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Ecology of the eastern rock blackfish Girella elevata across a latitudinal gradient

Author:
Stocks, Jerom

Publication Date:
2015

DOI:
https://doi.org/10.26190/unsworks/18136

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Ecology of the eastern rock blackfish *Girella elevata* across a latitudinal gradient

Jerom R. Stocks

A thesis in fulfilment of the requirements for the degree of
Doctor of Philosophy

School of Biological, Earth & Environmental Sciences
Faculty of Science
University of New South Wales

March 2015

THE UNIVERSITY OF NEW SOUTH WALES

Thesis/Dissertation Sheet

Surname or Family name: Stocks

First name: Jerom | Other name/s: Raymond

Abbreviation for degree as given in the University calendar: PhD

School: Biological, Earth and Environmental Sciences | Faculty: Faculty of Science

Title: Ecology of the eastern rock blackfish *Girella elevata* across a latitudinal gradient

Abstract 350 words maximum:

Spatial and temporal variation in growth and latitudinal clines in the reproductive biology of a temperate marine herbivore, the eastern rock blackfish *Girella elevata*, was examined from 3 regions of the south-east Australian coast. Biological sampling covered 780 km of coastline, encompassing the majority of the species distribution. The sampling range incorporated 3 distinct oceanographic regions of the East Australian Current, a poleward-flowing western boundary current of the Southern Pacific Gyre and climate change hotspot. Latitudinal gradients in life-history characteristics were examined to shed light on expected changes in fish productivity associated with climate and oceanographic shifts off south-east Australia. *Girella elevata* exhibited great longevity, displaying spatial variation in growth and reproductive fitness. The highest growth rates were observed within the centre of the species distribution. An inverse relationship was observed between growth and reproductive fitness, attributed to variation in energy allocation and trade-offs between life-history traits. Furthermore, analysis of otolith growth chronologies showed decreased growth rates during El Niño events characterised by cooler ocean temperatures in the western Pacific. In addition, spatial metrics of habitat use were investigated to determine the latitudinal connectivity of populations, contribute important data for the development of spatial management measures and provide further insight into the functioning of temperate rocky-reef marine ecosystems. To examine the movements and site fidelity of *G. elevata* a comprehensive array of acoustic receivers were deployed at two near-shore coastal sites in south-east Australia. Prior to the array deployment a study on the performance of acoustic-tracking technology in near-shore marine environments was conducted. This study demonstrated the importance of *in situ* range-test studies to array design, transmitter choice and interpretation of acoustic telemetry data. *Girella elevata* exhibited varying residency periods to the arrays, but all fish had small activity-space sizes. Life-history traits of longevity, slow growth, late maturation, restricted home range, and high residency potentially make *G. elevata* populations vulnerable to fishing pressure. Suggested management arrangements are proposed to ensure the sustainability of the population taking into consideration life-history traits and spatial metrics of habitat use. Furthermore, latitudinal clines in life-history traits of *G. elevata* and the associations with climate and oceanographic conditions suggest potential alterations to the latitudinal productivity of *G. elevata* populations in response to expected climate and oceanographic shifts in south-east Australia.

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Photo: Juvenile *Girella elevata* within intertidal rockpool, South Coast New South Wales (Photo: Sasha Schulz).

Publications

The information in this thesis is entirely the result of investigations conducted by the author with guidance from supervisors Dr Matthew Taylor, Dr Charles Gray, Professor Iain Suthers and Dr Adriana Vergés, and has not been submitted in part, or otherwise, for any other degree or qualification. This thesis consists of six chapters, including four data chapters prepared as standalone manuscripts. All four data chapters have been accepted in peer-reviewed journals as detailed below.

Chapter 2: Jerom R. Stocks, Charles A. Gray & Matthew D. Taylor (2014a) Synchrony and variation across latitudinal gradients: The role of climate and oceanographic processes in the growth of a herbivorous fish. *Journal of Sea Research* 90, 23-32.

Chapter 3: Jerom R. Stocks, Charles A. Gray & Matthew D. Taylor (2015) Intra-population trends in the maturation and reproduction of a temperate marine herbivore *Girella elevata* across latitudinal clines. *Journal of Fish Biology, 86,* 463-483.

Chapter 4: Jerom R. Stocks, Charles A. Gray & Matthew D. Taylor (2014b) Testing the effects of near-shore environmental variables on acoustic detections: implications on telemetry array design and data interpretation. *Marine Technology Society Journal* 48, 28-35.

Chapter 5: Jerom R. Stocks, Charles A. Gray & Matthew D. Taylor (in press) Out in the wash: Spatial ecology of a temperate shallow rocky-reef species derived using acoustic telemetry. *Marine and Freshwater Research.*

Acknowledgements

I must first gratefully acknowledge my supervisors Dr Matthew Taylor, Dr Charles Gray, Dr Adriana Vergés and Professor Iain Suthers for your guidance and input throughout my PhD. Furthermore, this project would not have been possible without the assistance and technical advice from New South Wales Department of Primary Industries (NSW DPI) and University of New South Wales (UNSW) personnel particularly Dr John Stewart, Dr Julian Hughes and Dr Nicholas Payne. I would also like to thank Joshua Aldridge for his tireless contribution and dedication in the lab, Jim Craig for his contribution to database management, Dylan van der Meulen and Dr Nicholas Payne for their acoustic telemetry expertise and David Barker for aquaria support and the housing of fish. Thank you to all those at the Cronulla Fisheries Research Centre of Excellence, your expertise and friendship made my time at Cronulla a pleasure.

Thank you to those who were involved in the collection of fish including Dylan van der Meulen, Grant Clark, Sasha Schulz, Tim Wilson, Jared Barnes, John Higgins, Mitch van der Meulen, Kyle van der Meulen, Aaron Puckeridge, Ian Puckeridge, Peter Walsh and Mitch Burns. Thank you also to the South Coast Barracudas, St George spearfishing Club, Sans Souci Dolphins Spearfishing Club and The North Shore Underwater Club for the donation of biological samples. I must also thank those who were involved in fish tagging including Alex Bellissimo, Grant Clark, Steph Brodie, Derrick Cruz, Cameron Doak and Jared Barnes. Also thank you to Grant Clark, Jared Barnes, Steph

Brodie and Derick Cruz who help with receiver downloads. Finally, to my friends and family, thank you all for your support and encouragement throughout.

This project was carried out in collaboration with NSW DPI and the UNSW. This project was funded by the NSW Saltwater Recreational Fishing Trust. The collection and use of animals was conducted under the Animal Research Act 1985 (Animal Research Authority 10/03 – CFC) and a Section 37 Scientific collection permit P01/0059(A), (Fisheries Management Act 1994) issued by NSW DPI.

Thesis Abstract

Threats to fisheries resources operate over a range of spatial and temporal scales, from broad-scale impacts of climate and oceanographic shifts to localised impacts of fishery exploitation. Therefore knowledge of species-specific life-history traits including age, growth, reproduction and movements, at a range of spatial and temporal scales, are of particular importance to: 1) assessing the productivity of fisheries; 2) assessing the vulnerability of a species to exploitation, and; 3) the development of biologically informed management strategies. In addition, information on spatial variation in life-history characteristics coupled with data on abiotic environmental conditions may provide information on latitudinal clines in population productivity, the habitat optima of a species and the biological response of a species to variation in abiotic conditions. These data can then contribute to predicting future trends in the latitudinal biology of a species in response to a changing climate and oceanographic conditions.

The eastern rock blackfish, *Girella elevata*, is a large perciform fish of the family Girellidae that inhabits temperate near-shore coastal regions of South-eastern Australia. The species geographic distribution stretches across approximately 13 degrees of latitude in an oceanographic region defined as a climate change hotspot. Prior to this study existing biological data on *G. elevata* was sparse. Given the broad latitudinal distribution of *G. elevata*, the accessibility of the species habitat and the absence of key life-history information, *G. elevata* is an ideal model species to investigate latitudinal clines in life-history characteristics of a temperate marine teleost over a highly variable oceanographic region.

Spatial and temporal variation in growth and latitudinal clines in the reproductive biology of *Girella elevata* was examined from 3 regions of the south-eastern Australian coast. Biological sampling covered 780 km of coastline, encompassing most of the species distribution. The sampling range incorporated 3 distinct oceanographic regions of the East Australian Current, a poleward-flowing western boundary current of the Southern Pacific Gyre and climate change hotspot. A validated ageing method using sectioned sagittal otoliths was developed to enumerate both daily (juvenile fish) and annual otolith increments. *Girella elevata* exhibited great longevity with a maximum recorded age of 45+ years. Spatial variation in growth from length-at-age data was observed, with the highest growth rates within the centre of the species distribution (von Bertalanffy growth parameter: Central Region $L\infty$=51.00, k=0.16, t_o=-1.47; Southern Region $L\infty$=54.35, k=0.09, t_o=-4.45). Analysis of otolith growth chronologies of 33 years showed a positive relationship with the Southern Oscillation Index. *Girella elevata* displayed decreased growth rates during El Niño events characterised by cooler ocean temperatures in the western Pacific.

Girella elevata are a highly fecund (mean ± S.E. batch fecundity: 69.2 x 10^4 ± 29.2 x 10^3) group synchronous (multiple batch) spawner. Mean fork length (L_F) and age at maturity was greater for females than males within all regions, with both male and female *G. elevata* of the Southern Region maturing at a greater size and age (mean ± S.E. males: 36.2 cm FL, 7.0 ± 0.4 yrs; females: 39.8 ± 0.8 cm FL, 9.5 ± 0.5 yrs than those from the Central Region (mean ± S.E. males: 31.2 ±1.3 cm FL, 3.5 ± 0.4 yrs; females: 37.2 ± 1.4 cm FL, 5.8 ± 1.5 yrs). Estimates of batch fecundity (F_B) were greatest in the Northern and Southern Regions, relative to the Central Region where

growth rates were greatest. Significant positive relationships were observed between F_B and $L_{F,}$ and F_B and total fish mass. Gonado-somatic indices indicated latitudinal synchrony in spawning seasonality between *G. elevata* at higher latitudes, spawning in the late austral spring and summer. A late or prolonged spawning period is evident for *G. elevata* from the Northern Region. Juvenile recruitment to intertidal rockpools within the Central and Southern Regions was synchronous with the spawning season, however no juveniles were found within the Northern Region.

Defining the spatial ecology of fish is a fundamental component to our understanding of the latitudinal connectivity of populations; it contributes important data for developing spatial management measures and provides further insights into the functioning of marine ecosystems. A comprehensive array of acoustic receivers were deployed at two near-shore coastal sites in south-east Australia to examine the movements, activity-space size and site fidelity of *G. elevata*. Prior to the array deployment a study on the performance of acoustic-tracking technology in near-shore marine environments was conducted. Specifically, the influence of a number of major environmental variables on detection range and detection frequency was assessed. This study demonstrated the importance of *in situ* range-test studies to array design, transmitter choice and interpretation of acoustic telemetry data. To examine the spatial ecology of *G. elevata*, twenty-four fish (274 – 447 mm fork length) were internally tagged with pressure-sensing acoustic transmitters across these two arrays (North Sydney, n=12 fish, and 15 VR2W monitoring stations and Wollongong, n=12 fish, and 10 VR2W monitoring stations) and monitored for up to 550 days. An existing network of coastal receivers was also incorporated into the study to examine large-scale movement patterns. Individuals exhibited varying residency (0.55 – 84.91% residency index), but all had small activity-

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Life-history traits of longevity, slow growth, late maturation, restricted home range, and high residency potentially make *G. elevata* populations vulnerable to fishing pressure and susceptible to the localised depletion of larger individuals. Suggested management arrangements are proposed to ensure the sustainability of the population taking into consideration life-history traits and spatial metrics of habitat use. Furthermore, latitudinal clines in life-history traits of *G. elevata* and the associations with temperature suggest potential alterations to the latitudinal productivity of *G. elevata* populations in response to expected climate and oceanographic shifts in south-east Australia.

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Chapter 1: General Introduction

Threats to fisheries resources operate over a range of spatial and temporal scales, from broad-scale impacts of climate and oceanographic shifts to localised impacts of fishery exploitation. Information on spatial variation in life-history characteristics coupled with data on abiotic environmental conditions may provide information on latitudinal clines in population productivity, the habitat optima of a species and the biological response of a species to variation in abiotic conditions. These data can then contribute to predicting future trends in the latitudinal biology of a species in response to a changing climate and oceanographic conditions. Furthermore, knowledge of species-specific life-history traits including age, growth, reproduction and spatial ecology, are of particular importance when assessing the productivity of fisheries and to the development of biologically informed management strategies.

1.1 Latitudinal gradients in life-history characteristics in the context of climate and oceanographic variability

Poleward range shifts in species latitudinal distributions are one of the most widely documented responses to climate change. However other biological responses including changes to population productivity through alterations in growth and reproduction are of particular importance to the sustainability of fisheries. All species have a temperature tolerance range, and typically, energy allocation towards growth and reproduction declines at temperatures near the range extremes. Exploring latitudinal gradients in life-history characteristics of a species may shed light on expected changes in fish

productivity associated with both basin- and decadal-scale climate and oceanographic shifts.

Climate change can affect species, communities and the functioning of ecosystems directly through alterations in abiotic conditions such as water temperature and ocean acidification (Doney, 2006), or indirectly through food web dynamics and other interspecies associations (Portner and Peck, 2010). For marine fish populations the implications of climate variability can be identified at multiple interlinked levels of biological organisation: 1) An ecosystem-level, altering the productivity of marine fish populations; 2) A population-level, altering phenologies and life-history traits; 3) An individual-level, resulting in behavioural changes such as the avoidance of unfavourable conditions and movement into suitable areas, and; 4) A organismal level, resulting in physiological changes (Cheung et al., 2010, Portner and Peck, 2010).

Age, growth rates, and reproductive characteristics are key life-history traits that determine the productivity of fish populations (Campana, 2001, Morgan and Brattey, 2005). Consequently, it is important to understand their association with abiotic conditions, in order to assess potential changes arising as a result of climate and oceanographic shifts. Fish have indeterminate growth patterns influenced by their environment (Stocks et al., 2011, Morrongiello et al., 2014). Reproductive characteristics may also vary with latitudinal clines in abiotic environmental conditions (Lappalainen et al., 2008, Leal et al., 2009, Thorsen et al., 2010). Information on a species age, growth and reproductive traits, and associations with environmental conditions, are therefore important when predicting the effects of environmental change on fish productivity (Campana and Thorrold, 2001, Morgan and Brattey, 2005).

Examining latitudinal gradients in life-history characteristics and identifying links with oceanographic variability is one method that may shed further light on the expected changes associated with climate and oceanographic shifts. Furthermore, sclerochronological approaches examining multi-decadal variation in growth rates can provide insight into the biological response of fish to long-term climate and oceanographic variation with minimal temporal sampling (Thresher et al., 2007, Black et al., 2008, Stocks et al., 2014a). Assessing variation in reproduction and growth is particularly important for fish populations off south-eastern Australia given the observed and predicted climate and oceanographic shifts of the region (Cai et al., 2005, Ridgway, 2007).

The predominant oceanographic feature off eastern Australia is the East Australian Current (EAC). The EAC is the poleward-flowing western boundary current of the Southern Pacific Gyre, extending from the Coral Sea into Tasmanian waters. The EAC is primarily composed as a current of eddies (Mata et al., 2006), and thus displays high oceanographic variability. The EAC is considered amongst the fastest changing oceanic water bodies in the world in response to climate change (Matear et al., 2013). The EAC has recently displayed a poleward advancement of ~350 km over a 60 year period, resulting in a >2°C century^{-1} warming rate in the Tasman Sea region (Ridgway, 2007). Modelling indicates that the poleward migration of the EAC is expected to further strengthen. The spatial variation in the EAC is categorised by three distinct water bodies, which are delineated by a highly variable region of water where the EAC separates from the coast (at approximately 31.5ºS) to form an eastward flowing frontal region off Sydney (Figure 2.1). The resulting three regions thus represent a strong southward flowing northern section dominated by warm Coral Sea water, a highly

variable separation zone dominated by a persistent eddy field, and a cooler southern zone that is seasonally dominated by either EAC flow-through water from the north or the cooler waters of the Tasman Sea. Given the large latitudinal variation in the oceanographic conditions of the EAC and the region's distinction as a climate change 'hotspot', the region presents an ideal scenario to examine latitudinal variation in life-history characteristics of marine teleosts and the associations with abiotic conditions.

In addition to the applications of a species latitudinal life-history data in assessing potential impacts of climate and oceanographic shifts, understanding life-history traits of individual species is also an integral component to assess vulnerability to over exploitation. This data may then be used in the development of biologically informed management strategies.

1.2 The spatial ecology of fish and near-shore coastal acoustic telemetry

The movement of fish can occur over a range of spatial and temporal scales. Meso-scale movements may involve localised movements within a species home range associated with feeding excursions, avoidance of poor conditions or diel variation in habitat preferences. Alternatively, macro-scale movements may include large scale migrations associated with spawning behaviours or home range shifts (Koehn and Crook, 2013). Characterising such spatial metrics of movement and exploring the associations with environmental parameters can provide an insight into the functioning of marine ecosystems and the processes driving habitat use (Lowry and Suthers, 1998,

Overholtzer and Motta, 1999, Childs et al., 2008, Taylor and Ko, 2011, van der Meulen et al., 2014).

Acoustic-tracking technology is frequently used to study both large and fine-scale movements of free-living aquatic organisms (Taylor et al., 2006, Hindell, 2007, Childs et al., 2008, Taylor and Ko, 2011, Walsh et al., 2012). Acoustic-tracking technology has been applied in a variety of habitat types including freshwater rivers and lakes, coastal estuaries and bays, and increasingly in open coastal waters. Given the large variability in the prevailing environmental conditions within and across each of these environments, researchers are now paying increasing attention to the performance of acoustic technology in the target environment prior to deploying full-scale acoustic arrays. *In situ* range-testing used for initial array design, coupled with control-transmitters (Payne et al., 2010, Topping and Szedlmayer, 2011, How and Lestang, 2012), provides increased validity to assumptions made in home range and habitat association studies. Preliminary range-test studies may also increase habitat coverage or reduce costs of array deployments by appropriate receiver spacing (Stocks et al., 2014b). As our understanding of array design and operation in near-shore coastal environments improves (Chapter 4, Stocks et al., 2014b), research is increasingly targeting the movements of exploited species in these environments (Bryars et al., 2012, Ferguson et al., 2013). Such studies are providing important data for spatial management measures such as marine protected areas (MPAs) (Bryars et al., 2012, Ferguson et al., 2013) and to further understand the latitudinal interactions of marine populations.

1.3 The eastern rock blackfish *Girella elevata*

The eastern rock blackfish, *Girella elevata*, is a large perciform fish of the family Girellidae. The genus *Girella* is comprised of 17 named species found in temperate to subtropical waters along the continental margins of the pacific and south-western Australia (Froese & Pauly 2009). *Girella elevata* inhabit near-shore coastal waters along the New South Wales (NSW) coast, as well as southern Queensland, Victoria and north-eastern Tasmania. The species geographic distribution stretches across approximately 13 degrees of latitude (Kuiter, 1993). However, shifts in the southern extremities of the species distribution have been observed, with gravid individuals reported in Tasman waters (Last et al., 2011). *Girella elevata* is relatively cryptic, often taking shelter in shallow caves and crevices (Kuiter, 1993). Juveniles are dependent on rockpools (Bell et al., 1980, Silberschneider and Booth, 2001, Griffiths, 2003b), before moving to coastal shallow rocky reefs (Kingsford, 2002, Curley, 2007) where they reportedly reach up to 76 cm total length (Kuiter, 2001). *Girella elevata* are frequently targeted by both recreational anglers (Kingsford et al., 1991) and spearfishers (Smith et al., 1989). The feeding habits, diet composition and digestive mechanisms of *G. elevata* have been examined in previous studies (Bell et al., 1980, Clements and Choat, 1997, Kingsford, 2002). However, prior to this study the existing biological data on *G. elevata* was sparse (Curley et al., 2013 b), with little to no published information regarding *G. elevata* age and growth, population structure, reproductive biology, movements and role in the ecological function of near-shore marine ecosystems. Therefore current management arrangements, including bag and size limits, are not underpinned by key biological and ecological data resulting in an exploitation status of ‘undefined’ (Fisheries NSW 2014).

Given the broad latitudinal distribution of *G. elevata* and the accessibility of the species habitat, *G. elevata* is an ideal model species to investigate latitudinal clines in life-history characteristics of a temperate marine teleost over a highly variable oceanographic region. In addition, information on the movement and habitat use is particularly lacking for temperate-reef species and *G. elevata* serves as a prime candidate to further understand this component of temperate rocky reef dynamics.

1.4 Thesis objectives

Each data chapter of this thesis consists of one primary goal addressed through a series of specific objectives. The primary goals and objectives of this thesis were to:

1. Examine *G. elevata* growth in the context of climate and oceanographic variation through a sequential series of objectives: (1) Develop a validated ageing method for *G. elevata* using sectioned sagittal otoliths; (2) Analyse spatial and intersexual variation in the growth of *G. elevata* across a broad-latitudinal range using size-at-age information, and; (3) Reconstruct multi-decadal otolith growth chronologies to examine climatic/oceanographic processes correlated with temporal trends in fish growth.

2. Describe the latitudinal variation in the reproductive fitness of *G. elevata*. Specifically the objectives were to: (1) Define the spawning period across latitudinal gradients; (2) Estimate length and age at maturity and deviations with latitude, and; (3) Examine spatial variation in reproductive output from fecundity estimates.

3. Addresses knowledge gaps in regards to the performance of acoustic technology in near-shore marine environments by: (1) Quantifying the detection distance and detection frequency of acoustic transmitters under varying environmental conditions in two near-shore habitat types; (2) Simultaneously assessing the relative importance of each variable affecting detection range and detection frequency in two near-shore marine environments, and; (3) Use results from the aforementioned objectives to design an array and interpret data from an acoustic telemetry study of *G. elevata.*

4. Employ acoustic telemetry technology to examine the movements and habitat use of *G. elevata*. More specifically to: (1) Investigate *G. elevata* movements across a range of spatial and temporal scales; (2) Determine *G. elevata* long-term site fidelity and home range size; and (3) Examine the behavioural response and habitat usage of *G. elevata* in relation to a number of abiotic environmental variables.

Chapter 2: Synchrony and variation across latitudinal gradients: The role of climate and oceanographic processes in the growth of a herbivorous fish

Abstract

Spatial and temporal variation in the growth of a widely distributed temperate marine herbivore, *Girella elevata*, was examined using length-at-age data and multi-decadal otolith increment growth chronologies. In total 927 *G. elevata* were collected from three regions of the Australian south-east coast, extending 780 km and covering a large proportion of the East Australian Current, a poleward-flowing western boundary current of the Southern Pacific Gyre and climate change hotspot. A validated ageing method using sectioned sagittal otoliths was developed to enumerate both daily (juvenile fish) and annual otolith increments. *Girella elevata* exhibited great longevity with a maximum recorded age of 45+ years. Spatial variation in growth from length-at-age data was observed with the highest growth rates within the centre of the species distribution. Analysis of otolith growth chronologies of 33 years showed a positive relationship with the Southern Oscillation Index. Identifying links between life-history characteristics and variation in oceanographic conditions across latitudinal gradients may shed light on potential impacts of expected climate shifts on fish productivity.

2.1 Introduction

Exploring latitudinal gradients of age and growth rates can provide insight into relationship between the biological attributes of a species and variability in the environment in which it lives. Growth variation may be a result of trade-offs among other life-history traits such as fitness and reproduction, including onset of maturity and fecundity (Vila-Gispert et al., 2002), or restrictions imposed by latitudinal gradients in environmental conditions such as temperature (Lappalainen et al., 2008) and productivity (Sogard, 2011). For coastal and marine species, identifying links between oceanographic variability and latitudinal gradients in life-history characteristics may shed light on expected changes associated with both basin- and decadal-scale climate shifts. In addition, such climate shifts may result in altered species distributions and community structures, which have already been observed in a number of fishes of south-eastern Australia (Last et al., 2011) and elsewhere throughout the world (Perry et al., 2005, Hiddink and Ter Hofstede, 2008, Booth et al., 2011).

Sclerochronological approaches, primarily employing fish otoliths (earstones), are being increasingly used to examine long-term temporal trends in fish growth (Thresher et al., 2007, Black, 2009, Morrongiello et al., 2010, Neuheimer et al., 2011, Godiksen et al., 2012). Due to the indeterminate nature of otolith deposition, long-term otolith growth chronologies can be constructed to deduce life-history traits (Stocks et al., 2011) and reflect environmental conditions and climate change (Thresher et al., 2007). Multiple climate and oceanographic processes have been correlated to otolith increment chronologies, such as sea-surface temperature (SST) (Black et al., 2008), El Niño

Southern Oscillation (ENSO) (Black et al., 2008), and localised upwelling (Boehlert et al., 1989).

Girella elevata occur on shallow near-shore rocky reefs along the south-east coast of mainland Australia and north-eastern Tasmania, with their geographic distribution stretching across approximately 13 degrees of latitude (Kuiter, 1993). The species is often found during the day in caves and under rocky ledges or in surge regions, although post-settlement fish use rockpools as nurseries before moving to shallow rocky reefs as they grow (Bell et al., 1980, Burchmore et al., 1985, Griffiths, 2003b). The species experiences considerable pressure from recreational fishing, particularly spearfishing and anglers from rock platforms (Lincoln Smith et al., 1989, Kingsford et al., 1991).

The broad latitudinal distribution of *G. elevata* spans a large proportion of the East Australian Current (EAC). The EAC is the poleward-flowing western boundary current of the Southern Pacific Gyre, extending from the Coral Sea into Tasmanian waters. The EAC is primarily composed as a current of eddies (Mata et al., 2006), and thus displays high oceanographic variability. The EAC is considered amongst the fastest changing oceanic water bodies in the world (Matear et al., 2013), displaying a poleward advancement of ~350 km over a 60 year period that consequently warms the Tasman Sea at >2°C century^{-1} (Ridgway, 2007). Modelling indicates that the poleward migration of the EAC is expected to further strengthen, and this will produce greater mesoscale variability (Cai et al., 2005). The spatial variation in the EAC is categorised by three distinct water bodies, which are delineated by a highly variable region of water where the EAC separates from the coast (at approximately 31.5ºS) to form an eastward

flowing frontal region off Sydney (Figure 2.1). The resulting three regions thus represent a strong southward flowing northern section dominated by warm Coral Sea water, a highly variable separation zone dominated by a persistent eddy field, and a cooler southern zone which is seasonally dominated by either EAC flow-through water from the north or the cooler waters of the Tasman Sea.

In this study we aimed to address fish growth in the context of climate variation, through the unique combination of a long-lived (45+ years) marine herbivore with a wide distribution across a highly variable oceanographic region. This combination was selected to provide a dataset of sufficient spatial and temporal variation, and our broad aim was addressed through a sequential series of objectives: (1) Develop a validated ageing method for *G. elevata* using sectioned sagittal otoliths; (2) Analyse spatial and intersexual variation in the growth of *G. elevata* across a broad-latitudinal range using size-at-age information, and; (3) Reconstruct multi-decadal otolith growth chronologies to examine climatic/oceanographic processes correlated with temporal trends in fish growth.

2.2 Methods

2.2.1 Study area

The dominant oceanographic features of this region include the poleward flowing EAC and its associated eddies (Suthers et al., 2011), a western boundary current of the Southern Pacific Gyre. Biological sampling of *G. elevata* was conducted within three regions of the Australian south-east coast (Figure 2.1), which align with the three broad regions of the EAC. These regions included the, 1) Northern Region (30.38ºS, 153.11ºE

to 29.89ºS, 153.28ºE): a strong southward flowing northern section dominated by warm Coral Sea water; 2) Central Region (34.60ºS, 150.90ºE to 34.04ºS, 151.21ºE): a highly variable separation zone where the EAC separates from the coast to form an eastward flowing frontal region dominated by a persistent eddy field, and; 3) Southern Region (37.27ºS, 150.06ºE to 36.72ºS, 149.99ºE): a cooler southern zone which is seasonally dominated by either EAC flow-through water from the north, or the cooler waters of the Tasman Sea. The coastline from which samples were collected was composed of headlands and coastal temperate-reefs punctuated by sandy beaches. Annual water temperatures (mean ± S.E) at 3 m depth from the 2011/2012 sampling years within the Northern, Central and Southern Regions were 20.54°C ± 0.38, 19.2°C ± 0.36 and 17.70°C ± 0.35 respectively.

2.2.2 Sample collection and processing

Biological samples of *G. elevata* from the Central and Southern Regions were collected approximately every second month for a 33 month period (October 2009 – June 2012), whereas in the Northern Region collection was performed bi-annually (October 2009 – June 2012) due to logistic constraints. Samples within each of the three regions were collected from coastal headlands nested along a 60 km stretch of coastline (Figure 2.1, Appendix: Table A.1.). Each sample of *G. elevata* (>15 individuals) was collected by free-dive spearfishing at 2 to 5 randomly selected headlands within each region to reduce any potential influence of site specific biological traits. Within each Region, juvenile *G. elevata* (1 – 15 cm fork length, L_F) were also collected from several intertidal rockpools using scoop nets. All fish collected were measured to the nearest 0.1

cm L_F and total length (L_T), weighed to the nearest gram and gonads were macroscopically examined to determine sex.

2.2.3 Age estimation and precision

Estimates of age and measurements of annual otolith increment widths were made from transverse sections of sagittal otoliths (Figure 2.2). Otoliths were embedded in resin and 0.6 mm sections were taken through the otolith core using a diamond saw (Gemmasta, Shelleys Lapidary, South Australia). Sections were mounted on glass microscope slides and polished using 500 grit waterproof silicon carbide paper on a Struers LaboPol-4 polishing machine (Struers Australia, Milton, Queensland, Australia). Sectioned otoliths were examined under a compound microscope (Olympus BX41, Tokyo, Japan) using reflected light with a 4x objective lens. Opaque zones (validated as annuli, see below) visible in the internal structure were counted along a radius from the primordium to the outer edge of the ventral lobe following the outer margin of the sulcus acusticus. A camera (Q-Imaging, MicroPublisher 5.0 RTV, Canada) attached to the compound microscope collected an image of each otolith examined (Figures 2.2b and 2.2c). Counts of opaque zones and increment widths (perpendicular distance between opaque zones) were obtained using Image J, a digital image analysis program (http://rsb.info.nih.gov/ij/). A 10% re-read of randomly chosen otoliths was used to calculate a coefficient of variation for the two reads using the equation described in Campana (2001).

To examine and enumerate daily growth rings in otoliths of juvenile *G. elevata* (<6 cm L_F), otoliths were mounted on a microscope slide using crystalbond mounting adhesive

(Structure Probe Inc., West Chester, Pennsylvania, USA). Otoliths were polished to the core from the dorsal and ventral ends by hand on 9 µm lapping film followed by 0.05 µm alumina powder until daily growth increments became visible. Multiple images were collected throughout the polishing process and the images re-stitched prior to ageing due to the varying ring visibility with section thickness between primordium and otolith margins. Sectioned otoliths were viewed under a compound microscope using transmitted light and a 20x objective lens. Daily rings were counted radially from the primordium to outer otolith edge (Figure 2.2a).

A random selection of cleaned, dried and undamaged otoliths of 187 *G. elevata* from the Northern and Central Regions were weighed on an electronic balance (Sartorius CP225D), accurate to 0.1×10^{-5}g, to examine the relationship between fish age and otolith mass. This was done to assess the utility of using otolith mass to estimate fish age in future studies.

