Movement, connectivity and population structure of *Acanthopagrus australis* (Yellowfin Bream) along the New South Wales coast

Holly Gunton

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and Dr. John Stewart (NSW DPI)

University of Technology Sydney

Faculty of Science

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Certificate of original authorship

I, Holly Gunton declare that this thesis, is submitted in fulfilment of the requirements for the award of Master of Science (Research), in the School of Life Sciences at the University of Technology Sydney. This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis. This document has not been submitted for qualifications at any other academic institution. This research is supported by the Australian Government Research Training Program.

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Abstract

In this thesis, I investigate the population structure of Yellowfin Bream, *Acanthopagrus australis*, an important and popular fish species in eastern Australia. Archival collections of otoliths (ear stones) and long-term tag-recapture data were used to examine movement and potential stock segregation in New South Wales (NSW) at a range of spatial and temporal scales.

In Chapter 2, cooperative tag-recapture data was examined using generalized additive models, to assess potential environmental and intrinsic drivers of *A. australis* movement. Over 24 000 individuals were tagged along ~ 800 km of the NSW coastline, with anglers recapturing 2036 (8.2 %) individuals during a 19-year period. A broad range of movements were observed (up to 832 km), however a substantial proportion (37%) of individuals were recaptured at their release location, with only 8.6 % of individuals moving further than 100 km. Fish were more likely to move if they spent greater time at liberty, were of larger body length at release, or were released during Autumn. Fish that spent greater time at liberty and those released at more southerly latitudes were more likely to move a greater distance, with those that travelled in a northerly direction (61.5%) significantly more likely to move a greater distance.

In Chapter 3, connectivity of *A. australis* among estuaries was examined during recent life history using otolith elemental edge signatures, and throughout life history using otolith shape indices. Archived otoliths (n = 355) from estuaries covering ~850 km of the NSW coastline were examined using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) and Elliptical Fourier Analysis. The results indicate complex stock structure of *A. australis*, with considerable differences in elemental edge signatures among a range of estuaries and sites at a variety of spatial and temporal scales. Differences in

elemental signatures from the juvenile region of adult otoliths were consistent with patterns of adult separation, suggesting they were established early in life. Differences in otolith edge signatures revealed at both the smallest (sites within estuaries) and largest scale of investigation (100s of km) highlight the importance of investigating multiple spatial scales.

The use of multiple techniques provided a more holistic understanding of population structure of *A. australis* in NSW. Overall, the results indicate that movement of *A. australis* is likely restricted over spatial scales considerably smaller than that of fisheries management in the region.

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Chapter 1   General Introduction

In Australia and throughout the world pressure on our fisheries is continuing to grow, with effort increasing and yields either constant or in decline (Hutchings et al. 2000; Mora et al. 2009). Anthropogenic impacts on fisheries may be most pronounced in coastal and estuarine systems, where the cumulative impacts of high human presence have led to these areas becoming some of the most degraded aquatic ecosystems worldwide (Lotze et al. 2006; Halpern et al. 2008). As our population continues to grow, so will the weight of these stresses on aquatic systems, and in turn the necessity of understanding the biology and ecology of estuarine and coastal fishes, in order to inform effective management and conservation strategies (Cloern et al. 2016).

1.1 Importance of understanding population connectivity and movement patterns

An important component of the life history of fish and how their populations and assemblages interact in space and time is the degree of connectivity of groups of a species throughout their range, because it determines stock structure and genetic transfer (Hawkins et al. 2016). The subject of spatial structure and connectivity has gained increased recognition over the past decade or so as knowledge has developed of its strong influence on population productivity and dynamics (Cadrin & Secor 2009; Kerr 2010b). The spatial structure within, and connectivity between, populations may have a strong influence on a species resilience and persistence (Kerr et al. 2010b). Understanding movement patterns and intraspecific levels of exchange between spatially segregated areas is vital in determining how populations will respond to stressors such as exploitation and climatic changes.

Levels of connectivity and resulting population structure are controlled through both dispersal during the larval period and movement during juvenile and adult stages (Cowen & Sponaugle 2009; Frisk et al. 2014). Movement and dispersal may affect the distribution and

abundance of organisms, local and metapopulation dynamics, genetic diversity, resilience to exploitation and thus population persistence (Kritzer & Sale 2004; Hastings & Botsford 2006; Cowen & Sponaugle 2009). In the past, fish populations were predominantly considered 'open' with broad dispersal, however evidence has led to recognition that populations may operate at much finer scales (Warner & Cowen 2002; Cowen et al. 2007). Much of the research into population connectivity has focused on larval dispersal, particularly in reef fishes, that generally have a bipartite life cycle, with a pelagic larval phase followed by more sedentary juvenile and adult phases (Fogarty & Botsford 2007; Thorrold et al. 2007). However larval dispersal may be considerably more limited than suggested by passive dispersal alone, for example some estuarine-associated species exhibit limited dispersal due to larval retention (North & Houde 2001; Bradbury et al. 2008).

While connectivity through larval dispersal is an important force in driving connectivity among areas, movement of post-settlement individuals may influence population dynamics at much finer temporal and spatial scales with regards to replenishment of mature, reproductive individuals (Frisk et al. 2014). An area that has received much less attention than early life history stages, adult connectivity is thought to play a pivotal role in population structure and function for some species (Frisk et al. 2014; Archambault et al. 2016). Certain fishes have been seen to display greater mobility as adults than larvae (Tobin et al. 2010), indicating the significance of adults in maintaining connectivity (Moore et al. 2012).

Successful management and monitoring of fisheries require an understanding of the spatial organisation of exploited species, as it informs the spatial scale at which management measures should be applied and populations assessed (Cooke et al. 2016). If population structure of a species is unknown, the default is to assume a species forms a single well-mixed population over a given management area, with homogenous demographic

characteristics (Forgarty & Botsford 2007; Cadrin et al. 2013). Unfortunately, this is unlikely to be the case for most exploited fishes, with complex spatial structure and movement patterns more typical than spatial homogeneity (Cope & Punt 2011). Failure to recognise or account for potentially complex spatial structure may degrade fish populations and spawning components (Stephenson 1999).

Despite advances in stock assessment models used to inform management decisions, data constraints mean assumptions of single stocks across management areas remain in order to increase parsimony in stock assessments (Cotter et al. 2004; Cope & Punt 2011). If management measures are applied which fail to accurately define levels of exchange and opportunity for replenishment to local populations, it may result in over-exploitation of localised subpopulations (Stephenson 1999). In turn, this may lead to substantial changes in demography and productivity of isolated subpopulations and eventually localised depletion or even extinction (Ying et al. 2011). Over-exploitation due to insufficient information on population structure has led to depletions to the point of collapse for Atlantic cod *Gadus morhua* (see Hutchings 1996) and several other important exploited species (Orensanz et al. 1998; Mullen et al. 2005).

Estimates of demographic connectivity are also essential in the effective design of marine protected areas (MPAs), informing the spatial scale at which such areas may be most advantageous to targeted species (Burgess et al. 2014). Growing evidence of limited adult movement in putatively mobile species suggests MPAs may benefit exploited species more than previously thought (Willis et al. 2003; Malcolm et al. 2018). Additionally, several studies into fish movement indicate intraspecific variation in movement behaviour. This occurrence where some individuals are relatively sedentary or exhibit strong homing ability, while others display less fidelity and undertake larger migrations, is increasingly being

reported in marine taxa (Parsons et al. 2011; Gillanders et al. 2015). The spatial organisation of fish populations may be associated with the behavioural response (i.e. resident or migratory) of individuals to their fitness in relation to environmental conditions (Jonsson & Jonsson 1993). Such movement strategies are an important consideration for management in regard to stock complexity (Kerr et al. 2009).

Despite the importance of understanding movement patterns and degrees of connectivity, it remains poorly understood for the majority of fish species. Uncertainty surrounding connectivity and population structure for many exploited fish species is a central issue for fisheries management (Begg et al. 1999a; Cowen et al. 2007; Fogarty & Botsford 2007). Assessment and management controls need to be applied at the unit stock level (Cadrin & Secor 2009). If what is assumed to be a homogeneous stock is actually composed of several smaller populations with distinct demographics and dynamics, it may lead to overfishing in less productive populations (Goethel et al. 2016). Similarly, if management units only comprise a portion of a larger population, it may lead to inaccurate understanding of population dynamics and incomplete control over fishing mortality (Kerr et al. 2017). Understanding if a species contains separate populations, how these interact and to what degree they are exploited are all essential for developing appropriate spatial management of a species (Begg & Waldman 1999; Hamer et al. 2012; Fairclough et al. 2013).

1.2 Methodological approaches to estimating movement and population structure in fishes

A wide range of methodological approaches exist for assessing post-settlement fish movement and estimating population connectivity. with each individual methodology having benefits and drawbacks (Cadrin et al. 2013). The development of tag-recapture techniques enabled movement estimates of individual fish to be obtained, and while they may be limited

by their simplicity and underlying assumptions (Begg & Waldman 1999), cooperative strategies may allow economical investigations at large temporal and spatial scales (Gillanders et al. 2001). Developments such as acoustic tagging can provide more comprehensive data on individual fish movement, however increased cost means they often lack resolution over large spatial scales (Thorstad et al. 2013; Crossin et al. 2017; Taylor et al. 2017b). To address the limitations associated with direct tagging, a number of indirect methods have been generated. These include comparisons of life history parameters (Begg et al. 1999b; Abaunza et al. 2008a), otolith shape and morphological characteristics (Campana & Casselman 1993; Keating et al. 2014), population genetics (Hawkins et al. 2016) and otolith elemental signatures (Elsdon et al. 2008), among others (Cadrin et al. 2013).

Although the aforementioned methods address some of the limitations of other approaches, each of these methods has inherent limitations of its own. For instance, genetic techniques endeavour to test spatial homogeneity in gene flow and interbreeding, by investigating the degree of genetic divergence or distribution-wide existence of genetically related individuals (Reiss et al. 2009). In contrast, otolith elemental signatures and parasite assemblages reflect residence and movement through differing environments throughout an individual's life, and may allow genetically homogenous populations to be resolved into discrete groups that exist over more recent ecological timescales (Buckworth et al. 1998; Thorrold et al. 2001; Cowen & Sponaugle 2009). The effectiveness of different approaches varies, dependent on the temporal and spatial scales of investigation (Welch et al. 2015). Choice of the methodology used to assess connectivity and population structure is dependent upon the species or life history period being studied, the data available, the time period that the methodology provides information over and the specific research or management questions being addressed (Begg & Waldman 1999).

The most powerful method of reliably detecting whether there is movement among areas and whether different stocks exist involves a holistic approach that integrates information gathered from multiple complementary techniques (Begg & Waldman 1999; Izzo et al. 2017). The application of such approaches increases the power of detecting patterns of movement and stock structure by providing a 'weight of evidence' and thus greater confidence in results (Welch et al. 2015). Failure to detect stock structure using a single technique may merely reflect the discriminatory power of the chosen technique or a mismatch between the temporal and spatial scales over which structure exists and the scales over which the method is capable of detecting differences. Such potential mismatches are unknown prior to investigation; therefore, using multiple techniques greatly increases the likelihood of detecting separate stocks if they exist (Welch et al. 2015). Multiple techniques also allow for the limitations of individual methods to be less critical, and increase the scope of the temporal and spatial scales that may be examined (Begg & Waldman 1999; Abaunza 2008a).

1.3 Study species: *Acanthopagrus australis*

1.3.1 Biology and ecology

Acanthopagrus australis (Sparidae), commonly known as Yellowfin Bream, are an estuarine-dependent species endemic to the east coast of Australia (McGilvray et al. 2018). Ranging from Townsville in Northern Queensland to the Gippsland lakes in Eastern Victoria they are thought to comprise one stock (Stewart & Hughes 2008; Curley et al. 2013; McGilvray et al 2018). Mainly associated with estuarine and inshore areas, *A. australis* occupy a variety of habitats, including seagrass beds, mangroves, rocky reefs and bare substrates (Stewart et al. 2015). *A. australis* is known to hybridize with the estuary-restricted congener *Acanthopagrus*

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butcheri (black bream) in areas of greatest sympatry in southern NSW (Roberts et al. 2009; Roberts et al. 2010).

The NSW fishery for *A. australis* is dominated by individuals ranging from 2 to 10 + years, with individuals greater than 400 mm uncommon (Gray et al. 2000; Stewart & Hughes 2008). Length has been found to be a poor predictor of age for *A. australis*, with large variations recorded in length at age (Ochwada et al. 2008). Differences in growth rates of *A. australis* have been recorded and appear dependent on geographical area (Pollock 1982b; Griffiths 2001), which may be linked to latitudinal differences in temperature (Curley et al. 2013). The diet of *A. australis* also varies with geographic location, demonstrating their generalist feeding habits (Curley et al. 2013).

Acanthopagrus australis have a bipartite life cycle, spawning pelagic eggs that remain over the continental shelf prior to hatching, at which point larvae begin to swim towards and then along the coast when they are ready to settle (Trnski 2002; Leis et al. 2006). It is reasonably well established that a proportion of adult *A. australis* undertake spawning migrations to coastal areas near estuary mouths and surf bars (Pollock 1982b; Gray et al. 2000), with spawning periods recorded at varying times of year dependent on location (Stewart & Hughes 2008).

1.3.2 Significance to fisheries

Acanthopagrus australis is a popular species both commercially and recreationally on the east coast of Australia. The majority of the catch of *A. australis* is taken in NSW waters, with the NSW commercial catch accounting for approximately two thirds of the total catch of all jurisdictions (McGilvray et al. 2018). In addition to being a valuable commercial species, *A. australis* is also a major target for recreational fishers owing to its extensive distribution within estuaries and its relative ease of capture and accessibility nearshore (Broadhurst et al.

2007; Stewart et al. 2015). *A. australis* is the most common species caught recreationally in NSW (West et al. 2015), with recreational catch estimated to account for ~ 32 % of the total catch within NSW (Murphy et al. 2020 in press), half of which is concentrated in the Sydney and mid-south coast fishing zones (West et al. 2015). Currently, *A. australis* are treated as a single biological stock throughout their range for stock assessment purposes. This biological stock has components in three separate jurisdictions, QLD, NSW and VIC, with each jurisdiction managing the part of the stock that occurs in its waters separately (McGilvray et al. 2018).

The *A. australis* stock was most recently classified as "fully-fished" in NSW (Stewart et al. 2015), which is a state-based stock status classification analogous to the "sustainable" classification in the national Status of Australian Fish Stocks (SAFS) reports (Fisheries Research & Development Corporation 2020). The status is supported by size-frequency distributions in both commercial and recreational fisheries remaining relatively stable since the 1960s (Stewart & Hughes 2008). Despite this, it is acknowledged that due to the large recreational popularity of this species, any increase in catch effort is undesirable (Stewart & Hughes 2008). Fishing effort for *A. australis* varies spatially between estuaries and coastal areas within NSW, with the greatest coastal and estuarine exploitation taking place in central NSW (Gray et al. 2000; West et al. 2015). Just five areas (Port Stephens, Tuggerah Lakes, Lake Macquarie, Clarence River and Botany Bay) were estimated to account for approximately half of commercial catch in estuaries between 1992 and 1997 (Gray et al. 2000). Such estimates indicate substantial differences in exploitation spatially, establishing the need to understand the demographic structuring of *A. australis*. If segregation exists for this species, areas of higher exploitation may be at risk of localised depletions, because individuals removed through fishing may not be replenished from surrounding areas. Limited

replenishment from surrounding areas may lead to shifts in morphological and life history characteristics of *A. australis*.

1.3.3 Movement, connectivity and population structure

Despite the need for information on the stock structure of *A. australis*, few studies have investigated the broad scale movement patterns and stock structure of this species in NSW (but see West 1993; Curley et al. 2013). West (1993) conducted a tagging study within two estuaries in Northern NSW, with only 4% of recaptured fish found to have emigrated to areas outside the estuary in which they were tagged. Those that have investigated *A. australis* movement have been constrained by spatial scales of investigation, generally examining fine scale (> 100 km) movement patterns, predominately within single estuaries or between estuaries and coastal spawning locations (Pollock et al. 1982a; Sheaves 1993; Gillanders & Kingford 2003; Meynecke et al. 2008; Butcher et al. 2010; Payne et al. 2013; Taylor et al. 2013; Gannon et al. 2015; Taylor et al. 2017; Lowry et al. 2017; Taylor et al. 2018). The majority of research has found *A. australis* display strong residence behaviour, for instance research in NSW has identified small home ranges (< 0.3km^2) (Gannon et al. 2015) and strong site fidelity (Meynecke et al. 2008; Taylor et al. 2017; Taylor et al. 2018).

The estuarine association and high degree of fidelity displayed by *A. australis* would suggest this species may be segregated along the east Australian coast, with limited movement among areas separated by > 100 km, however genetic surveys of allele frequencies have revealed high levels of genetic diversity and no genetic differentiation among areas separated by several 100s of kilometres (Roberts & Ayre 2010). Due primarily to the latter finding, *A. australis* are assessed as a single biological stock throughout their range, and are managed at a state-wide level by each of the three jurisdictions they inhabit (McGilvray et al. 2018). Although genetic techniques may successfully delineate stocks when structure is distinct and

long term, populations found to display genetic panmixis may still form discrete units over the shorter timescales relevant to fisheries assessment and management (Buckworth et al. 1998; Thorrold et al. 2001). The level of exchange required to maintain genetic panmixia is considerably lower than that required to maintain demographic homogeneity (Cowen & Sponaugle 2009; Hawkins et al. 2016). Furthermore, exchange leading to genetic panmixia may be achieved through larval connectivity, despite considerable segregation of later developmental stages subject to fishing pressure (Frisk et al. 2014).

A number of studies in NSW have recorded *A. australis* moving substantial distances (>300 km) despite identifying predominantly small-scale movement and residency (West 1993; Lowry et al. 2017; van der Meulen 2018). Limited and conflicting information on the broad-scale movement patterns of *A. australis* within NSW warrants further research into the degree of population connectivity and stock structure of this important exploited species (Curley et al. 2013).

1.4 Objectives and thesis structure

The broad objective of this thesis was to investigate the movement and connectivity of *A. australis* within NSW using multiple methods, and thereby help clarify how this population is structured spatially, in order to assist in monitoring, assessment and management of this important resource in NSW. Specific aims and objectives are to:

1. Examine broad-scale movement patterns of *A. australis* along the NSW coast (Chapter 2)

2. Examine factors contributing to movement of *A.australis* along the NSW coast (Chapter 2)

3. Determine whether *A. australis* are spatially segregated across estuaries during their recent and more extended life history (Chapter 3)

4. Examine whether patterns of adult *A. australis* connectivity relate to their juvenile life-stage (Chapter 3)

This project incorporates data from complementary methods of fish tracking to examine patterns of movement, associated connectivity and resultant population structure of *A.australis*. Otolith elemental signatures, otolith shape indices and tag-recapture data are used to examine movement and population structure at multiple spatial and temporal scales along the NSW coast, to ensure a holistic and robust understanding of *A. australis* population structure.

