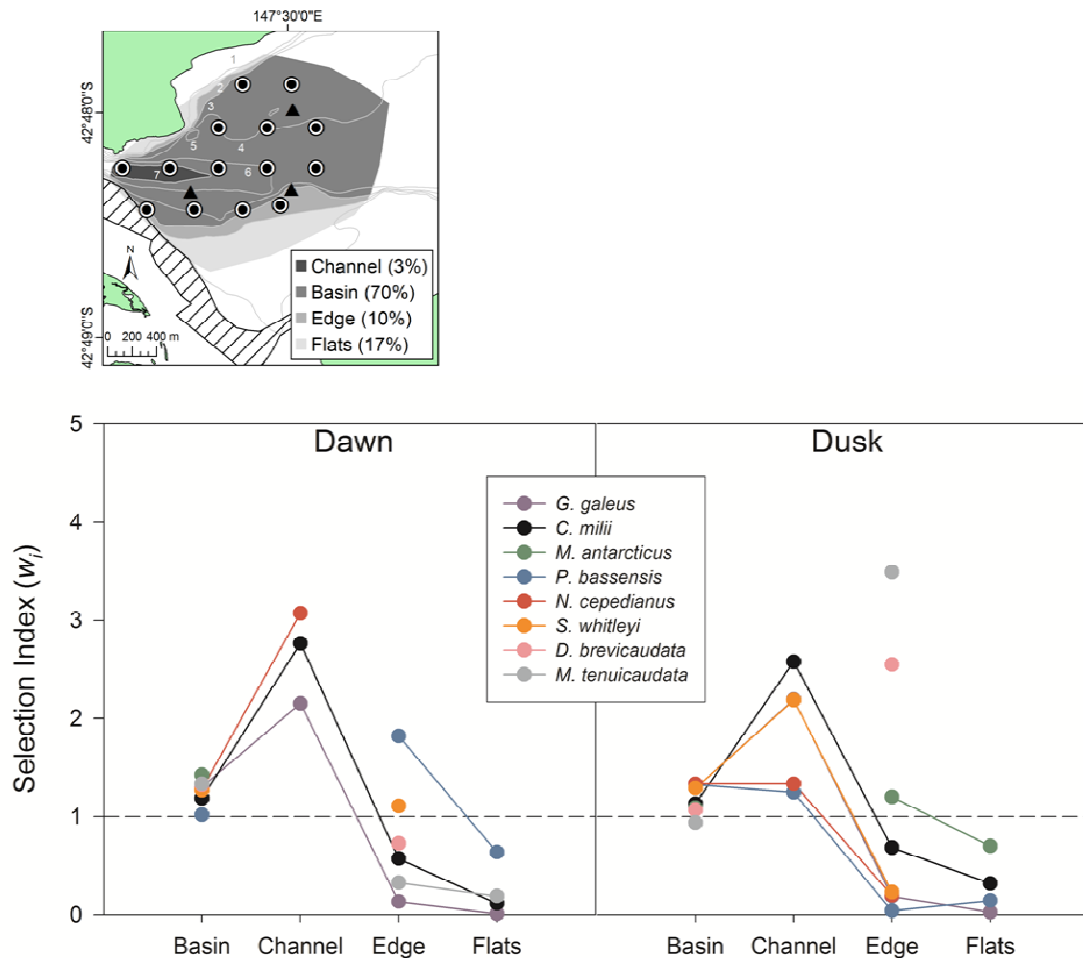
Figure 5.5 Selection index for each habitat category ($w_i \pm$ s.e.) (filled circles and line) for animals positioned in the VPS. Selection ratios greater than one (dashed line) indicate a preference for a particular habitat whereas values less than one indicate avoidance.

5.4.2 Trophic niches and niche overlap

Average δ^{13}C values ranged from -17.6 to -15.5 ‰ and δ^{15}N ranged from 13.8 to 15.9 ‰ (Table 5.3). Both δ^{13}C and δ^{15}N varied among species (Table 5.3), indicating differences in prey composition/carbon sources. *Notorynchus cepedianus* had the widest range in δ^{13}C, ranging from -18.0 ‰ to -13.5 ‰, and *P. bassensis* had the lowest (-16.6 to -14.6 ‰) (Fig. 5.5). *Mustelus antarcticus* had the widest range in δ^{15}N, ranging from 12.2 ‰ to 17.2 ‰, and *C. milii* had the lowest (12.9 to 14.5 ‰) (Fig. 5.6). Overall, the different species were separated into separate isotopic niches forming discrete clusters (Fig. 5.6). *Mustelus antarcticus* had the largest standard ellipse area (SEA = 4.9 ‰^{2}), followed by *N. cepedianus* (3.3 ‰^{2}), whereas the other species had smaller and similar SEAs (0.7-1.0 ‰^{2}) (Table 5.3; Fig. 5.7). There was no or small overlap in isotopic niches between most species captured in UPW with the exception of

M. antarcticus and *P. bassensis* (SEA overlap = 0.9 ‰^{2}, corresponding to 19% and 88% of the total SEA for *M. antarcticus* and *P. bassensis*, respectively) (Table 5.3; Fig. 5.6).