2.2.4 Age validation

Wild caught, captive-held *G. elevata* from the Central Region were periodically examined for aquaria-based validation of annual and daily otolith growth increments. Three separate age validation experiments were conducted to examine the formation of: 1) daily growth increments (3.2 – 4.5 cm L_F); 2) the second annual increment of juvenile *G .elevata* (6 – 9 cm L_F), and; 3) annual increments of larger/older individuals (15 – 35 cm L_F). For validation experiments 1 and 2, fish were immersed in an Alizarin Complexone (ALC) bath at a concentration of 50 mg L^{-1} for 9 hrs to achieve maximum mark quality (Taylor et al. 2005). Prior to the addition of ALC to the immersion tank, a

pH buffer was dissolved to stabilize the pH at 8.2 – 8.4. Pure oxygen was supplied to the alizarin immersion tank through a ceramic air-stone. Dissolved oxygen and pH were monitored for the duration of the fish immersion as each have been show to fluctuate after the addition of ALC (Taylor et al., 2005). Daily validation fish (3.2 – 4.5 cm L_F, n = 6) were kept in a 40 L tank, with flow-through sea water at ambient temperature and salinity and were sampled at 18 days following the ALC treatment. Sectioned otoliths were view under ultraviolet light and rings distal to the inner edge of the alizarin stain were counted by a technician with no foreknowledge of the duration of the experiment. Moreover, to validate the formation of the second annual increment, fifty alizarin treated *G. elevata* (6 – 9 cm L_F) were kept in a 1000 litre tank with flow-through sea water at ambient temperature and salinity, and fed brine shrimp, prawn and 6 mm pellet (Ridley Aquatic feed, Narangba, Australia). Monthly, for 18 consecutive months, ≥ 2 *G. elevata* were sampled and their sectioned otolith (see methods 2.2.3) viewed under ultraviolet light to examine otolith growth and opaque zone formation subsequent to the ALC mark. Finally, to validate the formation of annual increments in larger/older individuals, 24 *G. elevata* of 15 – 35 cm L_F were injected with oxytetracycline hydrochloride (OTC) solution (Engemycin®, Intervet Australia Pty Ltd, Bendigo East, Victoria, Australia), into the coelomic cavity. These fish were kept in a 50 m^2 aquaria pen with flow-through sea water at ambient temperature and salinity and 12 fish were sampled annually for the 2 subsequent years. The otoliths were then extracted and the number of increments distal to the OTC mark was examined as detailed above.

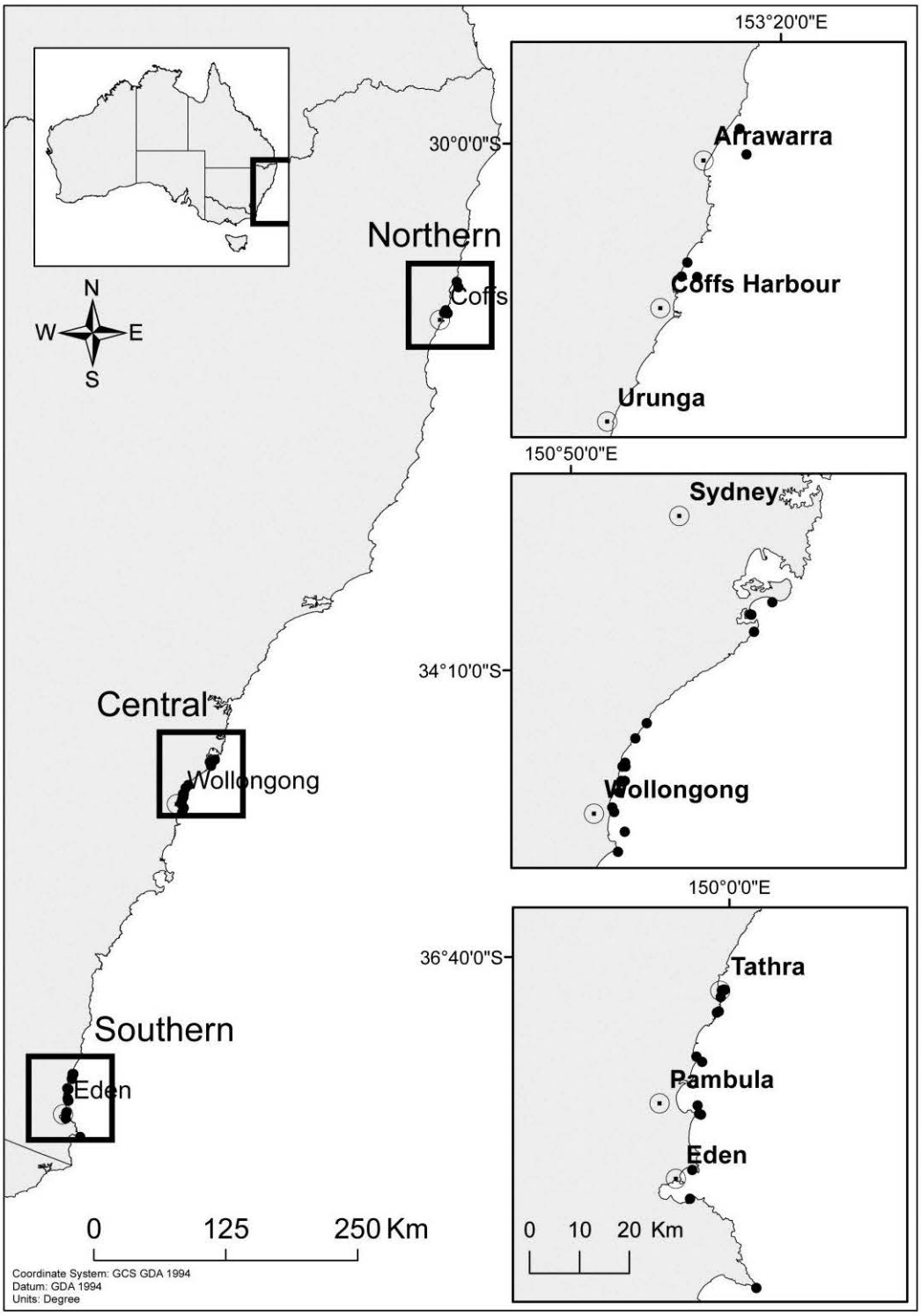

Figure 2.1 Spatial distribution of the Northern, Central and Southern sampling regions. Filled circles indicate the locations where *Girella elevata* were collected by free-dive spearfishing.

2.2.5 Ageing protocol

An ageing protocol was developed to convert counts of opaque zones (age class) in otoliths to fish age (decimal years). Firstly, a universal 'birth date' was assigned to all fish based on the peak of the spawning season/maximum female GSI (Chapter 3, Stocks et al., 2015). Back-calculation of the birth date from daily ring counts of juvenile fish from the primary recruitment pulse to intertidal rockpools was used to further validate the assigned universal 'birth date'. Secondly, fish age classes were adjusted to account for the age of formation of the first opaque zone; this was based on the number of months between the universal birth date and the month that the first opaque zone was deposited. The month of formation of the first opaque zone was calculated from monthly sampling of newly recruited juvenile *G. elevata* to intertidal rockpools in the Central Region. Finally, fish age classes were adjusted by adding the proportion of the year between the month of formation of the most distal opaque zone (determined through an age validation experiment, see 2.2.4) and the sampling date to give a final fish age. This ageing protocol was defined using the equation:

$$Age_F = \frac{Age_{R1}}{12} + (Age_{RC} - 1) + \frac{Mth_{MI}}{12} \qquad (2.1)$$

where Age_F is final age, Age_{R1} is age (months) of formation of the first opaque zone, Age_{RC} is the count of opaque zones and Mth_{MI} is the number of months between the deposition of the distal opaque zone and the sample date.

2.2.6 Age composition and growth rate analysis

The growth of male and female *G. elevata* sampled from the Central and Southern Regions and the growth of *G. elevata* for these two regions with sexes combined was modelled using the von Bertalanffy growth function (VBGF) and fitted to length-at-age data using the equation:

$$L_t = L_\infty \cdot (1 - e^{-k(t-t_0)}) \qquad (2.2)$$

where L_t is the fork length (cm) at age t, L_∞ is the asymptotic fork length (cm), k is the rate at which the function approaches L_∞ and, t_0 is the theoretical age (years) at length zero. Growth functions were compared across equal age ranges between regions and between sexes within regions using analysis of residual sum of squares (ARSS) method (Chen et al., 1992). Fish from the Northern Region were not modelled using VBGF due to the absence of smaller fish, despite considerable effort to locate and collect them. Consequently, a two-factor (sex, and age as a covariate) permutational analysis of variance (PERMANOVA) of a matrix of Euclidian distances, calculated from length data, was used to compare growth to *G. elevata* of the Northern Region.

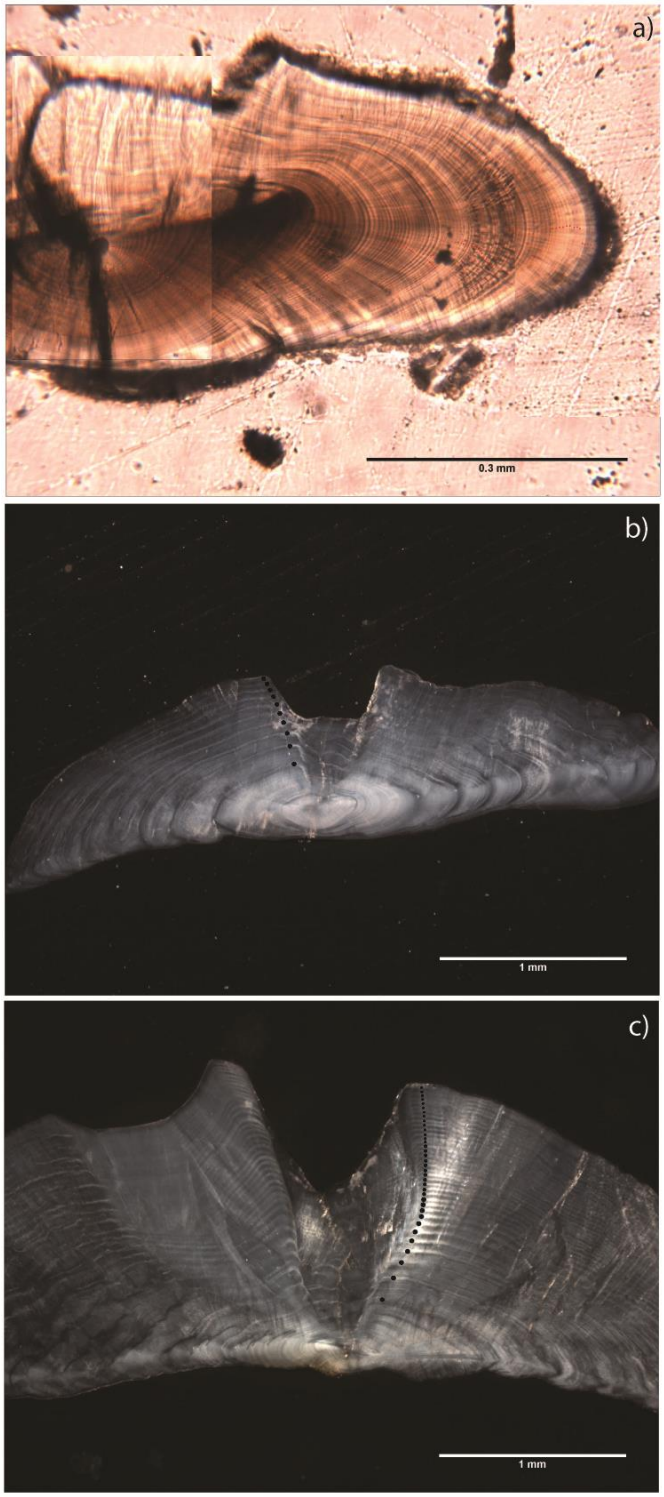

Figure 2.2 Transverse section of *Girella elevata* sagittal otolith showing: a) daily increments using transmitted light (106 days old); b) annual increments using reflected light (10 years old), and; c) annual increments using reflected light (36 years old). Opaque annuli are marked with solid circles.

2.2.7 Growth chronologies, climate and oceanographic processes

Increment measurements between opaque otolith zones (see methods 2.2.3) of fish of known sampling date were used to create multi-decadal mean otolith growth chronologies for each of the three regions. Partially formed marginal increments were removed from individual growth chronology to eliminate biases associated with varying sample dates. Increment chronologies were recorded from the marginal increment towards inner increments, as ageing error was primarily associated with the correct identification of the 1st and 2nd opaque otolith zones. The inner two increments were therefore removed from the growth chronology prior to analysis to reduce increment cross-dating error.

High-frequency variability in increment widths are shown to be induced by climatic processes (Black et al., 2008, Black et al., 2005). Other physiological and age related variables affecting increment width were removed in a process known as de-trending (Grissino-Mayer, 2001, Holmes, 1983). These low-frequency long-term trends were removed by fitting negative exponential functions to individual increment width time series. In instances where a negative exponential function did not fit the raw increment series a negative linear regression was fitted. Increment widths for each year were then divided by the predicted increment width from the fitted function. The average of all residual increment time series was used to create a final master chronology for each region. Values greater than 1 indicated wider than average increment widths, values less than 1 indicated narrower than average increment widths. Fish >10 years of age and years where the number of increment measurement exceeded 10 were included in the derivation of the master growth chronology. All the processes used for the creation of the de-trended master growth were automated in the ASTRAN program developed by

Ed Cook and Paul Krusic, available at http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html.

Pooled master increment chronologies dating back to 1995 (17 years), 1979 (33 years) and 1990 (22 years) for the Northern, Central and Southern Regions respectively were analysed in relation to the Southern Oscillation Index (SOI) using a simple linear regression. The SOI is a measure of the pressure differences between Darwin, Australia and Tahiti, a positive SOI implies a La Niña event, while negative values imply an El Niño event (SOI data was provided by the Australian Government, Bureau of Meteorology, http://www.bom.gov.au/climate/current/soihtm1.shtml).

2.3 Results

2.3.1 Ageing protocol and precision

Back-calculation of the birth date from daily ring counts of juvenile *G. elevata* from the primary recruitment pulse to intertidal rockpools was synchronous with the peak of the spawning season, occurring in January within the Central and Southern Regions. However, fine scale temporal knowledge of spawning periods within the Northern Region remains unclear (Chapter 3, Stocks et al., 2015). A similar spawning period was therefore inferred for the Northern Region and all fish were assigned a universal birth date of January 1. The centre of the 1st opaque zone was laid down in wild caught fish from the Central Region in September/October. It was therefore calculated that the first opaque zone formed at 9 months of age (number of months between the universal birth date and month of formation of the first opaque zone). Using this information and equation 2, counts of otolith opaque zones were converted to give a final age. The age

adjustment protocol was applied only to fish that had formed the 1st opaque zone; other fish were aged from daily ring counts (which required no age adjustments). A 10% re-read of randomly chosen otoliths yielded a coefficient of variation of 3.75%, well below the accepted reference point of 5% (Campana, 2001).

Significant relationships were observed between otolith mass and fish age for both the Central and Southern Regions (Central Region: $F_{1,97}$=938.485, P < 0.0001, R^2=0.906; Southern Region: $F_{1,87}$=689.084, P < 0.0001, R^2=0.888), (Appendix: Figure A.1). In interests of optimum accuracy otolith mass was not used to estimate fish age in this study.

2.3.2 Age validation

All juvenile *G. elevata* stained with ALC (n = 6) had counts of 18 rings distal to the inner edge of the ALC stain when euthanised at 18 days post the ALC treatment, thus validating daily deposition of rings. Secondly, monthly sampling of juvenile fish held in the aquaria over 18 consecutive months showed formation of a single second opaque zone in Oct/Nov during increasing water temperatures of the austral spring (Figure 2.3). Finally, annual sampling of larger fish injected with OTC showed the deposition of 1 opaque zone, forming annually around November, distal to the OTC stain for age-2+ to age-4+ fish.

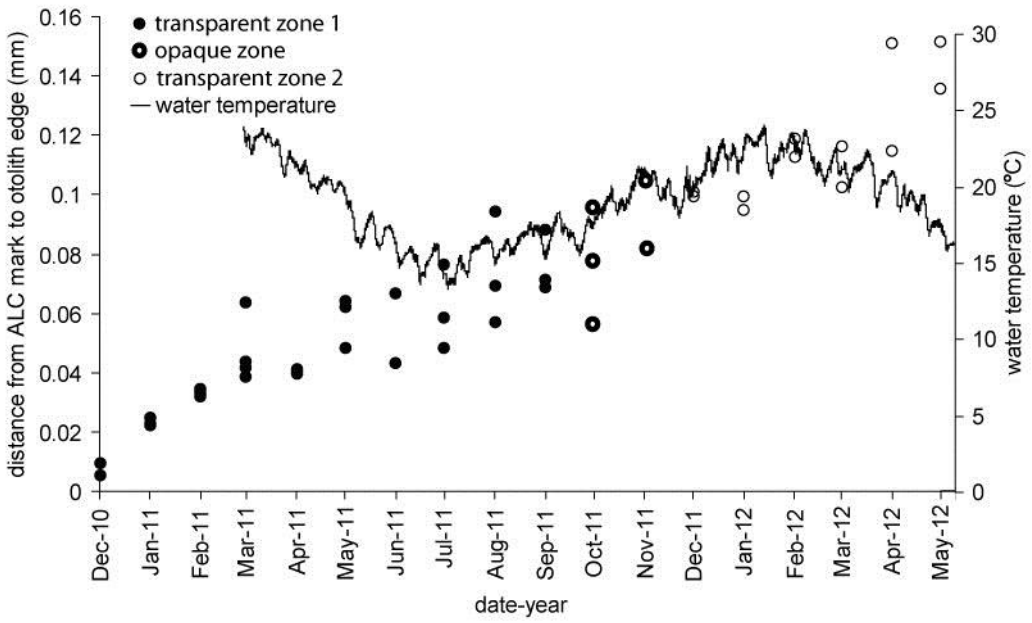

Figure 2.3 Otolith growth (distal to Alizarin Complexone (ALC) stain) of *Girella elevata* raised in captivity. Monthly sampling of fish shows the time of formation of opaque and translucent otolith zones when viewed under reflected light. Each data point represents a single fish (n=40). Flow-through aquaria water at ambient temperature is also indicated.

2.3.3 Age composition

In total, 957 *G. elevata* were aged, 70 from the Northern, 460 from the Central and 427 from the Southern Regions. The oldest fish sampled were 39, 45 and 42 years of age from the Northern, Central and Southern Region respectively. The youngest *G. elevata* collected from the Northern Region was age-4+ (Figure 2.4a). New recruits (age-0+) were collected from intertidal rockpools in both the Central and Southern Regions (Figure 2.4b & 2.4c). The Central Region was dominated by younger fish, but also had the largest proportion of fish older than 21 years (relative to the other regions), most of

which were male. Within the Northern and Southern Regions, proportions of older males were similar to the proportion of older females (Figure 2.4).

2.3.4 Growth

In general, *G. elevata* showed relatively fast growth rates to approximately 40 cm L_F, after which growth slowed (Figure 2.5). The oldest fish sampled was a male age-45+ and 57.6 cm L_F from the Central Region. The largest fish (L_F) sampled was a male of age-35+ and 59.4 cm L_F, also from the Central Region (Figure 2.5).

ARSS showed no significant variation in growth between sexes for the Central ($F_{1, 351}$ = 1.628, P = 0.182) and Southern ($F_{1, 325}$ = 0.928, P = 0.427) Regions. Significant spatial variation in growth occurred between the Central and Southern Regions when sexes were combined (ARSS, $F_{1, 840}$ = 66.302, P < 0.001), with fish from the Central Region growing faster and attaining larger maximum size (Figure 2.5 & Appendix Figure A.2).

These results were largely supported by the PERMANOVA, which indicated a significant *Region* · *Age* interaction term ($F_{2, 762}$ = 50.963, P < 0.01), but no significant differences between sex ($F_{1, 762}$ = 1.382, P = 0.231). The basis of the significant interaction was explored through pair-wise comparisons, which indicated that length-at-age was much greater in the Central Region than the Southern (t = 3.389, P < 0.001) and Northern (t = 3.934, P < 0.001) Regions, and greater in the Southern than the Northern Region (t = 3.297, P < 0.001).

2.3.5 Growth chronologies, climate and oceanographic processes

De-trended master otolith increment chronologies for each region showed large inter-annual variation (Figure 2.6). The de-trended master otolith increment chronology pooled for each sampling region showed a significant positive relationship with the SOI ($F_{1, 70} = 10.051$, $P < 0.01$), explaining 13% of interannual variation in growth (Figure 2.7).

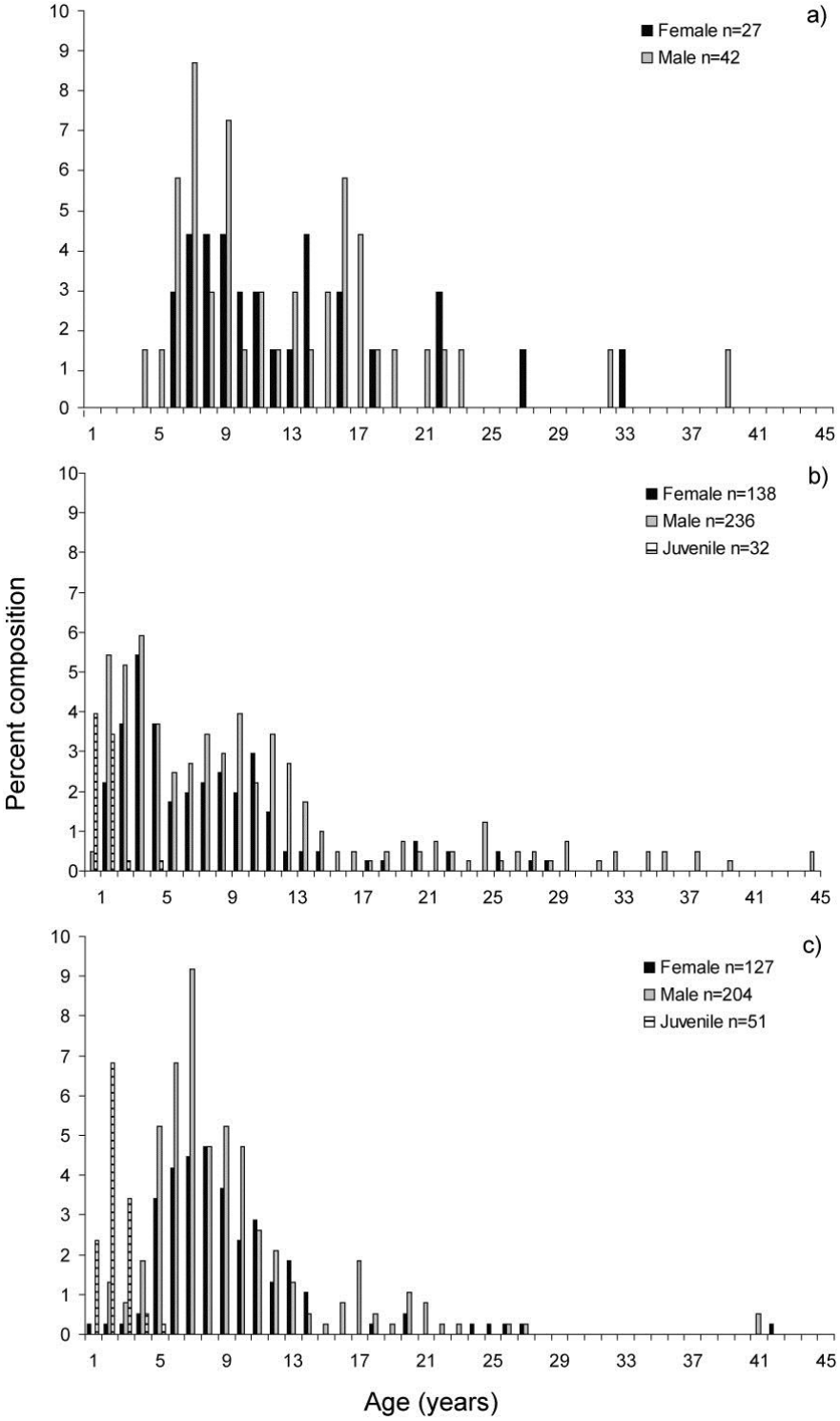

Figure 2.4 Age frequency of *Girella elevata* sampled by free-dive spearfishing temperate rocky reefs in the: a) Northern, b) Central and c) Southern Regions. Note: For fish classified as 'juvenile' the sex could not yet be determined from macroscopic gonad examination.

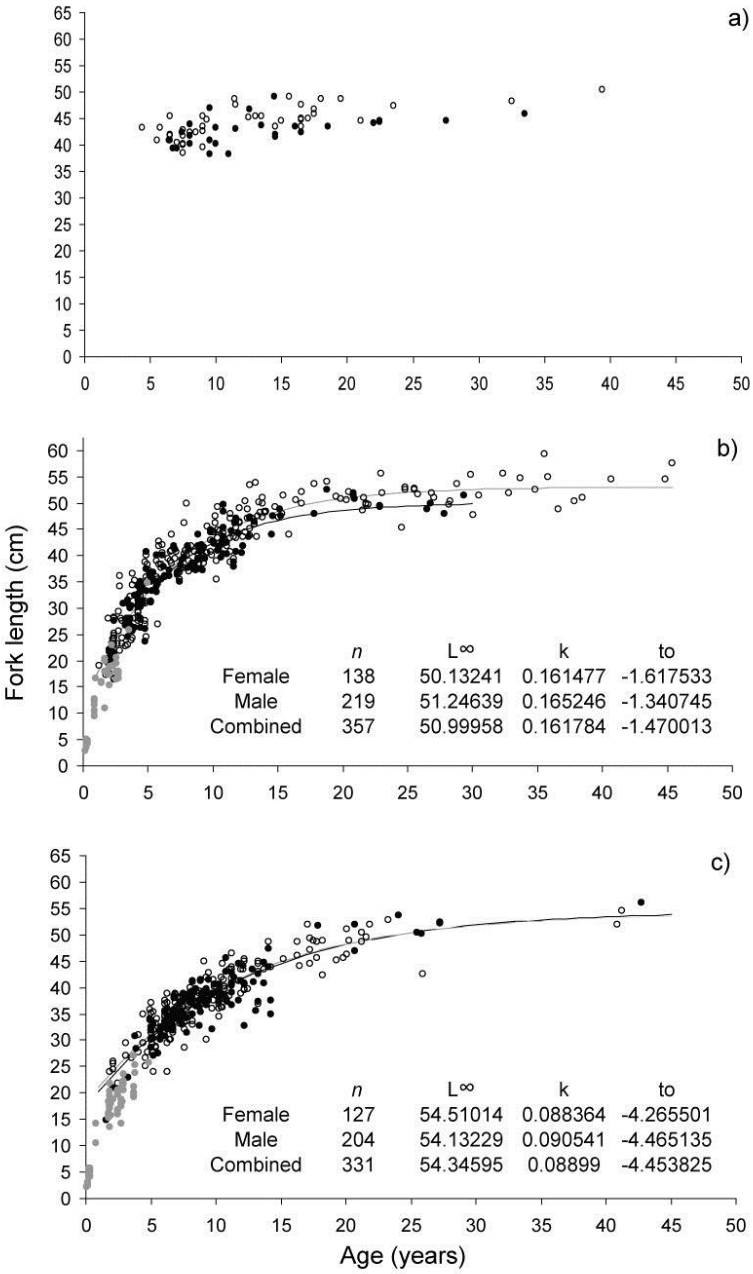

Figure 2.5 Length-at-age data of *Girella elevata* separated by sex for the: a) Northern Region; b) Central Region (von Bertalanffy growth function fitted), and; c) Southern Region (von Bertalanffy growth function fitted). Hollow circle/grey fitted curve = male; solid circle/black fitted curve = female; grey circle = juvenile. Note: For fish classified as 'juvenile' the sex could not yet be determined from macroscopic gonad examination.

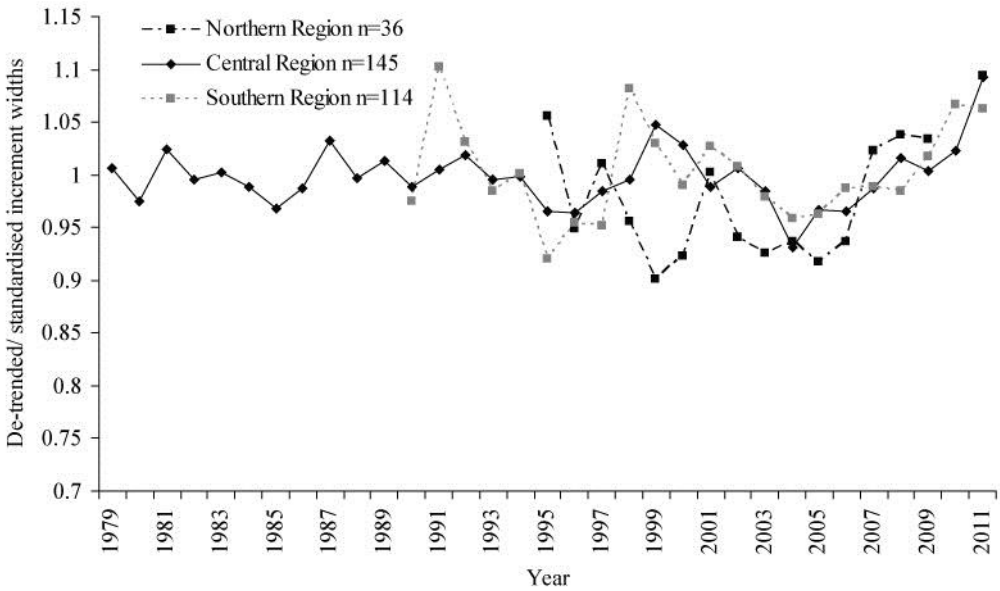

Figure 2.6 De-trended master otolith increment growth chronology for *Girella elevata* of the Northern, Central and Southern Regions. De-trending removed low frequency age related variation in otolith increment width, retaining climate induced high frequency variation.

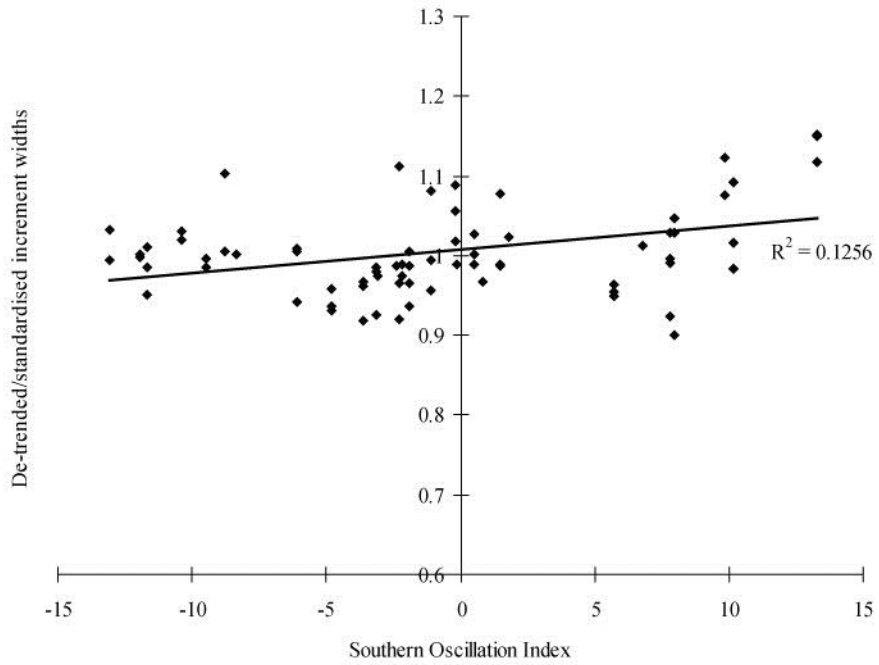

Figure 2.7 Regression of pooled de-trended otolith increment growth chronologies of *Girella elevata* with the Southern Oscillation Index, a common measure of El Niño Southern Oscillation (ENSO).

2.4 Discussion

2.4.1 Growth observations

Girella elevata exhibited great longevity (age-45+) with relatively fast growth to the age of sexual maturity (~31 and 37 cm L_F for male and females respectively; Chapter 3, Stocks et al., 2015) after which growth slowed, a common life-history trait among teleost fishes (Stewart and Hughes, 2007, Walsh et al., 2010). Spatial variation in growth was observed throughout the species distribution with *G. elevata* showing significantly faster growth rates within the Central Region. No differentiation in growth was observed between male and female *G. elevata* in the Northern, Central or Southern Regions. Similarly, the closely related *Girella tricuspidata* showed no intersexual

differentiation in growth within central and southern estuaries of the Australian south-east coast (Gray et al., 2010).

2.4.2 Assumptions of temporal and latitudinal growth studies

Comprehensive aquaria-based age validation experiments confirmed both the formation of daily and annual otolith increments that facilitated the development of an accurate ageing protocol. Such preliminary assays are necessary to deduce with confidence the biological consequences of temporal variation in abiotic variables in both ageing and sclerochronological growth studies.