Two research chapters are presented, structured as a progression of independent but complementary studies, followed by a general discussion. The research chapters form the basis of stand-alone manuscripts that are intended to be submitted for publication in peer-reviewed scientific journals. As such, this has resulted in some unavoidable repetition. Note that references are collated at the end of the document.

Chapter 2   Patterns and Drivers of movement in the estuarine associated sparid *Acanthopagrus australis* from a large-scale cooperative tagging program

Abstract

Knowledge of movement patterns is vital in determining how fishes will respond to stressors and thus in implementing appropriate spatial scales of assessment and management. This paper provides an examination of movement patterns of *Acanthopagrus australis* along the NSW coast through a cooperative tag-recapture program. Over 24 000 individuals were tagged and released over ~ 800 km of coastline, with anglers recapturing 2036 (8.2 %) individuals during a 19-year period (1980-1999). A broad range of movements were observed (up to 832 km), however a substantial proportion (37%) of individuals were recaptured at their release location, with only 8.6 % of fish moving further than 100 km. Generalized additive models were used to assess potential environmental and intrinsic drivers of movement and movement distance. Fish were more likely to move a detectable distance if they spent greater time at liberty, were of larger body length at release or were released during Autumn. The majority (61.5 %) of individuals travelled in a northerly direction and movement distance was likely to be greater if fish moved in a northerly direction, spent greater time at liberty or were released at more southerly latitudes. The results suggest restricted movement over a relatively small spatial scale (< 100 km), interspersed with occasional large-scale movements, implying multiple behavioural types may exist for *A. australis*. The findings indicate adult movement of *A. australis* in NSW primarily occurs over considerably smaller distances than the current spatial scale of management in this region, which may be more appropriate at more localised, regional scales.

2.1 Introduction

Understanding patterns of movement and levels of spatial connectivity of fish populations is critical in ensuring sustainable spatial management of exploited species (Kerr et al. 2017). Nonetheless, developing this knowledge presents unique challenges in marine species as aquatic systems are highly interconnected, linking different environments and enabling long distance movements which are often difficult to detect (Lennox et al. 2017). Knowledge of the spatial distribution of fish species not only assists in appropriate spatial management of fished populations, it contributes to the design, implementation and interpretation of both biological and fishery assessment and monitoring (Cooke et al. 2016). When a species is not managed at an ecologically appropriate scale, it may result in localised depletions (Hanselman et al. 2007), risks to sustainability (Hutchinson 2008) or inefficiencies that limit productivity (Kerr et al. 2010).

Patterns of movement and dispersal are the primary drivers of connectivity and mixing, and thus population structure (Cadrin et al. 2013; Izzo et al. 2017). Connectivity and resulting population structure can be dictated by movement and dispersal in specific life history stages, with some exploited species capable of broad scale post settlement movement (Cowen et al. 2007; Clarke et al. 2010; Frisk et al. 2014), the extent of which can influence biological characteristics such as growth across environmental gradients (Williams et al. 2012). Data on the range and extent of individual movements is necessary for comprehension of the spatial ecology and demography of mobile species. An understanding of patterns of movement and thus connectivity among populations is also imperative in the effective design of marine protected areas (MPAs) and conservation zones, as it allows for development of MPAs at spatial scales which provide adequate protection (Botsford et al. 2009).

The typical method of quantifying movement patterns of post-settlement fish is through tag-recapture programs, which provide movement estimates for individual fish based on the distance between release and recapture locations. Although developments in acoustic tagging technologies have allowed more detailed information on individual fish movement, they may be costly, in turn often lacking resolution and sufficient replication over large spatial scales (Thorstad et al. 2013; Crossin et al. 2017; Taylor et al. 2017b). Conventional studies using external tags allow for extensive programs with a relatively large number of individuals, and thus can provide valuable data on movement at spatial and temporal scales relevant to fisheries management and monitoring (Gillanders et al. 2001; Stewart et al. 2019).

Despite their utility, simple tag-recapture data provide an indirect measure of movement, and are limited by underlying assumptions, for instance that no additional movement has occurred between tag and recapture locations or that tagging has no effect on subsequent survival (see Gillanders et al. 2001 for a comprehensive review of assumptions). Additionally, tag-recapture studies may be limited by low recapture rates, owing to the dilution of tagged individuals among the greater population and the resulting low probability of recapture. Statistical power can be substantially increased by adopting cooperative strategies in long term, widespread programs with large numbers of individuals. Cooperative programs where research and government agencies work together with anglers have demonstrated success on providing data on movement patterns, as well as growth rates and habitat use (Brodie et al. 2018; Fowler et al. 2018; Stewart et al. 2019).

Acanthopagrus australis are an important fish species both recreationally and commercially along the east coast of Australia (Stewart & Hughes 2008). Commonly known as Yellowfin Bream, the species ranges from the Gippsland Lakes (38°S, 148°E) in eastern Victoria (VIC) to Townsville (19°S, 147°E) in northern Queensland (QLD), stretching over ~ 2000 km of

coastline (Rowland 1984; Curley et al. 2013). *A. australis* are thought to primarily inhabit estuarine and inshore areas (Stewart et al. 2015), and although understudied, are thought to undertake small scale migrations to spawn at estuary mouths and adjacent surf zones (Pollock 1982b, 1984). Fine-scale movement patterns of *A. australis* have been well studied, documenting strong site fidelity and small home ranges (Sheaves 1993; Meynecke et al. 2008; Taylor et al. 2017). Less is known about the broad-scale movement patterns of this species, with some studies documenting substantial movement distances in a small number of fish (West 1993; Lowry et al. 2017; van der Meulen 2018). Currently, the species is considered a single biological stock along the east coast, covering three jurisdictions, QLD, NSW and VIC (McGilvray et al. 2018). However, each jurisdiction assesses and manages their component of the stock separately (McGilvray et al. 2018). The majority of the catch of *A. australis* is taken in NSW waters, with the commercial catch from NSW accounting for approximately two thirds of the total catch of all jurisdictions (McGilvray et al. 2018). *Acanthopagrus australis* is the most common species caught recreationally in NSW (West et al. 2015), with recreational catch accounting for 32 % of the total catch within NSW (Murphy et al. 2020 in press), half of the which is concentrated in the Sydney and mid-south coast fishing zones (West et al. 2015).

The assumption that *A. australis* are a single stock along the entire east coast is based on the finding that they are genetically homogenous throughout their range (Roberts & Ayre 2010), yet tagging work to date suggests predominantly small-scale movement of post-settlement individuals (Pollock 1982; Sheaves 1993; West 1993; see Table 1). Given the evolutionary timescales involved with genetic divergence, a species may display genetic homogeneity despite considerable structure in post-settlement life stages, due to limited exchange among areas (Coyle 1998). From a fisheries management perspective, it is important to understand movement of adults and resulting stock structure over ecologically relevant timescales (Kerr

et al. 2017). If a high degree of mixing is occurring, the effects of over exploitation may be offset via replenishment from adjacent areas, however if there is little movement and mixing, over exploitation may lead to lasting depletion as areas are not replenished (Edmonds et al. 1991; Hanselman et al. 2007). As research to date suggests *A. australis* primarily undertake small-scale movements, the disproportionate fishing effort throughout this species' range may lead to localised depletions and thus risks to sustainability, particularly if scales of management do not reflect scales of connectivity and movement patterns. Furthering our understanding on the movement patterns and associated connectivity of *A. australis* is crucial in order to ascertain how this species is structured spatially and whether the current scales of management reflect scales of connectivity.

Table 1. Summary of *Acanthopagrus australis* tag-recapture studies, including details of the number of fish tagged and recaptured, whether they were recaptured within or outside the estuary or embayment of tagging, and the maximum time at liberty in days for each study.

Study	Number of fish tagged	Number of fish recaptured	Remained within tag estuary/embayment	Emigrated outside tag estuary/embayment	Maximum time at liberty (days)
Sheaves 1993	137	36	36	0	519
Pollock 1982	2162	147	147	0	Not available
West 1993	12588	589	560	29	1002

A long-term tag-recapture dataset spanning 19 years exists for the Australian east coast stock of *Acanthopagrus australis* (Sparidae). These data were briefly summarised in a fisheries data workshop focusing on the Australian Longfinned Eel (Pease 1993), however the data have not been extensively analysed for *A. australis.* The current study aims to examine broad-scale patterns of movement of *A. australis* on the east coast of Australia using this long-term tag-recapture dataset. Specifically, we examine whether recaptured individuals moved a detectable distance from their tagging location, and if so, the extent and direction (north or south) of that movement. We then investigate potential drivers of movement,

including release latitude, season of release, fork length, time at liberty and direction. The results are considered in terms of informing appropriate scales of stock assessment and fisheries management.

2.2 Methods

Tag-recapture data were available for *A. australis* from two separate tagging programs that were conducted by NSW Fisheries (see Table 2 for details), with individuals tagged between 1980 and 1994, and recaptures reported from 1980 to 1999. The programs used plastic dart tags and metal opercular strap tags (Crossland 1982), with fish being tagged by scientists and recaptured by anglers who reported to the NSW Department of Primary Industries, Fisheries. Details recorded at both tag and recapture included date, fish length and location (geographical place names). During this period, 24 869 individuals were tagged and released along ~ 800 km of coastline, between latitudes 28 and 36°S (Fig 1). The majority of releases were made between 28 and 31°S, with 54% of individuals released between 1988 and 1989 and only 11.7% released prior to 1988.

Table 2. Summary of tagging programs that provided data for this study, including the project investigators, tagging periods, estuaries where fish were tagged, sampling methods and tag types used.

Investigators	Tagging Period	Estuaries	Sampling Methods	Tag Type
John Virgona	1980 – 1981	Lake Macquarie	Beach seine	Metal opercular
Robert Kearney	1988-1994	Richmond River	Beach seine	Plastic dart
Ron West		Clarence River	Trawl	
Glen Cuthbert		Bellinger River		
Trudy Walford		Kalang River		
David Foster		Nambucca River		
		Macleay River		
		Shoalhaven River		
		St Georges Basin		
		Lake Conjola		
		Burrill Lake		

2.2.1 Data processing

Data were first checked for reporting errors prior to analysis and any records that were missing relevant fields (i.e. dates, locations) or contained implausible or conflicting information (i.e. shrinkage) at either release or recapture were excluded from further analysis. The distance moved (km) for each individual was estimated using the straight-line distance between release and recapture locations. However, the reporting of release and recapture locations using place name, rather than coordinates, affected the precision with which geographical positions could be resolved. Recaptured *A. australis* were therefore allocated as having moved or not, based on the distance between tag and recapture locations relative to the precision of the reported location names. The precision of reported locations was determined by the length of coastline of the location, as defined by council boundaries. Records that had generic location names were assigned latitudes and longitudes at their centres using Google Earth. For instance, individuals with a reported tag and recapture location of 'Burrill Lake' would be recorded as 'zero' movers, despite the individual potentially moving up to 5 km within this geographical location (maximum length of the jurisdictional boundary). Precision estimates for locations ranged from 0.1 to 10 km, with 88 % of individuals subject to ≤ 2 km precision.

2.2.2 Data analysis

Nonlinear statistical modelling was used to assess potential drivers of movement. As 37 % of recaptured individuals were deemed as having no movement, a two-step modelling approach was used, to first examine what factors influenced the likelihood of recapturing the individual at the location of release, and then subsequently examine the factors that influenced the distance of movement, for the subset of individuals that did move.

A Generalised Additive Model (GAM) was used to examine whether the likelihood of recapturing the individual at the location of release (binary variable i.e. 'yes' or 'no', hereafter referred to as the "Odds of movement") was influenced by time at liberty (measured in days; hereafter "Days"), body size at release (fork length in mm; hereafter "Length"), Austral season of release (hereafter "Season") or latitude of release (in degrees; hereafter "Latitude"). A second GAM was used to investigate whether the distance moved was influenced by the aforementioned factors, as well as an additional variable - direction of movement (north or south; hereafter "Direction"). This GAM only incorporated individuals that were deemed to have moved from their tagging location (see explanation above). The model terms were selected because they were either of direct interest (i.e. spatial and temporal factors), or they are known to influence fish movement and need to be accounted for when attempting to understand the effect of primary spatial and temporal factors (e.g. Days and Length; Gillanders et al. 2001; Fowler et al. 2018). The model terms Latitude, Direction and Season were included, because they have previously been observed to influence movement in several fish species (Kuliskova et al. 2009; Fowler et al. 2018; Stewart et al. 2019).

A GAM was selected for both investigations as preliminary data exploration indicated potentially complex non-linear relationships between the response variable (odds/distance) and the continuous predictor variables for both datasets. For the odds of movement model, the binomial distribution with a logit link was selected due to the binary nature of the response variable. For the model of distance moved, the gamma distribution with a log link was adopted due to the positive continuous response variable and pattern of model residuals relative to that from an equivalent model using the normal distribution. Model improvement using the gamma distribution relative to the normal distribution was confirmed through

comparison of Akaike's Information Criterion (AIC). Model selection was based on AIC, with the lowest value representing the best model.

Modelling was completed using the gam function in the 'mgcv' package (v.1.8.31, Wood 2017) in R (v.3.6.3). Smooth model terms were integrated for all continuous predictor variables. Season was retained as a parametric predictor variable in both models, with Direction included as an additional parametric predictor in the Distance model. Selection of model terms and optimisation of smoothing functions was completed automatically by using the 'select' argument within the gam function in the 'mgcv' package. The 'select' argument adds an additional penalty to each smooth so that terms with parameters that tend towards infinity are penalised to zero and dropped from the model, in order to achieve a balance between goodness of fit and parsimony (Marra and Wood 2011). The upper limit to the effective degrees of freedom (edf) for smooth terms was set at k = 6 and the appropriateness of this choice was examined using the *gam.check* function to ensure edfs were not overly restricted. The quality of the model fit was assessed using the deviance explained by the final model. Prior to analyses, data were explored using boxplots, scatterplots and Cleveland plots following the protocol of Zuur et al. (2010). Concurvity among model terms was investigated using the concurvity function in the 'mgcv' package, which is a generalisation of collinearity that appears when a smooth model term can be approximated by one or more of the other smooth terms (Wood 2011).

2.3 Results

Of the 24 869 individuals tagged, 2 036 individuals were recaptured and reported along the NSW and QLD coast, accounting for ~ 8 % of tagged fish. Recaptured individuals were recorded over a 19-year period from 1980 to 1999, spanning 11° latitude between 25 and 36°S (Fig. 1). Days at liberty ranged between 0 and 1 467 days (~ 4 years), with straight-line

distance moved ranging from 0 to 832 km. Length at tagging of recaptured individuals ranged from 151 to 405 mm, with a mean fork length of 230 mm. *A. australis* have been reported to reach maturity at fork lengths ranging from 175 and 205 mm in QLD (Pollock 1982), thus the results of the current study mainly pertain to the adult population. Following data checking, 133 records were removed (~7 % of recaptures) (see Section 2.1), leaving 1903 individuals for further analysis.