Isotopic niches of supplementary *N. cepedianus* samples overlapped with *G. galeus* (0.3 ‰^{2}, corresponding to 29% and 9% of the total SEA of *G. galeus* and *N. cepedianus*, respectively), *M. antarcticus* (0.38 ‰^{2}, corresponding to 8% and 12% of the total SEA of *M. antarcticus* and *N. cepedianus*, respectively) and *P. bassensis* (0.24 ‰^{2}, corresponding to 24% and 7% of the total SEA of *P. bassensis* and *N. cepedianus*, respectively) (Table 5.3; Fig. 5.6). Isotopic niches of *S. whitleyi* overlapped with *G. galeus* (0.29 ‰^{2}, corresponding to 30% and 14% of the total SEA of *G. galeus* and *S. whitleyi*, respectively) and *M. antarcticus* (0.34 ‰^{2}, corresponding to 7% and 17% of the total SEA of *M. antarcticus* and *S. whitleyi*, respectively) (Table 5.3; Fig. 5.6).
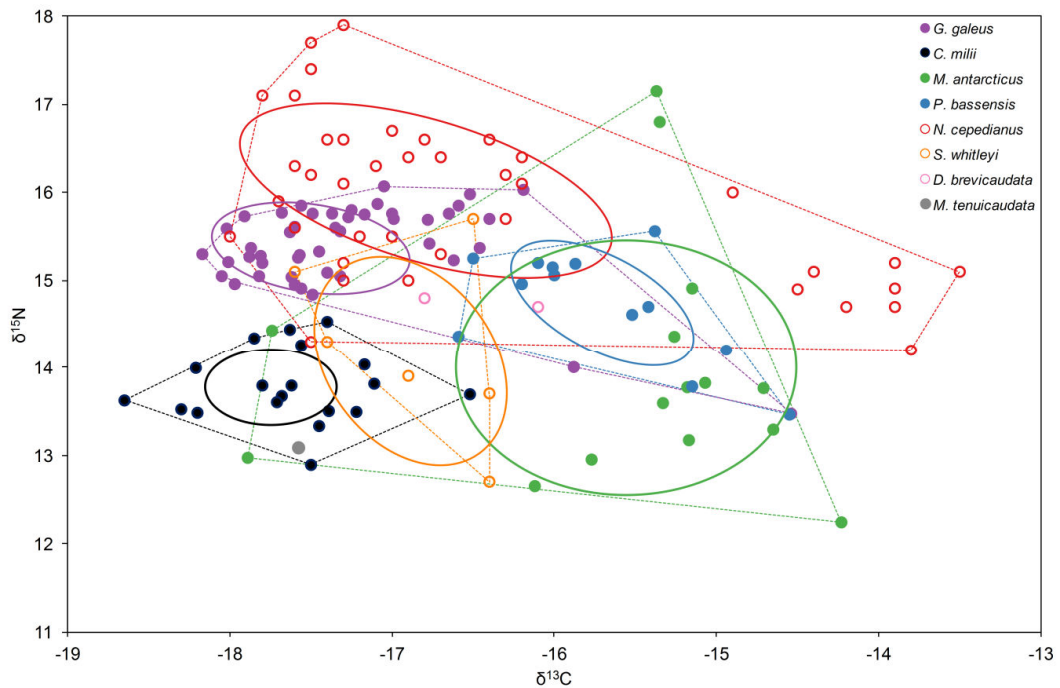
Figure 5.6 Stable isotope values (δ^{13}C and δ^{15}N) for each species captured in UPW (solid circles) and NB (open circles). Solid lines are the Bayesian standard ellipses (SEA$_C$),used for comparing isotopic niche overlap between species. Convex hulls (i.e. isotope extent) are also shown for each species (dashed lines).
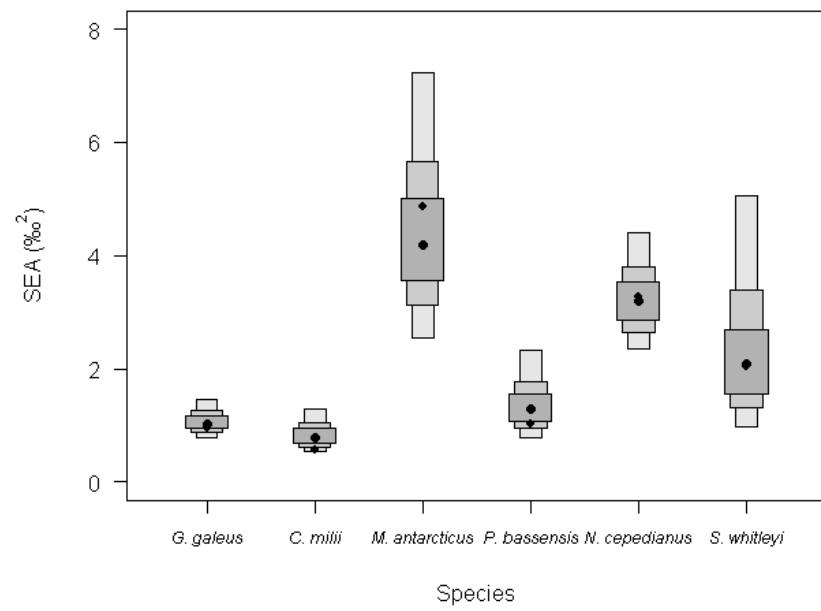
Figure 5.7 Density plots showing the credibility intervals of the standard ellipse areas (SEA). Black diamonds are the mode SEA, and the shaded boxes indicate the 50, 75 and 95% credible intervals from dark (wide) to light (narrow) grey, respectively. Black circles are the sample size-corrected SEA (SEA$_C$).