Temporal analyses of life-history traits in relation to environmental variables operate under the assumption of minimal movement of the species in question. Acoustic telemetry and tag-recapture studies conducted within the centre of the species distribution suggest *G. elevata* are highly resident, with small home ranges and high habitat affinities. *G. elevata* showed movement at scales <2 km with no movement between adjacent reef systems (Chapter 5, Wilson, 1984, Stocks et al., in press). Such attributes made *G. elevata* a suitable species to examine the response of growth to spatial and temporal variations in climate and oceanographic variables. However, age frequencies of the Northern Region were defined by an absence of small fish (<37 cm L_F and <age 4+). Potential explanations for the absence of smaller fish include: 1) Poor recruitment during years prior to sampling; 2) Habitat availability: although not quantitatively assessed, rocky headlands within the Northern Region were generally observed to be steeper with fewer rockpools containing cover for juvenile *G. elevata*; 3) Sampling biases: unlike juveniles in the south that recruit to rockpools, juveniles in the

north may be recruiting to alternate habitats that were not sampled (e.g. the entrance of estuaries); 4) Southward larval drift within the EAC and/or the migration of a proportion of the population to the north. The northern migration with ontogenetic development is common life-history strategy of coastal south-east Australian marine invertebrates (Montgomery, 1990, Stewart and Kennelly, 1998) and teleosts (Stewart et al., 2011, Gray et al., 2012, Miller and Stewart, 2013) that utilize the southward flowing EAC to deliver larvae to higher latitudes (Gray et al., 2012). Further studies examining otolith chemistry, larval drift and genetic analyses may shed light on the life-history of this enigmatic northern population.

2.4.3 Growth, climate and oceanographic processes

The growth of *G. elevata* showed a significant positive relationship with the SOI, explaining 13% of interannual variation in *G. elevata* growth. The SOI is a common measure of the ENSO phenomenon. The ENSO phenomenon is a natural inter-annual oceanographic perturbation of the South Pacific. In eastern Australia, La Niña brings increased rainfall and warmer ocean temperatures while El Niño is characterised by a reduction in winter and spring rainfall and cooler ocean temperatures (Stone and Auliciems, 1992). The effects of El Niño and La Niña events upon marine organisms have been widely studied in the Eastern Pacific, and have been shown to affect both the growth and abundance of fish (Hernandez-Miranda and Ojeda, 2006, Williams et al., 2007b, Sogard, 2011), algae and invertebrates (Castilla and Camus, 1992) primarily due to decreases in ocean nutrients associated with El Niño events.

Girella elevata showed decreased growth during El Niño events, characterised by cooler ocean temperatures in the western Pacific. Environmental temperature is commonly regarded as the principal factor influencing metabolic rates, in turn affecting somatic growth. Positive relationships are often observed between growth and temperature (Thresher et al., 2007, Stocks et al., 2011), provided temperatures do not rise above species-specific thermal windows (Portner, 2002) and resources are not limited (Cowan et al., 2000). Despite decreased growth in cooler El Niño years, latitudinal variation in *G. elevata* growth does not reflect a simple positive relationship with water temperature. Fish from intermediate water temperatures of the Central Region exhibited the highest growth rates. Whereas warmer waters of the Northern Region resulted in the slowest growth rates. It is apparent that latitudinal variation in *G. elevata* growth cannot be simply predicted by gradients in water temperature but likely is a complex intermixing of thermal habitat windows (Righton et al., 2010, Neuheimer et al., 2011), resource limitation (Persson et al., 2000), energy allocation and trade-offs among other life-history traits (Vila-Gispert et al., 2002, Morgan et al., 2010).

2.4.4 Implications of climate change

Recent decades have seen rates of ocean warming of coastal south-east Australia exceed ~3-4 times that of the global average (Matear et al., 2013), giving rise to the region's distinction as a 'hotspot' for climate induced environmental change (Booth et al., 2011, Byrne et al., 2011). Such warming is attributed to the strengthening of the southward-flowing EAC and associated incursions of warmer waters to increased latitudes.

The identification of latitudinal gradients in *G. elevata* growth and the association of growth with oceanographic conditions provide evidence that the southern migration of the EAC will likely result in alterations to *G. elevata* growth rates. Such alterations in environmental conditions have seen shifts in the southern extremities of the distribution of some species of fish in south-east Australia (Poloczanska et al., 2007, Last et al., 2011), including *G. elevata*, likely due to warming Tasman waters (Last et al., 2011). Climate model projections further suggest the optimal thermal habitat of *G. elevata* will continue to shift polewards in the coming decades (Sen Gupta et al., in press). Furthermore, increased eddy activity in the Tasman Sea associated with the strengthening of the EAC is expected to increase nutrient supplies to the upper ocean (Matear et al., 2013). In the eastern Pacific, increased growth during La Niña events suggests a bottom-up effect of nutrient levels on fish growth irrespective of trophic level (Hernandez-Miranda and Ojeda, 2006). A similar trend may result in *G. elevata* populations as a result of changes in EAC transport and nutrient supplies.

The relationship between temporal patterns in *G. elevata* growth and climate/oceanic perturbations associated with the ENSO phenomenon further contributes to the complexity of issues encountered when predicting the biological consequences of climate change. Some studies predict possible enhanced ENSO variability (Fedorov and Philander, 2000, Zhang et al., 2008) with climate change, while others believe it is too soon to predict whether ENSO activity will be enhanced or damped, or if the frequency of events will change (Collins et al., 2010). Nevertheless, the identification of the relationship between growth and the SOI means future change in ENSO will likely result in changes to the growth rates of *G. elevata*.

The sclerochronological approach adopted in this study provides a means for assessing the response of growth to long term climate and oceanographic variation. With continued temporal sampling, populations may be re-examined in the future to monitor potential changes in growth. This technique, coupled with the monitoring of other important life-history parameters, including reproduction, may be particularly useful in monitoring fishery productivity and assessing the biological consequences of a changing climate.

Chapter 3: Intra-population trends in the maturation and reproduction of a temperate marine herbivore *Girella elevata* across latitudinal clines

Abstract

Latitudinal variation in the reproductive characteristics of a temperate marine herbivore, the eastern rock blackfish *Girella elevata*, was examined from 3 regions of the south-eastern Australian coast. Biological sampling covered 780 km of coastline, including the majority of the species' distribution. The sampling range incorporated 3 distinct oceanographic regions of the East Australian Current, a poleward-flowing western boundary current of the Southern Pacific Gyre and climate change hotspot. *Girella elevata* are a highly fecund, group synchronous (multiple batch) spawner. Mean fork length (L_F) and age at maturity was greater for females than males within all regions, with both male and female *G. elevata* of the Southern Region maturing at a greater size and age than those from the Central Region. Estimates of batch fecundity (F_B) were greatest in the Northern and Southern Regions, relative to the Central Region where growth rates were greatest. Significant positive relationships were observed between F_B and $L_{F,}$ and F_B and total fish mass. Gonado-somatic indices indicated latitudinal synchrony in spawning seasonality between *G. elevata* at higher latitudes, spawning in the late austral spring and summer. A late or prolonged spawning period is evident for *G. elevata* from the Northern Region. Juvenile recruitment to intertidal rockpools within the Central and Southern Regions was synchronous with the spawning season, however no juveniles were found within the Northern Region. Current management

arrangements, including the minimum legal length of *G. elevata* in New South Wales, should be revised to take into consideration this new biological data. The implications of latitudinal variation in reproductive characteristics are also discussed in context of climate and oceanographic conditions of south-east Australia.

3.1 Introduction

Exploring latitudinal gradients in reproductive fitness can provide insight into relationships between the biological attributes of a species and environmental variability (Leal et al., 2009, Thorsen et al., 2010). Spatial variation in population reproductive characteristics may be a result of trade-offs among other life-history traits, result from restrictions imposed by latitudinal gradients in environmental conditions (Fleming and Gross, 1990, Lappalainen et al., 2008) or come as a result of fishing pressures (Swain, 2011). For marine organisms, identifying links between climate, oceanographic variability and latitudinal gradients in life-history characteristics may provide insight into the potential biological consequences associated with both basin- and decadal-scale climate shifts. Changes in such climatic and oceanographic processes has led to altered species distributions, changes in breeding populations and alterations in community structures in a number of teleosts throughout the world (Perry et al., 2005, Hiddink and Ter Hofstede, 2008, Last et al., 2011).

At a species-specific level, understanding the latitudinal clines in reproductive biology may provide information on the latitudinal fitness, thermal tolerance windows and energy allocation of a species. Gradients in reproductive characteristics are commonly linked to varying environmental conditions (Lappalainen et al., 2008, Thorsen et al., 2010). The response of a species to such environmental variation may result in phenotypic plasticity or intraspecific life-history evolution due to localised selective pressures (Olney and McBride, 2003). Variation in fecundity, onset of sexual maturity, oocyte size and reproductive lifespan are traits often related to latitudinal clines in abiotic environmental factors (Lappalainen et al., 2008, Leal et al., 2009, Thorsen et al., 2010).

The broad aim of this study was to address the reproductive characteristics of the eastern rock blackfish *Girella elevata* (Macleay 1881), in the context of climate and oceanographic variation across a highly variable oceanographic region. The latitudinal distribution of *G. elevata* spans 3 distinct oceanographic regions of the East Australian Current (EAC), a poleward-flowing western boundary current of the Southern Pacific Gyre. The EAC extends from the Coral Sea into the Tasman Sea, and is heavily dominated by eddies (Mata et al., 2006) which contribute to high oceanographic variability. The spatial variation in the EAC is categorised by several distinct water bodies, which are delineated by a highly variable region of water where the EAC separates from the coast (at approximately 31.5ºS) to form an eastward flowing frontal region. The resulting 3 regions thus represent a strong southward flowing northern zone dominated by warm Coral Sea water, a highly variable separation zone dominated by a persistent eddy field, and a cooler southern zone which is seasonally dominated by either EAC flow-through water from the north, or the cooler waters of the Tasman Sea (Ridgway and Dunn, 2003, Suthers et al., 2011).

Latitudinal variation in reproductive fitness of *G. elevata* was examined by addressing three aims: (1) Define the spawning period across latitudinal gradients; (2) Estimate length and age at maturity and deviations with latitude, and; (3) Examine spatial variation in reproductive output from fecundity estimates. Such life-history data not only provides insight into the relationships between latitudinal clines in reproductive biology and abiotic conditions, but are also critical to assess the species vulnerability to exploitation and to the development of informed management strategies.

3.2 Methods

3.2.1 Study area

Biological sampling of *G. elevata* was conducted within 3 regions of the east Australian coast which correspond to the 3 broad zones of the EAC. These regions were, 1) Northern (30.38ºS, 153.11ºE to 29.89ºS, 153.28ºE): a strong southward flowing northern section dominated by warm Coral Sea water; 2) Central (34.60ºS, 150.90ºE to 34.04ºS, 151.21ºE): a highly variable separation zone dominated by a persistent eddy field, and; 3) Southern (37.27ºS, 150.06ºE to 36.72ºS, 149.99ºE): a cooler southern zone which is seasonally dominated by either EAC flow-through water from the north, or the cooler waters of the Tasman Sea (Figure 3.1). Water temperature loggers were deployed within each of the 3 sampling regions, and mean annual water temperatures (± S.E) at 3 m depth for the 2011/2012 sampling years within the Northern, Central and Southern Regions were 20.54 °C ± 0.38, 19.12°C ± 0.36 and 17.70°C ± 0.35 respectively.

3.2.2 Sample collection and processing

Biological samples of *G. elevata* were collected approximately bimonthly for a two year period (June 2010 – June 2012). Due to logistic constraints, biological sampling of *G. elevata* in the Northern Region was performed bi-annually. Samples within each of the 3 regions were collected from coastal headlands nested along a 60 km stretch of coastline (Figure 3.1, Appendix: Table A.1.). Each sample of *Girella elevata* (>15 individuals) was collected by free-dive spearfishing at 2 – 5 randomly selected headlands within each region to reduce any potential influence of site specific biological traits. The catchability of *G. elevata* did vary with fish size when spearfishing however this bias was equally applied in all regions. Within the Central and Southern

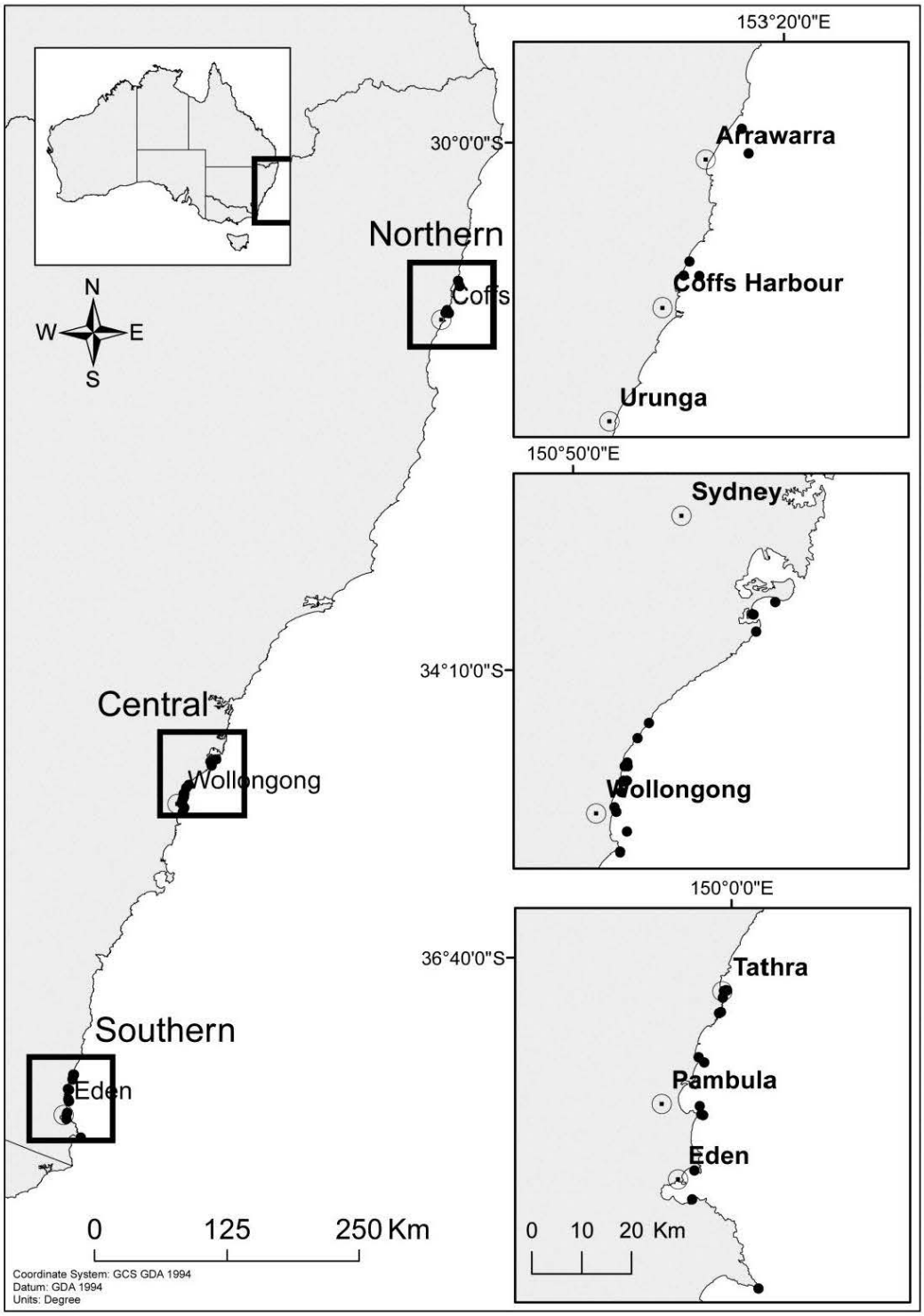

Figure 3.1 Spatial distribution of the 3 sampling regions: Northern, Central and Southern, and locations within each regions where *Girella elevata* were sampled (filled circles).

Regions, juvenile *G. elevata* (1.2 – 15 cm fork length, L_F) were collected from several intertidal rockpools using scoop nets. No juveniles were collected from rockpools within the Northern Region despite extensive efforts to detect and sample them. All fish collected from spearfishing and scoop nets were measured to the nearest 0.1 cm L_F, weighed to the nearest gram and their gonads removed and weighed to 0.01 g. Ripe female gonads and a representative sample of each identifiable sex and stage of development were fixed in a solution of 10% formaldehyde, 5% glacial acetic acid, 1% anhydrous calcium chloride and 84% water (FAACC fixative) for two weeks before being transferred to 70% ethanol for storage.

3.2.3 Macroscopic staging and gonad histology

The gonads of *G. elevata* were assigned a stage of reproductive condition according to their macroscopic appearance (adapted from Stewart et al. (2011)) as described in Tables 3.1 and 3.2. To validate macroscopic staging and provide further detail on ovarian and testicular development, 5 male and 5 female gonads of each macroscopic stage were histologically examined. The fixed gonad tissue was embedded in paraffin wax and a 5 µm cross-section was taken through the middle of the gonad. Sectioned gonads were then stained with haematoxylin and eosin. Histological sections were examined under a compound microscope and a microscope mounted camera (Q-Imaging, MicroPublisher 5.0 RTV, Canada) collected images of each gonad stage (Figure 3.2 and 3.3).

3.2.4 Sex ratios and size distributions

Sex ratios within the Northern, Central and Southern Regions were compared using a Chi-squared (X^2) test. The size-frequency distributions for male and female *G. elevata* within each region collected by free-dive spearfishing were compared using Kolmogorov-Smirnov (K-S) Tests.

3.2.5 Maturity and spawning seasonality

The L_F and age at sexual maturity for male and female *G. elevata* in each region were estimated using the gonad stage assignments detailed in Tables 3.1 and 3.2. *Girella elevata* ages were estimated by counting opaque zones in sectioned sagittal otoliths (Chapter 2, Stocks et al., 2014a). Fish collected in the spawning season (defined from the GSI, see below) were classified as being immature (Stages I and II) or mature (Stages III, IV and V). The proportion of mature fish in each 1 cm L_F size class and 1 year age class were plotted for males and females of each region and a logistic curve was fitted. The length and age at 50% maturity was calculated from the logistic curves. The effect of factors (i) sex, and (ii) region, on length and age at maturity was evaluated using a generalised linear model, with data modelled using a binomial variance function and logit link.

To examine latitudinal variation in spawning seasonality gonado-somatic indices (GSI) were calculated for individual *G. elevata* using the equation:

$$GSI = W_G * W_W^{-1} * 100 \quad (3.1)$$

where W_G is gonad mass (g) and W_W is the whole fish mass (g). Monthly mean GSI values for fish >Stage I were used to describe the period of peak reproductive activity within each region. Water temperature loggers deployed at each sampling region were used to explore relationships between spawning periods and water temperature.

3.2.6 Fecundity

Batch fecundity (F_B) estimates (as defined in Murua *et al.*, (2003)) were made from pre-spawning Stage III ovaries. Batch fecundity counts of 12 - 21 fish from each region covering the size distribution of all mature fish sampled were analysed. Whole ovaries were weighed to 1^{-5} g and a sub-sample of approximately 0.1 g was removed from the centre of the ovary. The ovary sub-sample was then placed in a sonic bath (Unisonics FXP4) to separate the oocytes from the connective tissue (Barnes et al., 2013). The loose oocytes were then transferred to a petri dish, shallow filled with 70% ethanol, and scanned (CanoScan 8600 F). Gravimetric estimates of F_B were made from automated counts of vitellogenic oocytes in the scanned ovary sub-samples using image analysis software (Image J Version 1.38 l), as described by Klibansky and Juanes (2008). A validation experiment of the automated oocyte count methodology was used to compare fecundity estimates between manual counting and the automated count technique described above. Secondly, to examine for potential biases associated with sub-sample location on oocyte counts, fecundity estimates were calculated from sub-samples collected from the anterior, centre and posterior of the gonad. Mean oocyte counts were then compared between sub-sample locations using ANOVA. Finally, the size of oocytes from ovaries fixed in FAACC solution for 2 weeks and stored in ethanol were compared to those collected from fresh ovaries using ANOVA.

Both linear and non-linear models were fitted to F_B estimates to examine relationships with length and mass. Linear models provided the best fit therefore batch fecundity estimates were compared among regions with length and weight as covariates using Analysis of Covariance (ANCOVA) in R v. 2.14.1 (R Development Core Team, 2012).

The relative fecundity (F_R) for individual *G. elevata* was calculated using the equation:

$$F_R = F_B * (W_W - W_G)^{-1} \quad (3.2)$$

where F_B is batch fecundity, W_W is whole fish mass and W_G is gonad mass. An ANOVA and SNK-test, was used to compare mean F_R amongst regions, and the effects of latitudinal patterns in water temperature on F_R was evaluated.

3.2.7 Oocyte development

To examine oocyte development throughout ovarian maturation the size frequency of oocytes for each reproductive stage (Stages II – V, Table 3.1) from 4 randomly chosen *G. elevata* were examined. Using the methodology described above (Section 3.2.6) the diameter of all oocytes within the ovarian sub-sample was then plotted in a size-frequency distribution.

3.3 Results

3.3.1 Macroscopic staging and gonad histology

Stage I (immature) ovaries of *G. elevata* were characterised by the chromatin nuclear stage of previtellogenic primary oocyte growth where oocytes were formed within the ovarian epithelium. Chromatin nuclear oocytes were characterised by a large nucleus and thin cytoplasm layer (Figure 3.2). In Stage II (developing/resting) ovaries perinuclear and chromatin nuclear oocytes were present within the ovaries (Figure 3.2). In Stage III (ripe) gonads, cortical alveoli (yolk vesicle) formation occurred within the cytoplasm and vitellogenic oocytes were predominant (Figure 3.2). The hydration of oocytes occurred in Stage IV (running ripe) ovaries, the membrane of the nucleus was dissolved as it migrated to the periphery of the oocyte. In stage IV ovaries, oocytes were released into the ovarian lumen following hormonal stimulation (Figure 3.2). Stage V (spent) post spawning ovaries were microscopically similar in appearance to Stage II gonads, although densities of perinuclear and chromatin nuclear oocytes were reduced. Stage II gonads were best distinguished from Stage V ovaries macroscopically (Table 3.1 and Figure 3.2).

Stage I (immature) testes contained primary spermatogonia, these were the largest germ cells generally found near the periphery of the testes. Primary spermatogonia then differentiated into secondary spermatogonia where the nuclei took a deeper stain. The secondary spermatogonia were found in varying numbers within cysts (Figure 3.3). In Stage II (developing/resting) testes small spherical spermatocytes, developed from the spermatogonia, and early spermatids were the most predominant germ cells within the testes, each strongly stained (Figure 3.3). Stage III (ripe) testes contained spermatozoa,

spermatids and spermatocytes. Lobules that contain the more advanced stages of spermatogenesis were located towards the centre of the testes (Figure 3.3). In Stage IV (running ripe) testes the accumulation of spermatozoa continued. The sperm duct wall thickened, became less convoluted and was filled with sperm (Figure 3.3). In Stage V (spent) testes there was substantially fewer spermatocytes and spermatids distributed throughout the tissue though residual spermatocytes were still present within the lumen (Figure 3.3).

3.3.2 Sex ratios and size distribution

Significant differences in sex ratios were observed within the Central (1.66:1, X^2 = 23.38, d.f. = 1, n = 378, P < 0.01) and Southern Regions (1.58:1, X^2 = 16.59, d.f. = 1, n = 330, P < 0.01) with a greater proportion of males relative to females. However, no significant differences were observed between sexes in the Northern Region (1.48:1, X^2 = 2.72, d.f. = 1, n = 72, P >0.05). Results from the K-S Tests indicate no variation between male and female length-frequency distributions within the Northern (D = 0.04, P = 0.99), Central (D = 0.09, P = 0.88) and Southern Regions (D = 0.13, P = 0.62), (Figure 3.4). Fork length/total body mass and fork length/total length relationships are presented in the Appendix, Figures A.3 and A.4 respectively.

3.3.3 Maturity and spawning

Within the Central Region 50% of male and female *G. elevata* reached sexual maturity at 31.2 ± 1.3 cm and 37.2 ± 1.4 cm L_F respectively (Figure 3.5: 1a). The age at which 50% of *G. elevata* from the Central Region reached sexual maturity was 3.5 ± 0.4 and 5.8 ± 1.5 years for males and females respectively (Figure 3.5: 1b). *G. elevata* of the

Southern Region matured at a larger size (deviance = 15.68, P < 0.001) and age (deviance = 75.86, P < 0.001) than the Central Region, with males reaching 50% maturity at 34.8 ± 0.9 cm L_F and 7.0 ± 0.4 years and females at 39.8 ± 0.8 cm L_F and 9.5 ± 0.5 years (Figure 3.5: 2a and 2b). Statistical comparison confirmed that overall males achieved sexual maturity at a smaller size (deviance = 26.81, P < 0.001) and age (deviance = 9.28, P < 0.01). No sexually immature fish were sampled during periods of increased GSI in the Northern Region. The smallest and youngest fish sampled during periods of increased GSI within the Northern Region were 38.4 cm L_F and 6.0 years and 38.3 cm L_F and 4.0 years for male and female respectively.

Peaks in the GSI of *G. elevata* were synchronous between the Central and Southern Regions. Temporal sampling over 24 months showed little deviation in spawning seasonality, occurring during periods of increasing water temperature in the late austral spring and summer (Figure 3.6). The GSI of *G. elevata* rose in late October/November reaching a peak in January, returning to baseline levels by late February (Figure 3.6). Limited temporal sampling within the Northern Region did not provide adequate data to accurately define the spawning period. However, ripe females with GSI values up to 9.00% were collected in August, September and October within the Northern Region.

3.3.4 Fecundity

Minimal variation was found between manual and automated oocyte count methodologies (3.21% ± 1.48 S.E). No significant differences were found between anterior, centre and posterior sub-sample oocyte counts ($F_{2, 6}$ = 1.53; P = 0.29). Vitellogenic oocytes of Stage III *G. elevata* gonads fixed in FACC solution were

significantly smaller than those measured from fresh ovaries ($F_{1, 116}$ = 10,240, P < 0.001), with a mean reduction in diameter of 15.01%.

The mean F_B of *G. elevata* was highly variable, ranging from 97,196 ± 4,199 (mean ± S.E) for a 41.0 cm L_F fish from the Southern Region to 2,327,658 ± 162,559 (mean ± S.E) for a 52.0 cm L_F fish from the Southern Region. Significant relationships between F_B and L_F were best described by the linear relationship $F_B = 114.07 * L_F – 4{,}388.10$ (r^2 = 0.37) in the Northern Region, $F_B = 66.30 * L_F – 2{,}565.00$ (r^2 = 0.35) in the Central Region and $F_B = 162.76 * L_F – 6{,}417.00$ (r^2 = 0.75) in the Southern Regions. The F_R (mean ± S.E) for the Northern, Central and Southern Regions were 349 ± 82, 223 ± 22 and 411 ± 51 oocytes per gram body mass respectively. Significant relationships between F_B and body mass were best described by the linear relationship $F_B = 0.92 * W_W – 1{,}118.00$ (r^2 = 0.75) in the Northern Region, $F_B = 0.54 * W_W – 723.52$ (r^2 = 0.76) in the Central Region and $F_B = 0.82 * W_W – 938.82$ (r^2 = 0.59) in the Southern Regions.

Batch fecundity (F_B) differed between the Central and Southern Regions when length and weight were included as covariates, with no significant difference between Central and Northern Regions and Northern and Southern Regions (Table 3.3). Significant differences in F_R were observed between regions ($F_{2, 40}$ = 3.64; P < 0.05). Relative fecundity (F_R) in the Northern and Southern Regions was significantly greater than that of the Central Region, although no differences were observed between the Northern and Southern Regions. The higher F_R within the Northern and Southern Regions indicates a non-linear latitudinal relationship between fecundity and latitudinal variation in water

Table 3.1 The macroscopic and microscopic characteristics of each stage in the development of *Girella elevata* ovaries. Adapted from Stewart et al. (2011).

Stage	**Macroscopic Characteristics**	**Microscopic Characteristics**
I. Immature	Determination of sex difficult. Ovaries fine and threadlike.	Contain perinuclear and chromatin nuclear oocytes.
II. Developing/Resting	Ovaries yellow-orange in colour, translucent and jelly-like. No oocytes visible through ovary wall.	Perinuclear and chromatin nuclear oocytes are present within the ovaries.
III. Ripe	Yellow-orange in colour, vitellogenic oocytes visible through ovary wall, but no hydrated oocytes. Extensive vascularisation of ovary wall.	Cortical alveoli (yolk vesicle) formation occurs within the cytoplasm and vitellogenic oocytes are predominant.
IV. Running ripe	Hydrated oocytes visible through ovary wall, oviduct full of hydrated ova and shed through genital pore with gentle pressure on abdomen. Ovaries are large and occupy most of visceral cavity. Occur during the spawning season.	Hydrated oocytes. The membrane of the nucleus is dissolved as it migrated to the peripheral of the oocyte. Oocytes may then be released into the ovarian lumen following hormonal stimulation.
V. Spent	Ovary flaccid, rubbery and bloodshot. Occur at the end of spawning season.	Microscopically similar in appearance to stage II gonads. Post-ovulatory follicles indicative of recent spawning may be present.

Table 3.2 The macroscopic and microscopic characteristics of each stage in the development of *Girella elevata* testes. Adapted from Stewart et al. (2011).

Stage	**Macroscopic Characteristics**	**Microscopic Characteristics**
I. Immature	Determination of sex difficult. Testes small and threadlike in cross section.	Contain primary and secondary spermatogonia. Secondary spermatogonia are found in varying numbers within cysts.
II. Developing/Resting	Testes cream-brown in colour, threadlike and tough.	Small spherical spermatocytes and early spermatids are the most predominant germ cells within the testes.
III. Ripe	Testes pinkish-white in colour, soft and easily ruptured, no milt expelled with pressure on abdomen. Much larger than Stage II.	Contain spermatozoa, spermatids and spermatocytes. Lobules that contain the more advanced stages of spermatogenesis are located towards the centre of the testes.
IV. Running ripe	Testes pinkish-white in colour, milt expelled with gentle pressure on abdomen. Testes are large and occupy most of visceral cavity. Occur during the spawning season.	Accumulation of spermatozoa continues. The sperm duct wall thickens, becomes less convoluted and is filled with sperm.
V. Spent	Testes brownish, rubbery and bloodshot. Small amount of residual milt may be expelled with pressure on abdomen. Occur at the end of spawning season.	Substantially fewer spermatocytes and spermatids are distributed throughout the tissue though residual spermatocytes are still present within the lumen.

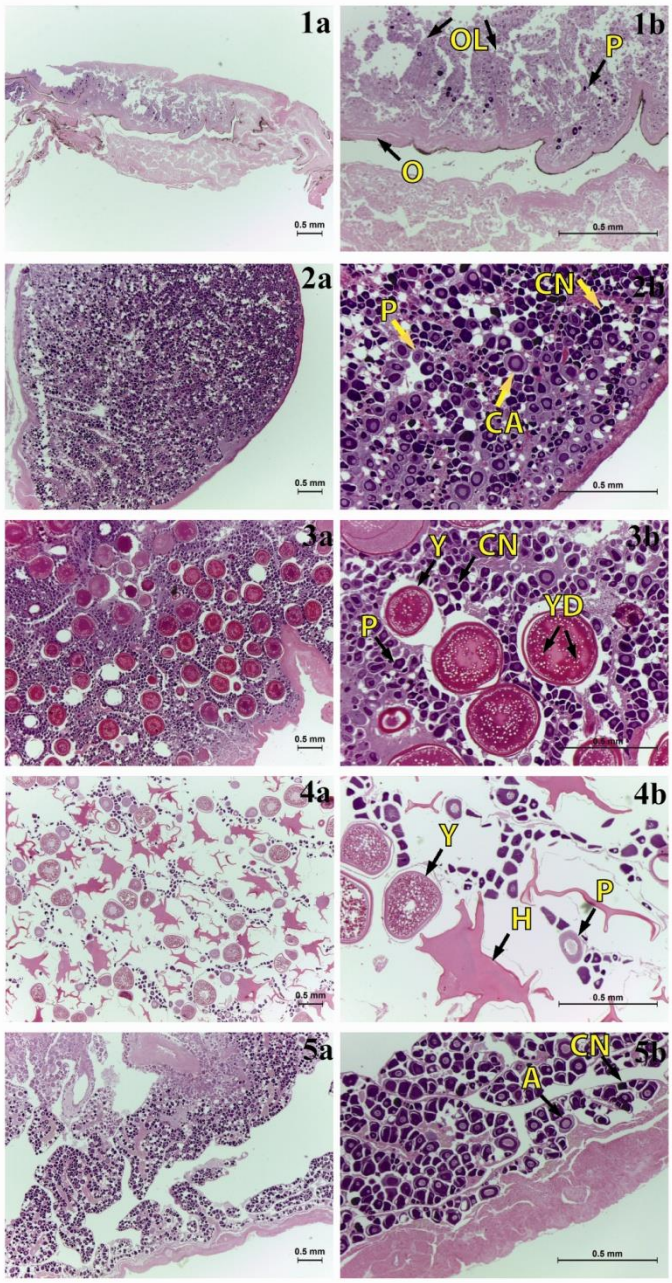

Figure 3.2 Histological sections under 2x (a) and 10x (b) magnification illustrating the development of *Girella elevata* ovarian tissue as described in Table 3.1: 1) Stage I (immature); 2) Stage II (developing/resting); 3) Stage III (ripe); 4) Stage IV (running ripe), and; 5) Stage V (spent). Abbreviations: ovigerous lamellae (OL); ovarian wall (O): chromatin nuclear oocyte (CN); perinuclear oocyte (P); cortical alveolar oocyte (CA); Vitellogenic/yolk granule oocyte (Y); hydrated oocyte (H); atretic yolk granule oocyte (A); yolk droplet (YD).