Of the 1 903 individuals available for analysis, 86.3 % were recaptured within 20 km of their tagging location, with 77.8 and 61.7 % recaptured within 10 and 5 km, respectively. Median distance between release and recapture location was ~ 2.5 km, which did not increase when individuals at liberty < 30 days were excluded. Of the 1 903 recaptures, 37 % (712) were deemed as having no detectable movement from their tagging location, with these individuals at liberty for an average of ~ 236 days. Of the individuals that did move a detectable distance, ~ 81 % were recaptured within 25 km or their release location, with ~ 13 % of individuals moving farther than 100 km and only ~ 4 % of individuals moving farther than 300 km (Fig. 2). Individuals that moved distances greater than 100 km were at liberty for an average of ~ 434 days. Of the individuals that moved, 62% travelled in a northerly direction.
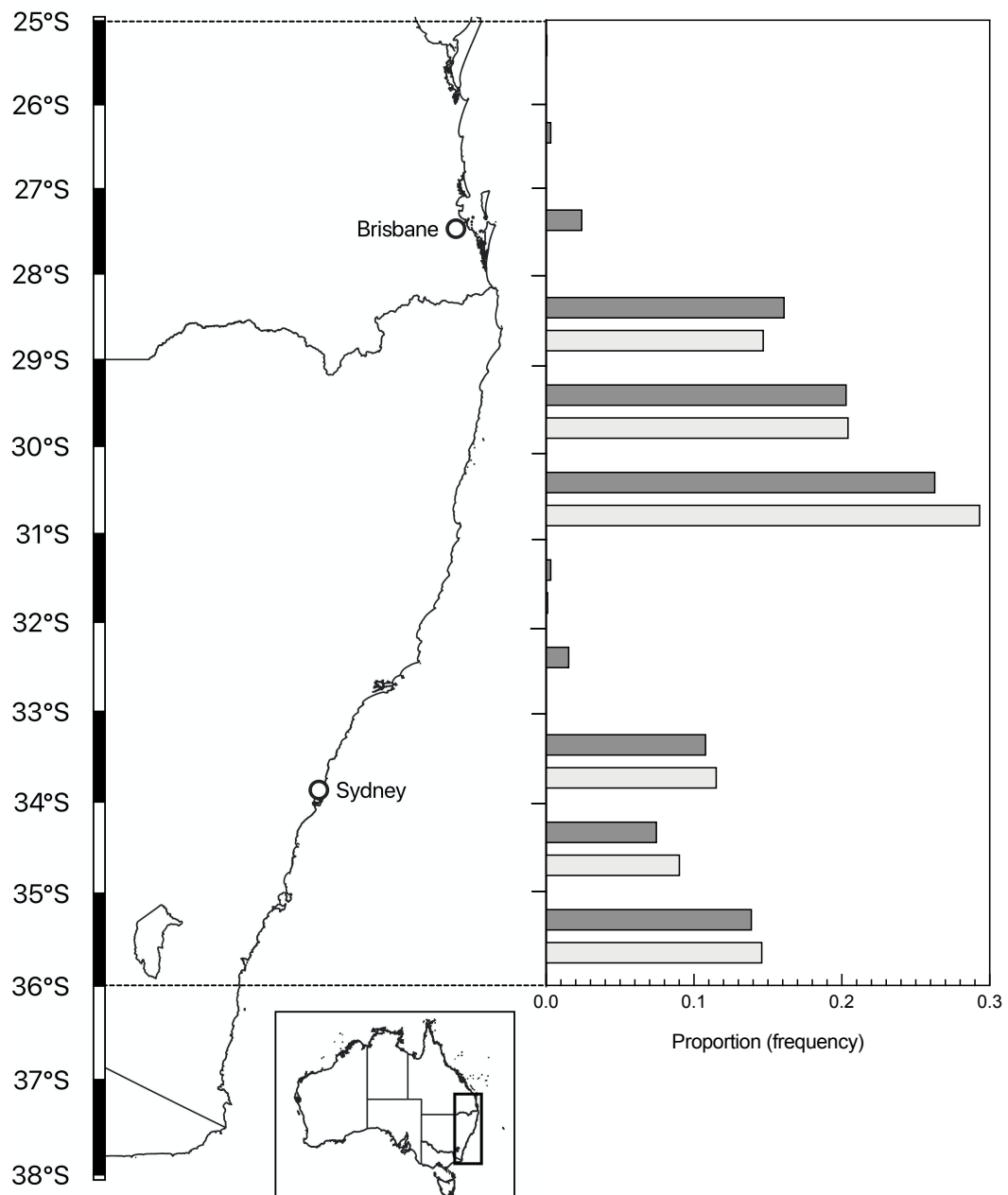
Figure 1. Map of the NSW coast indicating the proportion of releases (light bars) and recaptures (dark bars) of *Acanthopagrus australis* at each degree of latitude. Release proportion includes all individuals tagged and released (~25 000), while recapture proportion includes all individuals recaptured and reported (~ 2 000).
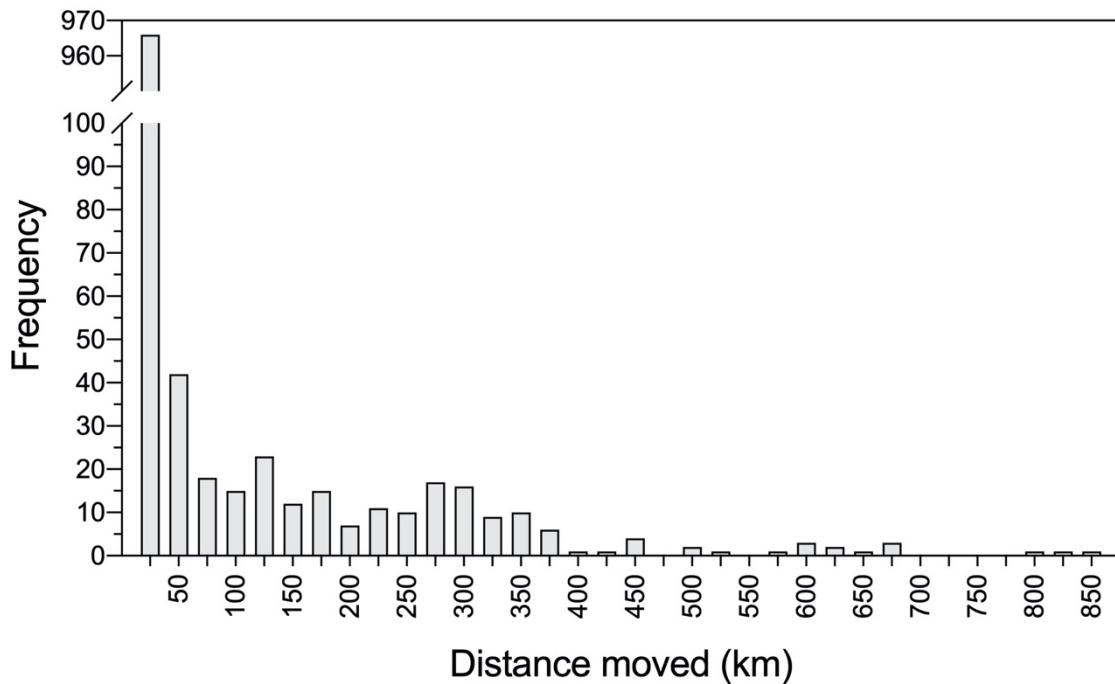
Figure 2. Distribution of movement distance for *Acanthopagrus australis* that were deemed as having moved a detectable distance from their tagging location (*n* = 1191). Note the break in the y-axis.

For the odds of movement modelling (*n* = 1889), the model selection procedure retained the predictors Days, Length and Season. The smooth term Latitude was penalised out of the model, with an edf approaching 0 (Table 3). Days was a significant predictor of odds of movement, with odds increasing linearly with days at liberty until a plateau at ~ 800 days, after which the relationship flattened (Fig. 3). Length was also a significant predictor of odds of movement, with odds increasing linearly with length (Fig. 3), as indicated by the edf (β) approaching 1 (Table 3). Odds of movement were significantly greater in Autumn relative to all other seasons (Fig. 3; Table 3). Despite the significant relationships detected, the selected model explained only 1.9% of null deviance.

For the model of distance moved (*n* = 1185), model selection retained all predictor variables (Table 4). Days was again a significant predictor of distance moved, with distance increasing with days at liberty until ~ 650 days, beyond which the relationship flattened (Fig 4; Table 4). Latitude was also a significant predictor, with distance moved generally greater at

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intermediate latitudes, and two peaks observed at ~33.5° and ~31°S (Fig 4; Table 4). Body

length had little influence on distance moved and was not found to be a significant predictor

(Fig 4; Table 4). A southerly direction of movement decreased the distance moved by a

factor of 0.22 relative to northerly movements (Fig. 4; Table 4). Season had a marginal

impact on distance moved, with the apparently reduced movement in winter relative to

autumn approaching significance, and intermediate values in spring and summer (Fig 4;

Table 4). Overall the model explained 34.4 % of null deviance.

Table 3. Model results for the generalised additive model of *Acanthopagrus australis* likelihood of movement. Values in parentheses specify 95% confidence limits around parametric estimates, which are back transformed from the modelled (log) scale. *s()* signifies smooth terms; β signifies effective degrees of freedom (degree of nonlinearity) for smooth terms or the coefficient estimate for the parametric Season terms. * denotes significant results.

Model term	Data range	β	p
s(Days)	0 – 1370	1.255	0.005*
s(Length)	151 – 342 mm FL	0.954	< 0.001*
s(Latitude)	-28.9 to -35.4° S	0.001	0.655
Season_Spring		0.679 (0.504-0.915)	0.011*
Season_Summer		0.584 (0.452-0.755)	< 0.001*
Season_Winter		0.600 (0.456-0.790)	< 0.001*

Table 4. Model results for the generalised additive model of movement distance for *Acanthopagrus australis*. Values in parentheses specify 95% confidence limits around parametric estimates, which are back transformed from the modelled (log) scale. *s()* signifies smooth terms; β signifies effective degrees of freedom (degree of nonlinearity) for smooth terms or the coefficient estimate for the parametric Season terms. * denotes significant results.

Model term	Data range	β	p
s(Days)	0 – 1293	3.817	<0.001*
s(Length)	159 – 342 mm FL	1.109	0.405
s(Latitude)	28.9 – 35.4° S	4.804	<0.001*
Direction_South		0.223 (0.178-0.281)	<0.001*
Season_Spring		0.895 (0.640-1.250)	0.515
Season_Summer		1.053 (0.783-1.414)	0.734
Season_Winter		0.726 (0.526-1.002)	0.052
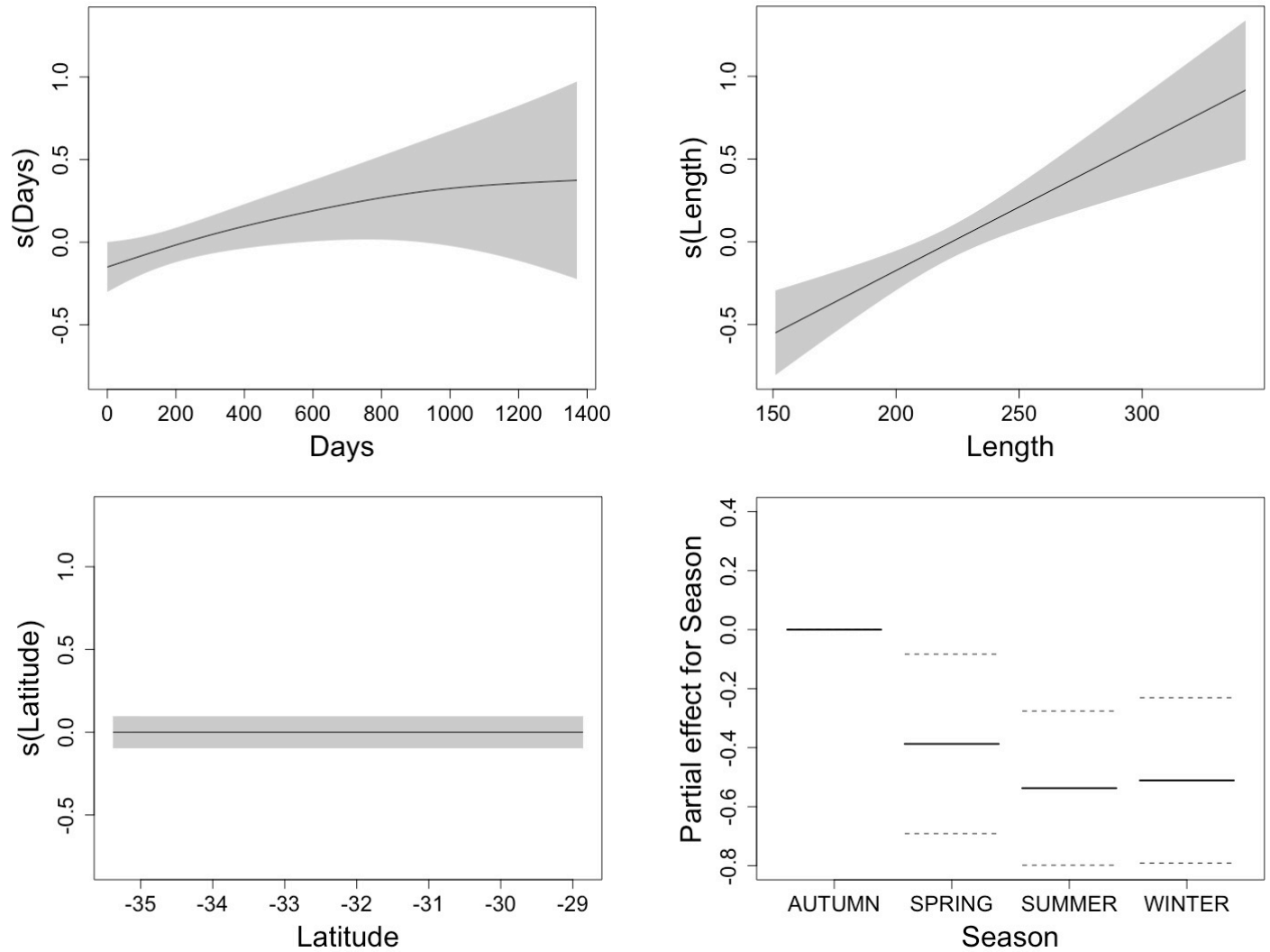
Figure 3. Partial effects of smooth terms and the parametric term Season for the generalised additive model of the odds of movement for *Acanthopagrus australis*. The contribution of the smoother to the model's fitted values are shown on the *y*-axis. Solid lines represent the model estimates; shaded regions and dashed lines indicate 95% confidence intervals. Length is fork length in mm and latitude is degrees south. The values for Season are on the modelled (log) scale.
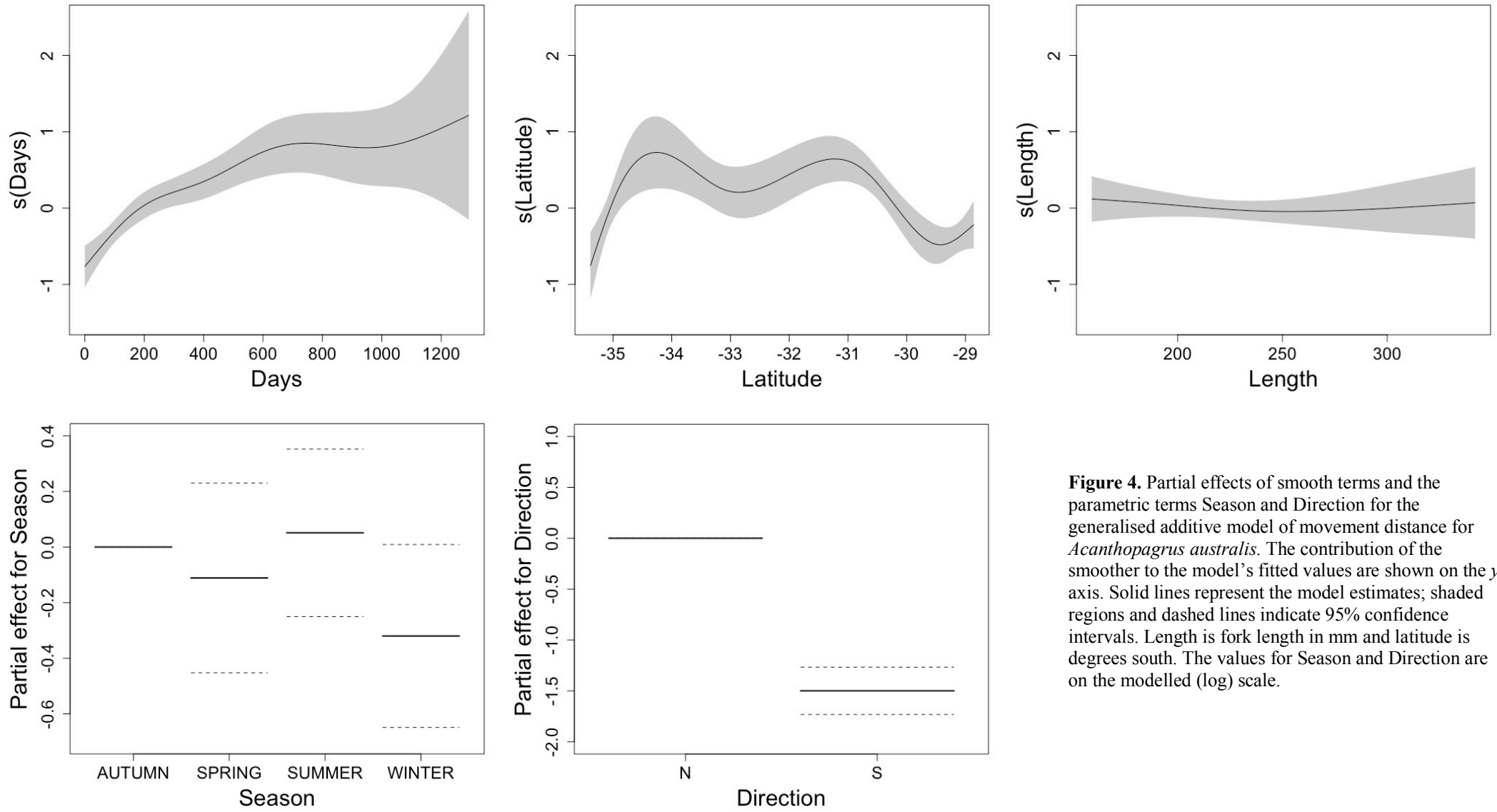
Figure 4. Partial effects of smooth terms and the parametric terms Season and Direction for the generalised additive model of movement distance for *Acanthopagrus australis*. The contribution of the smoother to the model's fitted values are shown on the *y*-axis. Solid lines represent the model estimates; shaded regions and dashed lines indicate 95% confidence intervals. Length is fork length in mm and latitude is degrees south. The values for Season and Direction are on the modelled (log) scale.

2.4 Discussion

The current study confirms and extends our knowledge of the movement of *Acanthopagrus australis* on Australia's east coast. Despite this species' propensity to move long distances, our results suggest that movement of adult *A. australis* may be restricted over the scale of fisheries management in the region (~1000 km), as a high proportion of individuals remain resident with only a minority undertaking long distance movements. The results imply management of *A. australis* at a statewide scale may require re-assessment, taking into consideration that occasional larger movements between areas may not be sufficient to ensure replenishment of localised mortality and subpopulations may be unknowingly depleted due to the uneven spread of fishing effort along the NSW coast (Coyle 1998; West et al. 2015; Kerr et al. 2017).

Results from the current study indicate movement of *A. australis* is largely restricted over small (1 - 10 km) spatial scales, which is consistent with smaller scale tag-recapture studies from QLD and NSW (Pollock 1982; Sheaves 1993; West 1993). The median distance moved by *A. australis* in the present study was just 2.5 km, with > 75 % of individuals recaptured within 10 km of their release location. Research in QLD has found juveniles and adults generally move at scales < 6 km and apart from some large (10 – 90 km) scale movements to or from coastal spawning areas this study found no indication of movement outside an embayment (Pollock 1982). Similarly, Sheaves (1993) conducted a small-scale tag recapture study within a creek in Northern QLD and found that 75% of recaptured *A. australis* were within 240 m of their release location, with no individuals recaptured outside the creek. Acoustic tracking of 10 adult *A. australis* in NSW found that of the seven that were subsequently detected by receivers, all individuals displayed a small home range (< 0.3 km^2) suggesting a high degree of site fidelity (Gannon et al. 2015).

In contrast to some work in QLD and NSW, we did observe movements outside the estuary in which individuals were tagged, likely due to the broader temporal and spatial scales examined. One individual was recaptured over 800 km north, travelling from Lake Conjola on the NSW south coast, to Kingscliff near the QLD border. This is the largest movement recorded for this species. This is consistent with tagging research from NSW, which indicates a small proportion of individuals undertake larger migrations (>200 km) (West 1993; Lowry et al. 2017; van der Meulen 2018). West (1993) conducted a long-term tag recapture study in Northern NSW, and found that 4 % of individuals emigrated outside their release estuary, while the majority of individuals remained in close proximity to their release location. Acoustic tracking of 39 *A. australis* at natural and artificial reefs in Lake Macquarie NSW also detected longer range movements (>200 km), however the majority of tagged fish tended to remain associated with their release site, with 36 % of fish detected by the array for > 1 year (Lowry et al. 2017). Acoustic tracking of 14 *A. australis* within the Shoalhaven River estuary in NSW identified small core areas (< 5 km), however six individuals appeared to make offshore movements at the conclusion of their detection period, with one individual recaptured > 250 km to the north (van der Meulen 2018). The contrasting scales of movement between studies may reflect differences in movement behaviours between locations or habitats, with possibly smaller movements occurring in QLD, the northern part of this species range. Alternatively, the disparities may reflect differences between the techniques, spatial and temporal scales employed in these studies.