Table 5.3 Summary of mean stable isotope values (in ‰; ±s.e.), and sample size corrected standard ellipse areas (SEA$_c$, in ‰^{2}) and SEA overlap (‰^{2}) between species. CM = *C. milii*, MA = *M. antarcticus*, PB = *P. bassensis*, NC = *N. cepedianus*, and SW = *S. whitleyi*. *denotes samples from NB.

Species	n	Size range (cm; ±s.e.)	$\delta^{13}C$	$\delta^{15}N$	SEA$_c$	CM	MA	PB	NC*	SW*
G. galeus	46	35-47 (±1)	-17.3 (±0.1)	15.4 (±0.1)	1.03	0	0	0	0.30	0.29
C. milii	19	60-95 (±3)	-17.6 (±0.1)	13.8 (±0.1)	0.67	-	0	0	0	0
M. antarcticus	15	34-144 (±8)	-15.5 (±0.3)	14.0 (±0.4)	4.87		-	0.94	0.38	0.33
P. bassensis	13	20-41 (±1)	-15.7 (±0.2)	14.7 (±0.2)	1.02			-	0.24	0
*N. cepedianus**	40	120-270 (±5)	-16.4 (±0.2)	15.9 (±0.1)	3.28				-	0
*S. whitleyi**	6	100-106 (±10)	-16.8 (±0.2)	14.2 (±0.3)	2.03					-
*D. brevicaudata**	2	87-88 (±1)	-17.5 (±0.3)	12.6 (±0.8)	-					
M. tenuicaudatus	1	90	-17.6	13.1	-					

5.5 Discussion

The results of this study provide evidence that dietary and spatial partitioning play an essential role in allowing multiple species to coexist in a shared environment where competition was expected. With the exception of *M. antarcticus* and *P. bassensis* there was no overlap in isotopic niches between species indicating that most species are foraging on different prey. Dietary variation may also explain the low overlap in core habitat use between species within the VPS if individual prey preferences reside in their own unique habitats within UPW. Dietary partitioning is a common strategy used in shared habitats (e.g. DeAngelis *et al.*, 2008; Kinney *et al.*, 2011; Speed *et al.*, 2011) and there are emerging views that this may be in response to limited resources (Bethea *et al.*, 2004; Kinney *et al.*, 2011). Whilst the relative abundances and distribution of the different prey in UPW are largely unknown, the dissimilarities and low overlap in diet between most species suggest certain food resources may be limited. For example, Kinney *et al.* (2011) suggest that sharks and teleosts occupying a similar trophic level in a communal shark nursery reduce competition for possibly limited prey types by partitioning on the basis of basal dietary resources and foraging on prey from different trophic pathways or carbon sources.

High trophic niche overlap between *M. antarcticus* and *P. bassensis* suggests they are either competing for or sharing similar food resources in UPW (Croxall *et al.*, 1999; Tinker *et al.*, 2008). Previous dietary studies indicate both species predominantly forage on similar benthic crustaceans in Tasmanian waters, such as mottled shore crabs (*Paragrapsus gaimardii*) (Edgar and Shaw, 1995; Yick *et al.*, 2012). However, a preference for shallower areas by *M. antarcticus* (i.e. edge habitats) and low spatial overlap with *P. bassensis* indicates that spatial partitioning may be a strategy used to alleviate competition for similar prey between these species in UPW. Competition for similar dietary sources is often associated with a spatial segregation in habitat use between sharks (Bethea *et al.*, 2004; Papastamatiou *et al.*, 2006; DeAngelis *et al.*, 2008). However, of the few studies that have examined resource sharing between sharks and teleosts, most report dietary partitioning (e.g. Kinney *et al.*, 2011).

Most batoids (i.e. *M. tenuicaudatus*, *S. whitleyi*, and *D. brevicaudata*) also utilised shallower edge habitats, more so than other chondrichthyans. Batoids typically utilise shallow habitats for foraging (Vaudo and Heithaus, 2009; Ajemian *et al.*, 2012), and there is also some evidence that suggests shallow water may be important for batoid thermoregulation (Matern *et al.*, 2000). Although dietary or stable isotope data are required to determine the foraging behaviour of batoids in UPW, the use of shallow habitats may be in response to reducing competition with other chondrichthyans with similar dietary composition that forage in deeper areas. In UPW stable isotope data of *S. whitleyi* suggests that there is some trophic niche overlap with *G. galeus*. Given that dietary studies have shown *S. whitleyi* also predate on teleosts (Treloar *et al.*, 2007), perhaps feeding on teleosts in shallow areas of UPW is a strategy this species uses to reduce competition with *G. galeus*. Likewise, *M. tenuicaudatus* and *D. brevicaudata* may also adopt a similar shallow-water foraging behaviour to reduce competition with their nearest rivals. *Myliobatis tenuicaudatus* and *D. brevicaudata* diets mostly consist of benthic molluscs and crustaceans (Le Port *et al.*, 2008; Sommerville *et al.*, 2011), which is similar to the prey of *C. milii* (Di Giacomo and Perier, 1996) and *M. antarcticus* (Yick *et al.*, 2012). Although sample sizes are low and were not statistically tested, stable isotope data indicates that dietary niches may indeed be similar in UPW for these species (Fig. 5.6). However, the use of shallow habitats by *M. tenuicaudatus* and *D. brevicaudata* compared to *C. milii* and *M. antarcticus* which more frequently occurred in deeper areas, further supports some degree of spatial separation is occurring for species which feed on similar diets in UPW.