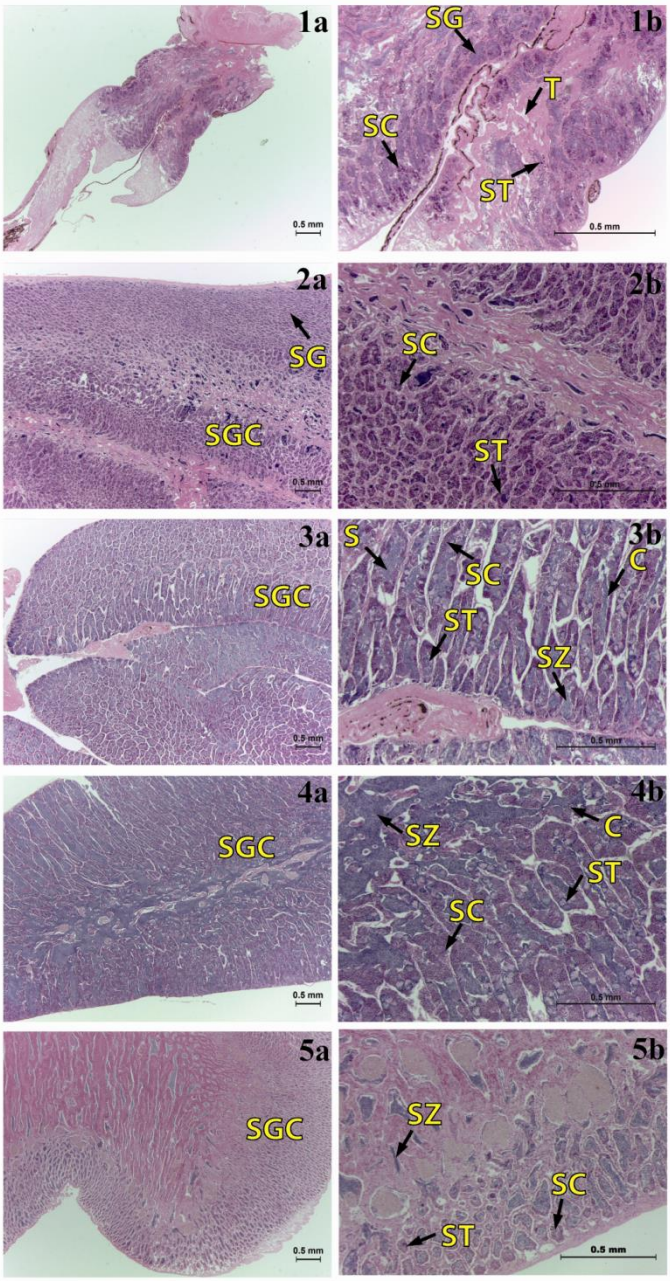

Figure 3.3 Histological sections under 2x (a) and 10x (b) magnification illustrating the development of *Girella elevata* testicular tissue as described in Table 3.2: 1) Stage I (immature); 2) Stage II (developing/resting); 3) Stage III (ripe); 4) Stage IV (running ripe), and; 5) Stage V (spent). Abbreviations: collecting duct (C); spermatocytes (SC); sperm duct (S); spermatogonia (SG); spermatogenic cyst (SGC); spermatids (ST); spermatozoa (SZ); seminiferous tubule (T).

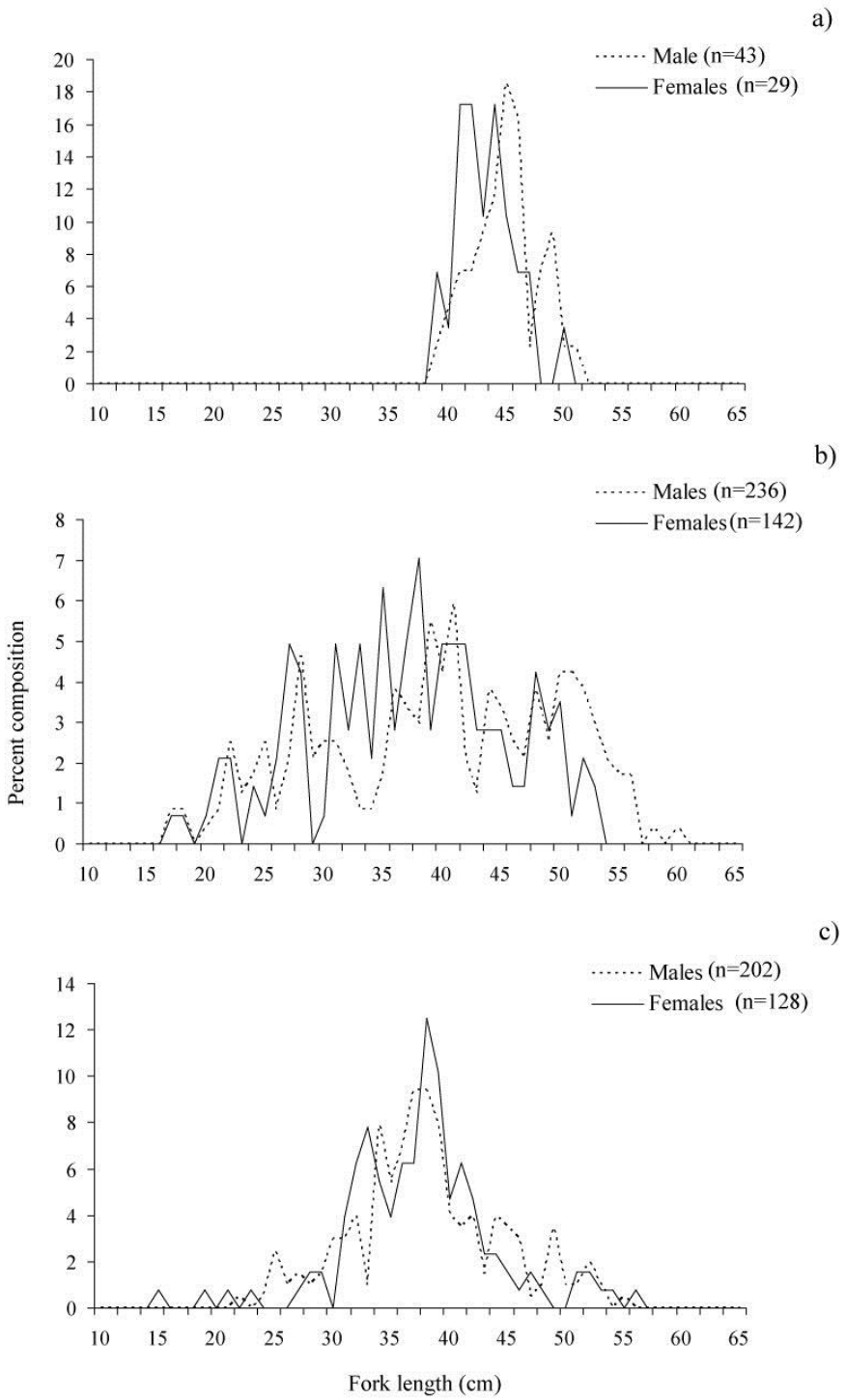

Figure 3.4 Length frequency composition by sex of *Girella elevata* collected by free-dive spearfishing from the: a) Northern; b) Central, and; c) Southern Regions between June 2010 – June 2012.

temperature between the 3 sampling regions (i.e. increasing water temperature with increasing latitude).

3.3.5 Oocyte development

Developing/resting (Stage II) ovaries of *G. elevata* fixed in FAACC solution showed a single mode of oocytes ranging in diameter from 0.10 – 0.25 mm (Figure 3.7a). Ripe (Stage III) ovaries exhibited a mode of oocytes of 0.10 – 0.15 mm in diameter and an additional mode of larger vitellogenic oocytes ranging in diameter from 0.40 – 0.55 mm (Figure 3.7b). Ovaries of running ripe (Stage IV) *G. elevata* had oocytes of 0.10 – 0.40 mm present in similar quantities and two relatively larger peaks in size frequency for the vitellogenic oocytes of 0.40 – 0.55 mm and the hydrated ova of 0.70 – 0.90 mm (Figure 3.7c). Spent ovaries (Stage V) were characterised by a single mode of oocytes of 0.10 – 0.25 mm, with few to no hydrated ova remaining (Figure 3.7d).

3.3.6 Juvenile recruitment

Juvenile *G. elevata* were collected from intertidal rockpools in the Central and Southern Regions, but none were collected from rockpools within the Northern Region despite significant effort to sample them. Post-larval *G. elevata* recruited to intertidal rockpools within the Central and Southern Regions at approximately 1.4 cm L_F, where they remained to approximately 15.0 cm L_F (Figure 3.8) and 1 year of age (Chapter 2, Stocks et al., 2014a) . The timing of the primary recruitment pulse of post-larval *G. elevata* to these pools in the Central and Southern Region varied by a number of months, between years, over the 24 month sampling regime. The first year of sampling saw the primary recruitment pulse to the Central and Southern Regions in November (2010), whereas the

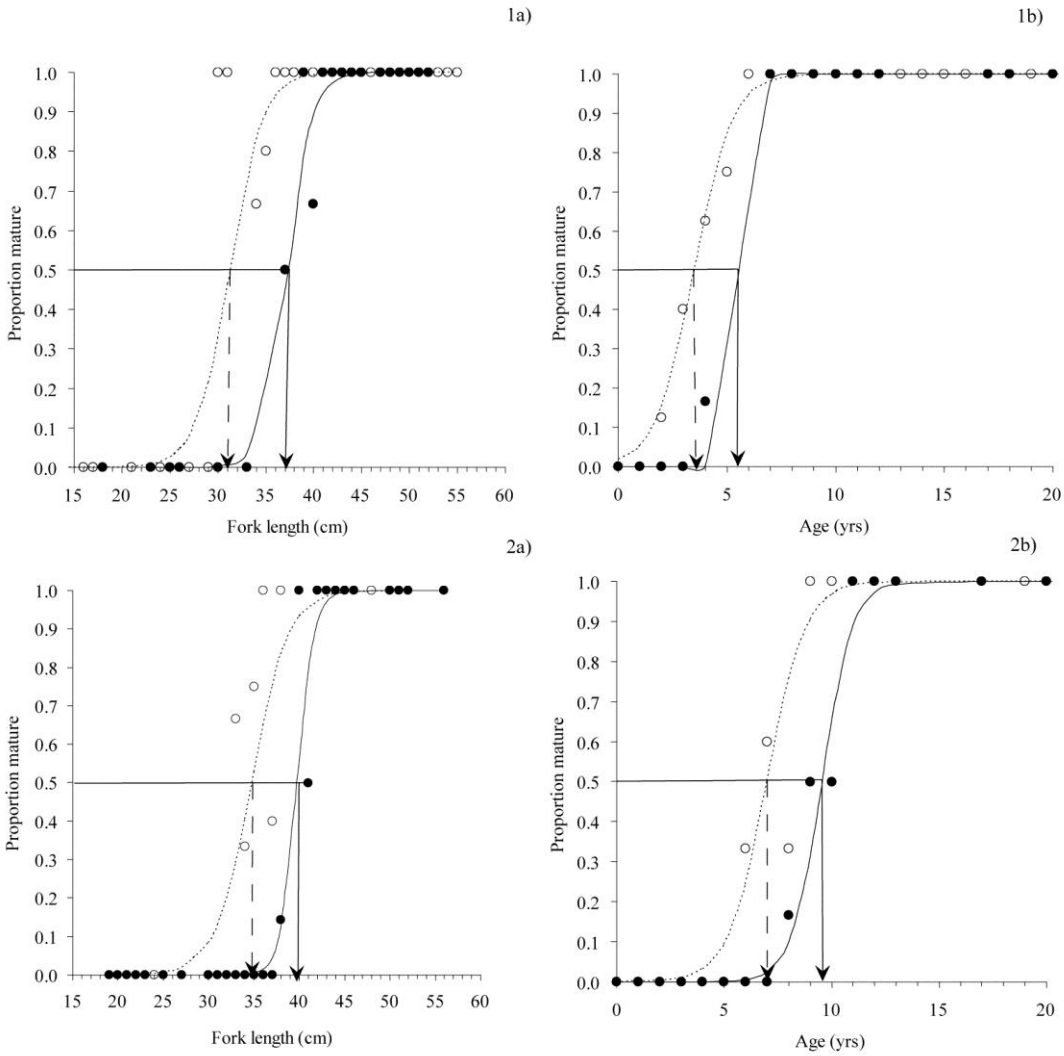

Figure 3.5 Reproductive maturity data and logistic curves of male (hollow circles) and female (filled circles) *Girella elevata* sampled from the: 1) Central Region, and; 2) Southern Regions between June 2010 – June 2012. Arrows indicate: a) fork length and b) age at 50% maturity for males (broken line) and females (solid line).

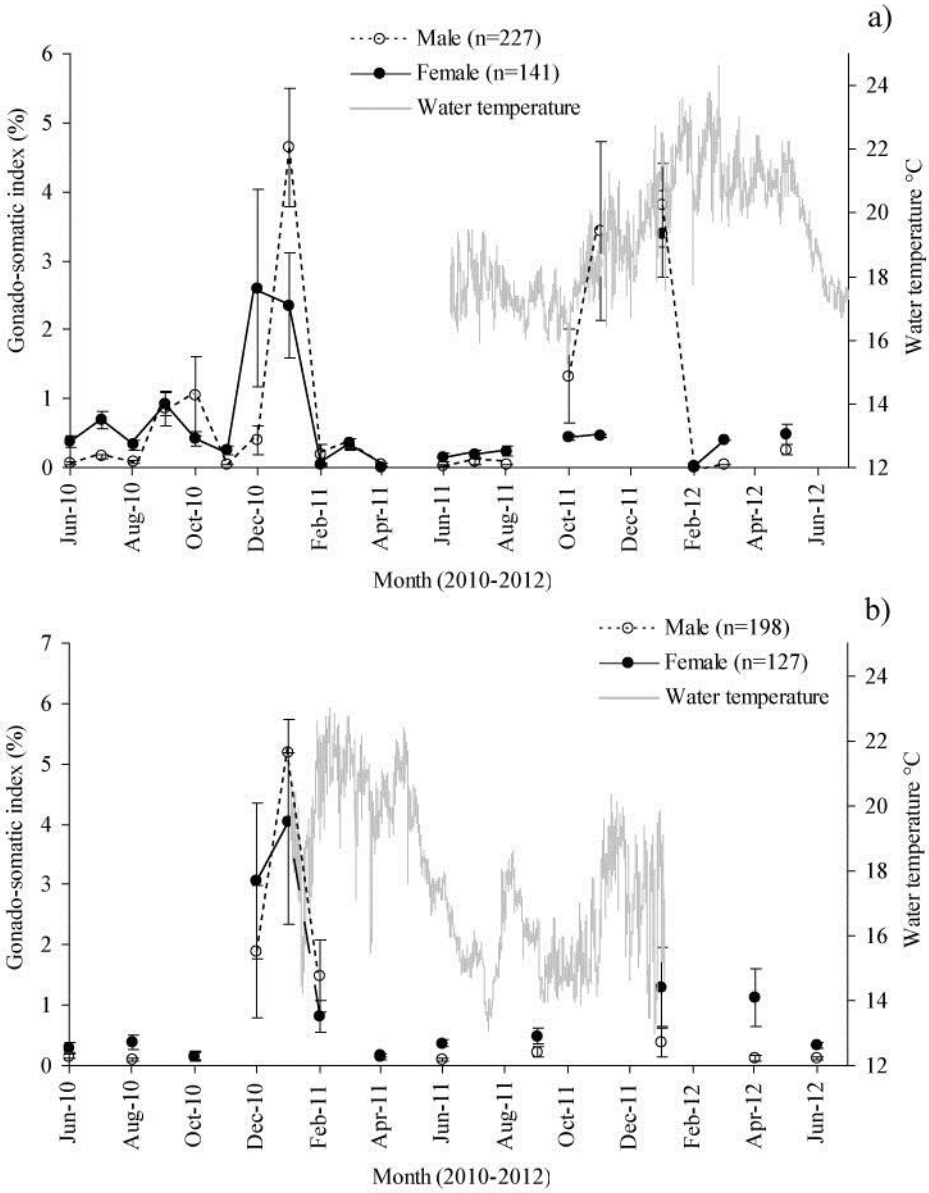

Figure 3.6 Water temperature and gonado-somatic index by month of male (hollow circles) and female (filled circles) *Girella elevata* sampled from the: a) Central Region, and; b) Southern Region.

Table 3.3 Analysis of covariance examining batch fecundity of *Girella elevata* of the Northern, Central and Southern Regions with: a) fork length and b) mass as covariates.

a) Covariate fork length

	d.f.	SS	MS	F	P
Fork length	1	5.509×10^{12}	5.509×10^{12}	32.302	<0.001
Region	2	1.816×10^{12}	9.082×10^{11}	5.325	<0.05
Fork length x Region	2	6.267×10^{11}	3.133×10^{11}	1.837	>0.05
Res	30	5.116×10^{12}	1.706×10^{11}		

Pair-wise	P
Central, Northern	>0.05
Central, Southern	<0.05
Northern, Southern	>0.05

b) Covariate body mass

	d.f.	SS	MS	F	P
Body mass	1	6.396×10^{12}	6.396×10^{12}	37.530	<0.001
Region	2	1.323×10^{12}	6.614×10^{11}	3.881	<0.05
Body mass x Region	2	2.375×10^{11}	1.187×10^{11}	0.697	>0.05
Res	30	5.113×10^{12}	1.704×10^{11}		

Pair-wise	P
Central, Northern	>0.05
Central, Southern	<0.05
Northern, Southern	>0.05

following season it was January (2012) (Figure 3.8). Relatively small numbers of *G. elevata* also recruited to the intertidal rockpools a number of months either side of the primary recruitment pulse (Figure 3.8). From personal observations abundances of *G. elevata* in intertidal rockpools immediately after the primary recruitment pulse exceeded that of all other fish species on the rock platform.

3.4 Discussion

3.4.1 Maturity

Girella elevata from the cooler Southern Region matured at a greater size (L_F) and age than those from the Central Region. This variation in maturation may be attributed to a number of factors including abiotic environmental conditions and/or life-history trade-offs. Fish from warmer waters have been shown to mature at younger ages and smaller sizes than their conspecifics from colder waters (Morgan and Colbourne, 1999, Heibo et al., 2005). Alternatively, life-history traits of a species are often correlated (Heibo et al., 2005), consequently variation in maturation may be a result of trade-offs with growth, or other reproductive features such as fecundity and/or oocyte size (Fleming and Gross, 1990, Lappalainen et al., 2008). Notably, *G. elevata* displayed earlier maturation within the Central Region where fish were characterised by higher growth rates (Chapter 2, Stocks et al., 2014a) and lower fecundity (223 ± 22 and 411 ± 51 oocytes per gram body mass for the Central and Southern Regions respectively). This is consistent with findings for other teleosts where earlier maturation has been associated with higher growth rates (Alm, 1959, Morgan and Colbourne, 1999, Haugen, 2000).

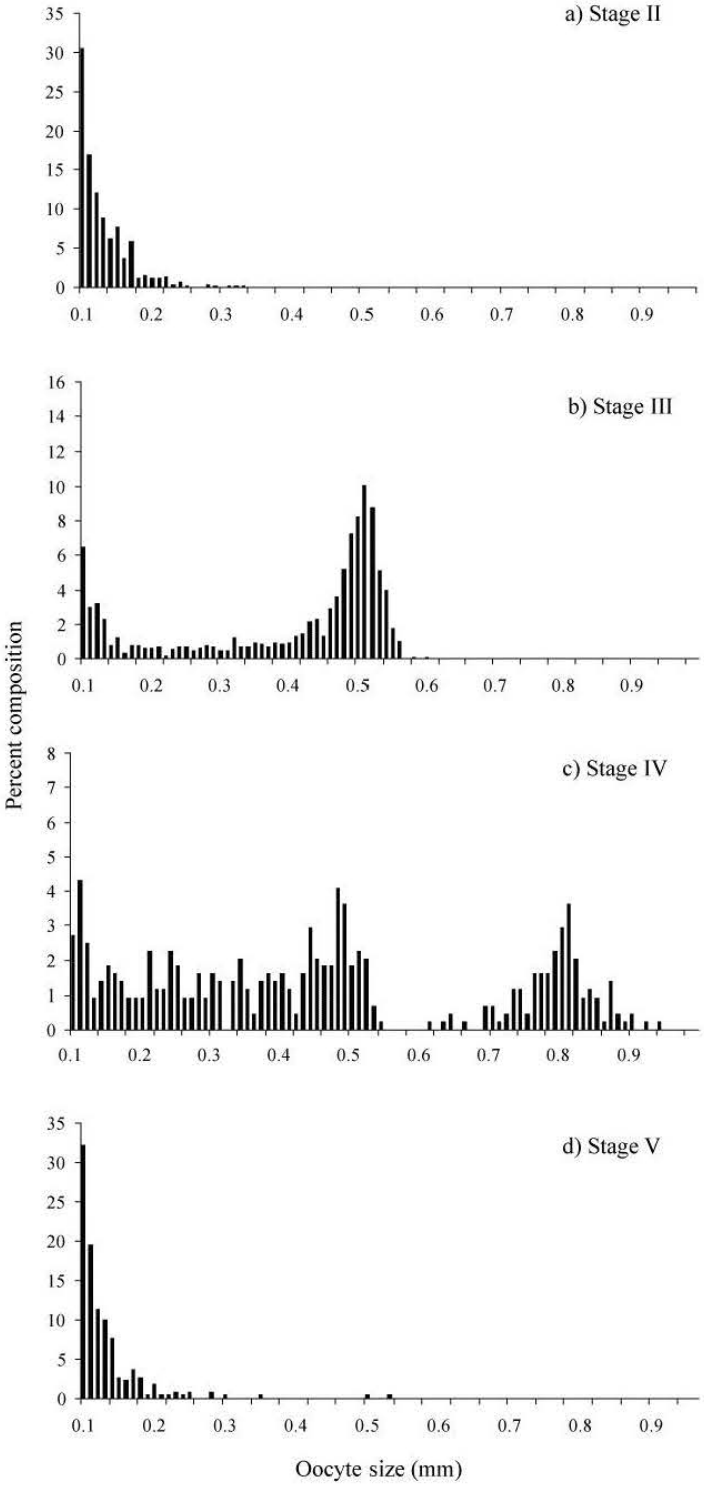

Figure 3.7 Oocyte size frequency of: a) Stage II (developing/resting); b) Stage III (ripe); c) Stage IV (running ripe), and; d) Stage V (spent), female *Girella elevata* gonads fixed in formalin solution.

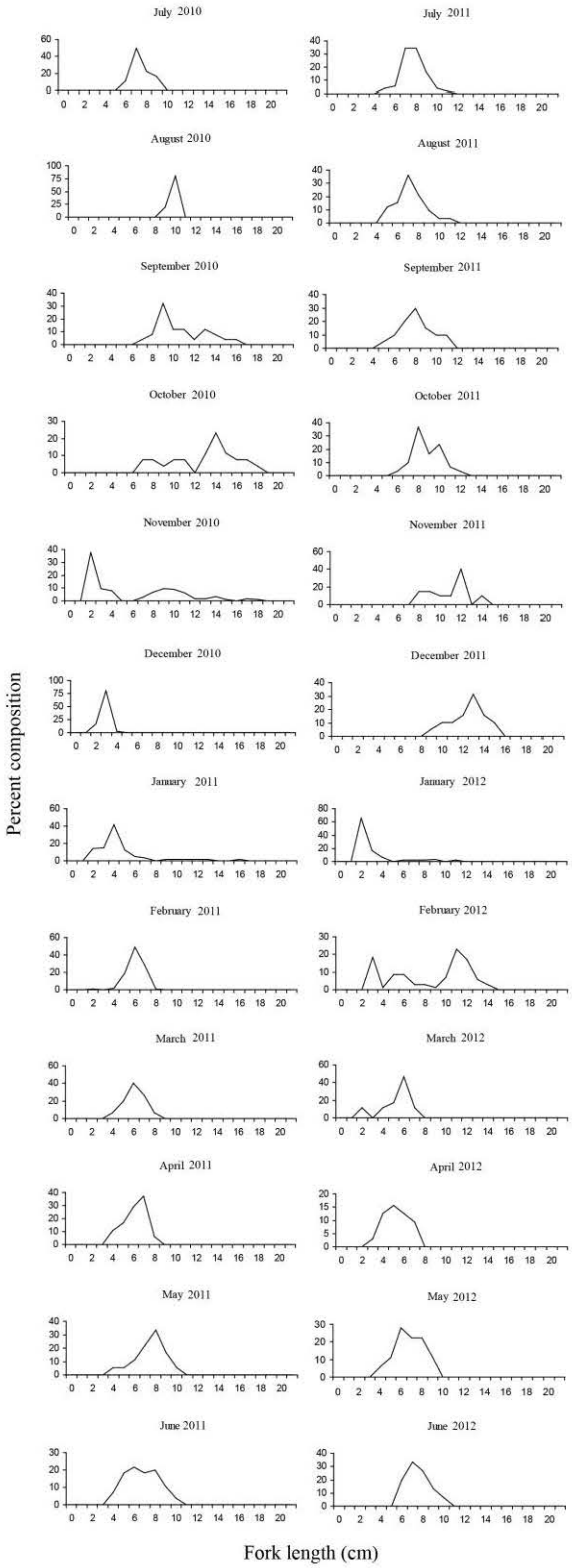

Figure 3.8 Length frequency composition by month of juvenile *Girella elevata* sampled from intertidal rockpools within the Central Region (n >40 for each sampling month).

Girella elevata displayed sexual variation in maturation, with females maturing at a greater length and age than males within each of the regions examined. Such sexual variation in maturation is common among teleosts (Silberschneider and Gray, 2005, Stewart and Hughes, 2008, Walsh et al., 2011), though not previously observed in Australian Girellidae (Gray et al., 2012). Given fecundity is positively related to fish size, female *G. elevata* have likely adopted a life-history strategy to delay maturation, allocating energy to increased somatic growth, which will in-turn result in increased fitness at maturity.

3.4.2 Fecundity

Peaks in GSI were synchronous between the Central and Southern Regions corresponding to the austral spring and summer. The timing of spawning events within the Northern Region remains uncertain due to the restricted temporal sampling. Nonetheless, ripe male and female *G. elevata* were sampled throughout the austral winter and spring (August, September and October) suggesting a late or prolonged spawning period within the northern population. Similarly, the congeneric species *Girella tricuspidata* of south-eastern Australia has been shown to spawn later at higher latitudes (Gray et al., 2012).

Batch fecundity showed a positive relationship with both body mass and L_F within each of the 3 regions. The relationship between batch fecundity and biometrics, also observed in the closely related *G. tricuspidata* (Gray et al., 2012), illustrates the importance of larger individuals to the reproductive potential of the population. Selective fishing of larger more fecund individuals across the species range could

reduce the total population fecundity, though the impacts to juvenile recruitment and population maintenance remain unclear. Further investigations into the frequency of individual spawning events within the reproductive season will also provide additional information on the potential total reproductive output of this multiple batch spawner.

Girella elevata exhibited latitudinal variation in F_R, fish of the Northern and Southern Regions had significantly greater fecundity than those of the Central Region, though no differences were observed between the Northern and Southern Region. Results from the present study and those of Stocks et al. (2014), who examined latitudinal variation in *G. elevata* growth rates, indicate an inverse relationship between growth and F_R. *Girella elevata* of the Central Region exhibited the highest growth rates though fish of this region also had the lowest F_R. Yoneda and Wright (2005) attribute the negative correlation between somatic growth and oocyte development to varying energy allocation. Environmental variables may also be responsible for latitudinal clines in fitness (Wootton, 1990). Processes through which temperature can influence reproductive performance include hormone synthesis, metabolic rates and gametogenesis (Pankhurst, 1997). Studies by Yoneda and Wright (2005) indicate that food availability may also affect reproductive investment.

3.4.3 Juvenile recruitment

The timing of the primary recruitment pulse of juvenile *G. elevata* to intertidal rockpools varied between years. The primary recruitment pulse of juvenile *G. elevata* to intertidal rockpools of the Central and Southern Region occurred in the austral spring and early summer months of November 2010 and January 2012, as observed in previous

rockpool ichthyofauna studies (Griffiths, 2003c). Given the synchrony between peak GSI periods and juvenile recruitment to intertidal rockpools within each region the pelagic larval duration is likely <1 month. Daily aging of newly recruited fish to intertidal rockpools would provide more precise estimates. Additional minor recruitment pulses occurred throughout the months surrounding each primary pulse. Actual spawning cues are not known, however they may be related to oceanographic conditions that are suitable for successful recruitment (Sponaugle and Pinkard, 2004). The relatively few female *G. elevata* sampled with hydrated oocytes suggests rapid oocyte development in the final stages of spawning, often a response to particular environmental cues (Hoffman and Grau, 1989), or the movement of ripe (Stage IV) females to regions outside the sampling localities.

Juvenile *G. elevata* were absent from sampling conducted in the Northern Region. Distinct from the lower 2 regions, the Northern Region is characterised by a strong southward flowing section of the EAC. The poor recruitment in the northern portion of the population may be due to larval drift associated with the strong southward pushing EAC. The dispersal of larvae in south-east Australian waters have been linked to mesoscale oceanographic processes (Bruce et al., 2001). The presence of exclusively mature *G. elevata* within the Northern Region may suggest the northern migration of a proportion of the population. Northern migration with ontogenetic development is common life-history strategy of coastal south-east Australian marine invertebrates (Montgomery, 1990, Stewart and Kennelly, 1998) and teleosts (Stewart et al., 2011, Miller and Stewart, 2013) that utilise the southward flowing EAC to deliver larvae to higher latitudes (Gray et al., 2012). Further studies of the early life stages of larvae, including mechanisms of dispersal, as well as genetic analyses and otolith

microchemistry are required for assessing population connectivity, and the utility of larval seeding from marine protected areas (Christie et al., 2010).

3.4.4 Implications to species management

The current minimum legal length of *G. elevata* in NSW is 30 cm L_T (approximately 28.6 cm L_F, Appendix: Figure A3). Based upon recent maturity data of *G. elevata* provided in this study, a minimum legal length of 39 cm L_T (37 cm L_F) and 42 cm L_T (40 cm L_F) within the central and southern regions respectively would be required to allow approximately 50% of females at the stated lengths to reach sexual maturity and spawn before they are subject to fishing mortality. However, increasing the minimum legal length may place increased strain on the adult stock already devoid of older/larger individuals of higher fecundity (Chapter 3, Stocks et al., 2015). Further population modelling is therefore required to assess the utility of an increase in the minimum legal length for *G. elevata.*

3.4.5 Effects of a changing climate and oceanographic processes

Recent decades have seen rates of ocean warming of coastal south-east Australia exceed ~3 – 4 times that of the global average (Matear et al., 2013), giving rise to the region's classification as a climate change ‘hotspot’ (Booth et al., 2011, Byrne et al., 2011). This warming has been attributed to the strengthening of the southward flowing EAC and associated incursions of warm waters to higher latitudes. This poleward extension of the EAC (~350 km over a 60 year period) is warming the Tasman Sea at >2°C century^{-1} (Ridgway, 2007). The identification of latitudinal clines in reproductive characteristics and the non-linear associations of fecundity with water temperature provide evidence

that the southern extensions of the EAC and the poleward advancements in isotherms will likely result in alterations to the latitudinal variation in *G. elevata* reproductive fitness. Studies by Last et al. (2011) have observed recent poleward shifts in the range limits, abundance and distribution of gravid *G. elevata*. Such changes may be due to a combination of the poleward migration of isotherm providing appropriate temperatures for *G. elevata* survival and/or increased larval dispersal due to the extension of the EAC into Tasman waters. Furthermore, if the poor recruitment of juveniles in the northern portion of the population is a result of the hypothesised larval drift associated with the strong southward pushing EAC, the expected strengthening of the EAC may negatively impact juvenile recruitment at higher latitudes further altering the population distribution.