Movement distances observed for *A. australis* in the current study show the potential for demographic structuring of this species along the east coast. Only 8.5 % of individuals were recaptured > 100 km from their release location, suggesting limited exchange between areas separated by such distances, with exchange decreasing with increasing distance. Adult exchange is likely restricted between some subgroups of the population, considering the large

geographic range of *A. australis* along the coast (~2000 km). The lack of extensive

connectivity suggests this species may be organised as a series of overlapping

subpopulations, distributed linearly along the south-east Australian coast, with a small

proportion of the population displaying sporadic long-distance movements. This population

structuring may lead to demographic variation along the coast, due to varying environmental

conditions spatially and/or differential fishing pressure. Growth dynamics of *A. australis*

have been found to vary spatially along the NSW coast (Gray 2015). Growth rates, and thus

relative productivity, may be reduced as water temperatures decrease from north to south.

Latitudinal gradients in demographic characteristics are well known for teleosts distributed

over broad geographic distances (Heibo et al. 2005; Sala-Bozano & Mariani 2011; Stocks et

al. 2014).

Research from different geographic regions suggests latitudinal variations in growth rates for

A. australis, which may be related to latitudinal variation in temperature, as rates of growth

after settlement are temperature dependent (Pollock 1982b; Worthington et al. 1992; Griffiths

2001). Fish in their first year have been found to grow to only 78-100mm in NSW estuaries

(West 1993; Griffiths 2001), while they grow to 100-145mm in the warmer jurisdiction to the

north, QLD (Pollock 1982b; Pollock et al. 1983). Regions that experience greater fishing

pressure may in turn experience truncation of length and age structure, as larger, older

individuals are lost and not subsequently replenished due to generally limited movement

(Walsh et al. 2010).

Although our model on the odds of movement explained little deviance, it did indicate that

individuals were significantly more likely to move in Autumn relative to other seasons. This

coincides with known seasons of movement for *A. australis*, which commence pre-spawning

migrations to estuary mouths and coastal surf bars during Autumn (April to June) in NSW

(Rowland 1984; West 1993; Gray et al. 2000; Roberts & Ayre 2010). Migration is thought to

be related to spawning activity for many teleosts (Ward et al. 2003), and is the major driver of movement in species with otherwise generally sedentary adult stages (Sheaves et al. 1999; Tracey et al. 2020).

Movement of *A. australis* was also found to be significantly more likely with increasing body length, however length had little influence on movement distance. This is possibly related to the close association of juvenile *A. australis* with estuaries (Pollock 1982; Griffiths 2001), leading to a greater likelihood of registering movement of larger individuals that were at a critical size, enabling them to move into coastal areas. *A. australis* that did move a detectable distance were more likely to travel in a northerly direction and individuals that travelled in a northerly direction were more likely to move a greater distance than those that moved in a southerly direction. Northerly migration of adult *A. australis* has previously been suggested (Roberts & Ayre 2010) and is supported by observed variations in age structures along the coast (Gray et al. 2000). Previous tagging studies have also observed predominantly northerly movement, particularly for individuals emigrating out of estuaries (West 1993). Northerly migration of numerous teleosts along Australia's south east coast has been documented (Sumpton et al. 2003; Hughes et al. 2015), and is suggested to be an evolved compensation for the corresponding southerly movement of larvae via the East Australian Current (EAC) to suitable habitat (Ward et al. 2003).

The large variation in movement distances among *A. australis* individuals suggests multiple behavioural types may be present. This occurrence in which both resident and migratory movement patterns occur within a single species, known as partial migration, was initially recognised in species that undertake extensive diadromous migrations (Jonsson & Jonsson 1993), but is increasingly being documented in various teleosts, including several sparids (Robichaud & Rose 2004; Kerr et al. 2009; Parsons et al. 2011; Gillanders et al. 2015; Stewart et al. 2019). Partial migration is thought to indicate population resilience and may

increase both productivity and abundance (Kerr et al. 2009; Kerr et al. 2010). The drivers that determine whether individuals migrate or remain resident are not known for *A. australis*, but may be associated with environmental factors or individual genetics. Length at tagging did not have much of an effect on movement distance in the current study, suggesting ontogeny is unlikely a driving factor for migration in adult *A. australis*. Environmental factors may be important in influencing whether *A. australis* remain resident or migrate. Habitat quality and population density have been suggested as potential drivers of different movement behaviours for another sparid, *P. auratus* (Parsons et al. 2011; Stewart et al. 2019). Individuals may assume residency when high quality habitat with low population density is available, and choose to move due to poor habitat quality and/or high population densities (Parsons et al. 2011). Further research is evidently necessary to understand these differences in movement behaviour in *A. australis*. This partial migration strategy apparent in the current study may explain why *A. australis* display genetic homogeneity throughout their range, with the small number of migrating individuals coupled with larval distribution sufficient to maintain panmixia (Roberts & Ayre 2010). Additionally, genetic homogeneity of *A.australis* may reflect structure unfolding over evolutionary timescales, rather than potential segregation occurring over the shorter ecological timescales which are relevant to fisheries management (Kritzer & Sale 2004).

Our finding that *A. australis* exhibit restricted movement patterns supports the growing body of literature that supposedly mobile species can benefit from relatively small marine protected areas (MPAs) (Apostolaki et al. 2002; Willis et al. 2003; Curley et al. 2013b; Harasti et al. 2015). A study into a small (0.1 km^2) partial-take marine protected area in NSW demonstrated increased densities of legal-sized *A. australis* within the MPA (Curley et al. 2013b). Similarly, Pillans (2006) found relative densities and mean size of *A. australis* to be significantly higher in two small (1.9 and 5.7 km^2) coastal marine reserves in Morton Bay,

QLD. Increased densities of *A. australis* in MPAs is unsurprising in such populated coastal areas that experience substantial fishing pressure, considering only a minority of individuals move long distances, as demonstrated in our results. The benefit of protected areas to overall stock status is uncertain, however increased biomass of *A. australis* identified within MPAs (Pillans 2006) may increase reproductive potential through larval dispersal beyond MPA boundaries (Harrison et al. 2012). Although levels of spill-over from MPA boundaries are unknown for *A. australis*, if individual migrations are partially driven by habitat productivity and capacity, the potential partial migration strategy identified in the current study may increase levels of adult spill-over from such areas. Further research focused on how population density might affect *A. australis* behaviour would aid in assessing the benefits of MPAs to the stock and fisheries for *A. australis*.

The tag recapture data employed in the current study allowed investigation of movement at spatial and temporal scales rarely achieved through other methods, providing individualised estimates of movement. The broad spatial scale investigated afforded us a greater likelihood of identifying long-distance movements, which otherwise, may have gone unnoticed. Nonetheless, tag-recapture datasets have specific limitations that may reduce their efficacy relative to other methods (Gillanders et al. 2001). One limitation present in the current dataset, and common to all physical tag-recapture studies, is that the location of each individual was only available at two time points, with no information on fish movement between these times. Consequently, it is possible individuals moved considerable distances from their tagging location before returning to this area prior to recapture, however, this is considered unlikely among estuaries due to the temporal scale of this study, and any intermediate scale movement that may have occurred at least indicates homing of *A. australis* at small spatial scales (< 20 km). Further, acoustic tagging work provides support that this limitation was unlikely to influence our findings (Lowry et al. 2017). Lowry et al. 2017

conducted a long-term (3 years) acoustic tagging study which found fish tended to reside at their release location, with 36% of fish detected by the array for > 1 year and the seven fish known to have left the array not recorded returning to the area.

The current study supports a growing body of evidence that fishes able to move long distances (> 500 km) may exhibit limited adult movement (Fowler et al. 2018; Stewart et al. 2019). Despite being considered as a single biological stock, and managed as such by each jurisdiction, there is evidence suggesting that *A. australis* may need to be assessed and managed at more local scales, particularly considering their close association with estuaries. In south-eastern Australia, the idea that many mobile fish species represent single stocks for management purposes, on the basis of the strong southward flow of the EAC and observed long-distance movements by some individuals, is being increasingly contested as more comprehensive stock structure studies are performed (Izzo et al. 2017). Understanding patterns of movement and connectivity is especially critical for species managed by multiple jurisdictions, as scales of multiple management programs may not sufficiently reflect population structure (Fowler et al. 2018). The current study demonstrates the utility of tag-recapture datasets in contributing to our understanding of fish movement patterns, as they allow examination at broad spatial scales with large numbers of individuals, complementing more intricate approaches like acoustic telemetry.

Chapter 3   Otolith elemental signatures and shape descriptors demonstrate potential population structuring of the estuarine obligate sparid *Acanthopagrus australis*, in southeastern Australia.

3.0 Abstract

Effective management of marine fishes requires knowledge of the degree of connectivity among areas, however for many species it remains poorly understood. This paper provides a broad-scale examination of connectivity of *Acanthopagrus australis* among estuaries over ~ 850 km of Australia's south-east coast, integrating information obtained from multiple approaches: otolith elemental signatures and otolith shape indices (n =355). Elemental signatures obtained from the otolith edge using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) differed among estuaries, with differences more apparent among estuaries separated by greater distances. Differences in elemental signatures from the juvenile region of adult otoliths were consistent with patterns of adult separation, suggesting this separation was established early in life. A combination of both elemental data and elliptical Fourier (shape) descriptors of otoliths allowed allocation of individuals to their estuary of capture with varying degrees of accuracy at the differing spatial and temporal scales (overall: 35.3 – 61.3 %, range: 19.0 – 70.0 %). Differences in otolith edge signatures revealed at both the smallest (sites within estuaries) and largest scale of investigation (100s of km) highlight the importance of investigating multiple spatial scales and suggest that the scale of elemental variation may sometimes be too fine for testing segregation at scales of interest to management. The results indicate restricted movement of *A. australis* along the NSW coast, with limited exchange between estuaries > 300 km apart suggesting a series of overlapping subpopulations along the coast and indicating more complex spatial structure than the current scale of management.

3.1 Introduction

Globally, coastal marine fisheries are subject to increasing pressures that threaten their persistence (Hutchings et al. 2000; Mora et al. 2009). Yields are either constant or in decline, effort is increasing and multiple anthropogenic impacts are degrading the systems on which fisheries depend (Worm 2018; Lotze et al. 2019). Stock structure provides the foundation for sustainable fisheries management, as it is the unit at which populations are assessed, and management measures are applied (Hawkins et al. 2016). Recent advances in research into the spatial ecology of fisheries have demonstrated that marine species with little population structure are rare, while the majority exhibit complex spatial structure (Ciannelli et al. 2013). Research has historically focused on the impact spatial structure and connectivity have on population persistence and recovery (Pulliam 1998), but more recently has shifted to address the temporal scales addressed by fisheries scientists, focussing on the resilience and stability of species over ecologically relevant time scales (Kritzer & Sale 2004; Kerr et al. 2017).

Despite the importance of understanding population structure, it remains poorly understood for the majority of fish species. Individuals are typically arranged in a series of local sub-populations that comprise a larger meta-population (Kritzer & Sale 2004; Hawkins et al. 2016). These local populations may be connected through the movement of individuals via either larval transport and/or the movement of post-settlement juveniles and adults (Botsford et al. 2009). The levels of connectivity between such local populations controls the degree to which they are influenced by demographic processes of adjacent populations (Kritzer & Sale 2004). An understanding of this meta-population structuring and the degree of intraspecific exchange between local populations is fundamental in determining spatially appropriate scales of management (Kritzer & Sale 2004, Kerr et al. 2017). Fisheries assessment and management is often jurisdictional rather than biological, and implicitly assumes a species

displays homogenous ecological characteristics across management areas when there is a lack of specific information on population structure (Cadrin 2020), or when there is limited resourcing available for management at sub-jurisdictional scales. In the absence of sufficient information about population dynamics, spatially discrete populations can unknowingly be subjected to localised depletion which threatens their persistence, due to limited replenishment from neighbouring populations (Cianelli et al. 2013).

Analysis of elemental signatures of otoliths provides a useful approach for examining patterns of connectivity and population structure (Elsdon et al. 2008; Fowler et al. 2018). Otoliths, located in the inner ear of teleost fish, are structures composed of calcium carbonate laid down over time. As fish age, elements are accreted and incorporated into this calcium structure in minor and trace quantities, largely facilitated by environmental and endogenous factors, for instance ambient concentration, salinity and diet (Elsdon & Gillanders 2004; Webb et al. 2012). Because otoliths are metabolically inert, this deposition of elements remains intact through time, creating an elemental signature which relates to the environment/s an individual experiences throughout its life. This allows fish movement to be tracked through time, due to the differing water chemistry experienced throughout an individual's life history, which acts as a natural tag. These signatures can be used to investigate long distance movement of fish, as well as spatial and temporal separation, revealing patterns of separation and connectivity among sub-populations (Campana & Thorrold 2001). Otolith elemental composition is commonly measured using either laser ablation (LA) or solution based inductively coupled plasma mass spectrometry (ICP-MS). Solution based methods measure elemental concentrations in whole otoliths, thereby revealing an integrated signature of an individual's entire life history (Ludsin et al. 2006). In contrast, LA-ICP-MS can target discrete areas of the otolith, which allows investigation of distinct portions of a fish's life history (Fairclough et al. 2011).

Otoliths have many applications when studying population structure in fisheries research. Not only can they be used as natural tags via their chemistry, morphological characteristics of otoliths are an efficient tool for identifying groups of fish that have been spatially or temporally structured at some stage in their life history (Campana & Casselman 1993; Keating et al. 2014; Moreira et al. 2019). The shape of an otolith is species specific, however there can also be intraspecific differences in shape due to the effects of environmental and genetic factors on otolith growth patterns (Campana & Neilson 1985; Lombarte & Castellón 1991). Thus differences in otolith shape partly reflect different environmental exposure histories, and can potentially assist in identifying groups of fish which have been spatially structured at some stage during their life history (Keating et al. 2014; Mahé et al. 2019). Elliptical Fourier Analysis is a quantitative, objective method for describing otolith shape that has been increasingly adopted in population discrimination studies (Bird et al. 1986; Keating et al. 2014; Moreira et al. 2019). The use of multiple methodologies when studying population structure and patterns of connectivity has been recommended in order to obtain comparative results, as together, they provide more power and greater accuracy, while allowing the limitations of each individual method to be less influential (Begg and Waldman 1999; Fowler et al. 2015; Izzo et al. 2017).

The sparid Yellowfin Bream (*Acanthopagrus australis*) is one of the most significant fishery resources on Australia's east coast, being particularly popular with recreational fishers, as they tend to inhabit estuaries as well as inshore areas such as rocky reefs (Gannon et al. 2015; West et al. 2015). *A. australis* are distributed along the entire NSW coast, spanning three states and over 2000 km of the east Australian coastline. Classified as fully fished within NSW, *A. australis* are treated as a single stock for management purposes, due to limited knowledge of their movement patterns and population dynamics on a state-wide scale (Curley et al. 2013; West et al. 2015). As population structure and connectivity is poorly

understood for this species, it may be at risk of inadvertent localised depletion if spatial scales of management are not matched to scales of demographic exchange (Cope & Punt 2011). The majority of research into *A. australis* movement has been spatially constrained, often investigating small scale movements within specific areas (Pollock et al. 1982a; Sheaves 1993; Gillanders & Kingford 2003; Meynecke et al. 2008; Butcher et al. 2010; Payne et al. 2013; Taylor et al. 2013; Gannon et al. 2015). Nonetheless, research suggests *A. australis* exhibit strong site fidelity, rarely moving significant distances (Gannon et al. 2015; Taylor et al. 2017; Taylor et al. 2018), suggesting there may be a series of localised sub-populations along the coast with limited demographic exchange. The lack of information on population structure for this important commercial species could threaten their persistence and resilience.

This study aims to examine the population structure and connectivity of *A. australis* on Australia's east coast, in order to inform spatial considerations for management of this fished species. We used otolith chemistry and otolith shape from specimens collected over three spatial scales to determine: (1) whether individuals were spatially segregated across estuaries during their recent life history (elemental signatures at the otolith edge) and over more extended time periods (otolith shape descriptors), and (2) whether patterns of spatial segregation identified for adult *A. australis* were similar to their juvenile life-stage. This aim was achieved by sampling chemistry from both the edge of the otolith and the juvenile zone. Elemental analysis of the juvenile zone of the otolith assumed that similarities in juvenile signatures were the result of individuals remaining in a similar area to their location of capture. Year classes varied among individuals, and thus inter-annual variability in water chemistry would presumably decrease the likelihood of identifying any distinction in juvenile signatures between estuaries. If differences were identified amongst estuaries, this would suggest inter-annual variability in water chemistry was not great enough to dilute distinct

juvenile signatures. Similar patterns between life stages would suggest that spatial segregation observed in adults was established early in life.

3.2 Methods

3.2.1 Study location and sample collection

Acanthopagrus australis are collected throughout the New South Wales (NSW) coast as part of ongoing fisheries monitoring programs undertaken by the NSW Department of Primary Industries (DPI) - Fisheries. The individuals in the current study were sourced from both the NSW DPI Resource Assessment (Port) Monitoring Program (Rowlings et al. 2010) and Perfluoroalkyl Substance Monitoring Program (Taylor & Johnson 2016). Population segregation was explored at three different spatial scales, regional, coastwide and at the site level within the regional scale study estuaries (Figure 5). The decision to test at these two spatial scales (regional & coastwide) was driven by sampling effort, and as such there is some overlap in the spatial scales examined in these individual datasets.