Overall detections in the VPS were seemingly low (ca. 9% of time at liberty) relative to the higher proportion of detections that occurred at receivers in UPW outside the VPS array (ca. 28%). The VPS monitoring site was selected based on previous reports of this being an area characterised by high catches of *G. galeus* and other chondrichthyans (Stevens and West 1997; R. Daley pers. comm.). However, the higher number of detections outside of the VPS array suggests that there may be more important habitats outside the VPS array in UPW that are preferentially utilised. Whether animals use these alternative areas in UPW in response to reducing competition between species with similar diets or because they provide more suitable foraging habitats remains unclear. Understanding the importance of these fringing habitats is essential because

their existence could largely contribute to the resource partitioning that is occurring in UPW.

Nurseries are traditionally thought to contain an abundance of resources and low predation risks (Springer, 1967; Branstetter, 1990; Simpfendorfer and Milward, 1993; Beck *et al.*, 2001a; Beck *et al.*, 2001b). Therefore, if food resources are limited, then perhaps animals "choose" to occupy UPW due to lower predation risks. Ecological theory predicts that animals will generally occupy areas where predation risks are low, even if that means foraging in areas where resources are less optimal (Lima and Dill, 1990; Heithaus *et al.*, 2007). For example, juvenile scalloped hammerhead sharks *Sphyrna lewini* are thought to reside in Kāne'ohe Bay where food resources are limited, resulting in poorer body condition, because predation risks from larger sharks is low (Bush and Holland, 2002). Given that *N. cepedianus* were not commonly captured during seasonal, dedicated longline fishing in UPW using larger hook sizes (unpublished data; Stevens and West, 1997), were rarely detected moving into UPW (Barnett *et al.*, 2011; Barnett and Semmens, 2012) and were seldom detected during this study, dietary partitioning may be the best strategy to avoid competition between species in an environment where food may be limited, but the risk of predation is relatively lower compared to surrounding areas such as Norfolk Bay where *N. cepedianus* abundances are higher (Barnett *et al.*, 2010c).

Although predation pressure is probably relatively low, sevengills still occur in UPW and have a high spatial overlap with all species, as such the use of deeper areas of UPW by most chondrichthyan species could be predator avoidance behaviour during periods when small numbers of *N. cepedianus* move into the estuary. Indeed, there was a strong preference for deeper areas in UPW, particularly around the channel, even though these formed a relatively low proportion of areas monitored (ca. 3%). Barnett and Semmens (2012) also found that *M. antarcticus* and *G. galeus* selected deeper parts of Norfolk Bay, and suggested that animals may opt to use these areas because they provide greater escape probability from *N. cepedianus* in an environment that lacks complex habitat in which to hide. Alternatively, it could be an innate behaviour or the fact that these deeper areas may contain greater resource availability (i.e. food) or preferred environmental conditions for these chondrichthyans. Regardless of the reason, the use

of deeper areas results in reduced competition for resources in shallow areas with batoids.

Despite stable isotope values indicating dietary partitioning between species, there are limitations that should be considered when interpreting these results. Muscle tissue stable isotope composition can reflect chondrichthyan diet for long periods (i.e. up to 18 months) (MacNeil *et al.*, 2006; Logan and Lutcavage, 2010), so short-term fidelity to UPW and movement to surrounding regions (e.g. Lower Pitt Water and Frederick Henry Bay) by species such as *C. milii* and *M. antarcticus*, means that their stable isotope composition may represent a combination of feeding in several areas, in contrast to *G. galeus* which are born in UPW (J. McAllister unpublished data) and have high site fidelity. Likewise, the greater amount of time spent in other habitats within UPW outside the VPS array also suggests that preferential utilisation of these habitats may also have greater influence on driving isotopic signatures. In addition, some caution should be applied in comparing chondricthyans and teleosts given differences in their physiology which may influence the isotopic incorporation rate of tissues and δ^{15}N values, such as the retention of urea and Trimethylamine N-oxide (TMAO) by chondricthyans (Dale *et al.*, 2011).

Knowledge of how competition and predation influence the structure of marine communities is essential to understanding how management of one species can affect the recovery of another when designing ecosystem based conservation strategies (Dill *et al.*, 2003; Baskett *et al.*, 2006). The results of this study suggest that the recovery of *G. galeus* has likely benefited from their diet dissimilarity and ability to coexist with species in an environment where there is relatively low predation pressure but potentially strong competiton for limited resources. Despite the lack of competition between *G. galeus* and the other species analysed in this study, research catch data from 1991-97 (Stevens and West, 1997) indicate there are at least 13 shark and 28 teleost species found in UPW. Although these other species during our study, determining their trophic position and spatial behaviour's would provide an even greater understanding on how community ecology affects the recovery of *G. galeus*. For example, dietary analysis of the white-spotted spurdog *Squalus acanthias* captured in NB indicate they prey on small benthic teleosts such as gobies (Yick *et al.*, 2012), an

important component of YOY *G. galeus* diet (Stevens and West, 1997). Stable isotope analysis also indicates that *S. acanthias* occupy a similar trophic position to *G. galeus* in these areas (Abrantes and Barnett, 2011), suggesting competition would result from increased numbers of *S. acanthias* in UPW, potentially impacting on *G. galeus*.