Chapter 4: Testing the effects of near-shore environmental variables on acoustic detections: implications for telemetry array design and data interpretation

Abstract

Acoustic technology is a common means to study the movements and habitat utilisation of aquatic organisms. This study simultaneously assessed the relative importance of a number of major environmental variables affecting the detection range and detection frequency of acoustic-tracking technology in near-shore marine environments. Transmitter power-output and diel index (in order of relative importance) were the most influential variables affecting detection range within a shallow temperate-reef habitat (5 m depth). Wave height, transmitter power-output and diel index (in order of relative importance) were the most influential variables affecting detection range within the wash zone. Similar models resulted when examining detection frequency at 100 m within the two habitat types. Attention is also drawn to the selection of transmitter power-output based upon the habitat type and environmental conditions of the study site. This study demonstrates the importance of *in situ* range-test studies in array design and interpretation of acoustic telemetry data.

4.1 Introduction

Acoustic-tracking technology is frequently used to study the movements and habitat utilisation of free-living aquatic organisms (Taylor et al., 2006, Hindell, 2007, Childs et al., 2008, Taylor and Ko, 2011, Walsh et al., 2012). Such technology has been applied in a variety of habitat types including freshwater rivers and lakes, coastal estuaries and bays, and increasingly in unenclosed coastal and oceanic waters. The type, frequency and magnitude of prevailing and stochastic environmental conditions varies across each of these environments, and researchers are now paying increasing attention to understanding the performance of acoustic technology in the target environment prior to deploying full-scale acoustic arrays (Bryars et al., 2012, Ferguson et al., 2013).

A fundamental concern when designing acoustic arrays using fixed station receivers is the distance at which an acoustic transmitter will be detected in a particular area, given the study design, habitat and the site-specific environmental conditions. Variables shown to influence detection range and detection frequency can be classified into three categories: 1) Equipment, including transmitter and receiver specifications (Klimley et al., 1998), receiver mooring systems (Clements et al., 2005) and transmission collisions (Singh et al., 2009); 2) Abiotic variables, including water column stratification such as thermo- and haloclines (Singh et al., 2009), vessel noise, wind, rainfall, wave height (Klimley et al., 1998), water flow, air bubbles and substrate (Thorstad et al., 2000, Berge et al., 2012); and, 3) Biotic variables, including biological noise (Payne et al., 2010), tracked animal behaviour, and biofouling (Heupel et al., 2008). Directly accounting for all these sources of variation in detection distance is difficult, and

researchers frequently resort to deploying small pilot receiver arrays with range-test transmitters to evaluate detection range *in situ* (Kessel et al., 2014).

Several technical papers examine the effect of environmental variables on detection range and frequency of acoustic transmissions (Logsdon, 2009, Singh et al., 2009, Shroyer and Cotton, 2010, Welsh et al., 2012, Cagua et al., 2013, Gjelland and Hedger, 2013) however such studies are limited in the near-shore coastal temperate rocky reef environments. Near-shore coastal temperate rocky reefs present some of the most acoustically variable conditions in aquatic environments, and thus present a unique suite of 'noise' from a multitude of sources which can interfere with the reliable detection of acoustic signals. The performance of acoustic technology in these environments remains largely untested, but this is essential in extending acoustic technology to study near-shore reef-associated fishes. This study addresses this gap by: 1) quantifying the detection distance and detection frequency of acoustic transmitters under varying environmental conditions in two near-shore habitat types; and 2) simultaneously assessing the relative importance of each variable affecting detection range and detection frequency in two near-shore marine environments. In addition, these data will be used in the design of an acoustic telemetry array that will examine the activity space size and residency of a temperate near-shore coastal species, *G. elevata*.

4.2 Methods

4.2.1 Study location and design

Range-testing was conducted off Flagstaff Point, Wollongong, New South Wales (NSW) (34.4225ºS, 150.9121ºE; Figure 4.1). Flagstaff Point was chosen because it provided representative wash zones and near-shore reef within close vicinity. The water depth at the study site ranged from 1 – 12 m on rocky reef with depth increasing seaward of the reef. Eight fixed-delay Vemco (Vemco Division Amirix Systems Inc., Nova Scotia, Canada) range-test tags of 144, 147, 150 and 159 dB power-outputs were deployed on fixed submersed moorings at two habitats (one of each power-output in each zone): 1) within the surge/wash zone adjacent to the rock platform at 1 m depth and; 2) at 5 m depth on a rocky reef 90 m from the surge/wash zone (Figure 4.1). Fixed delays of 8 minutes and staggered activation times were used to ensure there were no collisions of transmissions among the range-test tags. A line of ten VR2W (Vemco) monitoring receivers at 6 m depth were deployed on fixed, submersed moorings at 100 m intervals to a distance of 1000 m from the range-test transmitters (Figure 4.1). The bathymetry of the rocky reef along the receiver line was inspected to ensure no ridges or rises could cause acoustic shadows or backscattering of transmissions. Receivers were periodically inspected to ensure each were clear of biofouling, which is known to cause reductions in receiver performance (Heupel et al., 2008).

Equipment was deployed for a total of 45 days (29th August – 12th October 2011) to capture a wide range of oceanographic and weather conditions. Weather conditions for the duration of the experiment were monitored via a weather station (34.37ºS,

150.93ºE), while wave height and period was recorded by Manly Hydraulics Laboratory at the Sydney Directional Waverider Buoy (33.76ºS, 151.41ºE).

4.2.2 Data analysis

Linear models were used to explore the effects of monitored environmental variables within the wash and reef habitats on: 1) the detection range (maximum range), and; 2) the detection frequency (proportion of successful transmissions that were detected at 100 m), of the four varying power-output transmitters. Detection frequency data bound by 0 and 100% was arcsin transformed prior to the analyses. First-order autoregressive models were run using generalised least-squares (gls) regression (linear and non-linear mixed-effects models package, Pinheiro et al., 2012) to handle serial correlations in the data (sequential detections over the course of the experiment were linearly correlated when they came from the same tag). Bayesian Information Criterion (BIC) was used to determine the most parsimonious model which provided the best fit. Linear models tested the explanatory variables that had been standardised according to the approach described in (Kleijnen, 1997): power-output of the tag, diel period (expressed as an index calculated using the formula $5 \cdot \sin(0.2618 * h - 1.57)$, where h is the hour-of-day), wind speed, wave height, wave period, precipitation and water temperature. Explanatory variables were measured in 1 hr time-blocks over the 45 day experiment. The response variable of ‘detection ranges’ was calculated as the maximum detection range for each 1 hr time-block and the ‘detection frequency’ was the proportion of successful transmissions that were detected at 100 m for each 1 hr time-block. Correlation between environmental variables was assessed using correlation coefficients. Standardisation of

parameters involved determining the spread (a_h) and midpoint (b_h) of possible values each parameter h could take (Kleijnen, 1997):

$$a_h = \frac{h_{\max} - h_{\min}}{2} \tag{4.1}$$

$$b_h = \frac{h_{\max} + h_{\min}}{2} \tag{4.2}$$

and then calculating a standardised value of parameter h in the parameter set i (x_{ih}):

$$x_{ih} = \frac{z_{ih} - b_h}{a_h} \tag{4.3}$$

where z_{ih} is the original non-standardised value of parameter h. The magnitude of the parameter coefficient in the resultant linear model thus directly reflected the influence of that particular explanatory variable relative to all other variables in the model. All data analysis was performed in R v. 2.14.1 (R Development Core Team, 2012).

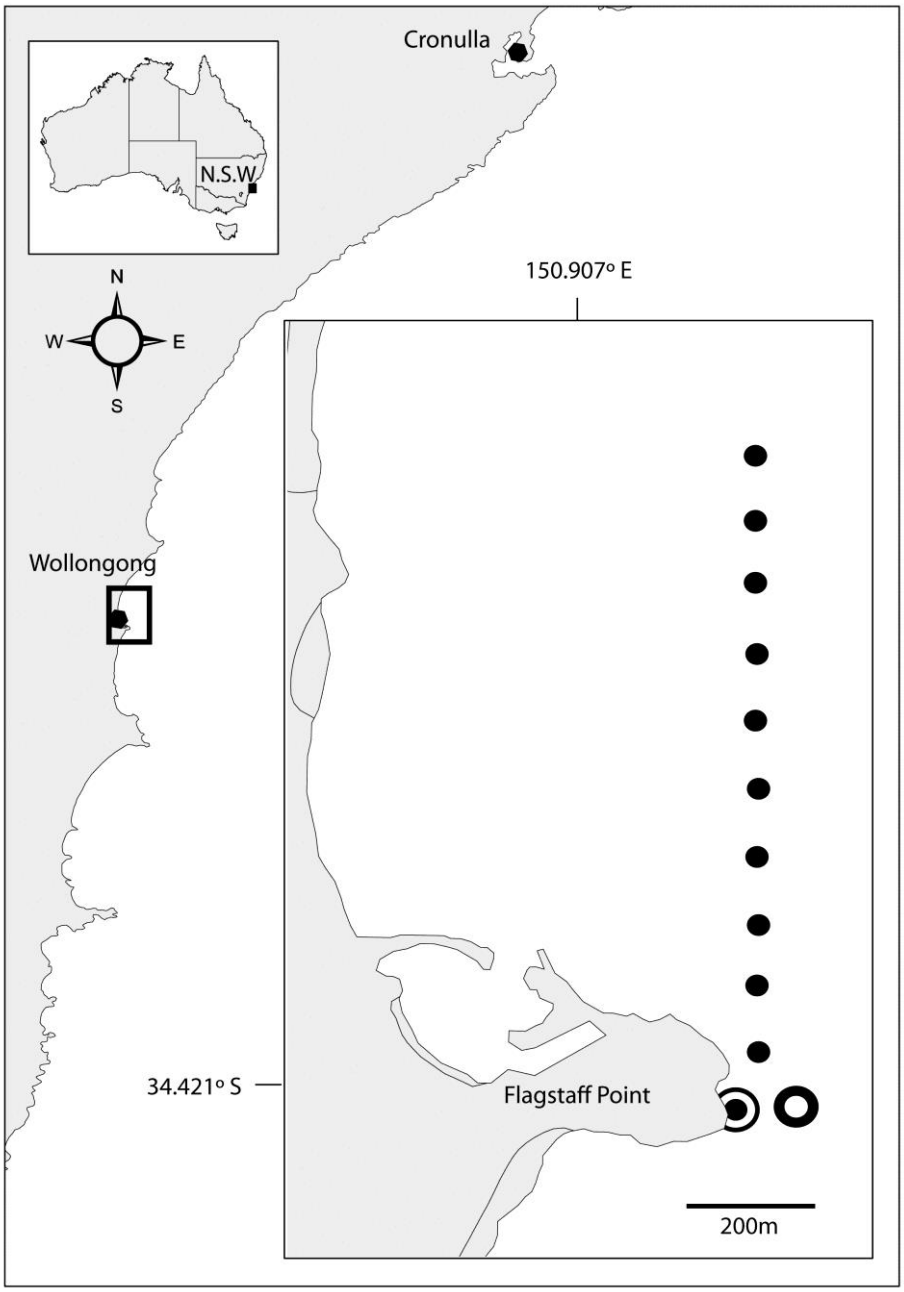

Figure 4.1 Map of study area showing deployment locations of acoustic equipment at Flagstaff Point, Wollongong. Wash transmitters were deployed at 1 m depth (black in white), reef transmitters were deployed at 5 m depth (white in black) and receivers (black) were deployed at 6 m depth.

4.3 Results

4.3.1 Environmental conditions

Water temperatures varied between 15.3 – 18.3 °C with a mean of 17.1 °C, while wind speed ranged from 0 – 52 km h^{-1}. Wave heights and wave period ranged from 0.66 – 4.12 m and 3.8 – 19.1 seconds respectively, with south-easterly swells dominating the study period. Correlation coefficients between environmental variables indicated that wave height and wind speed were moderately correlated (Table 4.1).

Table 4.1 Correlation between abiotic parameters examined in acoustic detection range and detection frequency models.

	Diel Index	Wind Speed	Wave Height	Wave Period	Precipitation
Wind Speed	0.20				
Wave Height	0.00	0.35			
Wave Period	0.04	-0.06	0.01		
Precipitation	0.03	0.16	0.12	-0.06	
Water Temp.	0.06	-0.26	-0.34	0.00	-0.04

4.3.2 Detection range

Several environmental variables were found to affect the detection range of acoustic signals, and these variables differed between reef and wash zones. In coastal reef habitat, the best model included transmitter power-output and diel index (Table 4.2a). Standardised parameter coefficients indicated that transmitter power had the greatest relative effect on detection range, followed by diel index (a positive relationship with diel index indicates greater detection range during the day) (Table 4.2b). In the wash

zone, the best model included parameters of wave height, power-output and diel index in order of relative importance (Table 4.2a and 4.2b).

4.3.3 Detection frequency

Large temporal variation was observed in the detection frequency at 100 m in both reef and wash habitat types. The proportion of successful transmitter detections increased as the power-output increased, and in each instance the detection frequency was higher on reef habitat compared to the wash zone (Figure 4.2).

The influence of environmental variables on the detection frequency of an acoustic signal at 100 m varied between the reef and wash habitats. Within the reef habitat the best model included transmitter power-output and diel index (Table 4.3a), with power-output having the greatest relative effect on detection frequency (Table 4.3b). In the wash habitat, the best model included transmitter power-output, diel index, and wave height (Table 4.3a). Parameter coefficients derived from standardised variables indicated that wave height had the greatest relative influence on detection frequency, followed by transmitter power-output and diel index (Table 4.3b).

The proportion of successful transmitter detections at 100 m ranged from a maximum of 54.60 % at 159 dB over reef habitat to 0.05 % at 144 dB when within the wash habitat. For all power-outputs and within each habitat type the proportion of successful transmitter detections decreased as the receiver distance from the transmitter increased. A maximum range of 600 m was recorded by the 159 dB transmitter over reef habitat though this equated to only 0.03 % of the maximum potential detections for that transmitter and range. The range over reef habitat for all higher power-output

transmitters (159, 150 and 147 dB) was greater than that of the equivalent power transmitters situated in the wash zone. The lowest power-output transmitter (144 dB) over reef habitat was outperformed by all transmitters with the exception of the equivalent power-output wash transmitter that had the lowest proportion of successful transmissions at a 100 m range (Figure 4.3).

4.4 Discussion

4.4.1 Environmental effects

Temporal variation in the detection frequency of the acoustic transmitter and receiver pairs demonstrates the sensitivity of the detection of an acoustic signal under varying environmental conditions. Within the wash habitat, wave height had the largest negative influence on detection range and detection frequency. This was likely due to the noise and air entrapment caused by wave impact increasing signal attenuation and decreasing signal transmission (Norton and Novarini, 2001). Although water temperature did not have a significant effect on detection range or frequency within the present study, increased water temperatures have been shown to decrease the proportion of successful detections (How and Lestang, 2012). How and Lestang (2012) have attributed this phenomenon to an indirect effect of increased noise from faunal activity. Thermocline stratification has also been shown to increase or decrease transmission distance depending on whether the signal must pass through the thermocline for detection (Singh et al., 2009, Topping, 2009). However, the shallow depths and strong water movement would prevent stratification at this study site.

The diel index was largely influential on detection range and frequency within each habitat type. Detection frequency markedly dropped with the onset of sunset then abruptly increased again at sunrise, similar to that found by Payne et al. (2010). Such patterns have been attributed to increased biological noise at night (Radford et al., 2008). Furthermore, the correlation between wind speed and diel index identified in the present study (Table 4.1) would also likely contribute to such an observation. Studies by Gjelland and Hedger (2013) found a reduction in detection frequency and range with increasing wind speed. In the present study the influence of environmental variables on detection frequency was examined at 100 m, however it should be noted that the patterns observed may vary with increasing detection distance.

4.4.2 Transmitter power-output

The choice of the transmitter used within acoustic studies should take into consideration the habitat type that the study species will utilise. Results from the present study illustrate the importance of appropriate transmitter choice based on habitat type in near-shore coastal environments. Detection range and frequency results indicate low dB output transmitters would be insufficient for species that inhabit coastal wash zones. The choice of power-output is largely a trade-off between the size of the fish to be tagged (as the size of a transmitter can influence fish behaviour and survival) (Thorstad et al., 2009), the desired duration of operability of the tag (as greater power-output consumes battery at a faster rate), the behaviour and fidelity of the study species, and the desired range (as larger transmitters have a greater power-output and range). These results indicate that lower powered tags are simply not a viable option under the

conditions experienced in the present study, unless receivers are deployed at an extremely high density (i.e., much less than 100 m apart).

4.4.3 Applications to array design and data interpretation

The type of acoustic array employed is largely determined by the specific objectives of the study and, when available, foreknowledge of the species scales of movement. Gridded arrays are commonly used to examine residency and behavioural rhythms of less mobile species, while those examining larger scale movements of more mobile species generally deploy ‘gates’ or ‘curtains’ (Kessel et al., 2014). Irrespective of the type of array, foreknowledge of the performance of the acoustic equipment in terms of detection range and detection frequency is critical to the array design and the interpretation of detection data collected from tagged animals. In studies deploying ‘gates’ or ‘curtains’, detection ranges must be known in order to place receiver stations at adequate distances to ensure overlap of detection range. Similarly, in studies using gridded arrays examining habitat residency and site fidelity, receiver stations should be deployed at distances to ensure complete habitat coverage. Understanding how detection frequency may vary across detection distance may also improve interpretation of data collected from tagged animals. Longer term range-test experiments that encompass a larger magnitude of the environmental conditions experienced at the study site, or the deployment of control-transmitters within the array, may provide a better understanding of this variation across the study period.

Significant relationships between detection frequency and various environmental variables demonstrate the potential bias involved in using detection frequency of

acoustic data to infer animal behaviour in the absence of adequate site-specific knowledge of the performance of the acoustic equipment (Payne et al., 2010). *In situ* range-testing used for initial array design, coupled with control-transmitters (Payne et al., 2010, Topping and Szedlmayer, 2011, How and Lestang, 2012), not only improves the validity of assumptions made in home range and habitat association studies, but can also increase habitat coverage or reduce costs of array deployments by appropriate receiver spacing.

Although sparse, existing data suggests that *G. elevata* move at small spatial scales <1km (Wilson 1984, Curley 2007), a gridded array will therefore be most appropriate to examine the residency and space utilisation for this species at two near-shore coastal sites. Range testing within the reef habitat indicated detection efficiencies for 159- and 150-dB transmitters were 54.6 and 24.0% when positioned 100 m from receivers. For transmitters positioned 200 m from receivers the detection efficiencies dropped to 24.0 and 4.6% for 159- and 150-dB transmitters. At 300 – 1000 m, detection efficiencies for each transmitter were <6%. Given the short nominal delays (240 and 310 seconds for the 159 and 150 dB transmitters respectively) of the transmitters to be implanted into *G. elevata*, the detection efficiencies at 100 m were deemed acceptable and receivers within each array will therefore be spaced at approximately 200 m intervals at 5 m depth. These detection ranges were significantly shorter than that observed by Lee et al. (2014) in similar near-shore temperate reef habitat off the Sydney region. In addition, detection frequency data of *G. elevata* will be used to infer diel activity patterns, so control-transmitters will therefore be deployed within each array to standardise the detection frequency data of fish.

Table 4.2 Details of models constructed to estimate the influence of standardised variables on the range of acoustic signals in the reef and wash zone, showing (a) BIC values and the best models (shown in bold), and (b) summary statistics for variables retained in the best model.

a.

Model	BIC
Reef	
Power-output + Diel Index + Wind speed + Wave height + Wave period + Precipitation + Water temperature	39819.08
Power-output + Diel Index + Wind speed +Wave height + Wave period + Precipitation	39810.89
Power-output + Diel Index + Wind speed + Wave height + Precipitation	39802.84
Power-output + Diel Index + Wind speed + Wave height	39794.89
Power-output + Diel Index + Wind speed	39789.22
Power-output + Diel Index	**39788.18**
Wash	
Power-output + Diel Index + Wind speed + Wave height + Wave period + Precipitation + Water temperature	37539.50
Power-output + Diel Index + Wave height + Wave period + Precipitation + Water temperature	37531.85
Power-output + Diel Index + Wave height + Precipitation + Water temperature	37524.53
Power-output + Diel Index + Wave height + Water temperature	37518.09
Power-output + Diel Index + Wave height	**37512.63**
Power-output + Diel Index	37520.62

b.

Parameter	β	s.e.	*t*-value	p-value
(Intercept)	97.64	2.81	34.77	<0.001
Power-output	81.51	3.63	22.49	<0.001
Diel index	32.27	3.07	10.52	<0.001
(Intercept)	18.15	2.20	8.24	<0.001
Power-output	24.18	1.96	12.31	<0.001
Diel index	14.98	1.86	8.06	<0.001
Wave height	-25.76	3.67	-7.02	<0.001

Table 4.3 Details of models constructed to estimate the influence of standardised variables on the detection frequency of an acoustic signal at 100 m in the reef and wash zone, showing a) BIC values and the best models (shown in bold), and b) summary statistics for variables retained in the best model.

a.

Model	BIC
Reef	
Power-output + Diel Index + Wind speed + Wave height + Wave period + Precipitation + Water temperature	-3300.63
Power-output + Diel Index + Wind speed +Wave height + Wave period + Water temperature	-3308.82
Power-output + Diel Index + Wind speed + Wave height + Wave period	-3316.88
Power-output + Diel Index + Wind speed + Wave height	-3323.89
Power-output + Diel Index + Wave height	-3327.71
Power-output + Diel Index	**-3331.21**
Wash	
Power-output + Diel Index + Wind speed + Wave height + Wave period + Precipitation + Water temperature	-5028.07
Power-output + Diel Index + Wind speed + Wave height + Wave period + Water temperature	-5036.21
Power-output + Diel Index +Wind speed + Wave height + Wave period	-5043.85
Power-output + Diel Index + Wind speed + Wave height	-5050.46
Power-output + Diel Index + Wave height	**-5055.95**

b.

Parameter	β	s.e.	*t*-value	p-value
(Intercept)	0.27	0.01	32.84	<0.001
Power-output	0.23	0.01	21.89	<0.001
Diel index	0.07	0.01	8.59	<0.001
(Intercept)	0.05	0.01	5.99	<0.001
Power-output	0.05	0.01	8.54	<0.001
Diel index	0.03	0.01	4.91	<0.001
Wave height	-0.06	0.01	-4.28	<0.001

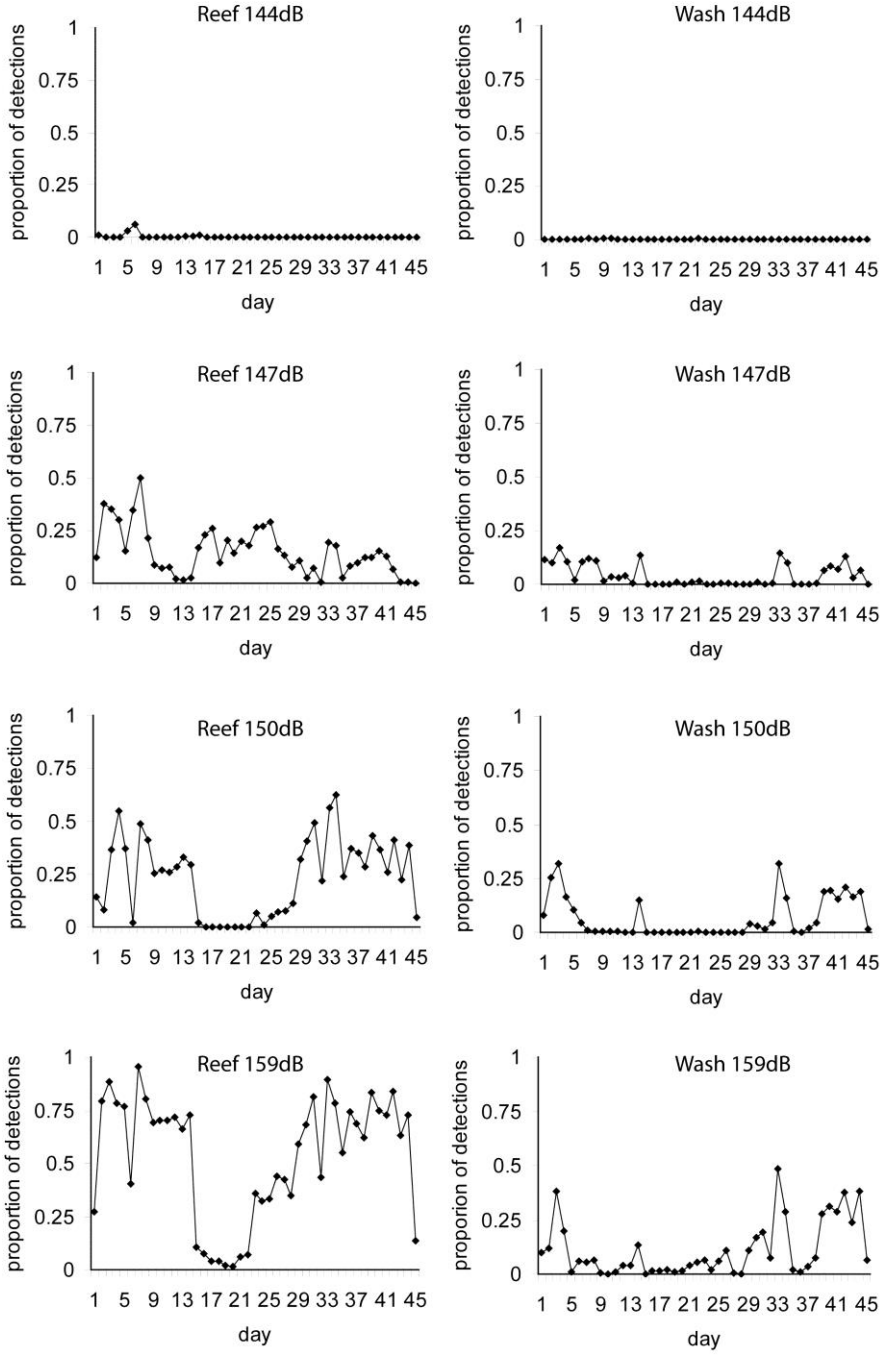

Figure 4.2 Proportion of successful detections for varying power-output transmitters at 100 m in reef and wash habitats.

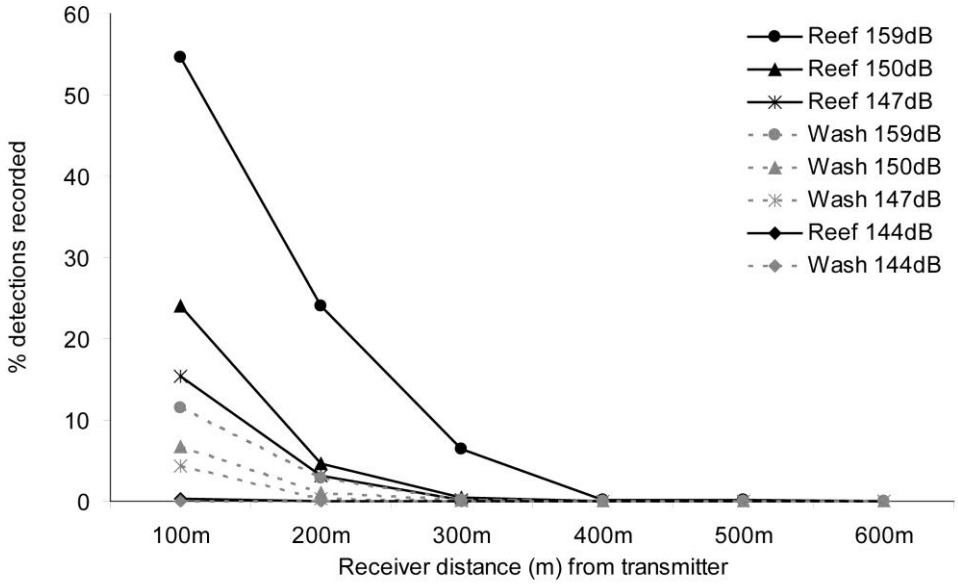

Figure 4.3 Proportion of successful transmitter detections of varying power-output transmitters in two habitat types over a 45 day period.

Chapter 5: Out in the wash: Spatial ecology of a temperate shallow rocky-reef species derived using acoustic telemetry

Abstract

Characterising the movement and habitat affinities of fish is a fundamental component in understanding the functioning of marine ecosystems. A comprehensive array of acoustic receivers was deployed at two near-shore coastal sites in south-eastern Australia to examine the movements, activity-space size and residency of a temperate rocky-reef, herbivorous species *Girella elevata*. Twenty-four *G. elevata* were internally tagged with pressure-sensing acoustic transmitters across these two arrays and monitored for up to 550 days. An existing network of coastal receivers was used to examine large-scale movement patterns. Individuals exhibited varying residency, but all had small activity-space sizes within the arrays. The species utilised shallow rocky-reef habitat, displaying uni-modal or bi-modal patterns in depth use. A positive correlation was observed between wind speed and the detection depth of fish, with fish being likely to move to deeper water to escape periods of adverse conditions. Detection frequency data, corrected using sentinel tags, generally illustrated diurnal behaviour. Patterns of habitat usage, residency, and spatial utilisation highlighted the susceptibility of *G. elevata* to recreational fishing pressure. The results from the present study will further contribute to the spatial information required in the zoning of effective marine protected areas, and our understanding of temperate-reef fish ecology.

5.1 Introduction

Defining the spatial ecology of fish is a fundamental component in understanding the functioning of marine ecosystems. Associations among movement, environmental parameters and biotic factors provide insight into processes driving habitat use (Lowry and Suthers, 1998, Overholtzer and Motta, 1999, Childs et al., 2008, Taylor and Ko, 2011, van der Meulen et al., 2014). Spatial metrics of residency and population structure are also important parameters in the management of aquatic resources (Zeller, 1997, Fromentin and Powers, 2005). Given the importance of such data, an increasing number of studies are employing passive acoustic monitoring to examine the movements, home range and residency of free-living aquatic organisms (Heupel and Webber, 2011). As our understanding of array design and operation in temperate near-shore coastal environments improves (Payne et al., 2010, Stocks et al., 2014b), research is increasingly targeting the movements of exploited species in these environments (Bryars et al., 2012, Ferguson et al., 2013). Such studies are providing important data for spatial management measures such as marine protected areas (MPAs) (Bryars et al., 2012, Ferguson et al., 2013) and increasing our understanding of the latitudinal interactions of fish populations.

No-take MPAs have been adopted throughout the world as a conservation tool to protect biodiversity and ecological processes within the marine environment. Positive effects on biomass, abundances, species richness and size of organisms have been attributed to the implementation of no-take MPAs at varying trophic levels (Edgar et al., 2009, Lester et al., 2009, Chiappone et al., 2000, Babcock et al., 2010). However, understanding the movements and spatial metrics of habitat use is central to the development of effective

no-take MPAs (Kramer and Chapman, 1999, Bryars et al., 2012, Curley et al., 2013 b, Ferguson et al., 2013). Design of MPAs should consider such spatial indices as residency, migration, home range size and the habitat utilisation of resident fish, to ensure reserve scale is appropriate for the species being protected (Kramer and Chapman, 1999). Curley et al. (2013 b) identified such spatial metrics as a critical knowledge gap required to improve spatial management using MPAs in near-shore coastal environments.

Girella elevata is a long-lived, primarily herbivorous, shallow temperate-reef species distributed between approximately 27°S and 39°S on the eastern coast of Australia (Kuiter, 1993, Last et al., 2011). Post-settlement fish use rockpools as nurseries before moving to shallow rocky reefs at approximately 1 year of age (Bell et al., 1980, Burchmore et al., 1985, Griffiths, 2003b, Stocks et al., 2014a, Stocks et al., 2015). They are distributed among rocky ledges or in surge regions, and reportedly reach up to 76 cm in total length (Kuiter, 2001). The species experience considerable recreational fishing pressure, primarily from spearfishing and anglers from rock platforms (Lincoln Smith et al., 1989, Kingsford et al., 1991). Life-history traits of slow growth, high longevity (>45 years; Stocks et al., 2014a) and late maturation (7 years for males and 9 years for females from the southern distribution; Stocks et al., 2015) make the species intrinsically vulnerable to exploitation. Constrained patterns of spatial utilisation (such as high residency and small activity-space size) may further exacerbate this vulnerability, particularly to localised depletion of larger individuals, but currently there is no data to verify this.

Wave-exposed coastal habitats represent some of the most highly variable and challenging marine environments in terms of abiotic conditions (Stocks et al., 2014b). In particular, the turbulence and dynamic pressure generated from wave exposure and currents can create particularly harsh environmental conditions for both mobile and sessile marine species. Such conditions have contributed to selection for various behavioural and morphological adaptations (Rolán et al., 2004, Depczynski and Bellwood, 2005, Fulton and Bellwood, 2005, Fulton et al., 2005, Harborne, 2013). The movement and habitat use of mobile temperate rocky-reef species in response to variations in environmental conditions are poorly understood. The development of passive acoustic-monitoring technology in association with depth-sensing transmitters provides an opportunity to examine the behavioural response of a species to changes in environmental conditions.