Coastwide estuaries were separated by distances ranging from 45 to 970 km, and spanned six of the seven estuarine fishing regions in NSW (DPI Fisheries 2003). The seven estuaries sampled from north to south were: Richmond River (RR), Clarence River (CR), Wallis Lake (WL), Lake Macquarie (LM), Tuggerah Lake (TL), St Georges Basin (GB) and Wallaga Lake (WA) (Figure 5; Table 5). Individuals ($n = 236$) were collected in two consecutive years, 2008 and 2009. For both years, collection dates were restricted between late January and early April, in order to limit the effect of potential seasonal differences in elemental signatures (Reis-Santos et al. 2012). Individuals were sourced from all seven locations in 2009, however, due to insufficient sampling overlap at WL and WA, only five locations could be examined in 2008 (Table 5). Samples were collected from between three and seven

separate sites within each estuary, in order to account for potential intra-estuarine variability (Reis-Santos et al. 2012). The aim of this was to create a homogenous elemental signature for each estuary by incorporating as much of the potential fine scale elemental variation as possible.
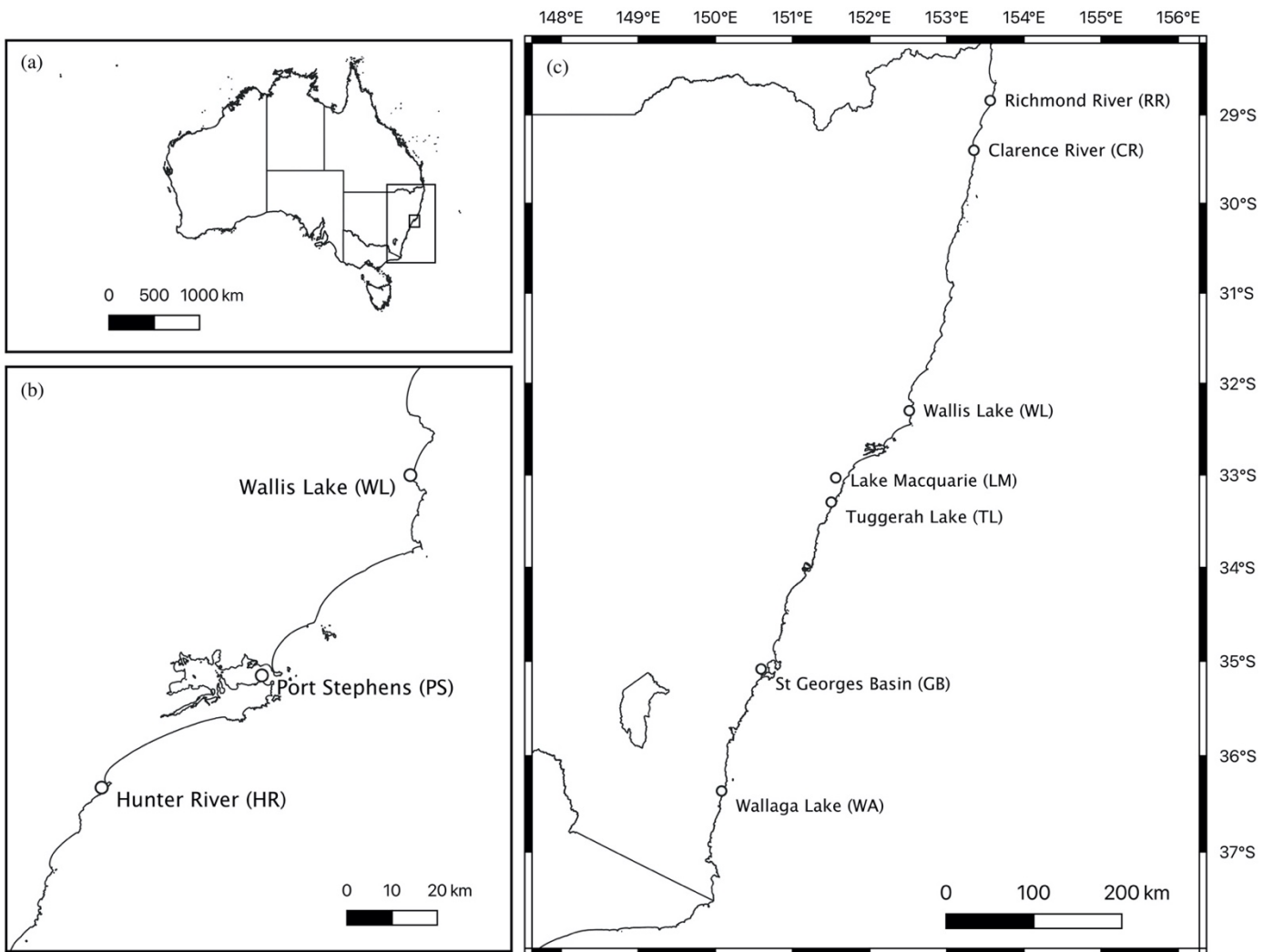
Figure 5. Locations of estuaries sampled on the NSW coast, South-eastern Australia, (a) insets showing locations of (b) and (c) within Australia, (b) the location of regional study estuaries and (c) the location of the larger scale, coastwide study estuaries

Table 5. Sampling summary of *Acanthopagrus australis* used for microchemical and shape analysis at two spatial scales, among region, spanning ~ 1000 km of the NSW coast, and within region, spanning ~ 100km of the NSW coast. Table includes estuary coordinates, date of capture (Year, Month), number of individuals (*N*), Mean fork length and range (in mm), and age range (in years). Estuary abbreviations included here are used in subsequent tables and figures.

Scale	Estuary	Coordinates	Year	Month	*N*	Mean size (range)	Age Range
Coastwide							
	Richmond River (RR)	28° 53' S, 153° 34' E	2008	Feb-Apr	20	249 (222-286)	2 - 18
			2009	Apr	20	238 (223-260)	3 - 13
	Clarence River (CR)	29° 24' S, 153° 20' E	2008	Feb-Mar	20	262 (225-335)	5 - 14
			2009	Feb-Apr	20	253 (225-274)	4 - 11
	Wallis Lake (WL)	32° 15' S, 152° 29' E	2009	Feb-Apr	20	267 (226-359)	6 - 20
	Lake Macquarie (LM)	33° 06' S, 151° 35' E	2008	Feb-Apr	23	255 (224-353)	4 - 14
			2009	Feb	20	251 (227-338)	5 - 16
	Tuggerah Lake (TL)	33° 18' S, 151° 30' E	2008	Feb-Apr	15	250 (224-288)	5 - 10
			2009	Jan	19	243 (221-275)	3 - 9
	St Georges Basin (GB)	35° 07' S, 150° 36' E	2008	Feb	21	250 (225-360)	3 - 23
			2009	Feb-Mar	20	266 (227-331)	2 - 12
	Wallaga Lake (WA)	36° 22' S, 150° 04' E	2009	Feb	18	248 (221-386)	4 – 13
Regional							
	Wallis Lake (WL)	32° 15' S, 152° 29' E	2016	Mar	40	253 (225-289)	
	Port Stephens (PS)	32° 42' S, 152° 9' E	2015	Dec	40	255 (225-295)	
	Hunter River (HR)	32° 55' S, 151° 47' E	2016	Feb	39	260 (225-315)	

Regional estuaries were situated within NSW Fisheries Region 4 (between 31°44' and 33°25' latitude) and included Wallis Lake (WL), Port Stephens (PS) and Hunter River (HR) (Figure 1c; Table 5). These estuaries were separated by distances ranging from 40 to 125 km. Again, individuals were selected to maintain a tight collection window of no more than four months as chemistry is known to vary temporally within estuaries (Reis-Santos et al. 2012). Individuals ($n = 119$) were sourced from two sites within each estuary between December 2015 and March 2016, with sites between 3 and 13 km apart.

3.2.2 Otolith preparation

Otoliths from 355 individuals were selected for otolith microchemistry and shape analysis. Juveniles (< 220 mm) were excluded as they may not have an adequate post-settlement section of their otolith, as well as to ensure findings were relevant to the fished population. A similar range of sizes were selected across estuaries, however age varied to some degree (Table 5). Wherever possible, the left otolith from each individual was used for both microchemical and shape analysis. This was done to avoid potential differences between an individual's two otoliths (Mahé et al. 2019). Otoliths were carefully inspected and cleaned prior to imaging, ensuring their outline was intact and no foreign material was present. Otoliths were imaged whole using transmitted light, a dissection microscope (Olympus SZ61 at 0.80 x magnification) and image analysis system (Teledyne QImaging Micropublisher™ 5.0 RTV). Otoliths were positioned with the distal surface facing upwards and the rostral-postrostral axis aligned vertically during imaging.

Post imaging, otoliths were sectioned transversely through their primordium, using a Gemmasta™ lapidary saw fitted with a lubricated diamond edged blade. Four sections were taken from each otolith, inspected microscopically and the optimum section selected to ensure the primordium of each otolith was included. Thermoplastic cement (Crystalbond™

509) was used to mount ~ 40 otolith sections on each slide, so that multiple otoliths could fit in the laser ablation (LA) chamber during each analytical session. Otoliths were randomly ordered throughout the process to avoid any confounding effects of separate analytical sessions (Campana et al. 2000). Slides were then ground and polished using 1200 grit wet and dry paper, followed by 9 μm and 3 μm lapping film. Age estimates obtained from sectioned otoliths were available for the archived otoliths. Sections were rinsed to remove any residue from polishing, sonicated for three mins to remove residual surface contaminants, air dried and stored individually.

3.2.3 Otolith microchemistry

LA-ICP-MS was carried out at the UTS chemical technologies analytical suite using an Agilent Technologies 7700 Series ICP-MS coupled to a Teledyne photon machines LSX-213 G2+ Laser Ablation unit. Preliminary analyses were conducted to identify a suite of elements that were consistently above detection limits, as well as to ascertain the ideal settings to obtain data with sufficient precision and accuracy, while maintaining a relatively small ablation size in order to acquire data for a small enough temporal window (Chang et al. 2012). As the specifics of analysis and data processing can have a profound effect on reported compositional data (Branson et al. 2019), we provide an outline of the instrument's operational parameters (Table 6).

Eight elements were initially assayed, with only four elements along with Ca^{43} consistently present above limits of detection (LOD). Sr^{88}, Ba^{138}, Mg^{24}, Na^{23} and Ca^{43} were selected for elemental analysis and were above LOD in > 94% of samples. The precision of the instrument was approximated from frequent analyses of the National Institute of Standards and Technology (NIST) 612 standard reference material throughout analytical runs (Pearce et al. 1997). Pre-ablations of 50 μm diameter were performed at each ablation site to remove

any remaining surface contamination. Duplicate 30 μm diameter ablations were then made on the most recently deposited material at the edge of the otolith, recording the signature prior to capture (hereafter "edge signature"), as well as in the juvenile zone of the otolith, between the core and the first annual increment (hereafter "juvenile signature", Figure 2). Duplicate ablations were performed at each area of investigation within the otolith, as multiple ablations are beneficial in accounting for elemental variation within individual otoliths (Payan et al. 1999; Di Franco et al. 2014). Otolith increments have been validated as being laid down annually for Yellowfin Bream (Gray et al. 2000; Gray 2015).

Table 6. Outline of Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) operational parameters used for elemental analysis of *Acanthopagrus australis* otoliths

Instrument parameter	Setting
Laser output	60 percent
Fluence	6.58 Joules/cm^2
Repetition rate	15 Hertz
Shot Count	225
Spot size	30 micrometres
Dwell time	15 seconds

For regional samples, additional ablations were made within the increment preceding the otolith edge, corresponding to growth during the previous year (Figure 2). These additional ablations were required for temporal replication as there was no additional collection year available for regional samples. This approach assumed that individuals were present at their site of capture in the previous year. Spots were examined after each ablation run, and those that were not optimally located were repeated, to ensure they represented the correct time period, while also avoiding potential edge contamination. Spot position was standardised throughout samples, located adjacent to the *sulcus acusticus* (Figure 6), in order to lessen
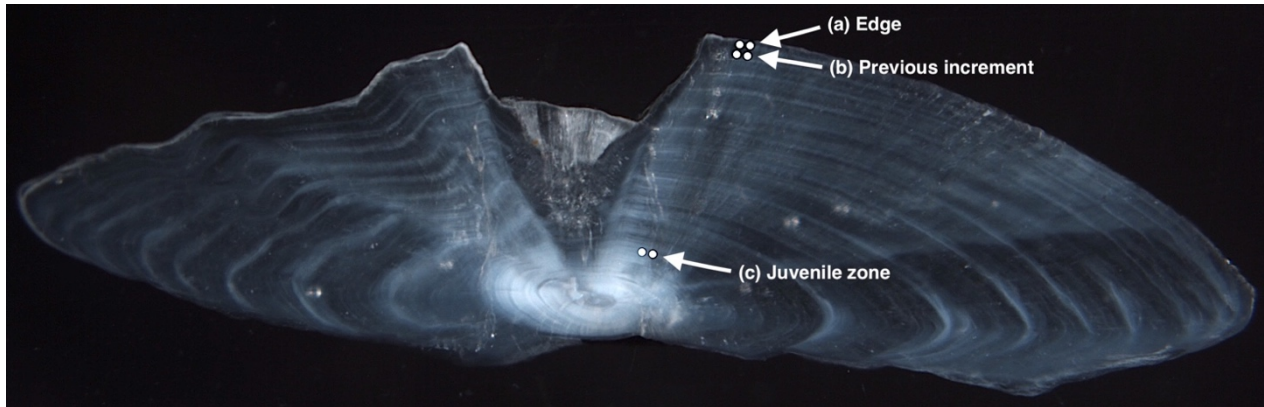
Figure 6. *Acanthopagrus australis* otolith section showing the location of laser ablation spots for ICPMS at (a) the otolith edge or margin, representing the period ~ 3 to 9 months prior to capture, (b) the previous increment, representing a similar amount of time, during the period 12 to 24 months prior to capture, and (c) the juvenile section of the adult otolith.

potential error that can arise from varying elemental concentrations within individual otoliths (Geffen et al. 2013; Di Franco et al. 2014).

An average elemental signature was calculated from the duplicate laser spots on each sample. The Python module *Latools* was used for data processing and reduction of LA-ICP-MS data, as this recent, semi-automated platform allows for reproducible reduction of the complex data sets associated with LA-ICP-MS (Branson et al. 2019). *Latools* performs similarly to other available data reduction methods, however allows for reproduction by other users in order to evaluate processing methodologies applied to a data set (Branson et al. 2019). LA-ICP-MS signals were plotted, de-spiked using exponential decay and noise functions to remove outliers, and background corrected. Data were separated from background counts using the *autorange*() tool, which excludes regions on both sides of the transition from both signal and background regions. This is based on the full-width-at-half-maximum (FWHM) of the Gaussian fit. Data were removed from the signal region at the beginning of the ablation at $2 \times$ FWHM and at the end of the ablation at $4 \times$ FWHM in order to select data points from the central region of the ablation to account for initial spikes in data and a diminishing signal over the 15 s dwell time. A ratio was calculated to normalise data to the internal standard,

Ca[43], and then a time sensitive calibration was generated using the standard reference material (NIST612) measurements, to correct for instrumental drift throughout each analytical session.

3.2.4 Otolith shape

Elliptical Fourier analysis (EFA) was used to quantify otolith shape, which describes the outline of the otolith edge using a series of increasingly high frequency ellipses (Kuhl & Giardiana 1982). EFA uses these ellipses, or harmonics, to describe any closed two-dimensional shape, and has been adopted in various fields in order to quantify biological shapes (Iwata & Ukai 2002; Neto et al. 2006; Keating et al. 2014). Before software processing, images were adjusted to ensure a solid outline was evident around each otolith. The software SHAPE (Iwata & Ukai 2002, v.1.3) was used to generate harmonics, which is based on Kuhl & Giardiana's (1982) concept of EFA. This program detects outlines using a threshold pixel value to convert the image data to binary silhouettes, which are then converted into a chain code (Freeman, 1974). Fifty harmonics were generated for each otolith, creating 200 standardised coefficients per sample (four per harmonic). The average Fourier power spectrum was calculated to identify the minimum number of harmonics needed to describe > 99.99% of the otolith shape, using the following formula:

$$PF_n = \frac{A_n^2 + B_n^2 + C_n^2 + D_n^2}{2}$$

$$PF_c = \sum_{1}^{n} PF_n$$

where A_n, B_n, C_n and D_n are the coefficients of the nth harmonic (Lord et al. 2012). Harmonics were normalised to account for any variations in size, rotation, and start point by setting the coefficients of the first harmonic at fixed values (A_1=1; B_1=C_1=0) (Tracey et al. 2006). The

power spectrum identified 99.99% of the otolith shape could be represented by 73 coefficients (19 harmonics), which were used as the shape characteristics for analysis.

3.2.5 Statistical analyses

Otolith microchemistry and shape data were compared between and within estuaries using multivariate permutational analysis of variance (PERMANOVA) using PRIMER-E v. 7.0 software with the PERMANOVA+ add on (Clarke and Gorley 2006). As this test uses permutations to test for significant differences among groups, the parametric assumptions of normality of distributions and homogeneity of variances are less critical (Anderson et al. 2008). When testing multifactorial designs, PERMANOVA is preferential to other multivariate procedures as it allows tests for factor interactions.

To establish whether elemental signatures supported recent separation of individuals among estuaries, trace elemental concentrations from otolith margins were compared among estuaries, while accounting for the potential effects of within-estuary variation, variation among years, and ontogenetic changes in otolith chemistry (Walther et al. 2010). Where applicable, fork length was used as a covariate as age data was not available for all samples and this continuous variable likely provided a more resolved covariate. Separate analyses were done for the coastwide and regional datasets. Prior to all analyses, data were graphically inspected using histogram and shade plots to evaluate the homogeneity of dispersions and optimal transformation and standardisation methods, as well as to ensure distributions were linear (Clarke et al. 2014). Data were fourth root transformed to balance the contribution of more and less abundant elements, and euclidean distances were used to construct dissimilarity matrices for each dataset.

For coastwide edge signature data, a two-factor PERMANOVA analysis was performed incorporating the factors 'estuary' (fixed) and 'year' (fixed), as well as their interaction, with 'fork length' included as a covariate to account for differences in size and age. This initial analysis identified a significant interaction effect between years and estuaries (Table 7a) and two additional estuaries were also available for the analysis during 2009, therefore edge signatures were also tested separately for each year. It was not possible to partition within-estuary variance for the coastwide dataset, because too few individuals were available from each site within each estuary. Individuals were therefore pooled across a minimum of three sites within each estuary, to ensure within-estuary variability was at least incorporated into statistical comparisons.

For regional edge signature data, a three-factor PERMANOVA analysis was performed, 'estuary', 'year' and an additional factor 'site' were incorporated in the statistical design, as enough individuals were available from numerous sites to ensure sufficient power to investigate this finer spatial scale. The factor 'site' (random) was nested within 'estuary', and 'fork length' was again used as a continuous covariate. The factor 'year' for this dataset denoted whether the data came from the otolith edge or the previous increment (i.e. previous year).

For both these analyses, Type I sum of squares (SS) were used, to ensure covariates were fitted to the data prior to the factor 'estuary'. The statistical significance of factors was tested using 9999 permutations conducted on residuals under a reduced model, as opposed to the raw data, in order to avoid inflated Type 1 error rates that can accompany covariates in multivariate analyses (Anderson et al. 2008). An *a priori* significance level of $\alpha = 0.05$ was used to assess the significance of results. Pairwise PERMANOVA tests were carried out on all statistically significant results to identify which estuaries were contributing to the

differences. To control for potentially increased Type 1 errors due to the multiple tests performed, all p-values from pairwise PERMANOVA tests were corrected for the coastwide analysis. P-values were only considered significant under a false discovery rate (FDR) of $q <$ 0.05, using the Benjamini-Hochberg procedure (Benjamini & Hochberg 1995).