The empirical data gathered in this study has provided an understanding of dietary and habitat partitioning that enables resource sharing in habitats shared by multiple species. Ecological theory would suggest that given the reduced predation threat from *N. cepedianus* compared to adjoining bays, there would be strong competition for resources between species. However, this study suggests that dietary and resource partitioning plays a role in reducing competition between chondrichthyans and teleosts in multi-species shark assemblages. In the case of *G. galeus* in UPW, partitioning resources with competing species such as *S. whitleyi* is likely key to maximising YOY survival in these areas. For a species currently undergoing a rebuilding process after decades of overfishing (AFMA, 2009), protecting functional sources of recruitment will form a fundamental step in their rebuilding process. Therefore knowledge of key behaviours such as dietary and habitat partitioning contributes to an understanding of how communities naturally maintain ecosystem function. Such knowledge provides critical information as to how ecosystem function may respond to the potential consequences of anthropogenic disturbance which will help in the development of effective ecosystem based management of areas important to species recovery and conservation.

6

General Discussion

6.1 Synthesis of main results

Spatial management based on the implementation of no-take area closures such as marine reserves is becoming an increasingly popular component of the management framework for the conservation and protection of overexploited species (Gell and Roberts, 2003; Halpern, 2003; Hilborn *et al.*, 2004b; Russ *et al.*, 2004; Roberts *et al.*, 2005). Therefore, evaluating the effectiveness of spatial management in helping to re-build overfished populations and meet conservation objectives is an essential requirement (Roberts, 2000; Halpern, 2003; Sobel and Dahlgren, 2004; Gaines *et al.*, 2010). The re-examination and presence of *Galeorhinus galeus* in the protected Shark Refuge Areas (SRAs) in south east Tasmania (Chapter 2) confirms that these areas represent an important habitat used for this species. Furthermore the as high or higher numbers of young-of-the-year (YOY) in UPW compared to the 1990s provides signs that re-building and recovery may be occurring in the *G. galeus* population.

Shark refuge areas were established to protect the nursery grounds of *G. galeus* based on evidence derived from extensive life history studies of pregnant females and the capture of mostly YOY in these areas during the 1940s (Olsen, 1954; Walker, 1999). Conventional mark-recapture studies have provided some understanding of migratory patterns and connectivity between nursery areas and the broader population (Olsen, 1954; Stevens and West, 1997; Walker *et al.*, 1999; Punt *et al.*, 2000a), however, knowledge of the spatial and temporal utilisation of nursery areas by YOY and juvenile

G. galeus has been scarce, limiting our understanding of the functional role of these areas during their early life history in addition to the ecological role of sharks within these areas. Indeed the functional role of many areas utilised by sharks is still poorly understood due to the limitations and difficulties of studying these often highly mobile animals (Heupel *et al.*, 2007). Only recently have studies begun to between understand the importance of shark nursery areas and their connectivity to adult populations (Yates *et al.*, 2008; Froeschke *et al.*, 2010). This study provides new information and greater understanding of the movement behaviours and functional role of SRAs and shark nursery areas for *G. galeus* and a range of other chondrichthyan species.

Nursery areas serve many functions, providing important habitats for reproduction (Castro, 1993), foraging (Bethea *et al.*, 2004; Barnett and Semmens, 2012), and refuge from predation (Heupel and Hueter, 2002; Heupel and Simpfendorfer, 2005a; Wetherbee *et al.*, 2007). The presence of mostly YOY *G. galeus*, particularly in upper Pitt Water (UPW), supports historical evidence that this area functions as an important pupping and natal area for this species (Olsen, 1954) (Chapter 2). Significant variations in the stable isotope composition of muscle tissue from similar size YOY captured in Frederick Henry Bay (FHB) also suggests that pupping is probably more widespread and extends throughout the SRAs in southeast Tasmania (Chapter 4). Traditional nursery area paradigms would suggest UPW is an ideal pupping site for *G. galeus* given its shallow, warm, turbid water, and low predator abundance (Springer, 1967; Heupel *et al.*, 2007): the occurrence of pupping in FHB was unexpected given its opposing environmental and ecological conditions. Multiple spawning or breeding sites are thought to represent a bet-hedging strategy used by animals to maximise reproductive success by accounting for environmental variability, intra-specific competition between offspring and risks of predation (Crean and Marshall, 2009; Nevoux *et al.*, 2010; Refsnider and Janzen, 2010). In the case of *G. galeus*, the use of multiple pupping sites may represent a strategy to reduce intra-specific competition for food and risk of predation if large concentrations of YOY are present in small discrete areas such as UPW. Therefore, although *G. galeus* largely use UPW specifically for pupping, maximum reproductive success may be dependent on other areas within SRAs also functioning as pupping sites.