Given the recreational importance and likelihood of some degree of site fidelity, *G. elevata* was selected as a study species to better understand space use and behavioural strategies employed by fish in these environments, and the implications of such strategies for place-based conservation. Using a multi-level and spatially replicated acoustic-telemetry array design, the present study addressed the following three specific aims: 1) to investigate movements across a range of spatial scales (within reefs, among reefs and broad-scale coastal migrations); 2) to determine residency periods and activity-space size; and 3) to examine behavioural response and habitat usage in relation to a number of abiotic environmental variables (i.e. wind speed, water temperature, tidal range and dial cycle).

5.2 Methods

5.2.1 Study site

Two-fixed receiver arrays separated by approximately 80 km (Figure 5.1) were deployed off North Sydney (33.79ºS, 151.29ºE to 33.75 ºS, 151.30 ºE) and Flagstaff Point, Wollongong (34.42ºS, 150.91ºE). The North Sydney study site is a narrow strip of wave-exposed coastal temperate-reef predominantly comprising complex near-shore reef habitat including caves, boulders and crevices in depths of approximately 0 – 15 m that extends to a sandy or broken bottom. The North Sydney Array encompasses three sections of rocky shoreline ranging from 0.5 to 2 km in length punctuated by sandy beaches 0.4 – 1 km in length. The Wollongong Array is a single area of temperate rocky reef extending seaward around a wave-exposed coastal headland. The near-shore reef habitat is comprised of caves, boulders and crevices (0 – 18 m in depth), also extending to a sandy or broken bottom. Adjacent rocky reef systems are approximately 0.6 km north and 7 km south, separated from the Wollongong Array by sandy beaches and harbours (Figure 5.1).

5.2.2 Array design

Vemco omni-directional VR2W receivers (Vemco Division Amirix Systems Inc., Nova Scotia, Canada) were deployed on fixed subsurface moorings within the North Sydney (n=15 VR2W receiver stations) and Wollongong Arrays (n=10 VR2W receiver stations). Spacing of receivers within the arrays was based on results from range-testing (Stocks et al., 2014b). Within the reef habitat the detection efficiencies for 159- and 150-dB transmitters were 54.6 and 24.0% when positioned 100 m from receivers. For transmitters positioned 200 m from receivers the detection efficiencies dropped to 24.0

and 4.6% for 159- and 150-dB transmitters. At 300 – 1000 m, detection efficiencies for each transmitter were <6%. Given the short nominal delays (240 and 310 seconds for the 159 and 150 dB transmitters respectively) of the transmitters used, the detection efficiencies at 100 m were deemed acceptable and receivers within each array were therefore spaced at approximately 200 m intervals at 5 m depth. A single Vemco VR2W receiver was also deployed on rocky-reefs both to the north and south of the tagging arrays, to capture potential movements between adjacent reef systems outside the two primary arrays. A further seven receiver stations were deployed approximately 100 m from the coastline between the two study arrays to further increase the spatial resolution for observing larger-scale movement patterns (Figure 5.1). In addition receivers of the Australian Animal Tagging and Monitoring System (AATAMS, a facility of the Integrated Marine Observing System), who operates intermittently positioned coastal stations along the south-eastern Australian coastline, were also included. Array receivers were replaced and downloaded every 3 months to reduce the effect of biofouling on detection range (Heupel et al., 2008) and minimise data loss in the event of mooring failure.

Within each of the two arrays, two fixed-position control-transmitters (V16-1x H 159 dB and V16-1x L 150 dB, fixed-delay 480 seconds), representative of the power-output of transmitters implanted into study fish, were attached to a single mooring 3 m above the sea floor. The control-transmitters were deployed for 378 and 167 days within the Wollongong and North Sydney Arrays respectively. Staggered activation times of the fixed-delay control-transmitters were used to prevent signal collisions (D. Allen, Amirix Systems, pers. comm.). The distances of the control-transmitter mooring to receiver stations within ‘line-of-sight’ were 100, 220, 260, 320 and 470 m at the Wollongong

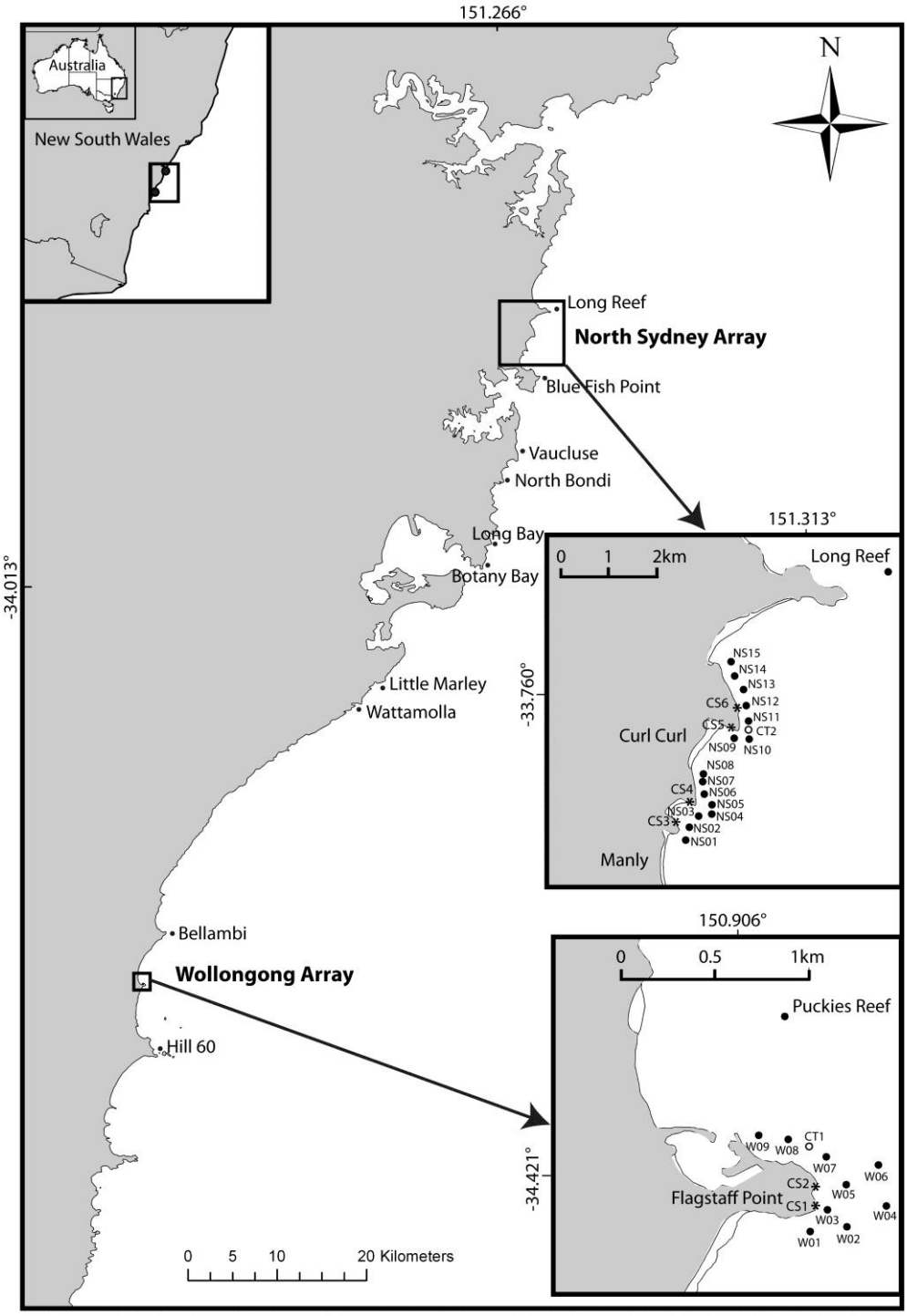

Figure 5.1 Location of the North Sydney and Wollongong Arrays. Filled circles indicate locations of fixed subsurface receiver stations within each array (figure insets) and intermittently positioned along the coastline (10 receiver stations), asterisk- fish capture and release site, hollow circles- control-transmitter mooring locations.

Array and 100, 350, 590 and 740 m at the North Sydney Array. The control-transmitters were used to estimate the influence of factors other than animal behaviour on the detection frequency of acoustic transmissions (Payne et al., 2010, Stocks et al., 2014b).

5.2.3 Transmitter retention experiment and acoustic tagging

Twelve *G. elevata* within each array were surgically implanted with Vemco depth-sensing acoustic transmitters (depth sensor error ± 2.5 m). Six *G. elevata* <35 cm fork length (FL) were internally tagged with V9TP-2x transmitters (nominal delay of 310 seconds, power-output 150 dB, transmitter life 366 days) and six fish >35 cm FL were tagged with V13TP-1x transmitters (nominal delay of 240 seconds, power-output 158 dB, transmitter life 550 days) within each array (Table 5.1). All fish were captured from the rock platform using baited circle-style hooks on monofilament line from depths <3 m. On capture, fish were immediately anaesthetised in a 25 mg L^{-1} eugenol solution (Aqui-S, Aqui-S NZ, Wellington, New Zealand) until equilibrium was lost and the fish became unresponsive to external stimuli (Barker et al., 2009). The fish were then weighed and their FL measured. Prior to surgery, all surgical equipment and the acoustic transmitter were sterilised in a povidone-iodine solution (Betadine, Sanofi-aventis Healthcare Pty Ltd, Sydney, Australia). A ≈20 mm incision was then made along the ventral midline posterior to the pectoral fins through the linea alba into the coelomic cavity, with care taken not to puncture internal organs. The acoustic transmitter was inserted into the coelomic cavity through the incision and one or two 4/0 glyconate monofilament absorbable sutures (Monosyn, B. Braun, Melsungen, Germany) were used to close the incision. A t-bar tag (Hallprint, Hindmarsh Valley, SA, Australia) was inserted below the anterior of the dorsal fin for external

identification. Throughout surgery a circulating pump system of diluted Aqui-S (15 mg L^{-1}) maintained water flow over the gills. Post-surgery fish were placed in a 60 L aerated holding tank and monitored for the return of operculation, correct orientation and response to external stimuli. Once fully recovered (within 15 – 30 minutes), fish were released at their capture location.

A preliminary aquaria tagging trial of 12 *G. elevata* was used to examine post-implant survival rates, animal behaviour, transmitter retention (Wagner and Cooke, 2005, Deters et al., 2010, Butler et al., 2009, Jepsen et al., 2002) and appropriate transmitter size (Thorstad et al., 2009). *Girella elevata* were implanted with Vemco V9 (400 – 700 g total weight and <35 cm FL, n = 6) or V13 (>700 g total weight and >35 cm FL, n = 6) transmitters on the basis of existing literature, suggesting that the proportion of transmitter weight of the total fish body weight should, as a guide, be approximately 2% (Pursche et al., 2014, Childs et al., 2011). Fish were held in 5000 L tanks with flow-through sea water at ambient temperature and salinity, and monitored for 8 months.

5.2.4 Activity-space size

A modified technique of minimum convex polygons (MCPs) was used as an index of activity-space size, which is a measure of the total area used and traversed by an individual when present within the array. MCPs were calculated by summing the detection areas of stations at which an individual was detected and the adjoining area between these stations. Station detection areas were defined as the spherical area created around a station with a radius of 100 m (the detection range at which 159- and 150-dB

transmitters had a respective detection efficiency of 54.6 and 24.0% as determined from a range-test study; Stocks et al., 2014b).

5.2.5 Residency

Residency of the 24 *G. elevata* passively tracked in each of the two arrays was quantified by calculating a residency index (I_R) for each fish. The I_R of each fish was calculated for each station and for the array in which they were tagged as a whole (I_R-Total). I_R-total was calculated by dividing the number of days an individual was detected within the array by the total potential detection period (number of days between the fish tagging date and conclusion of the study) then multiplying by 100. To examine finer scale residency and habitat use, I_R values were also calculated for individual receiver stations. Residency index values ranged from 0, indicating no residency, to 100, indicating a high level of residency.

5.2.6 Depth utilisation

Pressure-sensing data collected from 18 of the 24 *G. elevata* tagged was examined as a proportion of detections in each 1 m depth bin for the duration the fish remained within the array. In all, 18 of the 24 *G. elevata* implanted with acoustic transmitters provided useful data (i.e. >50 detections) to examine depth utilisation and residency indices. The detection depth of fish was also examined in relation to a number of abiotic environmental variables (see section 5.2.8).

5.2.7 Standardisation of detection frequency

To examine the average hourly detection frequency of individual *G. elevata* over a 24 hour diel period, the standardisation process developed by Payne et al. (2010) was applied. This standardisation process was employed to reduce the influence of environmental variables on detection frequencies.

To examine changes in *G. elevata* detection frequencies over a larger temporal scale and allow for association with abiotic environmental variables a modification of the approach developed by (Payne et al., 2010) was employed. A standardised sentinel detection frequency (SSDF) was calculated individually for the four control-transmitters (158- and 150-dB transmitters within each array). Detection frequencies of the control-transmitter were binned into consecutive 6 hour periods (0:00 – 5:59, 6:00 – 11:59, 12:00 – 17:59 and 18:00 – 23:59) for the duration of the control-transmitter deployments (378 and 167 days in the Wollongong and North Sydney Arrays respectively). The SSDF was calculated using the following equation:

$$SSDF_b = \frac{DF_b}{\mu} \qquad (5.1)$$

where DF_b is the detection frequency of the control-transmitter for the 6 hour binned period, and μ is the mean detection frequency for the control-transmitter over the duration of the experiment (when detection frequencies were binned into 6 hour periods). Once the SSDF for each 6 hour periods was calculated for individual control-transmitters the 6 hour binned detection frequencies of tagged *G. elevata* throughout the array as a whole were divided by the corresponding SSDF of the similar powered control-transmitter for the array at which the fish was tagged. Only fish that were

present within the array at the time the control tags were deployed had their detection frequencies examined. Corrected detection frequencies of individual fish binned into 6 hour intervals were plotted for the duration they were detected within the array.

5.2.8 Movement and abiotic variables

Weather conditions for the duration of the experiment were monitored at weather stations adjacent to each array (Bellambi: -34.3691, 150.9291 and Sydney -33.8607, 151.2050). Temperature loggers (HOBO pendant, Onset, Bourne, MA, USA) deployed at 3 m depth within each array recorded water temperature data.

For each array as a whole, corrected detection frequencies (SSDF) of nine fish from the two arrays (fish that were resident during the deployment periods of control-transmitters) were binned into 6 hour detection periods. A mean detection depths of each fish was also calculated for each 6 hour detection period. Corrected detection frequencies (SSDF) and detection depths were examined in relation to a number of abiotic variables specific to each array. Independent variables included diel index (expressed as a circular transform of hour-of-day calculated using the formula $5 \cdot \sin(0.2618 * h - 1.57)$, where h is the hour-of-day), wind speed, water temperature and tidal range. Parameters were standardised following the approach of Kleijnen (1997), and models were specified as first-order autoregressive to account for serial correlations in the data (Rogers and White, 2007). Explanatory variables were fitted using generalised least squares (nlme package, Pinheiro et al., 2012) in R v. 2.14.1 (R Development Core Team, 2012). Bayesian information criterion (BIC) was used to determine the most parsimonious model which provided the best fit.

5.3 Results

5.3.1 Recovery and transmitter retention trial

All *G. elevata* survived to the completion of the 8 month tag-retention experiment, with no obvious changes in fish behaviour apparent. Moreover, all 12 internal transmitters remained in the coelomic cavity to the completion of the experiment, with no sign of excretion. The incision made into the coelomic cavity was completely healed after <10 weeks and all sutures were expelled in <20 weeks. In total, 11 of the 12 external T-bar tags remained in the fish, with only 1 lost over the 8 month period.

5.3.2 General detection patterns

Over the 486 and 550 day study periods, a total of 10,211 and 16,081 acoustic detections of *G. elevata* were recorded at the North Sydney and Wollongong Arrays, respectively (Figure 5.2). In total, 18 of the 24 *G. elevata* implanted with acoustic transmitters provided useful data (i.e. >50 detections) to examine temporal patterns in detection frequency, depth utilisation and residency indices. Large variation was observed in detection periods of fish within the arrays. The minimum detection period (from first to last detection) within the array was 7 days, and the maximum was 550 days (the battery life of the transmitter; Table 5.1). Two fish were not detected within the arrays for more than 70 days after which they returned (Figure 5.2). Of the 24 *G. elevata* tagged with acoustic transmitters, five were still detected within the arrays at the completion of the studies (Figure 5.2).

5.3.3 Activity-space size

Girella elevata showed small activity-space sizes, with MCP measures ranging from 0.031 to 0.195 km^2 in the North Sydney Array and 0.031 to 0.218 km^2 in the Wollongong Array (Table 5.1). All fish displayed a single small region of habitat use within the rocky-reef at which they were tagged (Figure 5.3). No detections were recorded on receivers positioned on reefs immediately to the north and south of the tagging arrays or on receivers positioned intermittently along the coastline between the tagging arrays (Figure 5.1).

5.3.4 Residency

Large variability was observed among the residencies of individual *G. elevata.* Values of I_R-total for each array ranged from 0.55% to 67.21% in the North Sydney Array and from 0.55% to 84.91% in the Wollongong Array (Table 5.1). Fish generally showed the greatest residency at one or two receivers within each array (e.g. Fish 7, 19 and 20 in Figure 5.3). One fish from the Wollongong Array showed high I_R (I_R>10%) values at four stations within the array (Fish 5 in Figure 5.3). Approximately half of all fish within each array showed low I_R values (I_R<10%) at all stations at which they were detected (e.g. Fish 6 and 16 in Figure 5.3). The residency of 18 *G. elevata* tagged is shown in the Appendix (Figure A.5).

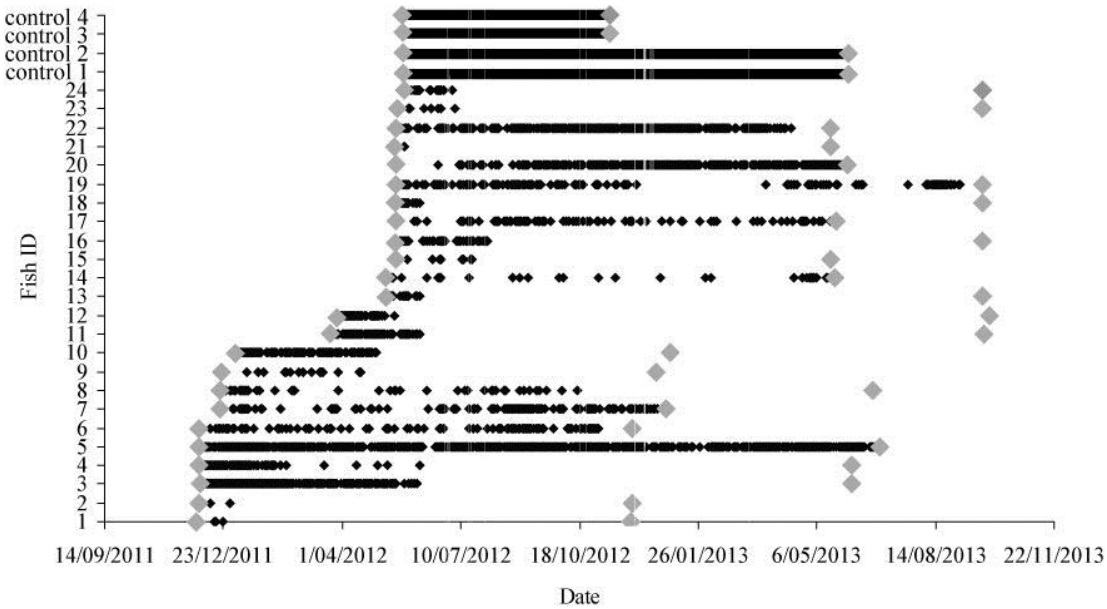

Figure 5.2 Raw temporal detections of *Girella elevata* surgically implanted with acoustic transmitters within the North Sydney Array (fish IDs 13 – 24) and Wollongong Array (fish IDs 1-12). Temporal detections of control-transmitters are also displayed (control 1: Wollongong 150 dB, control 2: Wollongong 159 dB, control 3: North Sydney 150 dB, control 4: North Sydney 159 dB). Grey diamonds indicate release or deployment dates and transmitter expiration or study conclusion dates.

Table 5.1 Biological and tagging details of the 24 *Girella elevata* surgically implanted with acoustic transmitters in the North Sydney and Wollongong Arrays. FL = fork length, potential detection days = release date to conclusion of study, detection period = days from release date to last detection, number of receivers = the number of receivers a fish was detected at within the array, I_R - total = residency index to the array as a whole, MCP = minimum convex polygon and activity-space size.

Array	Fish ID	FL (cm)	Transmitter	Release date	tag expiry	Capture/ release site	Last detection	Potential detection days	Total detections	Detection period (days)	Days detected	Number of receivers	MCP (km^2)	I_R - total
Wollongong	1	29.7	V9TP	30/11/2011	30/11/2012	CS2	16/12/2011	366	6	16	3	3	0.067	0.820
Wollongong	2	30	V9TP	2/12/2011	2/12/2012	CS2	28/12/2011	366	3	26	2	1	0.031	0.546
Wollongong	3	39.9	V13TP	2/12/2011	4/06/2013	CS2	3/06/2012	550	2358	184	151	7	0.194	27.455
Wollongong	4	36.4	V13TP	2/12/2011	4/06/2013	CS2	5/06/2012	550	366	186	58	3	0.095	10.545
Wollongong	5	44.7	V13TP	2/12/2011	4/06/2013	CS2	4/06/2013	550	8271	550	467	7	0.191	84.909
Wollongong	6	31	V9TP	2/12/2011	2/12/2012	CS2	3/11/2012	366	492	337	93	7	0.191	25.410
Wollongong	7	29.6	V9TP	20/12/2011	20/12/2012	CS2	20/12/2012	366	432	366	117	4	0.099	31.967
Wollongong	8	43.4	V13TP	20/12/2011	22/06/2013	CS2	19/09/2012	550	120	274	47	3	0.125	8.545
Wollongong	9	27.4	V9TP	21/12/2011	21/12/2012	CS2	14/03/2012	366	21	84	15	2	0.035	4.098
Wollongong	10	29.6	V9TP	3/01/2012	3/01/2013	CS2	30/04/2012	366	392	118	85	4	0.095	23.224
Wollongong	11	37	V13TP	23/03/2012	24/09/2013	CS1	3/06/2012	462	3439	72	60	7	0.178	12.987

Table 5.1 continued.

Wollongong	12	37.5	V13TP	28/03/2012	29/09/2013	CS2	15/05/2012	457	181	48	35	8	0.218	7.659
Nth Sydney	13	39	V13TP	8/05/2012	9/11/2013	CS5	5/06/2012	416	374	28	13	2	0.091	3.125
Nth Sydney	14	30.6	V9TP	8/05/2012	9/05/2013	CS5	9/05/2013	366	57	366	31	3	0.091	8.470
Nth Sydney	15	30.7	V9TP	16/05/2012	17/05/2013	CS5	19/07/2012	366	11	64	9	2	0.091	2.459
Nth Sydney	16	38.6	V13TP	16/05/2012	17/11/2013	CS5	1/08/2012	408	668	77	44	4	0.195	10.784
Nth Sydney	17	30.3	V9TP	16/05/2012	17/05/2013	CS5	17/05/2013	366	172	366	80	4	0.150	21.858
Nth Sydney	18	38.1	V13TP	16/05/2012	17/11/2013	CS5	5/06/2012	408	86	20	12	2	0.069	2.941
Nth Sydney	19	41	V13TP	16/05/2012	17/11/2013	CS5	4/09/2013	408	1146	476	132	4	0.150	32.353
Nth Sydney	20	30.5	V9TP	16/05/2012	17/05/2013	CS3	17/05/2013	366	3945	366	245	3	0.100	66.940
Nth Sydney	21	30.6	V9TP	16/05/2012	17/05/2013	CS3	23/05/2012	366	7	7	2	1	0.031	0.546
Nth Sydney	22	30.1	V9TP	16/05/2012	17/05/2013	CS3	14/04/2013	366	3637	333	246	3	0.100	67.213
Nth Sydney	23	36.7	V13TP	17/05/2012	18/11/2013	CS4	5/07/2012	407	16	49	7	3	0.126	1.720
Nth Sydney	24	40.9	V13TP	24/05/2012	25/11/2013	CS6	2/07/2012	400	92	39	18	4	0.150	4.500

5.3.5 Depth utilisation

The depth range used by *G. elevata* tagged within the North Sydney Array ranged from 0.4 to 11.4 m ± 2.5 m, whereas those in the Wollongong Array ranged from 0.4 to 16.9 m ± 2.5 m (Figure 5.4). Fifteen *G. elevata* showed a uni-modal pattern in detection depth, with the majority of fish being generally detected at 2 – 4 m depth (e.g. Fish 3 in Figure 5.4). However one fish from each array (Fish 8 and 16) was most commonly detected at 6 – 7 m depth (e.g. Fish 16 in Figure 5.4). In contrast to the general trend of uni-modal depth utilisation, three fish (Fish 5, 6 and 18) showed a bi-modal pattern in depth utilisation with the majority of detections at 2 – 3 and 9 – 10 m depth (e.g. Fish 6 in Figure 5.4). The detection depth of *G. elevata* in relation to a number of environmental variables is described in section 5.3.7 below. The depth utilisation of 18 *G. elevata* tagged is shown in the Appendix (Figure A.6).

5.3.6 Standardisation of detection frequencies

Within the Wollongong Arrays the detection frequency of control-transmitters showed a diurnal pattern, markedly dropping at sunset then abruptly increasing with the onset of sunrise (Figure 5.5). The magnitude of the variation between day and night control-transmitter detection frequencies was less apparent within the North Sydney Array (Figure 5.5). Similarly, the magnitude of variation in detection frequency between the two power-output control-transmitters (150 and 159 dB) was greater within the Wollongong Array (Figure 5.5). Large variability was observed in the corrected detection frequencies of *G. elevata* over the diel cycle (Figure 5.5); however, the majority of fish within both the Wollongong and North Sydney Arrays displayed a distinct day/night pattern in their corrected detection frequencies with higher detection

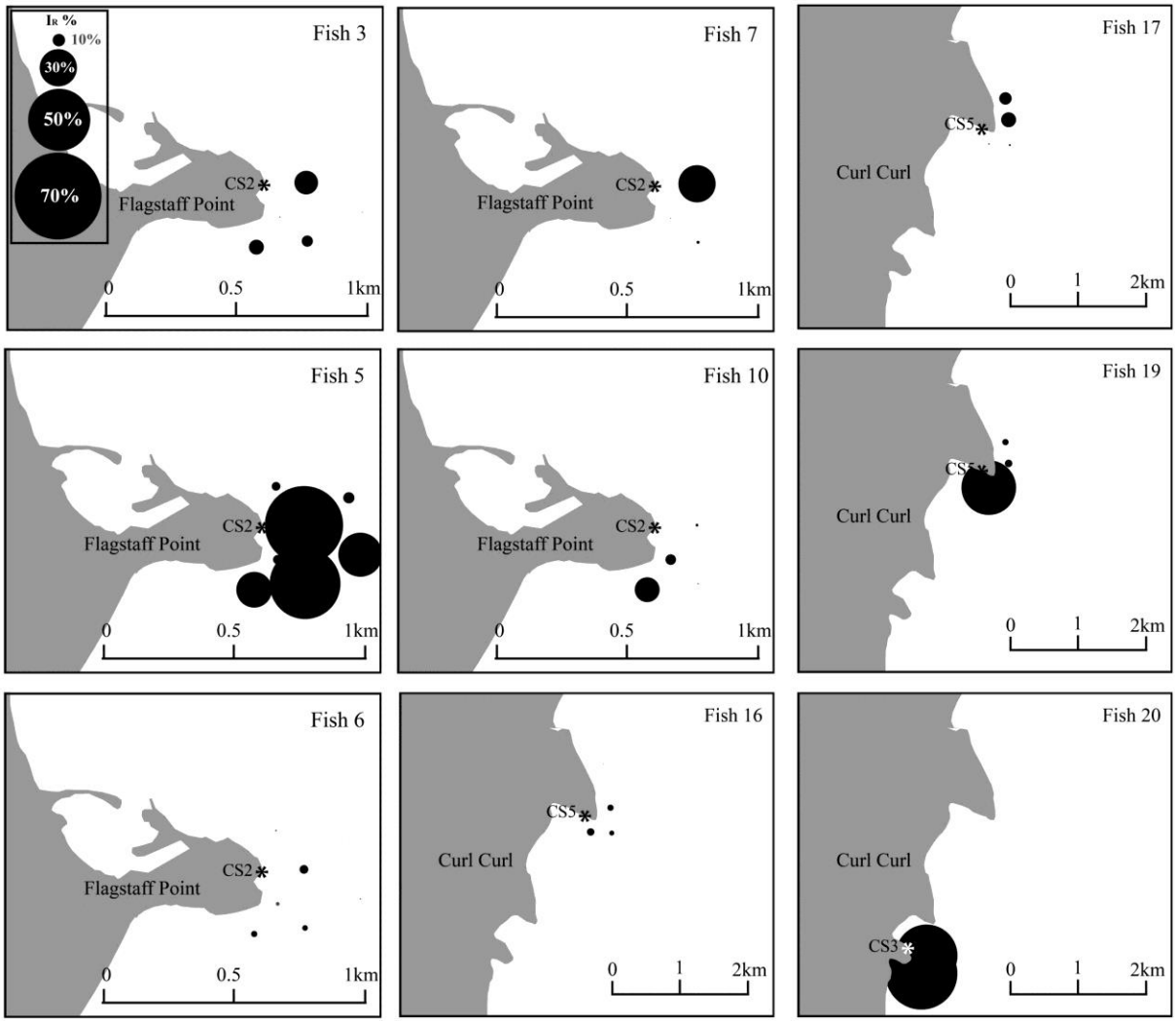

Figure 5.3 Residency index (I_R) by receiver of nine *Girella elevata* tagged with acoustic transmitters within the Wollongong Array (fish IDs 3 – 10) and North Sydney Array (fish IDs 16 – 20). Filled circles display IR values. Representative fish for different patterns in residency and habitat use are displayed.

frequencies observed during the day (e.g. Fish 3, 6, 10 and 22 in Figure 5.5). Of the 15 fish that displayed increased detections during daylight hours, one fish displayed increases in detection frequencies at sunrise and sunset (Fish 10 in Figure 5.5), while 2 fish displayed increases in detection frequencies at sunrise only (Fish 3 and 6 in Figure 5.5). There were three notable exceptions to this general trend of increased daylight detections, with one fish within each array (Fish 11 and 16) displaying increased detections at night (e.g. Fish 11in Figure 5.5) and one fish from the North Sydney Array displaying little variation between day and night detection frequencies (Fish 19 in Figure 5.5). The diel detection frequency of 18 *G. elevata* tagged is shown in the Appendix (Figure A.7). When examined throughout the duration of the experiment control-transmitters deployed within the Wollongong and North Sydney Arrays showed large temporal variation in detection frequency (Figure 5.6). Within the Wollongong Array, a peak in detection frequency of both the 150- and 159-dB control-transmitters was observed in August, although this variation was less apparent in the North Sydney Array (Figure 5.6).

5.3.7 Habitat usage and abiotic variables

Regression models indicated significant relationships between the abiotic variables and both SSDF and detection depth (Table 5.2). The best model indicated that SSDF positively correlated with diel index ($\beta = 0.114$; $t = 22.293$; $P < 0.001$), confirming that standardised detection frequency was elevated during daylight hours. Mean detection depths did not correlate with diel index, although few depth recordings were recorded at night (0:00 – 5:59 n=41; 6:00 – 11:59 n=349; 12:00 – 17:59 n=347, and; 18:00 – 23:59 n=15). However, there was a significant positive relationship with wind speed (β =

0.038; t = 3.932; P <0.001), indicating that during periods of high wind speed, fish were more likely to be found at greater depths.