To establish whether spatial separation may occur over longer time-periods for this species, Fourier descriptors were compared between estuaries of capture using a one-factor PERMANOVA for the coastwide analysis, and a two-factor PERMANOVA for the regional analysis. A 'fork length' covariate was again incorporated, to account for the slight differences in size ranges between sites, as ontogeny may influence otolith shape (Vignon 2012). Individuals from both years in the coastwide dataset were combined for shape analysis, as preliminary testing revealed no interaction between years and estuaries (Pseudo-$F_{4,164} = 1.2041$, p = 0.2128), and no significant effect of 'year' (Pseudo-$F_{1,164} = 0.5061$, p = 0.8708), allowing the two additional estuaries from the 2009 collection year to be incorporated. For the regional dataset the additional factor 'site' was again incorporated, nested within 'estuary'. Shape data were normalised to account for any variations in size, rotation, and start point, and Euclidean distance-based dissimilarity matrices were constructed. Type I sum-of-squares were used to ensure the covariate was fitted in the model prior to the factor 'estuary', with 9999 permutations performed on residuals under a reduced model. Pairwise tests were run on all significant results.

Additionally, to establish whether patterns of separation during the adult phase matched those during the juvenile phase, a one-factor PERMANOVA was performed on the coastwide juvenile chemistry data and a two-factor PERMANOVA was performed on the regional dataset incorporating 'site' as an additional factor (random; nested within estuary). The aim of this was to investigate whether individuals remain within or in close proximity to their

estuary of capture from the juvenile stage. This approach assumed that elemental composition from the juvenile zone accurately reflected the elemental composition from the location of capture across years as individuals were from various year classes. Pooling juvenile signatures across years has the potential to mask distinction among areas due to inter-annual variations in water chemistry. Nonetheless, if differences are identified it can provide a stronger result, as structure is still evident despite inter-annual variation in signatures. Data were fourth root transformed before constructing dissimilarity matrices based on Euclidean distances. Type III sum-of-squares were used with 9999 unrestricted permutations of the raw data. Pairwise PERMANOVAs were then used to investigate which estuaries were responsible for any significant results. A covariate to account for ontogenetic stage (e.g. body length) was not required for juvenile signatures as LA-ICP-MS was targeted at the same location within each otolith, representing the same period of life for each individual.

As PERMANOVA is sensitive to differences in both the location and dispersion of data, PERMDISP (PRIMER-E v. 7.0 +PERMANOVA) procedures were performed for all significant results to check for homogeneity of multivariate dispersions, as this test identifies significant differences in dispersion (Anderson et al. 2008; Anderson & Walsh 2013). Additionally, for both coastwide and regional datasets, linear regressions were constructed to compare the geographic distance with the Euclidean distance among centroids of individual estuaries for each methodology. This was used to investigate whether differences were related to the geographic distance between estuaries, with R-squared and p-values used to assess the strength and significance of any relationship. Multivariate data centroids of each estuary were used for comparison as they represent the centre of the data cloud, or spatial median, in multivariate space (Anderson 2006).

Canonical Analysis of Principal Coordinates (CAP; PRIMER-E v. 7.0 +PERMANOVA) were used to visualise multivariate differences following each PERMANOVA analysis, as well as to compare classification success, i.e. the likelihood individuals would be allocated back to their collection location. CAP is a constrained ordination which defines groups *a priori* and identifies axes which best separate these groups (Anderson & Willis 2003). This procedure determines the accuracy of re-allocating individuals to their original group using the 'leave-one-out' (cross-validation) method (Anderson & Willis 2003). CAP was also completed on combined otolith Fourier coefficients and elemental edge signatures, with data normalised prior to analysis to ensure variables were on the same scale (Anderson et al. 2008). Vector overlays were used to visualise which elements were responsible for driving differences among groups. Vectors were only displayed for elemental variables as the number of variables in the shape analyses made displaying them impractical. Vectors were established using Spearman rank correlations between elemental concentrations and CAP axes. The length of each vector corresponds to the strength of the relationship, and the direction corresponds to the CAP axes most responsible for these differences (Anderson et al. 2008).

3.3 Results

3.3.1 Elemental signatures at the otolith edge

Edge signatures differed between estuaries in both 2008 and 2009 in our coastwide analysis (Table 7b, c). Pairwise comparisons revealed differences between numerous estuaries, with the two northern estuaries (RR, CR) differing from the southernmost estuaries consistently across years (GB, WA) (Table 8a, b). Estuaries in closer proximity to one another also differed, with CR and RR, separated by 82 km, displaying differences in 2009, and LM and GB, separated by ~ 300 km differing in both years (Table 8b). No differences in multivariate

dispersions were observed in either 2008 (PERMDISP, Pseudo-$F_{4,94}$ = 1.951, p = 0.17) or 2009 (Pseudo-$F_{6,128}$ = 1.5706, p = 0.1972), indicating that the differences observed were due to differences in data location in multivariate space. Fork length influenced edge signatures in both years, however differences between estuaries were still evident following partitioning of this effect in the model.

Table 7. Summary of among-region PERMANOVA results for the multivariate analysis of (a)(b)(c) elemental signatures from the otolith edge, (d) otolith shape descriptors and (e) elemental signatures from the juvenile zone of adult otoliths for *Acanthopagrus australis*, sourced from multiple estuaries along the NSW coast. There were > 9500 unique permutations for each term in the models. **Bold** and * denote significant results.

		df	Pseudo-F	P(perm)
(a) Edge signatures (Both years)	Fork Length	1	8.7298	**0.0001***
	Year	1	4.7235	**0.0022***
	Estuary	6	7.5871	**0.0001***
	Year x Estuary	4	4.1897	**0.0001***
	Residuals	222		
(b) Edge signatures (2008)	Fork Length	1	3.6337	**0.0096***
	Estuary	4	4.4326	**0.0001***
	Residuals	93		
(c) Edge signatures (2009)	Fork Length	1	4.5780	**0.0215***
	Estuary	6	7.3564	**0.0001***
	Residuals	129		
(d) Shape coefficients	Fork Length	1	7.1939	**0.0001***
	Estuary	6	4.3190	**0.0001***
	Residuals	202		
(e) Juvenile signatures	Estuary	6	5.8927	**0.0001***
	Residuals	224		

Table 8. Summary of coastwide pairwise PERMANOVA results for *Acanthopagrus australis* collected from seven estuaries on the NSW coast, including (a)(b) elemental signatures from the otolith edge (split by collection year), (c) otolith shape coefficients, and (d) elemental signatures from the juvenile zone of adult otoliths. Letters denote estuaries and their position on the NSW coast relative to studied estuaries, locations are ordered by distances between estuaries, descending. **Bold** and * denote significant results, corrected for each PERMANOVA using the procedure outlined in Benjamini & Hochberg (1995), FDR *q* < 0.05. There were > 9900 unique permutations for each comparison in the model.

Region	Estuary	Distance (km)	(a) Edge (2008) t	(a) Edge (2008) P(perm)	(b) Edge (2009) t	(b) Edge (2009) P(perm)	(c) Shape t	(c) Shape P(perm)	(d) Juvenile t	(d) Juvenile P(perm)
N S	CR WA	970			2.3294	**0.0013***	3.1946	**0.0001***	2.7757	**0.0003***
N S	RR WA	888			6.08	**0.0001***	4.1653	**0.0001***	2.1850	**0.0019***
N S	RR GB	816	3.3906	**0.0001***	2.2656	**0.0023***	1.2379	0.1352	3.8425	**0.0001***
N S	CR GB	734	2.0801	**0.0146***	6.1819	**0.0001***	1.8769	**0.0027***	3.9855	**0.0001***
N C	RR TL	590	3.0241	**0.0005***	1.7125	**0.0018***	1.4939	0.0359	1.5401	**0.0286***
C S	WL WA	565			0.7204	0.6742	3.0924	**0.0001***	2.4251	**0.0022***
N C	RR LM	539	1.5211	0.0652	1.6727	0.0332	1.1825	0.1778	2.1384	**0.0049***
N C	CR TL	534	1.7115	0.0474	3.3955	**0.0001***	1.5164	0.0371	2.3555	**0.0004***
N C	CR LM	483	0.7082	0.6997	5.4933	**0.0001***	1.4455	0.0459	3.5276	**0.0001***
N C	RR WL	431			1.761	**0.0198***	1.1421	0.2206	2.0473	**0.0082***
C S	LM WA	431			1.9207	**0.0104***	3.5513	**0.0001***	2.6862	**0.0006***
C S	WL GB	411			0.9394	0.4605	1.4035	0.0558	1.8639	**0.0158***
C S	TL WA	380			1.1699	0.1902	3.2947	**0.0001***	1.2255	0.1979
N C	CR WL	349			4.8857	**0.0001***	0.7822	0.7527	2.7965	**0.0003***
C S	LM GB	301	2.4624	**0.0007***	2.048	**0.0051***	1.4582	0.0413	2.5624	**0.0007***
C S	TL GB	246	1.1437	0.2611	1.2633	0.1955	1.3069	0.1021	1.5849	**0.0140***
C C	WL TL	185			1.1411	0.2743	1.3194	0.1016	0.92017	0.5381
S S	GB WA	154			0.9650	0.4323	2.7577	**0.0001***	1.7028	**0.0231***
C C	WL LM	134			1.2017	0.2183	1.0928	0.2633	0.58647	0.8104
N N	RR CR	82	1.5934	0.0584	3.5567	**0.0001***	1.3808	0.0626	2.143	**0.0024***
C C	LM TL	45	1.7411	0.0315	1.3414	0.0875	1.4938	0.0382	0.93598	0.5232

Overall allocation accuracy of individuals back to their estuary of capture was low in both 2008 (32.3%) and 2009 (41.5%) (CAP) for the coastwide comparison. However, allocation accuracies for individual estuaries varied widely, for example, accuracy ranged from 5 to 94.7 % for CR among years (CAP, Table 9a, b). Some estuaries could be distinguished with moderate accuracy consistently across years, such as GB, where accuracies ranged from 61.9 to 65 %. Visual representations of CAP analyses suggested separation of the Northern two estuaries (RR, CR), with clear distinction of these estuaries from the more southerly estuaries investigated (GB, WA) (Figure 7a, b). Misallocated individuals were occasionally placed into adjacent estuaries, but typically dispersed throughout the study region. Estuaries in the mid-coast region (WL, LM & TL) didn't differ significantly from one another in either year (Table 8a, b), displaying overlap with adjacent estuaries in CAP ordinations and generally low allocation success (Figure 7a, b, Table 9a, b). Vector overlays indicated that Magnesium (Mg) was responsible for some of the separation apparent on CAP axis 2 in both 2008 and 2009 (Figure 7a, b). Barium (Ba) and Sodium (Na), and to a lesser extent Strontium (Sr), were responsible for separation on both axes in 2008 (Figure 7a). In 2009, Ba was responsible for the most of the separation apparent on CAP axis 1, while Sr was partly responsible for apparent separation on both axes (Figure 7b). Linear regressions showed positive but weak relationships between distance among centroids and geographical distance for both years (Figure 8a, b), with the relationship approaching significance in 2009 ($p = 0.053$).

In contrast to the coastwide comparison, no differences in otolith edge signatures were found among the regional study estuaries, however multivariate PERMANOVA did identify significant differences between sites within estuaries (Table 10a). Pairwise comparisons revealed significant differences between sites within estuaries for both WL (Pseudo-t = 1.9989, $p = 0.0104$) and HR (Pseudo-t = 4.0285, $p = 0.0001$).

Table 9. Summary of allocation success of *Acanthopagrus australis* individuals back to the estuary in which they were captured based upon canonical analysis of principal coordinates (CAP). Results presented for (a) 2008 elemental signatures from the otolith edge, (b) 2009 elemental signatures from the otolith edge, (c) fourier coefficients from the otolith outline (d) combined edge signatures and shape coefficients from 2008, (e) combined edge signatures and shape coefficients from 2009, and (f) juvenile elemental signatures from adult otoliths. The % allocation to each estuary in a random assignment would be ~ 20 % for (a) & (d) and ~14 % for (b), (c), (e) & (f). Locations are ordered corresponding to their position on the NSW coast, beginning with the northern most estuary.

	Original estuary	Allocated estuary							Total	% Allocated correctly
		RR	CR	WL	LM	TL	GB	WA		
(a) Edge (2008)	RR	11	4	N A	4	1	0	N A	20	**55.0**
	CR	7	1	N A	1	8	3	N A	20	**5.0**
	LM	9	4	N A	2	5	4	N A	24	**8.3**
	TL	0	1	N A	4	5	4	N A	14	**35.7**
	GB	1	0	N A	2	4	13	N A	21	**61.9**
(b) Edge (2009)	RR	8	4	0	4	1	1	2	20	**40.0**
	CR	1	18	0	0	0	0	0	19	**94.7**
	WL	2	0	3	4	3	4	4	20	**15.0**
	LM	4	0	4	8	1	1	2	20	**40.0**
	TL	0	0	2	2	5	2	7	18	**27.8**
	GB	0	0	4	0	1	13	2	20	**65.0**
	WA	0	0	3	3	7	4	1	18	**5.6**
(c) Shape	RR	9	6	9	5	3	1	1	34	**26.5**
	CR	6	13	5	6	3	3	0	36	**36.1**
	WL	6	5	5	2	1	3	1	23	**21.7**
	LM	5	3	5	13	3	9	1	39	**33.3**
	TL	1	4	1	3	18	2	0	29	**62.1**
	GB	4	2	2	4	6	15	0	33	**45.5**
	WA	1	0	0	1	0	0	14	16	**87.5**
(d) Edge & Shape (2008)	RR	9	6	N A	2	0	1	N A	18	**50.0**
	CR	3	7	N A	5	1	3	N A	19	**36.8**
	LM	0	5	N A	7	0	11	N A	23	**30.4**
	TL	1	0	N A	2	6	1	N A	10	**60.0**
	GB	2	3	N A	12	0	4	N A	21	**19.0**
(e) Edge & Shape (2009)	RR	9	3	2	3	0	3	0	20	**45.0**
	CR	4	14	1	0	1	0	0	20	**70.0**
	WL	4	0	5	6	3	2	0	20	**25.0**
	LM	1	0	3	10	2	4	0	20	**50.0**
	TL	0	0	2	4	8	4	0	18	**44.4**
	GB	4	0	3	2	2	6	3	20	**30.0**
	WA	2	0	2	1	0	1	11	17	**64.7**
(f) Juvenile	RR	9	10	7	4	4	5	0	39	**23.1**
	CR	0	24	4	2	4	0	3	36	**66.7**
	WL	1	0	4	5	2	6	2	20	**20.0**
	LM	7	1	12	5	7	5	4	44	**11.4**
	TL	5	3	8	3	4	3	7	33	**12.1**
	GB	1	1	6	1	3	23	6	41	**56.1**
	WA	1	0	2	2	1	1	11	18	**61.1**
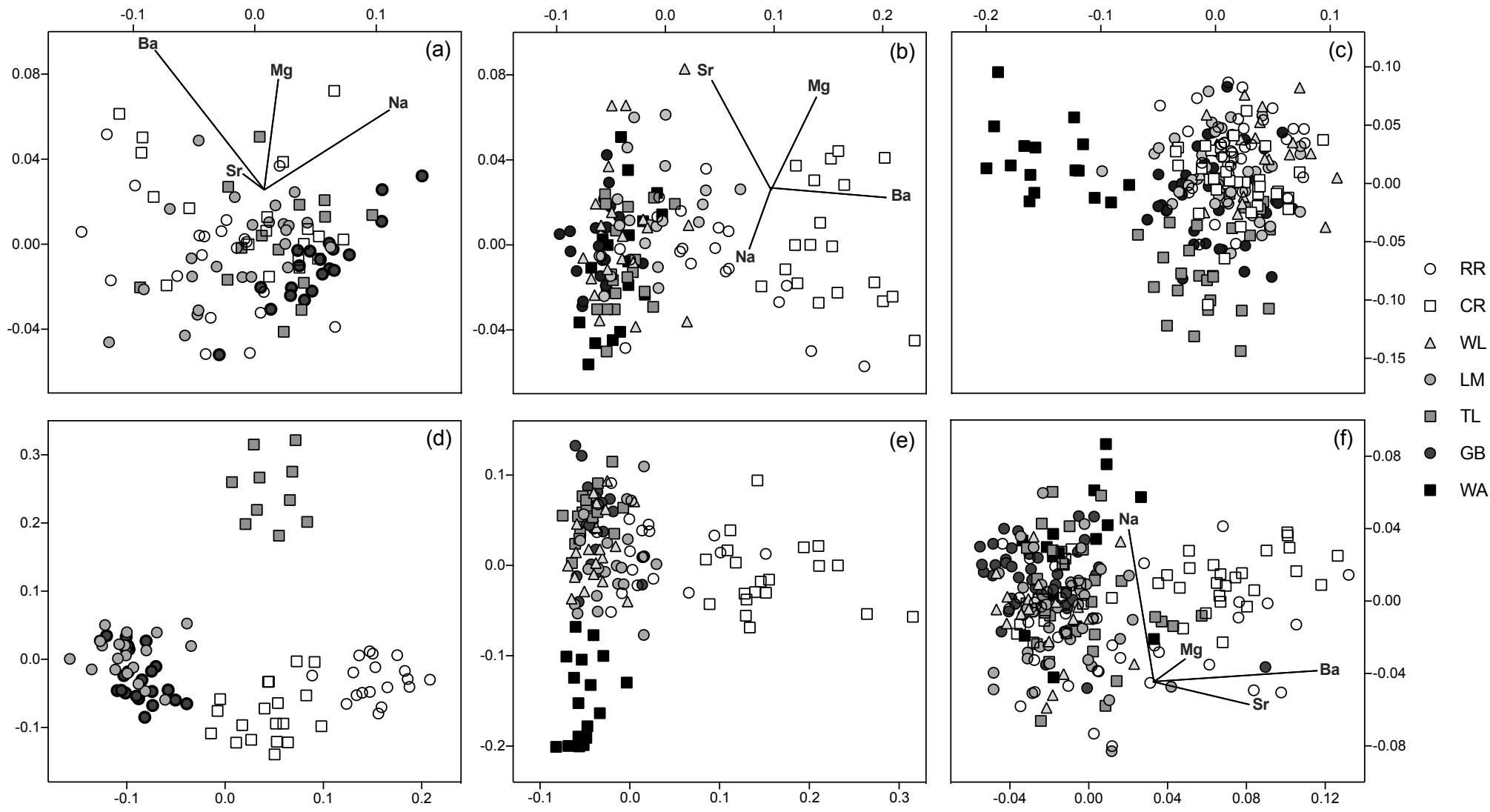
Figure 7. Canonical analysis of Principal Coordinates (CAP) for the coastwide component of the current study, for (a) 2008 otolith elemental edge signatures and (b) 2009 otolith elemental edge signatures, (c) Fourier descriptors of otolith shape, (d) 2008 Fourier descriptors and edge signatures combined, (e) 2009 Fourier descriptors and edge signatures combined and (f) elemental signatures from the juvenile zone of adult otoliths. Vector overlays in (a), (b) and (f) show correlations of individual elements with primary axis. Note different axis scales on each plot
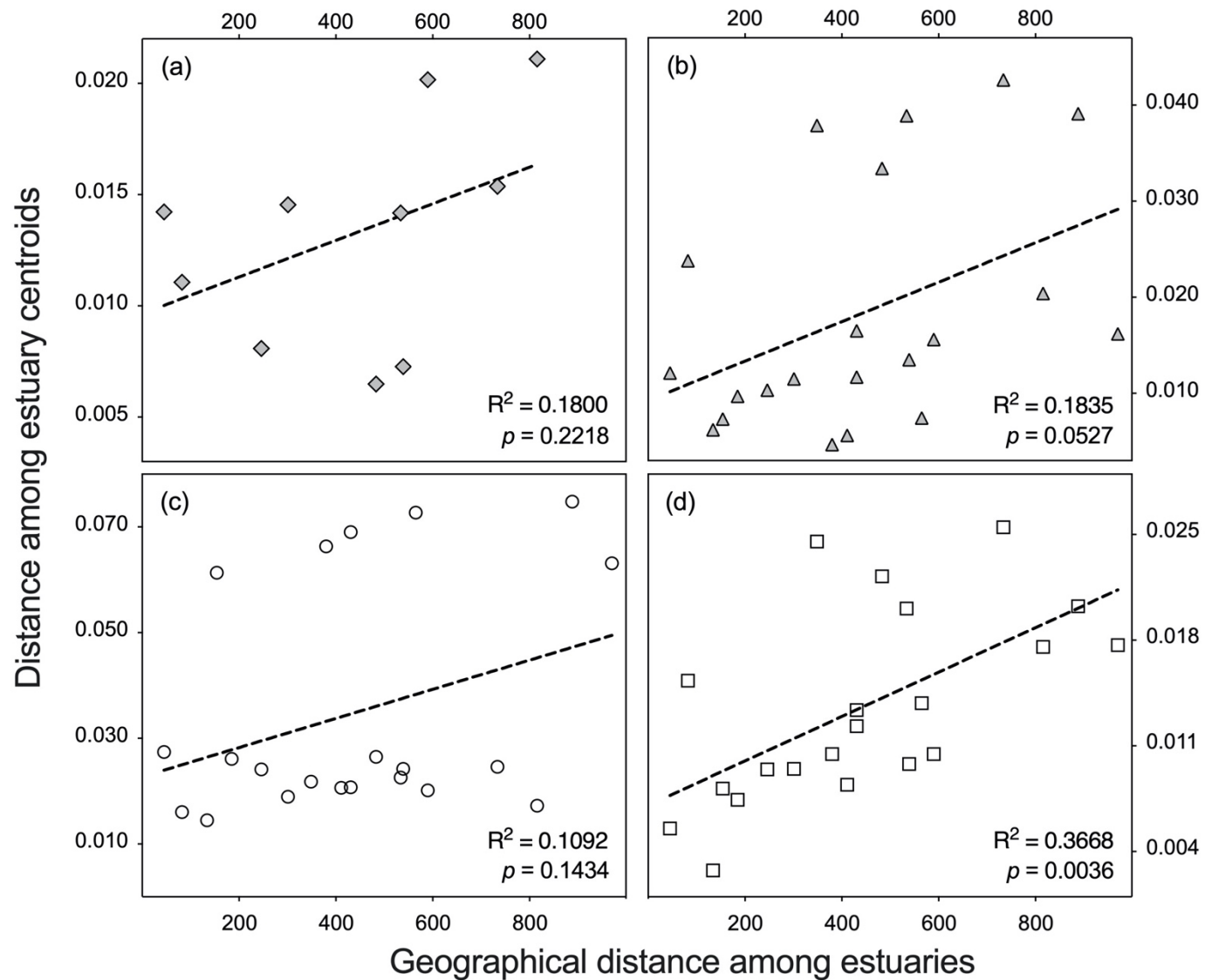
Figure 8. Linear regression of distance among centroids and geographical distance among estuaries for coastwide study estuaries. (a) otolith edge signatures (2008), (b) otolith edge signatures (2009), (c) otolith shape descriptors and (d) signatures from the juvenile zone of adult otoliths. R^2 value denotes the strength of the relationship and p value denotes the significance of the relationship ($p < 0.05$ is significant).