Ontogenetic changes in movements and habitat use are common among animals and typically follow changes in foraging needs, predator avoidance, and reproduction (Grubbs, 2010). Such behaviours are largely responsible for shaping population dynamics, inter- and intra-specific interactions, and ecosystem structure and function (Morris, 2003). Therefore knowledge of these behaviours is critical to designing and implementing effective management strategies throughout a species life history. In this study, acoustic telemetry demonstrated a clear separation in habitat use between YOY and juvenile *G. galeus* (Chapter 3). YOY showed strong site fidelity and utilisation of the shallow, turbid waters of UPW in their first 3-4 months, and upon leaving UPW occupied mostly shallow areas of FHB. In contrast juveniles rarely entered UPW and mostly occupied deeper areas of FHB. These behaviours and fine scale distributions appear largely driven by different life history strategies and suggest SRAs may function differently for chondrichthyans at various life stages. For example, the majority of *G. galeus* may choose to give birth to their offspring in UPW in what appears to be a trade-off between potentially limited resources (i.e. food) but a lower occurrence of *N. cepedianus*, a major predator of chondrichthyans in these waters (Barnett *et al.*, 2010a) (Chapter 5). In contrast, juvenile *G. galeus* are able to occupy the deeper, potentially riskier habitats of FHB where resources may be more abundant because they may be more experienced at avoiding predators (Chapter 3 and 5). However, given the dynamic nature of the estuarine conditions in UPW and the various physiological adaptations that chondrichthyans may require to exist in these environments, other factors such as ontogenetic tolerances to varying salinity levels (Morrissey and Gruber, 1993; Heupel and Simpfendorfer, 2008), may play a role in disparity of habitat choice between YOY and juvenile *G. galeus* and warrants further examination.

Whilst shark nursery areas typically support neonatal and juvenile sharks, they are sometimes seasonally occupied by a diversity of chondrichthyans at various life stages (Castro, 1993; Simpfendorfer and Milward, 1993) which often requires complex intra and inter-specific interactions that enable individuals to coexist. A common strategy used by animals that occupy similar areas is to partition resources such as food and habitat in order to reduce competition and increase survival (Schoener, 1974). Similarly chondrichthyans that move seasonally into UPW, appear to reduce competition by either feeding on different prey taxa or foraging in different habitats within the area

when species were competing for similar dietary requirements (e.g. gummy sharks *Mustelus antarcticus* and the teleost sand flathead *P. bassensis* had high diet niche overlap but low spatial overlap) (Chapter 5). Similarly, whilst the separation in the use of UPW and FHB, and shallow verse deep areas between YOY and juvenile *G. galeus* may be an innate strategy to reduce predation risks, this spatial partitioning may also be important for reducing competition for food (Chapter 3)?

6.2 Implications for conservation and management

Perhaps the most significant finding of this study was the earlier than expected emigration of YOY *G. galeus* from SRAs after 1-2 years, much less than the 3-4 years determined from historical abundance and tag-recapture studies (Olsen, 1954) (Chapter 3). Moreover, Olsen (1954) reported YOY and juveniles returning to these areas after winter, particularly into UPW, however, during the course of this study few YOY and no juveniles returned, and rarely into UPW (Chapter 3). Whether these earlier than expected emigrations and residency patterns are the result of using a finer resolution tracking method (i.e. acoustic telemetry) or represent a change over time in the functional role of these SRAs during *G. galeus* early life history, remains unclear. Despite these uncertainties, understanding key movement behaviours such as home range and site fidelity are fundamental aspects for effective design and implementation of non-take areas (Kramer and Chapman, 1999a; Grüss *et al.*, 2011). A major criticism of many no-take areas is the fact that they provide limited benefit to species which are highly mobile and have large home ranges (Gell and Roberts, 2003; Gerber *et al.*, 2003; Hilborn *et al.*, 2004b). Indeed the shorter than expected fidelity to SRAs by YOY and juvenile *G. galeus* and their ability to migrate long distances during early life history indicates that the protection benefits of these areas are temporally limited. Increasing the size of SRAs to encompass these movements would probably be inappropriate given the distances that YOY travelled and the vast areas that would need to be protected to cover their home range, further highlighting the difficulty of establishing area closures for highly mobile species. Therefore, although SRAs provide some protection for pregnant females and their offspring, effective fisheries management such as size limits,

gear restrictions (e.g. mesh size), and catch quotas are critical to minimising incidental mortality of juvenile and pregnant *G. galeus* outside of area closure boundaries.

In addition to offering protection to pupping adults and the early life history stages, being established nursery areas, SRAs may provide an ideal opportunity to independently monitor the recovery of chondrichthyan populations. Fishery independent surveys provide valuable and reliable measures of relative stock abundance because they are generally less subject to the unknown and often confounding factors that make fishery dependant data difficult to interpret (Hilborn and Walters, 1992; Musick and Bonfil, 2005). However, collecting fishery independent data is often difficult due to many fisheries no longer targeting species which have been overfished (Bonfil, 2004). In the case of *G. galeus* the species is now managed as incidental bycatch within the fishery since fishers no longer target the species (Huveneers *et al.*, 2013), thus traditional catch-rate indices of stock abundance are not available and alternative methods are required to monitor stock status. Given the relationship between YOY catch rates from research fishing in SRAs and modelled *G. galeus* stock size since the 1940s, monitoring YOY abundances in SRAs may provide an alternative method for monitoring trends and recovery in the overall stock (Chapter 2). Whilst some refinement and validation is needed, monitoring YOY catch rates in nursery areas represents a relatively cost-effective and less destructive sampling technique that may be applicable to other chondrichthyan populations that have no reliable means of monitoring stock abundance and recovery.