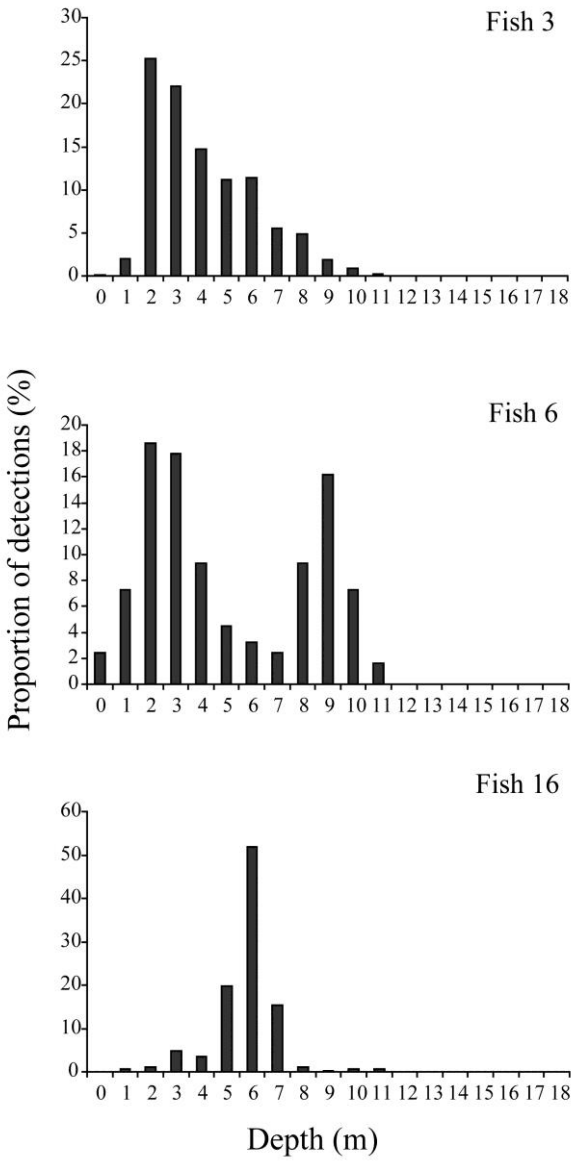

Figure 5.4 Percentage of detections in 1 m depth intervals of *Girella elevata* tagged with depth-sensing acoustic transmitters within the Wollongong Array (fish IDs 3 and 6) and North Sydney Array (fish ID 16). Three characteristic depth-utilisation behaviours are displayed.

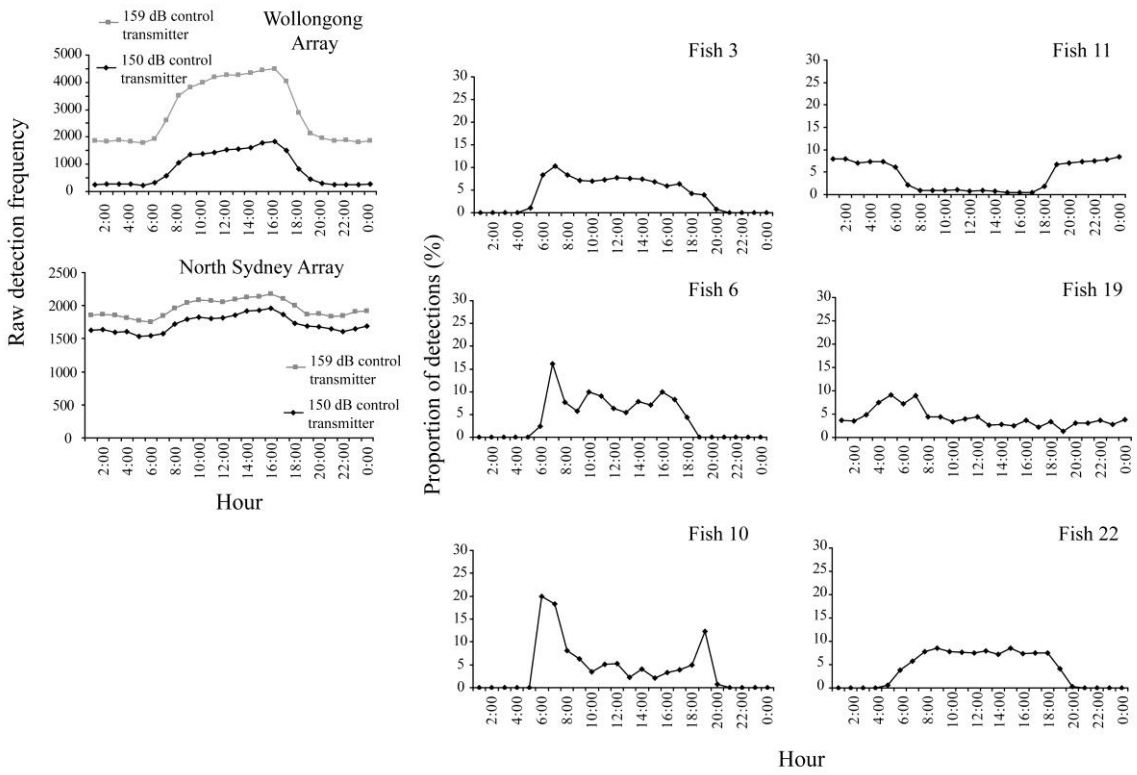

Figure 5.5 Diel detection frequency of 150 and 159dB control-transmitters and standardised detection frequencies of *Girella elevata* in hourly time bins for the Wollongong Array (fish IDs 3 – 11) and North Sydney Array (fish IDs 19 and 22). Representative fish for the different patterns in diel detections are displayed.

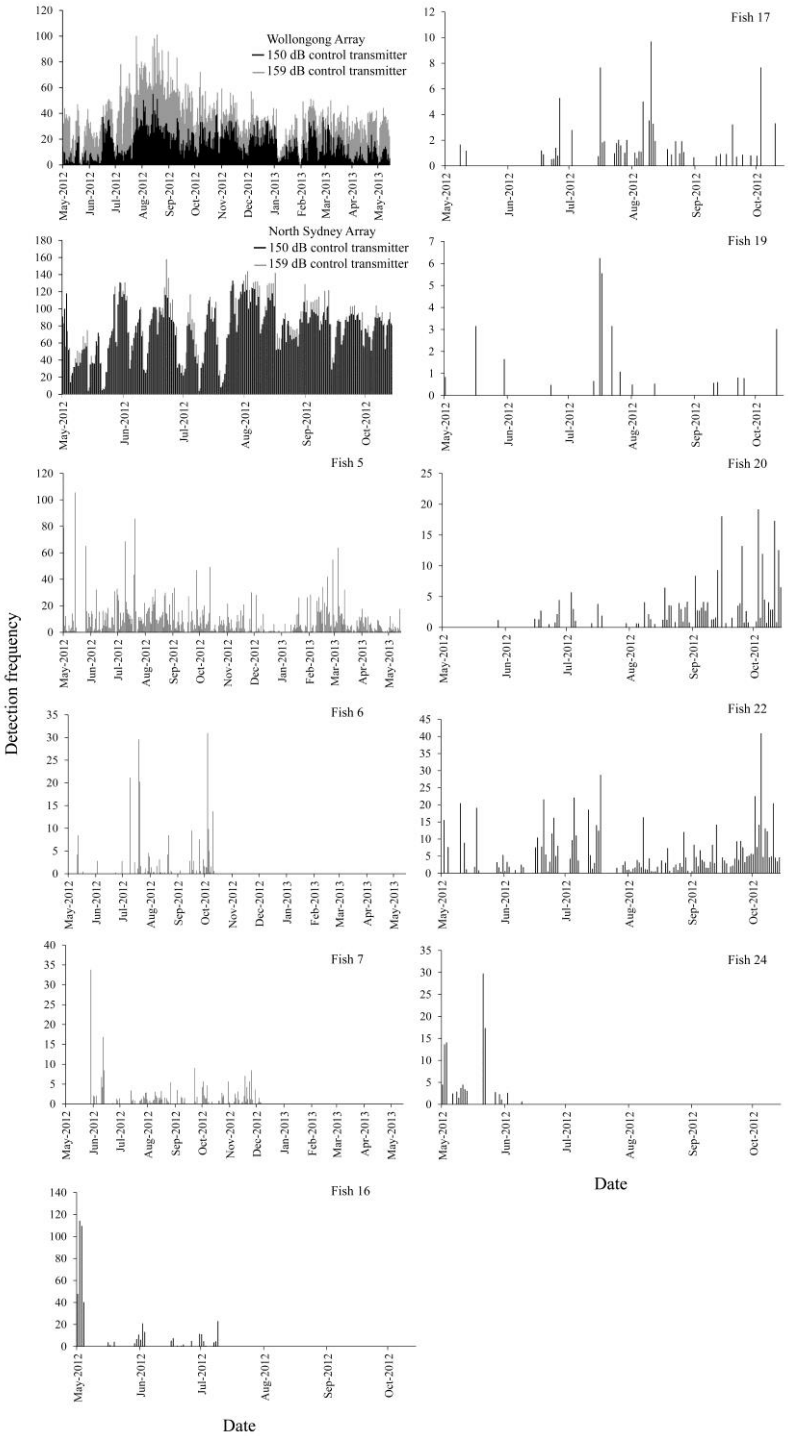

Figure 5.6 Six-hourly binned standardised sentinel detection frequency(SSDF) corrected detection frequencies of *Girella elevata* and control-transmitter detection frequencies within the Wollongong Array (fish IDs 5 – 7) and North Sydney Array (fish IDs 16 – 24).

Table 5.2 Details of full and best models (on the basis of Bayesian information criterion, BIC) constructed to estimate the influence of standardised variables on standardised sentinel detection frequency (SSDF), and detection depth.

Full model					Best model				
Parameter	*β*	*SE*	*t*-value	P-value	Parameter	*β*	*SE*	*t*-value	P-value
SSDF (BIC = 3256, φ = 0.573)					*SSDF* (BIC = 3234, φ = 0.557)				
Diel index	0.116	0.006	18.815	<0.001	Diel index	0.114	0.005	22.294	<0.001
Wind speed	-0.004	0.021	-0.175	0.860					
Water temperature	-0.035	0.051	-0.676	0.499					
Tidal range	-0.028	0.017	-1.749	0.080					
Detection depth (BIC = -933, φ = 0.937)					*Detection depth* (BIC = -950, φ = 0.936)				
Diel index	-0.007	0.006	-1.052	0.293	Wind speed	0.038	0.009	3.932	<0.001
Wind speed	0.046	0.011	4.061	<0.001					
Water temperature	-0.008	0.035	-0.241	0.809					
Tidal range	-0.006	0.009	-0.647	0.518					

~ First-order autocorrelation parameter

5.4 Discussion

5.4.1 Movements, residency and activity-space size

A population of fish can be comprised of both migrant and resident individuals (Lindholm et al., 2007). The data collected in the present study indicated that this may be the case for *G. elevata* within our study region at the temporal scales examined. Several fish left the arrays early in the experiment not to return, others returned to the array after extended periods of absence, whereas several fish continued to be detected within the array for the majority of the experiment. The majority of fish, however, showed high detection periods (>100 days) within the arrays. Interestingly, none of the fish that left the main arrays were detected on the adjacent reef systems or the intermittently positioned coastal receivers between the two arrays. There are several possible explanations for this, including: 1) Fish are non-migratory; however, the array may not have encompassed the entire home range of an individual, despite attempts to cover all available habitat at each rocky-reef; 2) At the temporal scale examined, a proportion of the population is migratory, though fish may not necessarily use a migration corridor that comprises near shore habitats covered by receiver stations, and; 3) The loss of detections of some fish within the arrays may have been a result of natural or recreational fishing mortality. All fish were externally tagged and signs were strategically positioned on the rock platforms adjacent to the arrays requesting recreational anglers to report re-captures. Four recaptures were reported during the course of the study (all of which were returned directly to the water), although unreported catches and natural mortality remain a possibility.

The small activity-space size of *G. elevata* (0.03 – 0.22 km^2) observed within each of the arrays is comparable to that of other near-shore temperate-reef marine teleosts (Lowry and Suthers, 1998, Bryars et al., 2012, Ferguson et al., 2013, Lee et al. 2014). However, estimates of activity-space size made from this study may be underestimates of the actual home range size. Although the arrays were designed to cover the majority of available habitat at each rocky-reef it is possible that fish may utilise regions outside the coverage of the array. All fish displayed a single small region of habitat use within each array, although several fish did show bimodal patterns in depth utilisation. These data support the observations of earlier studies that suggested that distribution and abundances of *G. elevata* are habitat dependent (Kingsford, 2002, Curley, 2007).

Despite the close proximity of suitable habitat to the tagging locations within the North Sydney Array, no movement of *G. elevata* was recorded between the adjacent reef systems within the array. The absence of movement between adjacent reef systems may be due to the advantages that are associated with habitat familiarity, including known foraging grounds (Warburton, 2003) and predator refuge sites (Forrester and Steele, 2004), that in turn may result in reduced energy expenditure, increased fitness and reduced mortality. Juvenile *G. elevata* of intertidal rock platforms showed a strong homing tendency to their original rockpool after experimental displacement (Griffiths, 2003a). Griffiths (2003a) proposed that the species remains within a restricted location for much of its life, using the same rockpool for up to 2 years until it reaches 90 – 100 mm FL, before moving to adjacent deeper subtidal waters. The spatial scales of movement identified by earlier tag recapture programmes suggest that *G. elevata* is a sedentary species, with both juveniles and adults moving within contiguous reef habitats at spatial scales of <1 km (Wilson, 1984, Griffiths, 2003a). Beaches between rocky

reefs within the North Sydney array may therefore dissect contiguous reef habitat and act as potential barriers to the movement of *G. elevata* to adjacent habitats. Similarly, the eastern blue groper, *Achoerodus viridis*, that utilises the same near-shore habitat as *G. elevata* exhibited high residency periods, small home ranges and no movement to adjacent reefs separated by sandy beaches (Lee et al., 2014).

This is one of few spatially replicated acoustic-tracking studies, although this study focused on the movement of fish from the centre of the species latitudinal distribution. *Girella elevata* from the northern and southern regions of the species latitudinal distribution may display different patterns in their movements and habitat affinities as a result of varying responses to latitudinal clines in biotic and abiotic variables. Observations of latitudinal variation in the size (Stocks et al., 2015) and age (Stocks et al., 2014a) structure of *G. elevata* have provided evidence to support larger-scale movements than those identified in the present study. The presence of exclusively mature *G. elevata* within the north of the species distribution suggests the potential migration of a portion of the population to the north (Stocks et al., 2015, Stocks et al., 2014a). This may be a larval dispersal strategy utilised by a number of south-eastern Australian invertebrates (Montgomery, 1990, Stewart and Kennelly, 1998) and teleosts (Stewart et al., 2011, Gray et al., 2012, Miller and Stewart, 2013) that use the strong southward moving East Australian Current to deliver larvae to increased latitudes. Further studies examining the movement patterns throughout the species latitudinal distribution would provide more information on latitudinal interactions and connectivity between populations.

5.4.3 Habitat use and behavioural strategies

Large temporal variation in detection frequencies of control-transmitters within the two arrays, and as identified in the range-test experiment (Stocks et al., 2014b), meant that detection frequency data could not be interpreted without standardisation (Payne et al., 2010). Following the standardisation of the data, the majority of fish displayed increased detections during daylight hours. This may reflect diurnal activity patterns on the basis of the assumption that increases in detection frequencies are associated with increases in activity. Similar diel patterns in detection frequencies have been observed in other temperate-reef teleosts (Bryars et al., 2012, Ferguson et al., 2013) and have been attributed to nocturnal sheltering and predator avoidance. Generalisations of diel variation in activity patterns have been associated with trophic level and feeding strategies (Helfman, 1986), with herbivores generally grazing by day (Choat and Clements, 1993). Increased detections of the herbivorous *G. elevata* during daylight hours may be associated with the need for vision when selectively grazing macrophyte beds (Stocks et al., unpubl. data) or an adaptation to diurnal variation in algal quality (Taborsky and Limberger, 1980, Polunin and Klumpp, 1989). The consistent movement of fish outside the array to deeper waters at night is unlikely, because no diel patterns in depth utilisation were recorded. Despite this general diurnal activity, two fish did display increased detections at night relative to the day. It is unclear whether these fish displayed nocturnal behaviour or if the cave or crevice that these fish used at night was orientated in such a way that it allowed for the successful detection of acoustic transmissions.

The positive relationship between detection depth of *G. elevata* and wind speed is likely to be due to the unfavourable conditions for *G. elevata* on near-shore coastal reefs

during periods of high wind. Other abiotic conditions correlated with increased winds include elevated wave height and reduced visibility (quantitatively assessed and inferred respectively). *G. elevata* appears to move to deeper habitat within its small activity-space to escape these adverse conditions. Bimodal patterns in depth utilisation observed for several *G. elevata* indicated that two distinct regions may be used within a small activity-space for feeding and refuge or under different environmental conditions. The zonation and community structure of wave-exposed marine communities can be influenced by physical disturbances in the form of water turbulence as a result of wind and wave action (Romer, 1990, Friedlander et al., 2003). In many studies, species abundance and diversity have been shown to decrease with wave exposure (Romer, 1990, Friedlander et al., 2003). Other studies have also suggested that fish may move to deeper water in adverse conditions (Cheal et al., 2002) or may have biomechanical adaptations (i.e. swimming modes) that provide energetic advantages and allow them to inhabit regions with high levels of water motion (Fulton and Bellwood, 2005).

5.4.6 Marine protected areas

The present study adds to a body of recent work aimed at understanding the biology, ecology and fishery of Girellidae (Gray et al., 2010, Gray et al., 2012, Ferguson et al., 2013, Stocks et al., 2014a). For *G. elevata*, life-history traits of longevity (>45 years), slow growth, late maturation (7 year for males and 9 years for females from the southern distribution), restricted activity-space, and high residency potentially make populations vulnerable to the localised depletion of larger individuals (Stocks et al., 2014a, Stocks et al., in press). Catch data indicated that Girellidae represent the greatest proportion of fish captured by recreational fishermen from rock platforms in New South

Wales, constituting up to 47% of seasonal catches (Kingsford et al., 1991). Furthermore, *G. elevata* was the third most commonly speared species (first in terms of biomass) in recreational spearfishing competitions in south-eastern Australia (Lincoln Smith et al., 1989).

The protection of spawning sites of a population is a key aspect for the sustainable management of a species (Lindeman et al., 2000, Claydon, 2004). Gravid individuals with hydrated oocytes have been collected from near-shore shallow rocky-reefs (Stocks et al., 2015). Further studies examining the early life stages of larvae, including mechanisms of dispersal and larval drifting periods are required to assess population connectivity, and the utility of larval seeding from MPAs (Christie et al., 2010). Given the small activity-space sizes and strong residency of a proportion of tagged individuals, resident populations of *G. elevata* would likely show a positive response to the protection provided by adequately sized and appropriately positioned no-take MPAs. However, the spatial utilisation of *G. elevata* is strongly habitat dependent, primarily associated with complex boulder and crevice habitat and wash zones that provide refuge and feeding grounds (Kingsford, 2002, Curley, 2007). For *G. elevata* to benefit from no-take MPAs, zoning arrangements must incorporate such critical habitat. Studies by Curley et al. (2013 a) found no evidence of an increase in size or abundance of *G. elevata* within a 0.1 km^2 partially protected MPA in Sydney. This was partly attributed to lack of protection of known aggregation sites which occurred on the boundary of the MPA. Other factors including the level of fishing effort and the associated effects on the population, should also be assessed to determine whether the implementation of no-take MPAs are advantageous to the sustainability of local populations.

Chapter 6: Key findings, management implications and future research

6.1 Latitudinal gradients in life-history characteristics in the context of climate and oceanographic variability

Assessing and predicting changes to the population productivity of a species as a result of alterations to climate and oceanographic conditions is of particular importance to the sustainable management of a fishery. Life-history traits of growth and reproduction are largely responsible for the productivity of a population (Campana, 2001, Morgan and Brattey, 2005). Temperature is the primary variable affecting the metabolic function of species and hence a species growth rates and reproductive fitness. Typically, the energy allocation towards growth and reproduction declines at temperatures near the range extremes (Roessig et al., 2004). Therefore, examining variation in life-history characteristics throughout a species' latitudinal distribution may shed light on expected changes associated with both basin- and decadal-scale climate and oceanographic shifts (Stocks et al., 2014a, Stocks et al., 2015).

Recent decades have seen rates of ocean warming of coastal south-east Australia exceed ~3-4 times that of the global average (Matear et al., 2013), giving rise to the region's distinction as a 'hotspot' for climate induced environmental change (Booth et al., 2011, Byrne et al., 2011). Such warming is attributed to the strengthening of the southward-flowing EAC and associated incursions of warmer waters to increased latitudes. The expected strengthening and southern migration of the EAC (Cai et al., 2005) is likely to

significantly affect marine ecosystems within this region (Suthers et al., 2011). The identification of latitudinal gradients in *G. elevata* reproductive fitness and both latitudinal and temporal variation in growth, and associations with temperature, provide evidence that the expected changes to climate and oceanographic conditions in south-east Australia will likely alter the productivity of *G. elevata* populations. In turn, latitudinal changes in the abundance, distribution and demographic traits of *G. elevata* could impact marine benthic ecosystems through changes in overall levels of consumption of algae by this herbivorous species though further studies are required. Indeed, recent research suggests that poleward shifts in the distribution of herbivorous fishes are already impacting benthic communities and in some instances leading to the overgrazing of algal beds and the creation of urchin-grazed barrens habitat (Vergés et al., 2014a; Vergés et al., 2014b).

Both latitudinal and temporal variation in the growth of *G. elevata* was observed. In regards to temporal variation in growth, *G. elevata* showed a significant positive relationship with the SOI, a common measure of the ENSO phenomenon. The ENSO phenomenon is a natural inter-annual oceanographic perturbation of the South Pacific. In eastern Australia, La Niña brings increased rainfall and warmer ocean temperatures while El Niño is characterised by a reduction in winter and spring rainfall and cooler ocean temperatures (Stone and Auliciems, 1992). Despite decreased growth in cooler El Niño years, latitudinal variation in *G. elevata* growth did not reflect a simple positive relationship with water temperature. Fish from intermediate water temperatures of the Central Region exhibited the highest growth rates. In contrast, warmer waters of the Northern Region resulted in the slowest growth rates. The expected strengthening of the EAC and incursions of warmer water to increased latitudes will likely result in

alterations to *G. elevata* growth rates, however predicting the response of *G. elevata* to such changes is difficult. It is apparent that latitudinal variation in *G. elevata* growth cannot be simply predicted by gradients in water temperature but likely is a complex intermixing of thermal habitat windows (Righton et al., 2010, Neuheimer et al., 2011), resource limitation (Persson et al., 2000), energy allocation and trade-offs among other life-history traits (Vila-Gispert et al., 2002, Morgan et al., 2010).

Similarly, latitudinal variation was also observed in the reproductive biology of *G. elevata*. *Girella elevata* from the cooler Southern Region matured at a greater size (L_F) and age than those from the Central Region. This variation in maturation may also be attributed to a number of factors including thermal habitat windows (Righton et al., 2010, Neuheimer et al., 2011), resource limitation (Persson et al., 2000), energy allocation and trade-offs among other life-history traits (Vila-Gispert et al., 2002, Morgan et al., 2010). Fish from warmer waters have been shown to mature at younger ages and smaller sizes than their conspecifics from colder waters (Morgan and Colbourne, 1999, Heibo et al., 2005). Alternatively, life-history traits of a species are often correlated (Heibo et al., 2005), consequently variation in maturation may be a result of trade-offs with growth, or other reproductive features such as fecundity and/or oocyte size (Fleming and Gross, 1990, Lappalainen et al., 2008). Notably, *G. elevata* displayed earlier maturation within the Central Region where fish were characterised by higher growth rates (Chapter 2, Stocks et al., 2014a) and lower fecundity (Chapter 3, Stocks et al., 2015). This is consistent with findings for other teleosts where earlier maturation has been associated with higher growth rates (Alm, 1959, Morgan and Colbourne, 1999, Haugen, 2000).

Girella elevata exhibited latitudinal variation in relative fecundity (F_R). Fish of the Northern and Southern Regions had significantly greater fecundity than those of the Central Region, though no differences were observed between the Northern and Southern Region. Results indicate an inverse relationship between growth and F_R. *Girella elevata* of the Central Region exhibited the highest growth rates though fish of this region also had the lowest F_R. Yoneda and Wright (2005) attribute the negative correlation between somatic growth and oocyte development to varying energy allocation. Environmental variables may also be responsible for latitudinal clines in fitness (Wootton, 1990). Processes through which temperature can influence reproductive performance include hormone synthesis, metabolic rates and gametogenesis (Pankhurst, 1997). The identification of latitudinal clines in reproductive characteristics and the non-linear associations of fecundity with water temperature provide evidence that the southern extensions of the EAC and the poleward advancements in isotherms will likely result in alterations to the latitudinal variation in *G. elevata* reproductive fitness.

The southern extensions of the EAC and the poleward advancements in isotherms may be responsible for the recent southward shifts in the range limits and abundance increases of *G. elevata* (Last et al., 2011). Shifts in the geographical distribution of a species in response to climate change are generally most evident at the northern and southern extremities of the population, where warming and cooling drives species to higher or lower latitudes (Portner and Peck, 2010). Recent observations of gravid *G. elevata* as far as 40°S (Last et al., 2011) may be a result of a combination of the poleward migration of isotherm providing appropriate temperatures for *G. elevata*

survival and/or increased larval dispersal due to the extension of the EAC into Tasman waters.

From this study latitudinal variation in the size and age structure of *G. elevata* was observed. No newly recruited or juvenile *G. elevata* were sampled within the northern range limits of the species distribution (Chapter 2 and 3). This absence may be attributed to: 1) Limited juvenile habitat availability: although not quantitatively assessed, rocky headlands within the Northern Region were generally observed to be steeper with fewer rockpools containing cover for juvenile *G. elevata,* and/or; 2) Sampling biases: unlike juveniles in the Central and Southern Regions that recruit to rockpools, juveniles in the Northern Region may be recruiting to alternate habitats that were not sampled (e.g. the entrance of estuaries).Two alternate hypotheses involving the EAC are proposed to explain their absence and predictions based on expected shifts in the EAC:

Hypothesis 1) the poor recruitment of juveniles in the northern portion of the population is a result of larval drift. In Queensland and northern NSW (the northern range limits of *G. elevata*) the intensification of the EAC and flow close to the coastline may entrain drifting larvae and disperse them south with little larval replenishment from the north. Furthermore the separation of the EAC from the coast at 31°S (Ridgway and Dunn, 2003) may result in the seaward loss of larvae. Girellidae larvae have been caught during summer surface and sub-surface ichthyoplankton trawls at the frontal regions (30 – 32°S) where the EAC separates from the coast (Syahailatua et al., 2011). The EAC has been illustrated as a mechanism to maintain coastal connectivity of populations or act as a barrier where it separates from the coast (Cresswell et al., 1983, Condie et al.,

2011, Roughan et al., 2011, Suthers et al., 2011). Larval dispersal models may provide further support for this hypothesis (Roughan et al., 2011).

Hypothesis 2) higher water temperatures of the northern region due to the delivery of warm Coral Sea water by the EAC is beyond the thermal tolerance of early *G. elevata* life stages. Studies examining the thermal tolerance windows of species at multiple levels of ontogenetic development indicate thermal windows are narrow in early life stages due to development constraints and insufficient capacity of organs in the larvae (Portner et al., 2006, Portner and Peck, 2010).

The *G. elevata* population in the Northern Region may be replenished by a migrating portion of the population from the south rather than localised juvenile recruitment. The northern migration with ontogenetic development is a common life-history strategy of coastal south-east Australian marine invertebrates (Montgomery, 1990, Stewart and Kennelly, 1998) and teleosts (Stewart et al., 2011, Miller and Stewart, 2013) that utilise the southward flowing EAC to deliver larvae to higher latitudes (Gray et al., 2012).

Irrespective of the mechanisms responsible for the absence of newly recruited and juvenile *G. elevata* in the northern region, the expected strengthening and poleward extension of the EAC (Cai et al., 2005) will likely result in alterations to the latitudinal distribution of these early life stages. At lower latitudes a range contraction of juveniles is proposed while poleward extensions in the distribution of *G. elevata* are expected at increased latitudes, each due to poleward advancements in isotherms and the strengthening of larval dispersing currents.

6.2 The spatial ecology of *G. elevata* and near-shore coastal acoustic telemetry

Acoustic telemetry was employed to examine the movement and habitat use of *G. elevata* and assess the potential for localised depletion, the effectiveness of MPAs and to further understand the latitudinal interactions of *G. elevata* populations. Measures of residency and movement of *G. elevata* suggested that at the temporal scale examined the species may be comprised of both migrant and resident individuals. A number of fish left the arrays early in the experiment not to return, others returned to the array after extended periods of absence, while a number of fish continued to be detected within the array for the duration of the experiment. The majority of fish, however, showed high detection periods (>100 days) within the arrays. Each fish also displayed a small activity-space size (0.03 – 0.22 km^2) within the arrays. In order to obtain these fine-scale estimates of activity space size, range testing of acoustic equipment forms an essential component in home range and habitat association studies. Knowledge of acoustic equipment performance improves habitat coverage and reduced costs of array deployments by appropriate receiver spacing (Stocks et al., 2014b, Payne et al., 2010).

Depth sensing acoustic transmitters and detection frequency data provided additional information to examine the behaviour and habitat use of *G. elevata*. Statistical modelling indicates *G. elevata* appears to move to deeper habitat within their small activity-space to escape periods of adverse conditions. Bimodal pattern in depth utilisation of a number of fish also support this hypothesis. A study by Cheal et al. (2002) also suggested that fish may move to deeper water in adverse conditions. The majority of *G. elevata* displayed increased detections during daylight hours. This may reflect diurnal activity patterns based on the assumption that increases in detection

frequencies are associated with increases in activity. However, caution should be taken when using detection frequency data to infer fish behaviour. In this instance the detection frequency data of fish was standardised using control transmitters to account for the influence of environmental variables on detection frequency. Significant relationships between detection frequency and various environmental variables demonstrated the potential bias involved in using the detection frequency of acoustic data to infer animal behaviour in the absence of adequate site-specific knowledge of the performance of the acoustic equipment (Chapter 4, Payne et al., 2010, Stocks et al., 2014b). *In situ* range-testing used for the initial array design, coupled with control-transmitters (Payne et al., 2010, Topping and Szedlmayer, 2011, How and Lestang, 2012), are essential to the validity of assumptions made based upon detection frequency data.

Information on the spatial ecology of fish is often collected to contribute to the effective design of MPAs (Bryars et al., 2012; Ferguson et al., 2013; Lee et al., 2014). Associations between MPA size and efficacy is an area of particular interest when designing MPAs (Halpern, 2003). Species specific effects of reserve size are likely to vary due to distinctive behaviours and spatial metrics of habitat use. If the goal of a MPA is to protect vulnerable resident fish species, an understanding of the target species' spatial metrics of habitat use is integral to the success of the reserve. The size of the reserve relative to fish home range size will influence the degree of protection provided to resident fish (Kramer and Chapman, 1999). An effective reserve should increase a species biomass and abundance, consequently increasing egg production. Adjacent fisheries should in time benefit through the emigration of fish as a result of

density dependent spillover (Abesamis and Russ, 2005) and dispersal of offspring with ocean currents (Roberts, 1997, Christie et al., 2010).

A positive response to the protection provided by MPAs has been observed in a multitude of sedentary species (Bohnsack, 1998). However positive impacts of MPAs are not restricted to sedentary species. MPAs may provide short-term refugia for highly mobile species provided they encompass preferred feeding and spawning sites (Apostolaki et al., 2002). Data from two acoustic arrays deployed for the current study (Chapter 5, Stocks et al., in press) showed the largest activity-space size of an individual *G. elevata* was 0.22 km^2. Although the acoustic arrays were designed to cover the majority of available habitat at each rocky-reef it is possible that fish may have used regions outside the coverage of the array or offshore reefs. Estimates of activity-space size made from this study may therefore be underestimates of actual home range size. However, given the small activity-space sizes and strong residency of a proportion of tagged individuals, small (~0.22 km^2) MPAs would provide considerable protection for resident populations of *G. elevata*. Similarly, Lee et al., (2014) indicates that small MPAs can provide effective protection for adult eastern blue groper, *Achoerodus viridis*, which utilises the same near-shore habitat as *G. elevata*. However, the spatial use by *G. elevata* is strongly habitat dependent, primarily associated with complex boulder and crevice habitat and wash zones that provide refuge and feeding grounds (Kingsford, 2002, Curley, 2007). For *G. elevata* to benefit from no-take MPAs, zoning arrangements must incorporate such critical habitat. Other factors including the level of fishing effort and the associated impacts on the population should also be assessed to determine if the implementation of no-take MPAs are advantageous to the sustainability of local populations.

6.3 Management recommendations

The development of biologically informed management strategies for a species is dependent upon knowledge of key life-history characteristics (Adkison, 2009). Traditional management strategies such as minimum legal lengths are often based upon knowledge of a species length at sexual maturity. The development of MPAs is an additional management strategy where the efficacy is dependent upon knowledge of the target species spatial ecology. Here we propose management arrangements for *G. elevata* based upon new knowledge of the species key life-history characteristics.