Table 10. Summary of regional PERMANOVA results for the multivariate analysis of (a) elemental signatures from the otolith edge, (b) otolith shape descriptors, and (c) elemental signatures from the juvenile zone of adult otoliths, of *Acanthopagrus australis* sourced from three estuaries along ~ 100 km NSW coast. There were > 9500 unique permutations for each term in the model, apart from the term estuary, which repeatedly had less than < 999 unique permutations, where Monte Carlo p-values were employed as there were not enough unique permutations to determine permutational p-values. **Bold** and ***** denote significant results. ~ denotes Monte Carlo p-values.

		df	Pseudo-F	P(perm)
(a) Edge signatures	Fork Length	1	4.6829	**0.0035***
	Year	1	6.2091	**0.0381***
	Estuary	2	2.9693	0.0563 ~
	Site(Estuary)	3	10.933	**0.0001***
	Year x Estuary	2	1.7050	0.2338
	Year x Site(Estuary)	3	0.1562	0.9996
	Residuals	223		
(b) Shape coefficients	Fork Length	1	1.2715	0.1591
	Estuary	2	1.409	**0.0309*** ~
	Site(Estuary)	3	1.0977	0.5509
	Residual	102		
(c) Juvenile signatures	Estuary	2	3.3841	**0.0477*** ~
	Site(Estuary)	3	1.5184	0.1405
	Residuals	117		

Table 11. Summary of allocation success of *Acanthopagrus australis* individuals back to the estuary in which they were captured based upon canonical analysis of principal coordinates (CAP). Results presented for (a) elemental signatures from the otolith edge, (b) otolith shape descriptors, (c) combined otolith shape and elemental edge signatures, and (d) elemental signatures from the juvenile zone of adult otoliths. The % allocation to each estuary in a random assignment would be ~ 33 % .

| | Original estuary | Allocated estuary | | | | |
		HR	PS	WL	Total	% Allocated correctly
(a) Edge signatures	HR	46	18	14	40	**59.0**
	PS	5	45	28	39	**57.7**
	WL	1	30	49	40	**61.3**
(b) Shape coefficients	HR	21	6	9	36	**58.3**
	PS	5	24	8	37	**64.9**
	WL	9	7	17	33	**51.5**
(c) Shape & edge signatures	HR	20	10	6	36	**55.6**
	PS	5	25	7	37	**67.6**
	WL	6	7	20	33	**60.6**
(d) Juvenile signatures	HR	25	7	7	39	**64.1**
	PS	10	9	20	39	**23.1**
	WL	7	10	23	40	**57.5**
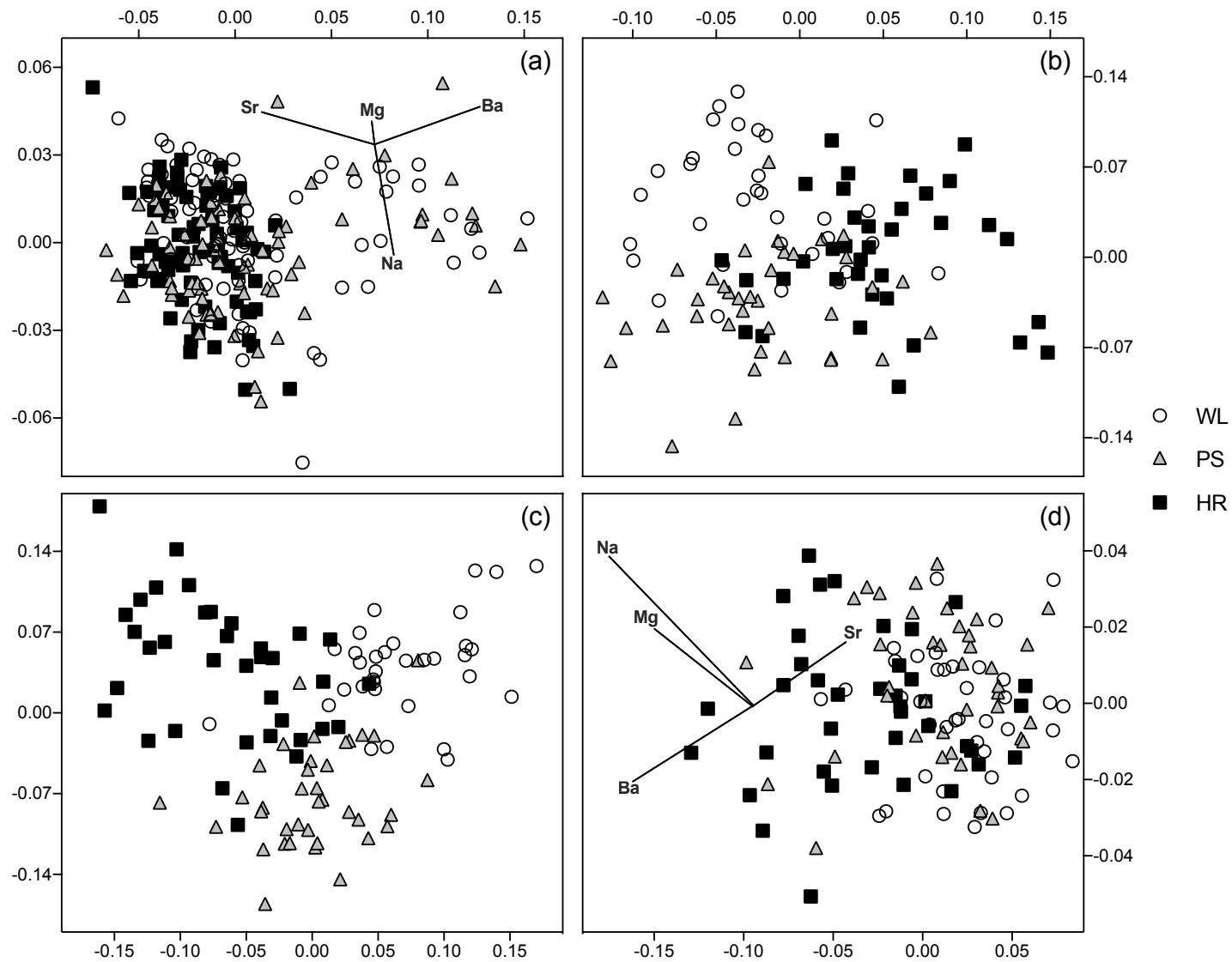
Figure 9. Canonical analysis of Principal Coordinates (CAP) for the within-region component of the current study, for (a) otolith elemental edge signatures, (b) elliptical Fourier descriptors of otolith shape, (c) combined Fourier descriptors and edge signatures and (d) elemental signatures from the juvenile zone of adult otoliths. Vector overlays in (a) and (d) show correlations of individual elements with the primary axis. Note differences in axis scales on each plot.

3.3.2 Otolith shape analysis

Otolith shape indices differed significantly between estuaries for the coastwide comparison (Table 7d). Pairwise tests revealed WA differed significantly from all other estuaries, while GB and CR also differed from one another (Table 8c). No differences in multivariate dispersion were apparent (PERMDISP, pseudo-$F_{6,203}$ = 1.8553, p = 0.128), indicating differences in otolith shape detected among estuaries were the result of differences in location, not dispersion. Overall allocation accuracy was low, with 41.43 % of individuals allocated back to their collection location. Classification success varied considerably however, with 87.5 % of individuals correctly allocated back to WA, the southern-most study estuary (Table 9c). Visual inspections of CAP ordinations showed overlap between some estuaries, however WA and TL exhibited little overlap with other estuaries (Figure 7c). Linear regressions showed a weak positive relationship between geographical and centroid distance among estuaries, however it was not significant (Figure 8c).

In contrast to edge chemistry, otolith shape indices differed significantly between regional estuaries, but not between sites within estuaries (Table 10b), with pairwise comparisons revealing differences between PS and WL (Pseudo-t = 1.672, p = 0.0457). No significant differences in dispersion were identified, signalling differences were due to data location, not dispersion (PERMDISP, pseudo-$F_{2,103}$ = 0.0767, p = 0.93). CAP ordinations showed partial separation of groups (Figure 9b), with allocation accuracy moderate overall (58.5 %), ranging from 51.5 % to 64.9 % (Table 11b).

3.3.3 Combined elemental edge signatures and shape data

For coastwide estuaries, combining shape data with elemental edge signatures improved allocation accuracy in both 2008 and 2009. Accuracy improved from 32.3 % to 36.3 % in

2008, and 41.5 % to 46.7% in 2009. Allocation accuracies for individual estuaries were less variable when data were combined, ranging from 19.0 % to 70.0 % (Table 9d, e). Some estuaries showed substantial increases in accuracy, for example, allocation of individuals from WA improved from 5.6 to 64.7 % in 2009. CAP ordinations showed clearer separation for combined data, with clear distinction between the northern- (CR, RR) and southern- (GB, WA) most estuaries in both years (Figure 7d, e). Mid-coast estuaries (WL, LM, TL) showed varying degrees of overlap in both years, however TL displayed clear separation from all other estuaries in 2008, as well as LM appearing distinct from all estuaries apart from GB in 2008.

Regional estuaries also showed improved allocation accuracy when otolith shape coefficients and elemental edge signatures were combined. Overall classification accuracy increased from 58.5 % to 61.3 %, with accuracies for individual estuaries ranging from 55.6 % to 67.6 % (Table 11c). CAP ordinations showed clearer distinction between the three estuaries than ordinations based on each of the separate datasets (Figure 9a, b, c).

3.3.4 Juvenile elemental signatures from adult otoliths

For the coastwide dataset, elemental signatures from the juvenile zone of adult otoliths were found to differ significantly between estuaries (Table 7e), with pairwise comparisons revealing significant differences between 81 % of estuaries (Table 8d). Differences in juvenile signatures concurred with differences found among estuaries using edge signatures (adult phase). Significant differences in the multivariate dispersion of individuals among estuaries weren't apparent (PERMDISP, pseudo-$F_{6,224}$ = 2.1928, p = 0.1087), indicating that observed differences between estuaries were due to differences in data location not data spread. Despite significant differences between most estuaries, allocation accuracy was low overall (CAP, 34.6 %), with individual accuracies ranging from 11.4 to 66.7 % (Table 9).

CAP ordinations revealed some separation of northern (RR, CR) and more southern estuaries (GB, WA), with considerable overlap among estuaries within these broader regions and the mid-coast region (Figure 9f). Vector overlays indicated that Barium (Ba) was responsible for most of the separation apparent on CAP axis 1, and to a lesser extent Stronium (Sr), and that Sodium (Na) was mostly responsible for differences evident on CAP axis 2 (Figure 9f). Juvenile chemical signature differences (multivariate Euclidean distance) increased significantly with geographical distance (Figure 4d; p <0.01, $n = 231$).

Elemental signatures from the juvenile zone of adult otoliths also displayed significant differences among estuaries in the regional comparison (Table 10c). Pairwise comparisons revealed significant differences between HR and WL (Psuedo-t = 2.4095, p = 0.0287~). These results were confirmed as being due to differences in data location, as no significant differences in dispersion were identified (PERMDISP, pseudo-$F_{2,115}$ = 1.4317, p = 0.323). The overall success of classifying individuals back to their capture origin was low (CAP, 48.31%), however classification success varied from 23.0 % at PS to 64.1% at HR (Table 11d). CAP ordinations of juvenile signatures showed a high degree of overlap (Figure 9d).

3.4 Discussion

Spatially structured populations must be managed at an ecologically appropriate spatial scale in order to ensure successful management (Kritzer & Sale 2004). *A. australis* are an important species both recreationally and commercially in south eastern Australia, yet knowledge of connectivity and population structure is limited. Currently treated as a single stock for assessment, and managed separately by the three jurisdictions they inhabit, they are known to comprise a single genetic stock throughout their range (Roberts & Ayre 2010; McGilvray et al. 2018)). However exchange of only a small number of individuals can produce genetic homogeneity (Botsford et al. 2009; Hawkins et al. 2016) and mask more

subtle population structure that is still important over the ecological timescales relevant to fisheries management (Kerr et al. 2017). Despite some tagging studies observing *A. australis* to move substantial (> 200 km) distances in NSW, the majority of individuals have been found to remain within or near the estuary in which they were tagged (West 1993; Lowry et al. 2017; van der Meulen 2018). The patterns of connectivity and population structure suggested by our analyses imply movement is likely restricted over the scale of fisheries management (~1000 km) in the region. If so, the current scale of management for *A. australis* may be too coarse to ensure sustainable harvest if fishing pressure is unevenly applied across regions.

Spatial differences in otolith characteristics were evident at all three spatial scales investigated, suggesting segregation over a broad range of geographical distances. Segregation appears to exist at the level of 10 to 100s of kilometres, suggesting movement may be occurring between adjacent estuaries. This is consistent with tagging research in Northern NSW, which indicates a small number (4 %) of individuals emigrate out of their release estuary (West 1993). Differences identified at multiple spatial scales within the current study may be the result of multiple behavioural types among individuals. Such differences in movement behaviour were initially identified in species that undertake extensive diadromous migrations (Jonnson & Jonnson 1993), but are increasingly being reported for marine species (Parsons et al. 2011; Gillanders et al. 2015). Despite possible movement among estuaries, differences were also identified at our smallest scale of investigation, suggesting restricted movement within estuaries. Several studies have documented small scale movement of *A. australis* (Sheaves 1993; Gannon et al. 2015; Taylor et al. 2017), with research in QLD recording movement generally at scales < 6 km (Pollock 1982), and a study in the Shoalhaven River, NSW identifying core areas < 5 km (van der Meulen 2018).

Our results suggest *A. australis* may be organised as a series of overlapping subpopulations distributed linearly along the South East Australian coast. Analysis of otolith elemental signatures and otolith shape descriptors revealed significant differences between numerous estuaries, with separation more apparent among estuaries separated by greater distances. The evidence suggests limited connectivity between the northern and southern most estuaries investigated, which concurs with various tagging studies, with the longest movement recorded to date < 500 km (West 1993). Coastwide analyses revealed no differences amongst the three mid coast estuaries, with a moderate amount of movement possibly occurring between estuaries at this spatial scale (< 160 km) rather than the southern and northern extremes of the estuaries examined. Nonetheless, edge signatures were found to differ significantly between Clarence and Richmond River (~ 80 km apart) and shape signatures were found to differ between Wallis Lake and Port Stephens (~ 80 km apart), suggesting similarities observed elsewhere could either be the result of mixing, or homogeneity in the factors influencing elemental deposition among locations (i.e. ambient concentration, diet, salinity).