Spatial movement behaviours are also a fundamental input for reliable fisheries stock assessment modelling as it provides the basis for understanding connectivity between populations and estimates of natural mortality (Booth, 2000). Historically, models have relied mostly on conventional tag-recapture data (Goethel *et al.*, 2011) and indeed these data are primarily used to estimate natural mortality in *G. galeus* stock assessments (Thompson and Punt, 2008). However, conventional tag-recapture data often lacks the resolution needed to understand fine-scale movement behaviours, can suffer from significant tag loss or shedding, and requires animals to be recaptured and reported (Walker *et al.*, 2008). Although not without their own limitations, acoustic telemetry and stable isotope analysis provides an opportunity to study fine-scale movement and

migratory behaviours of animals which can be used refine the understanding of population dynamics, develop stock assessments and management strategies. The application of these technologies in this study has provided a greater resolution of seasonal and migratory movement behaviours of YOY and juvenile *G. galeus* which may contribute to refining current stock assessment modelling. Moreover, although not examined in this study, these movement data could also provide a more refined indication of natural mortality during early life stages of *G. galeus* (Heupel and Simpfendorfer, 2002).

Whilst taking of sharks in SRAs is prohibited, both recreational and commercial fishing are still permitted in these areas using various gear types, and incidental captures of sharks do occur (Lyle *et al.*, 2009). Yet the full extent to which sharks are captured in SRAs and their post-release survival remains poorly understood. Gillnetting in shallow waters of FHB is one practice which should be reviewed in light of evidence that these habitats are regularly occupied YOY *G. galeus* (Chapter 3) and the fact that gillnetting can cause high incidental mortality in sharks (Frick *et al.*, 2010; Lyle *et al.*, 2014). Similarly, given the popularity of recreational hook and line fishing in SRAs (Lyle *et al.*, 2009), future studies are needed to ensure the post-release survival of *G. galeus* is not being compromised by current capture and handling practices using this method. Studies which examine different hook and line capture and handling techniques (e.g. Lyle *et al.*, 2007) may therefore provide management with evidence needed to refine current fishing regulations that maximise post-release survival of incidental shark captures in SRAs.

Identifying and understanding the importance of key habitats utilised during vulnerable life stages such as during an animals' early life history are also critical to establishing effective spatial management and protection of important habitats (Roberts, 2000; Heupel and Simpfendorfer, 2005b). Protection and restoration of key habitats is a fundamental component of current recovery plans for many over-exploited species, including chondrichthyans (e.g. Bethea *et al.*, 2007; Bensley *et al.*, 2009). For *G. galeus*, protection of known nursery areas has been identified as one of the highest priorities in their recovery (AFMA, 2009), as is the identification of the full extent of other areas used as nursery areas that may not currently be identified, noting that this

issue has not been studied in depth since the pioneering work of Olsen (1954) in the 1940s and 1950s. It has been hypothesised that additional nursery areas may exist for *G. galeus*, particularly along ocean beaches and in coastal waters of South Australia but these have yet to be confirmed (Stevens and West, 1997). Using the higher resolution of movement behaviours afforded by acoustic telemetry in this study, such as the strong preference for YOY to reside in UPW or shallower areas of FHB, provides management with a more focussed basis around which efforts can be directed to identify and protect similar habitats that are currently unidentified but may be critical to *G. galeus* recovery.

Anthropogenic disturbance and loss of key marine habitats is becoming increasingly common as urbanisation and development of coastal areas occurs. As a consequence many estuarine and coastal systems have suffered significant species loss, trophic collapse and loss of ecosystem structure and function (Dobson *et al.*, 2006; Ferretti *et al.*, 2010; Lotze *et al.*, 2011). In response, ecosystem-based management (EBM) is becoming widely recognised as an appropriate strategy for managing marine resources by considering the entire ecosystem, including human disturbance (Browman *et al.*, 2004; McLeod and Leslie, 2009). Fundamental to effective EBM is knowledge of community dynamics and the functional mechanisms that enable species to interact with their environment and how they might cope with and respond to anthropogenic disturbance (Latour *et al.*, 2003). For instance, competition and predation play a significant role in shaping community dynamics (Holt, 1977; Sih *et al.*, 1985; Cherrett and Bradshaw, 1989), therefore knowledge of how multi-species assemblages coexist in competitive environments (e.g. dietary and/or habitat partitioning) (Chapter 5) is critical in assessing how those communities may react in scenarios where resources (i.e. food or habitat) become limited as a result of habitat degradation or loss. Similarly, an understanding of how species depend on specific habitats for their survival (e.g. UPW), either to avoid predation (e.g. *C. milii* and *M. antarcticus*) (Chapter 5) or for reproduction (e.g. *G. galeus*) (Chapter 3), is essential to assessing their vulnerability to habitat degradation and loss. Given plans to alter land use practices such as increased irrigation schemes in the Coal River valley (Tasmanian Irrigation, 2013), and expansion of aquaculture Atlantic salmon (*Salmo salar*) farming in Norfolk Bay (DPIPWE, 2014), incorporating these species interaction data into ecosystem modelling and in the

development of environmental management plans may be important in assessing the impact of these practices on chondrichthyan community dynamics in SRAs.