The management goals for exploited species are generally aimed at maintaining stocks at sustainable levels and preventing overfishing. A commonly employed management strategy is limiting the size of retained individuals through minimum legal lengths (Stewart, 2008). However, the implementation of minimum legal lengths is not appropriate in all scenarios, particularly when fisheries catches are dominated by small individuals or there is a high mortality of discarded fish (Stewart, 2008). In instances where a minimum legal length is deemed an appropriate management response, the objective of setting the legal length can be to: 1) ensure that most of the fish in the population are able to grow to breeding size and spawn at least once before they are caught; 2) maximise catch value; 3) maximise the yield for the resource; 4) ensure sufficient reproduction to maintain stocks; 5) address growth overfishing; 6) minimise immediate losses to commercial and recreational fishers, or a combination of these objectives to produce an optimal minimum legal length (Stewart, 2008). Given the *G. elevata* fishery is almost entirely recreational (Lincoln Smith et al., 1989, Kingsford et al., 1991, Fisheries-NSW, 2014) and no recent creel survey data is available for the recreational fishery catch, the management response of a minimum legal length with an

objective to ensure most of the fish in the population have an opportunity to spawn at least once before they are subjected to fishing mortality was deemed most appropriate.

The current minimum legal length of *G. elevata* in NSW is 30 cm L_T (approximately 28.6 cm L_F, Appendix: Figure A3). Based upon recent maturity data of *G. elevata* provided in this study (Chapter 3; Stocks et al., 2015), a minimum legal length of 39 cm L_T (37 cm L_F) and 42 cm L_T (40 cm L_F) within the central and southern regions respectively would be required to allow approximately 50% of females at the stated lengths to reach sexual maturity and spawn before they are subject to fishing mortality. Because females mature at a larger size than males the minimum legal length was examined for females (Chapter 3; Stocks et al., 2015). The suggested minimum length would therefore automatically protect a larger proportion of sexually immature males. Knowledge of spatial variability in life-history traits allows for finer scale fishery management (Williams et al., 2007a), which may include varying catch quotas and legal lengths throughout a species distribution (Berg and Pedersen, 2001). However given the logistical constraints of assigning multiple minimum legal lengths, a precautionary approach that considers latitudinal variation in life-history traits should be adopted when applying uniform management strategies throughout the entirety of the species distribution. To further increase the complexity of stock management, increasing the minimum legal length may place increased strain on the adult stock already devoid of older/larger individuals of higher fecundity (Chapter 3, Stocks et al., 2015). Further population modelling is therefore required to assess the utility of an increase in the minimum legal length for *G. elevata.*

Information on the spatial ecology of *G. elevata* has provided information that will assist in the development of appropriately sized and positioned MPAs. Data from two acoustic arrays deployed for the current study (Chapter 5, Stocks et al., in press) showed the largest activity-space size of an individual *G. elevata* was 0.22 km^2. Given the small activity-space sizes and strong residency of a proportion of tagged individuals, small (~0.22 km^2) MPAs would provide considerable protection for resident populations of *G. elevata*. However, the spatial use by *G. elevata* is strongly habitat dependent, primarily associated with complex boulder and crevice habitat and wash zones that provide refuge and feeding grounds (Kingsford, 2002, Curley, 2007). For *G. elevata* to benefit from no-take MPAs, zoning arrangements must incorporate such critical habitat. Other factors including the level of fishing effort and the associated impacts on the population should also be assessed to determine if the implementation of no-take MPAs are advantageous to the sustainability of local populations.

6.4 Future research

- Examining the swimming energetics and thermal biology of *G. elevata* will provide further understanding of thermal tolerance windows, relationships between fitness and temperature and future biological impacts of changes in climate and oceanographic conditions. This can be achieved through a combination of field and laboratory approaches using swim tunnels and surgically implanting accelerometery transmitters.
- Finer scale temporal sampling within Northern Region should be conducted to examine spawning periods. This data would provide further information on the

relationships between fitness and temperature, and the species' fitness at its latitudinal range limits.

- This study focused on the movement of fish from the centre of the species' latitudinal distribution. Both northern and southern populations of *G. elevata* may display different patterns in their movements and habitat affinities as a result of varying responses to latitudinal clines in biotic and abiotic variables. The deployment of acoustic telemetry arrays within the northern and southern sampling regions would provide movement data throughout the species' latitudinal distribution.
- The deployment of an acoustic array that can triangulate the real time position of a tagged fish (i.e. Vemco Positioning System (VPS) or alike), coupled with habitat mapping would provide further information on the specific habitat requirements of *G. elevata*. Such data is required when implementing appropriately positioned MPAs to protect resident fish.
- Examining the otolith chemistry of *G. elevata* may provide further information on the large-scale movements of fish throughout their life. Such information is important in furthering our understanding of the species' susceptibility to localised depletion, the effectiveness of MPAs and to further understand the latitudinal interactions of *G. elevata* populations.
- Examining genetic markers of *G. elevata* throughout the species' latitudinal distribution would provide data to infer measures of dispersal and population connectivity.
- Investigating the feeding ecology and ecological impacts of *G. elevata* on benthic communities is necessary to understand the consequences derived from

any climate-mediated shifts in the distribution, abundance or demographic traits of this species.

6.5 Conclusion

The use of spatio-temporal survey techniques coupled with acoustic telemetry technology considerably broadened the knowledge of the life-history traits and movements of *G. elevata*. Examining latitudinal variation in life-history characteristics and the sclerochronological approach adopted in this study provides a means for assessing the biological response of fish to spatial and temporal climate and oceanographic variation. Such information is particularly useful in examining fishery productivity and assessing and predicting the biological consequences of a changing climate. Latitudinal clines in life-history traits of *G. elevata* and the associations with temperature suggest potential alterations to the latitudinal productivity of *G. elevata* populations in response to expected climate and oceanographic shifts in south-east Australia. Furthermore, life-history traits of longevity, slow growth, late maturation, small activity-space size, and high residency potentially make *G. elevata* populations vulnerable to fishing pressure and susceptible to the localised depletion of larger individuals (Stocks et al., 2014a, Stocks et al., 2015, Stocks et al., in press). Suggested management arrangements have been proposed to ensure the sustainability of the population taking into consideration life-history traits and spatial metrics of habitat use.

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Appendix

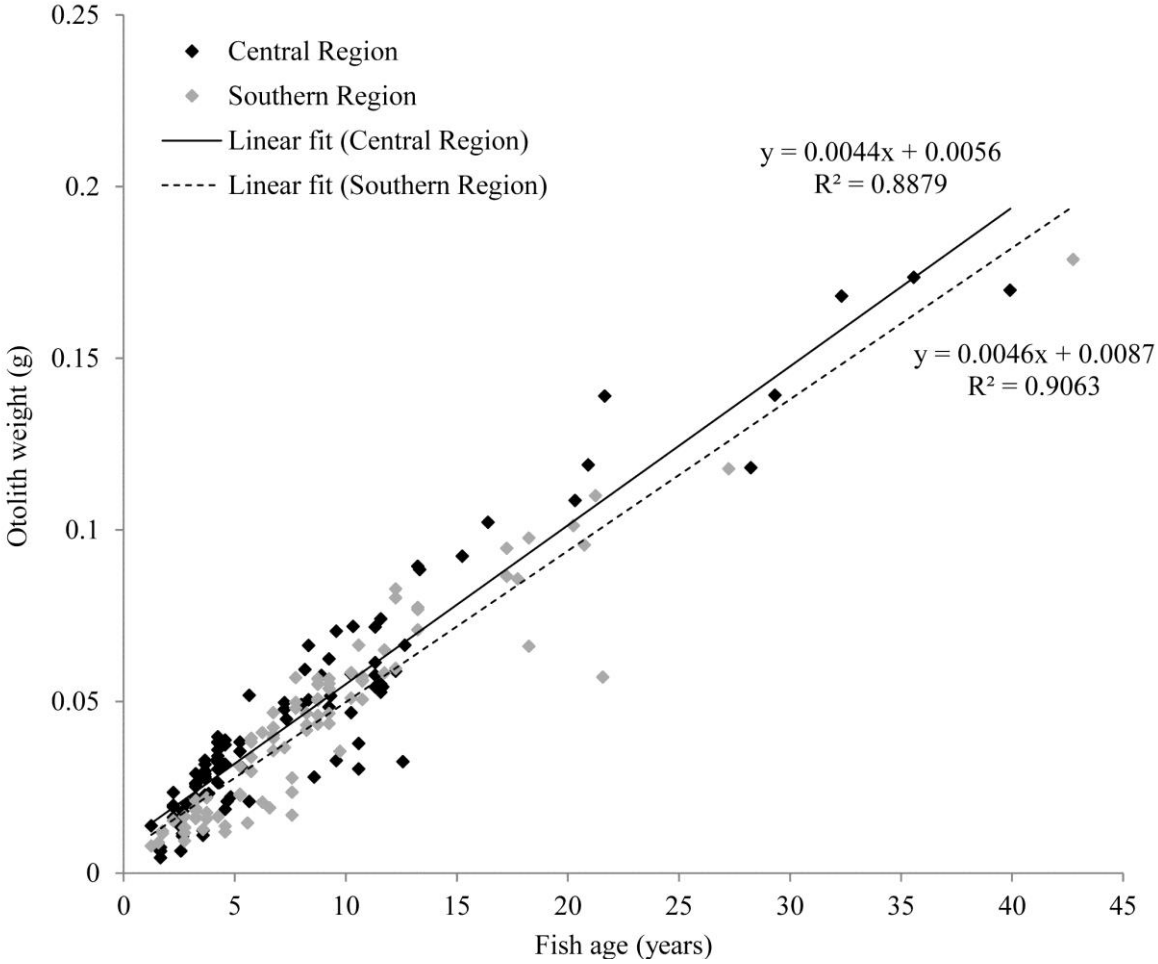

Figure A.1 Otolith weight-fish age relationship of *Girella elevata* sampled from two regions of the south-east Australian coast.

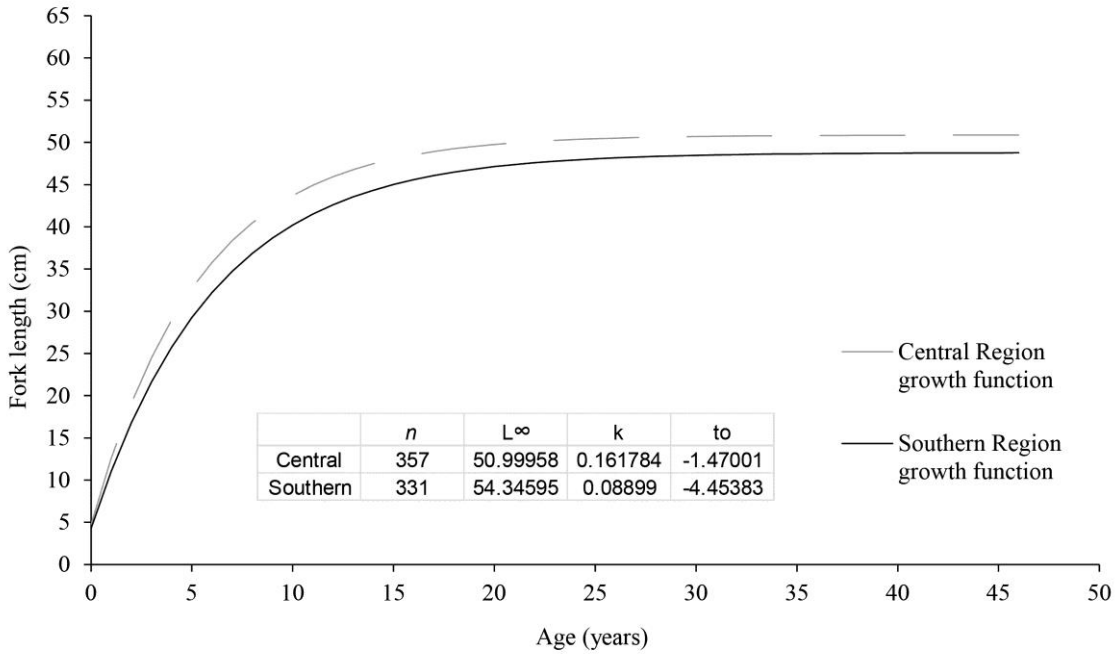

Figure A.2 Von Bertalanffy growth functions of *Girella elevata* from the Central and Southern Regions.

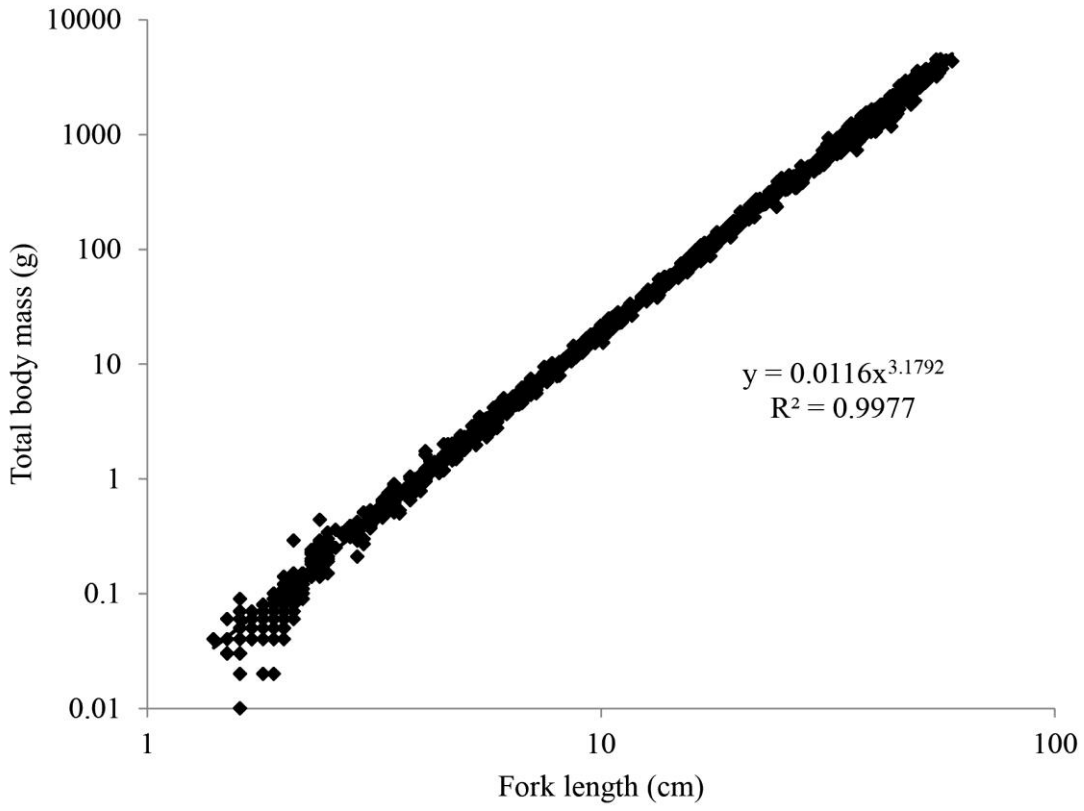

Figure A.3 Length (L_F)-weight relationship of *Girella elevata* sampled from three regions of the south-east Australian coast. Note log10 transformation of each axis.

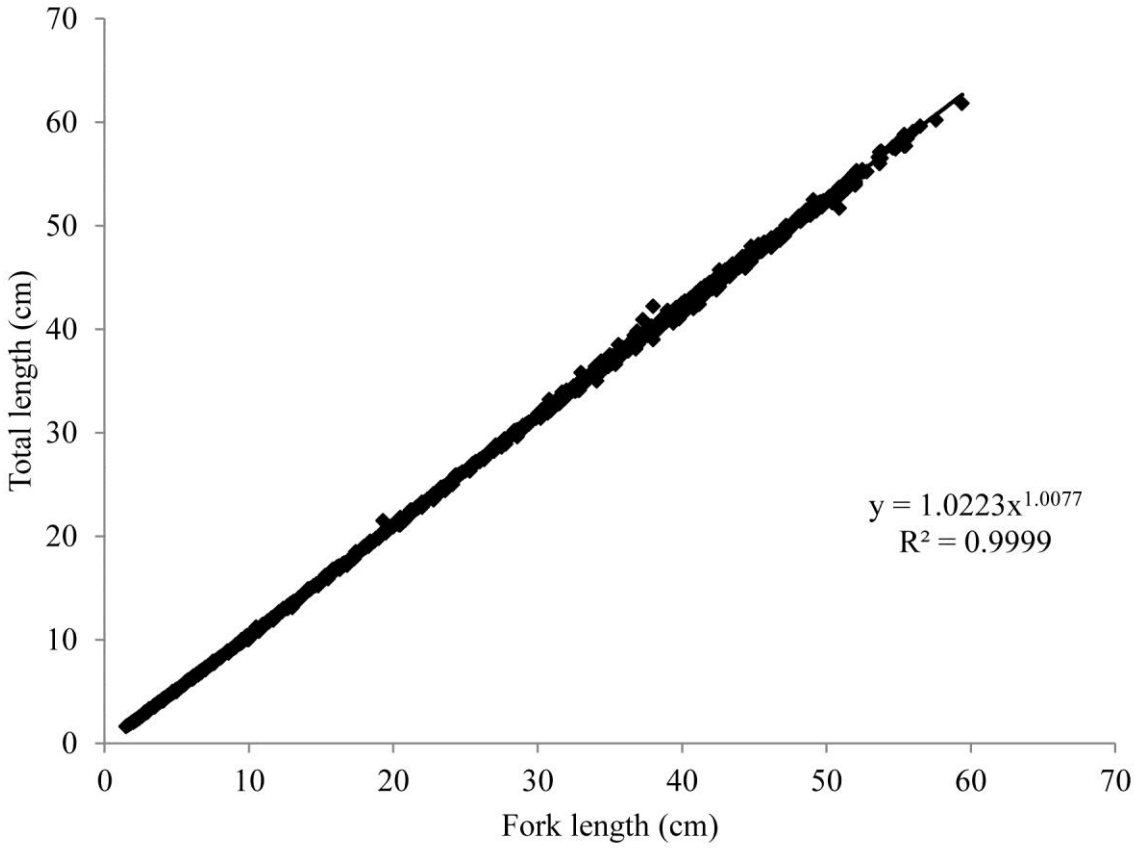

Figure A.4 Fork length-total length relationship of *Girella elevata* sampled from three regions of the south-east Australian coast.

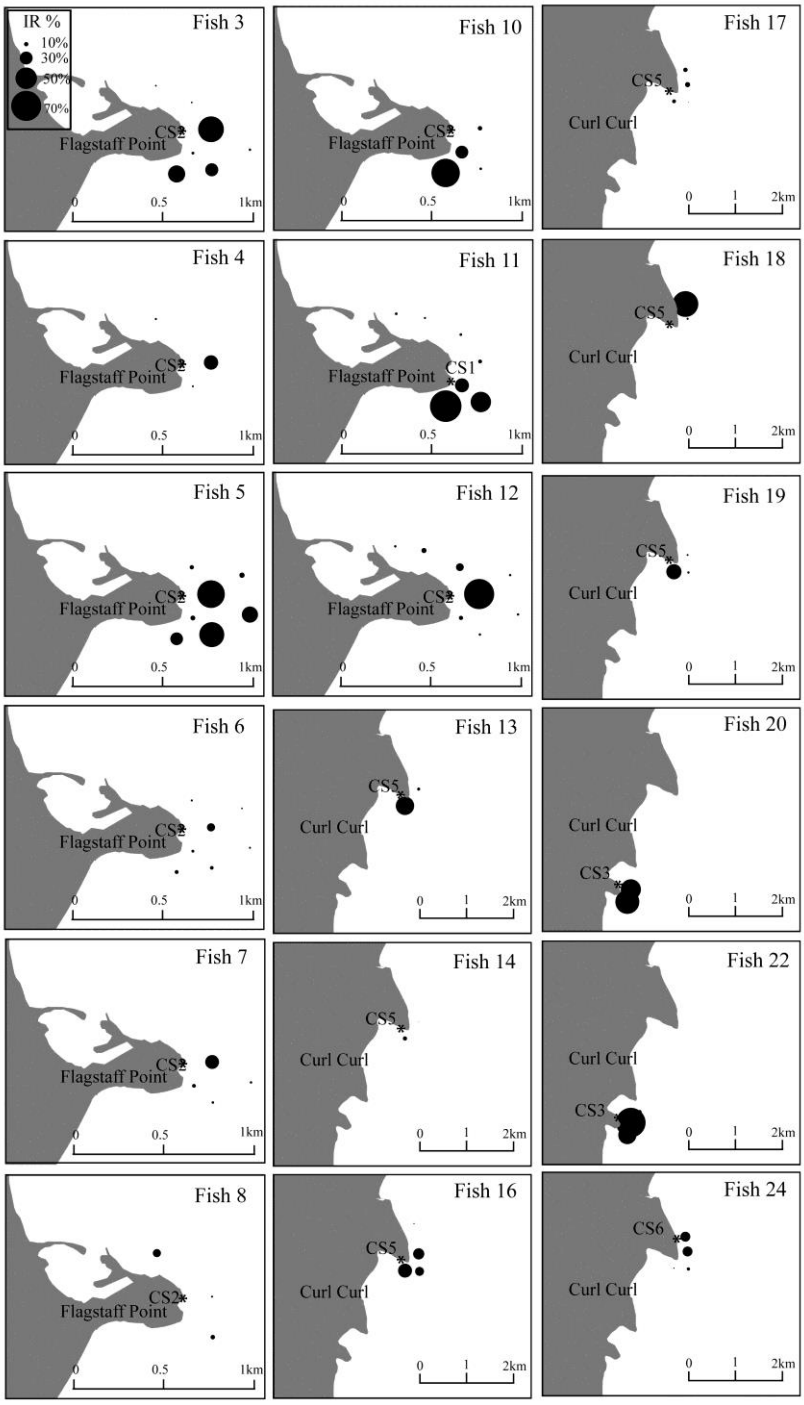

Figure A.5 Residency index (IR) by receiver of 18 *Girella elevata* tagged with acoustic transmitters within the Wollongong Array (fish IDs 3 – 12) and North Sydney Array (fish IDs 13 – 24). Filled circles display IR values.

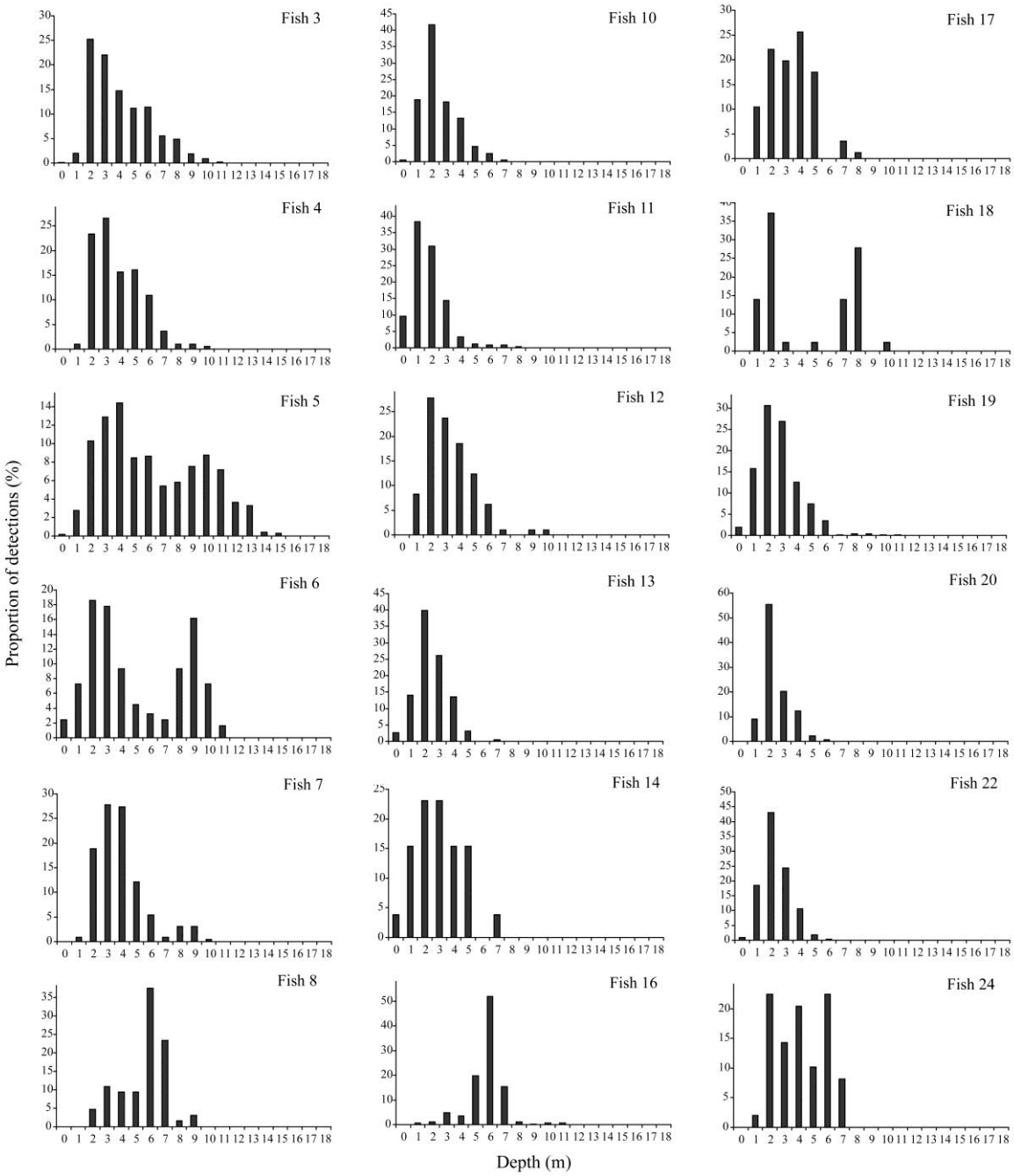

Figure A.6 Percentage of detections in 1 m depth classes of 18 *Girella elevata* tagged with depth-sensing acoustic transmitters within the Wollongong Array (fish IDs 3 – 12) and North Sydney Array (fish IDs 13 – 24).

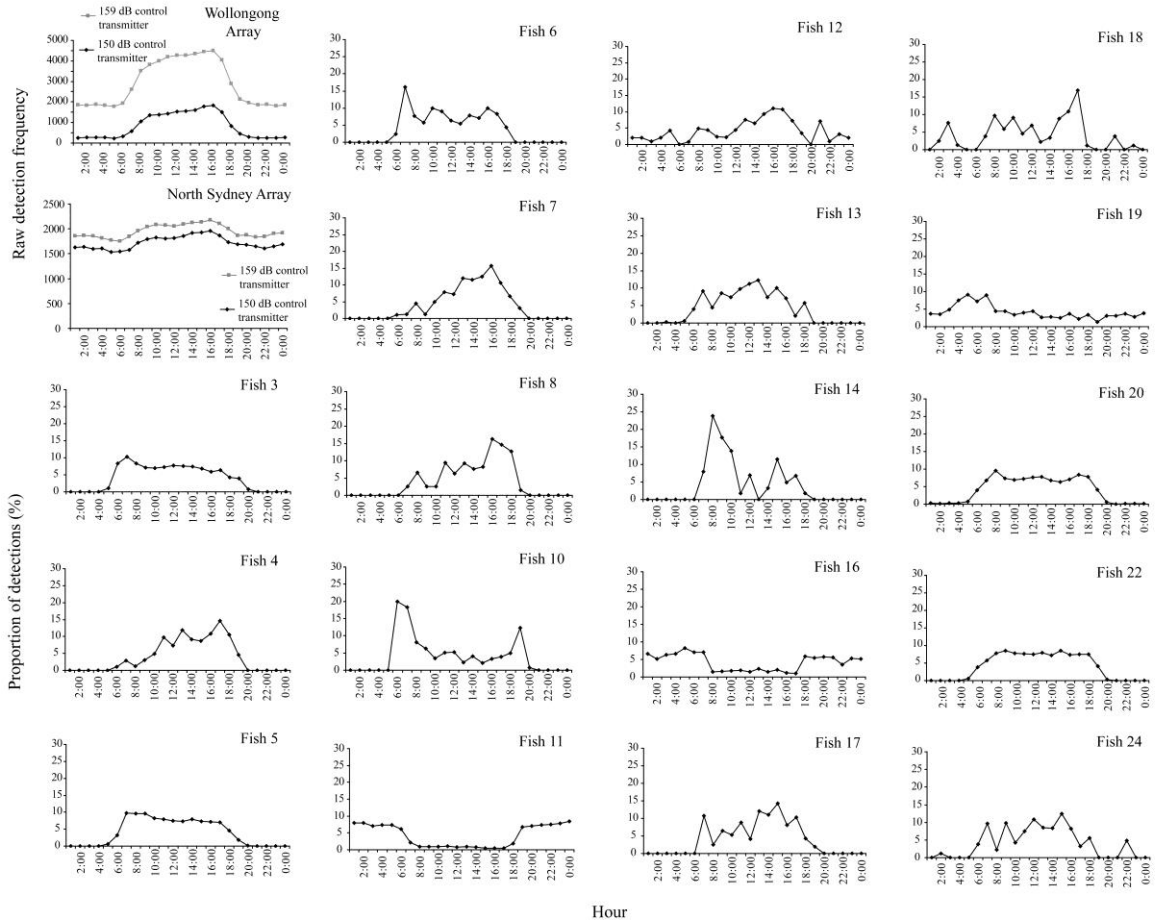

Figure A.7 Diel detection frequency of 150 and 159dB control-transmitters and SSDF corrected detections of *Girella elevata* in hourly time bins for the Wollongong Array (fish IDs 3 – 12) and North Sydney Array (fish IDs 13 – 24).

Table A.1 Coordinates of locations at which *Girella elevata* were sampled for biological data.

Latitude	Longitude	Site name
-37.26282042	150.048374	Green Cape
-37.10206322	149.92829	Wood Chip Mill
-37.05026591	149.932682	North Eden
-36.9503639	149.94821	Haycock Wreck
-36.94895445	149.945081	Haycock Point
-36.93406737	149.942148	Hunters
-36.85541018	149.950533	Tura East
-36.84620185	149.940342	Tura Nth
-36.76689128	149.977388	White Rock Juveniles
-36.76486557	149.980221	White Rock Bommy
-36.73852596	149.983885	Tathra Boat Ramp
-36.72638207	149.986326	Juvenile Rock Pools
-36.72574764	149.991713	Rod Holders
-36.72490988	149.990083	Tathra
-36.43034961	150.083033	Bermagui Blue Pools
-35.4578356	150.403426	Stokes Island
-35.24444195	150.534556	Bendalong Comp
-35.11112519	150.774551	Jervis Bay Comp
-35.0011499	150.830817	Currarong
-34.9644316	150.781418	Pluto
-34.78627652	150.815671	Black Head Bommy Gerroa
-34.59663816	150.903948	Bass Point
-34.59362234	150.892072	Ling Holes Bass Point
-34.59342779	150.886794	Juv. Rock Pool
-34.59300603	150.902893	Bass Point Wreck
-34.5797121	150.875833	Shellharbour
-34.49387179	150.918048	Hill 60
-34.4571187	150.930585	Toothbrush Isld
-34.42211349	150.911518	Wollongong
-34.4139815	150.908009	Puckies
-34.38624015	150.920496	Towradgi
-34.36734917	150.925145	Juv. Rockpool
-34.3660835	150.924698	Juv. Rockpool
-34.365833	150.930407	Bellambi
-34.34003683	150.93203	Bulli 15m
-34.34002354	150.926687	Bulli Pool Sth Corner
-34.33299524	150.931489	Sandon Point
-34.28897555	150.949821	Coaldale

Table A.1 (continued).

-34.26192187	150.969896	Clifton
-34.09742476	151.163873	Bundeena
-34.06645575	151.159131	Cronulla
-34.06593942	151.156898	Juv. Rock Pool
-34.06573656	151.15672	Juv. Rock Pool
-34.04416041	151.196315	Kurnel Boat Harbour
-32.43165006	152.535576	Seal Rocks Bird Shit Island
-32.43050252	152.525813	Seal Rocks Little Island
-31.45476185	152.935833	Shelly Bch Bommy
-30.89789744	153.084249	Whaler Bommy Sth Wst Rocks
-30.24020389	153.181947	Split Rock Solitary
-30.23915434	153.153908	Mooney Bommy Sth
-30.21424745	153.164216	Mooney Headland
-30.01959663	153.271248	Nth West Island
-29.97472554	153.258829	North Rock