6.3 Future directions for research

This study has provided a greater knowledge of the behavioural traits and spatial ecology of *G. galeus* and other chondrichthyans in a Shark Refuge Area, improving our understanding of the functional role area closures play in chondrichthyan conservation. Whilst these data provide management with a framework around which to refine current management and conservation strategies such as by reviewing gillnetting in shallow habitats of FHB (Chapter 3) or by examining the impact on changes to land use practices surrounding UPW (Chapter 5), there are still areas in which further research is required in order to better understand the importance and functional role of area closures to enhance recovery efforts for *G. galeus*.

Given that the *G. galeus* population appears to have stabilised or at best has increased in size, re-visiting other historically recognised nursery areas may be warranted. This study has examined one of eleven SRAs in Tasmania, albeit historically at least the most significant of the identified areas (Fig. 1.1), and whilst the increased abundances of YOY *G. galeus* supports a population recovery, understanding the relative contribution of different nursery areas to the overall stock is needed to determine whether there has been a shift in the functional role of SRAs and a greater dependency on fewer areas. Identifying nurseries which may be supporting a recovery in the population will give management much needed information as to where best to direct current conservation efforts in order to maximise re-building strategies.

YOY *G. galeus* catch rates in nursery areas have been determined at a point in time where the population appears stable and recovery is imminent (Chapter 2). Continuing to develop a time series of YOY *G. galeus* abundances in UPW would provide management with a useful indicator of relative stock size and a means to track population recovery. This study provides a baseline data set against which ongoing monitoring can compare and contrast with in order to detect change in the population. Whilst determining YOY *G. galeus* catch rates on an annual basis at present shows

some relationship with overall stock size, the high variability around catches suggests the frequency of monitoring may be more appropriate on a bi-annual or longer time frame until such a point in time that annual monitoring is more sensitive to detecting change in the population, such as during the 1950s.

Determining the long-term movement behaviours of *G. galeus* will be essential to understanding the long-term fidelity to and importance of area closures throughout their life history. This study has demonstrated that SRAs provide protection for YOY and juvenile *G. galeus* for up to 1-2 years. However, given that many of the *G. galeus* in this study were implanted with acoustic tags which last up to five years, continuing to monitor these areas would provide a long-term data set on which to assess the reliance of closed areas. Although, these tags will probably expire prior to these animals reaching sexual maturity (i.e. 9 years of age (Olsen, 1954)), investigating the use of longer life acoustic tags or genetic techniques such as kinship-based estimation (Palsbøll *et al.*, 2010) may provide a greater understanding of natal homing and the importance of these areas for pup production in later generations.

Broadening the acoustic array to cover areas adjacent to the closed areas would also benefit in understanding where YOY and juvenile *G. galeus* are migrating to in their early life history. Developing an acoustic array that monitors both other protected shark refuge areas around southern Australia and unprotected areas that include preferred habitat types like those determined in this study, would provide a greater understanding of the relative importance of protected verse unprotected areas during early life history. Determining movement into these areas would provide management with critical information needed to assess whether current management arrangements provide adequate protection of those areas and their susceptibility to anthropogenic disturbance. As suggested by Stevens and West (1997) other unidentified nursery areas may exist. Therefore identifying and understanding the importance of these areas utilising similar techniques as to those in the study are needed before any major changes in protecting and monitoring known nurseries occur.

Using a combination of sampling techniques in this study has demonstrated that chondrichthyan movements and habitat use are likely driven by innate responses to competition and predation within SRAs. Chondrichthyan movements in estuarine and

coastal waters are also influenced by environmental conditions such as temperature (Morrissey and Gruber, 1993), salinity (Heupel and Simpfendorfer, 2008), and rainfall (Knip *et al.*, 2011), however, the influence of these conditions on the distribution of chondrichthyans throughout southern Australia remain largely unknown. Altered climate scenarios, including a 1°C to 2°C rise in sea surface temperature and reduced rainfall and subsequent river flows by the year 2070 are predicted for eastern Tasmania at medium to high rates of current greenhouse gas emissions (Hobday and Lough, 2011). Therefore determining the relationships between chondrichthyan movements and environmental conditions will be important for understanding their future utilisation of SRAs and in predictive modelling of population spread and habitat selection (e.g. Avgar *et al.*, 2013). Moreover, understating these relationships may also be important in assessing the impact of upstream land practices, such as irrigation, which may alter river flows, increase nutrient loads and change primary productivity in areas like UPW.

6.4 General conclusion

Area closures have become increasingly popular in the management of marine resources and in helping to rebuild overexploited species, yet their effectiveness rely on a sound understanding of key animal behaviours which for many highly mobile species remains largely unknown. Ideally, it is desirable to gather knowledge of how and when an animal utilises important habitats prior to implementation of area closures, yet this is rarely achieved or is based on survey methods which lack the resolution needed to develop effective area closure design. Instead, adaptive management and research (i.e. not waiting until determining all unknowns before doing anything) by integrating modern sampling methodologies with more traditional survey approaches such as those adopted in this study are rapidly enabling researchers to gather the empirical evidence needed to monitor, evaluate and refine the effectiveness of current area closures and enhance our efforts to conserve and promote the recovery of overexploited marine resources.

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