Environmental homogeneity between estuaries in the dynamics which influence otolith development and elemental deposition may have masked differences and contributed to inconsistencies in results among years. Previous studies have identified difficulties in discriminating among estuaries due to similarities in the factors influencing otolith development and elemental uptake (Gillanders et al. 2002; Sturrock et al. 2012; Moore & Simpendorfer 2014), such as the varying influence of marine water (Schilling et al. 2018). It is of particular interest that Wallaga Lake was found to differ from all other estuaries in terms of otolith shape, as it is classified as an intermittently closed and open lake or lagoon (ICOLL), meaning it is a barrier estuary in which the entrance channel is open to the ocean intermittently (Roy et al. 2001; Hinwood & McLean 2015). Individuals were captured during

early 2009, when the mouth of Wallaga Lake was closed to the sea, and had been closed since November 2007 (Bega Valley Shire Council, 2016). The entrance closure could explain why otolith chemistry and shape differed significantly from the majority of estuaries examined, as individuals were confined to this ~ 9 km^2 estuary for over a year prior to capture (Roper et al. 2011). It also confirms that individuals had not moved outside this estuary for over 12 months, meaning the lack of differences found in otolith edge chemistry between Wallaga Lake and three other estuaries (WL, TL, GB) were not a result of mixing, but more likely a result of similarities between these estuary environments. Consequently, it is possible that the lack of edge signature differences identified among these three estuaries (WL, TL, GB) were the result of environmental homogeneity among these systems, as opposed to movement between them.

Spatial separation was also evident when examining signatures contained within the juvenile section of the otolith, supporting patterns observed in adult separation and suggesting individuals remain in proximity to their recruitment region throughout life. Distinct *A. australis* juvenile signatures have previously been identified among three estuaries on the NSW coast, however signatures were obtained from juvenile fish from the same year class (Gillanders & Kingsford 2003). Temporal differences in juvenile elemental signatures is well documented (Hamer et al. 2003; Reis-Santos et al. 2012), for instance Gillanders and Kingsford (2000) identified inter-annual differences in the elemental signatures of juvenile Trumpeter, and Hamer et al. (2003) identified variation in juvenile signatures between adjacent year classes, although this did not confound spatial discrimination. Temporal variation in juvenile signatures was not controlled for in the current study, as we were investigating whether patterns of adult separation could be linked to juvenile separation, not whether individuals could be assigned to recruitment estuaries (Elsdon et al. 2008). Despite the fact that cohorts were mixed among estuaries, which may have hindered our ability to

identify differences in juvenile signatures (Reis-Santos et al. 2012), the methodology still identified differences between estuaries. Although such results may also reflect inter-annual differences in local water chemistries and/or dietary sources, juvenile signatures from adult otoliths differed between the majority of estuaries examined, providing strong evidence of separation for extended periods.

The lack of edge signature differences between the regional estuaries was possibly driven by variations in water chemistry, as well as other factors such as diet, with this intra-estuarine heterogeneity potentially masking differences in signatures among estuaries (Roy et al. 2001; Reis-Santos et al. 2015). Estuarine systems are highly variable, influenced by both marine and freshwater systems, with the resultant variation in water chemistry often reflected in otolith elemental signatures (Roy et al. 2001; Elsdon & Gillanders 2003, 2004). Elemental signature variation among sites within estuaries, separated by as little as 3 km, suggests individuals have remained site associated within an estuary, with signatures differing due to distinctive water and environmental characteristics (Thorrold et al. 1998; Hamer et al. 2003; Reis-Santos et al. 2015). The different scales of variation identified in the current study, suggests the scale of elemental variation may sometimes be too fine for testing segregation at scales of ecological interest from a management perspective. Our results highlight the need to test at multiple spatial scales before drawing conclusions regarding actual segregation and movement. A lack of difference at the estuary level does not necessarily amount to connectivity, and may lead to Type II errors resulting in false assumptions that large scales of management are suitable.

It was not possible to partition within-estuary variance for the coastwide dataset, and although individuals were collected from a minimum of three sites within each estuary, intra-estuarine variation may have influenced coastwide analyses and contributed to the generally

low allocation accuracies. Nonetheless, if collection site within an estuary has an impact on otolith elemental signatures, it suggests that individuals have spent a significant portion of their recent life in a specific area within an estuary, implying little recent movement for the majority of individuals (Reis-Santos et al. 2015). The fact that we identified differences in otolith shape among estuaries in the regional comparison further supports the notion that edge signatures of these same individuals may have been influenced by short term intra-estuarine variation, as shape descriptors reflect processes occurring over longer time-periods (Sturrock et al. 2012). This further supports the need to use multiple methods when attempting to infer segregation of sub-populations, as each method has a different suite of limitations (Begg & Waldman 1999). If we had only explored edge chemistry in the present study, we may have inferred that there was mixing at the regional study level, however given the longer time integration of otolith shape, it evidences more prolonged separation between estuaries at a scale of 40 - 125 km.

Spatial patterns observed among estuaries in the current study were unlikely the result of temporal variation. Inter- and intra-annual variation in otolith elemental signatures has been documented in a number of studies, and has the potential to confound spatial comparisons (Hamer et al. 2003; Elsdon et al. 2008; Walther & Thorrold 2009; Reis-santos et al. 2012). In the present study, to counter the potential effects of intra- and inter-annual variation on spatial comparisons, individuals were collected within a four-month sampling window within discrete years. Notwithstanding, intra-annual variation in otolith edge signatures may have influenced discrimination and contributed towards generally low allocation accuracies. Additionally, differing year classes would have presumably influenced our ability to discriminate among individuals, with decreased otolith growth with development influencing the time period covered by ablations, and thus influencing comparisons of edge signatures (Elsdon & Gillanders 2006; Walther & Thorold 2009). Ablations of recently deposited

material at the otolith edge covered the period approximately ~ 3 to 9 months prior to capture, due to differing widths of annual bands among individuals, and although this may have influenced comparisons, the standardisation of sizes among estuaries would have minimised this effect.

Population structuring of *A. australis* supported in the current study could potentially promote demographic variation and localised depletion along the coast, due to spatial variability in environmental conditions and/or fishing pressure (Williams et al. 2003). Recreational and commercial catch for this species is disproportionate along the NSW coast, with > 65 % of recreational catch occurring between the NSW mid-south coast (36°S) and hunter regions (32°S) (West et al. 2015). The potential for restricted connectivity suggests *A. australis* may be vulnerable to localised depletion, with decline in a particular area unlikely to be compensated through immigration of individuals from outside this area. Regions with greater fishing pressure may thus undergo truncation of length and age structures due to the loss of older, larger individuals which are not subsequently replenished (Berkley et al. 2004). Existing management scales for this species may need to be re-examined to ensure they are consistent with population sub-structuring and differential fishing pressure along the coast. Management must also consider that sub-populations may extend over jurisdictional borders into QLD and VIC. Stock assessments conducted at the larger management scale may overlook depletions occurring at the level of individual estuaries, or groups of estuaries within particular coastal regions. Further investigation of abundance trends at fine scales is warranted, but may be challenging given the current reliance on commercial catch data for assessment, and the limited spatial resolution this offers.

Yellowfin Bream are known to hybridise with Black Bream (*Acanthopagrus bucheri*) at the southern end of their range (Rowland 1984; Roberts et al. 2009; Roberts et al. 2010). It is

acknowledged that a small number of individuals included in the current study may have been hybrids and possibly contributed to differences identified at the two Southern most estuaries examined. Nonetheless, hybridisation at the Southern end of this species range heightens the need to re-examine existing scales of management, to ensure they reflect the complex spatial structure of *A. australis* and account for *Acanthopagrus* complexes in areas of sympatry (Ochwada-Doyle et al. 2012).

The present study demonstrates the benefits of using multiple methodologies to investigate stock structure of marine species, and supports a growing body of literature on the advantages of integrating information obtained from multiple approaches (Abaunza et al. 2008; Izzo et al. 2017). Our results also highlight the utility of archived otolith samples in addressing unresolved questions relating to stock structure of exploited fishes, as well as the efficacy of juvenile signatures from adult otoliths in discerning population structure in conjunction with recent signatures from the otolith edge, even when collections are from multiple year classes. Differences revealed at both the smallest (sites within estuaries) and largest scale of investigation (100s of km) highlight the importance of investigating multiple spatial scales, and discrepancies between years for some estuaries emphasises the value of investigating multiple time periods when examining population structure. Although otolith chemistry presented some inconsistencies in spatial structure through time, results generally supported segregation at a scale of individual estuaries, suggesting assessment and management should be considered at that scale. If inconsistencies between years represent occasional mixing beyond this scale, the exchange of individuals may provide further buffer against localised depletion. Our approach of using archived otolith samples to examine stock structure was a cost-effective method of addressing important management questions relating to *A. australis*, and future studies examining stock structure could benefit from incorporating archived otolith samples in integrated approaches.

Chapter 4 General discussion

The east Australian population of *Acanthopagrus australis* predominantly occupies estuarine and coastal ecosystems. The human population is concentrated on coastlines, where diverse and growing anthropogenic pressures are degrading these systems at unprecedented rates (Lotze et al. 2006; Halpern et al. 2008; Cloern et al. 2016). Southeast Australia is considered a global hotspot for climate change, where it is experiencing some of the fastest increases in ocean temperatures globally (Ridgeway et al. 2007; Wernberg et al. 2011; Frusher et al. 2013). As such, there is an ever increasing need to understand how to best monitor and manage coastal fisheries in this region, to ensure resilience and persistence of populations. One of the most important considerations when managing aquatic organisms is the spatial scale of population connectivity, as the degree of movement among areas may influence the distribution and abundance of organisms, resilience to exploitation, the ability to recover from disturbance and the dynamics and persistence of populations (Cianelli et al. 2013; Kerr et al. 2017). Despite this, spatial scales of connectivity are poorly resolved for many exploited fishes, particularly over the ecological timescales relevant to fisheries management.

Acanthopagrus australis is an important species in east Australian fisheries and is the most common species caught recreationally in NSW (West et al. 2015). Despite considerable research into the biology and ecology of this species, there is still a lack of understanding of the levels of exchange among areas and thus their stock structure remains unclear. This thesis intended to address an important knowledge gap on the stock structure of *A. australis* by investigating movement patterns and levels of exchange among spatially segregated areas of NSW. By adopting a multidisciplinary approach, this thesis provides evidence of restricted connectivity over multiple temporal and spatial scales, presenting a 'weight of evidence' on how the population of *A. australis* is structured along the NSW coast. The findings of this

thesis contribute to the literature by providing one of the first broad-scale, multidisciplinary investigations on the population structure of *A. australis*. Below I provide a synthesis and discussion of this research and its implications for the management of *A. australis*, as well as future directions for research.

4.1 Multiple methods for detecting stock structure

Integrating information from multiple techniques to determine stock structure is a fairly recent development in the field of stock delineation (Abaunza et al. 2008b; Welch et al. 2015; Izzo et al. 2017). Such approaches allow limitations of individual methods to be less critical, increasing the likelihood of detecting separation among areas when it is present. Individual approaches may produce inconclusive information, and can present a skewed picture of spatial structure as each technique considers different aspects of the population. A holistic approach, where the results of different techniques are considered in combination can contribute to a 'weight of evidence', providing greater power in accurately identifying stocks (Begg & Waldman 1999; Welch et al. 2015).

Overall, there was moderate consensus among results from the three different techniques employed. Otolith elemental signatures and tag-recapture data suggest limited exchange of post settlement *A. australis* between northern and southern NSW. Less than 1.5% of the ~2000 tagged and recaptured individuals were > 350 km from their release location (Chapter 2). This was congruent with otolith elemental edge signatures (Chapter 3), which exhibited significant differences among most NSW estuaries that were > 300 km apart. In combination, these results suggest limited exchange of juveniles and adults is occurring at such spatial scales (> 300 km).

Nonetheless, there were some inconsistencies among techniques. Otolith shape differed significantly between only a few estuaries along the coast, with these differences not

appearing to be related to the distance between estuaries. Given otolith shape develops throughout an individual's entire lifetime, this divergent result may indicate sufficiently frequent exchange of individuals between adjacent estuaries to prevent the development of distinct otolith shapes. Alternatively, conditions affecting otolith shape may have been similar among estuaries irrespective of the distance between them. It is important to mention that a failure to identify differences among samples does not demonstrate the existence of extensive connectivity, rather it indicates that with the available data and statistical techniques employed, it is not possible disprove the null hypothesis of a single, well mixed stock (Welch et al. 2015).

In Chapter 3, estuaries as little as 82 km apart displayed differences in otolith elemental edge signatures, suggesting there may be restricted movement occurring between some estuaries at a relatively small scale. This is in concordance with movement of tagged *A. australis*, with 91.4 % of individuals recaptured within 100 km of their release location (Chapter 2). Restricted movement at such scales, along with the diversity in movement patterns observed, suggests there may be a series of subpopulations of *A. australis* along the NSW coast, with movement of individuals occurring between adjacent areas, rather than extensively along the coast. This notion is further supported by the finding that otolith edge signatures were more distinct with increasing distance among estuaries (Chapter 3).

Potential segregation identified among estuaries from the various methodologies employed in this thesis contrasts with research that has identified genetic homogeneity throughout the range of *A. australis*. The level of ecologically relevant exchange (i.e. exchange sufficient to impact on local demographic rates) required to form a single, well-mixed stock is much greater than the level of exchange required for the maintenance of genetic homogeneity (Slatkin 1993; Cowen & Sponaugle 2009; Welch et al. 2015; Hawkins et al. 2016). The lack

of genetic differences among *A. australis* on the NSW coast may be explained by occasional long-distance migrations identified in Chapter 2 and/or dispersal during the pelagic larval stage, rather than extensive mixing of post-settlement individuals along the coast.

Tag-recapture results highlighted the possibility of multiple behavioural types within the *A. australis* population, with the majority of individuals appearing resident and a small number exhibiting large movements (Chapter 2). The possible existence of multiple behavioural types could help explain generally low accuracy in allocating individuals back to their estuary of capture in Chapter 3, as a small proportion of individuals may have been migratory contingents. This flexibility in life history has been evidenced in another closely related sparid, *Acanthopagrus butcheri* (Gillanders et al. 2015). Intraspecific variation in movement behaviour, or partial migration, whereby both resident and migratory movement patterns exist within a single species, is being increasingly documented in exploited fishes (Robichaud & Rose 2004; Kerr et al. 2009; Parsons et al. 2011; Kerr & Secor 2012). If such variations in movement behaviour are not accounted for in fisheries assessment and management, it may have deleterious effects, such as localised depletion of resident individuals (Parsons et al. 2009). The potential presence of both migratory and resident fish may be an important strategy for *A. australis* (Kerr & Secor 2012), and the maintenance of both contingents could be significant in moderating population stability (Kerr et al. 2009).

Comparisons of juvenile signatures from adult otoliths between estuaries suggest that *A. australis* remain within proximity (~150 km) to their recruitment estuary throughout life. All but one pair of estuaries separated by > 200 km displayed significant differences based on the juvenile region of otoliths (Chapter 3). This is in keeping with tag-recapture data as < 6 % of individuals were found to move > 200km, suggesting resident individuals remain near their recruitment region through life (Chapter 2). Success of allocating individuals back to their

estuary of capture using juvenile signatures varied, and was generally low. This could perhaps be associated with the presence of migratory contingents and/or movement among adjacent areas leading to signatures distinct to estuaries in the region, as opposed to specific, individual estuaries. The integration of these findings suggests there are a series of subpopulations of *A. australis* along the NSW coast, with the majority of individuals appearing to remain within proximity (< 200 km) of their recruitment region throughout life history.

4.2 Implications for management

The results of this thesis have implications for the management of *A. australis* in NSW. The limited exchange of *A. australis* among estuaries separated by moderate spatial scales is contrary to that implicitly assumed for management purposes. *A. australis* are treated as a single biological stock throughout their range for stock assessment purposes. This biological stock has components in three separate jurisdictions, QLD, NSW and VIC, with each jurisdiction managing the part of the stock that occurs in its waters separately (McGilvray et al. 2018). For example, the minimum legal length of *A. australis* in NSW and QLD is 25 cm total length, while it is 28 cm in VIC, with bag limits for recreational fishers ranging from 10 to 30 fish between jurisdictions.

The restricted connectivity evident for *A. australis* across regions on the NSW coast suggests this species may be vulnerable to localised depletion if fishing effort is focused in particular regions. The loss of resident individuals may not be adequately compensated through replenishment of migratory contingents. *A. australis* may benefit from finer scale spatial management, to account for restricted movement of the majority of individuals, however while this may be best implemented at a local scale (i.e. individual estuaries) it is unlikely to be practical. Management may be more appropriate at regional (300-400 km) scales,

improving on the current disconnect of management by jurisdiction. Implementing catch and effort controls at a regional scale would strike a balance between practicality of management logistics and the restricted connectivity observed in the present study. While otolith chemistry results presented some inconsistencies in spatial structure through time, it is still advisable for assessment and management to be conducted at the spatial scale structure exists. Any occasional exchange or mixing of individuals at a broader scale can potentially provide compensation for localised mortality.

In addition, the results of this thesis suggest *A. australis* may be an appropriate candidate for protection in marine protected areas (MPAs) and reserves. Such areas of protection are becoming increasingly popular in maintaining productivity of exploited species (Botsford et al. 2009; Burgess et al. 2014) as evidence grows of their benefit to purportedly mobile fishes (Apostolaki et al. 2002; Willis et al. 2003; Curley et al. 2013b; Harasti et al. 2015). The restricted movement and residency evident for the majority of *A. australis* suggests MPAs may be beneficial to local populations, at least for resident contingents, while also providing spill over to surrounding areas through the smaller number of individuals that exhibit migratory behaviour. Initial results on the influence of such areas on *A. australis* support this idea, with two studies recording increased densities of *A. australis* within small (0.1 to 5.7 km^2) MPAs (Pillans 2006; Curley et al. 2013b). Additional research on *A. australis* behaviour is necessary to assess the usefulness of MPAs. Research concentrating on the dynamics of partial migration and the factors influencing behavioural shifts would help in estimating spill-over and in assessing the efficacy of such areas to the stock and fisheries of *A. australis*. Further research could also utilise acoustic tracking technologies to provide more detailed information on fine-scale movement inside and outside of MPA boundaries.

In a broader context, the results of this thesis add to the growing body of evidence that many exploited fishes are far more spatially structured than previously assumed (Abaunza et al. 2008b; Cadrin et al. 2010; Svedang et al. 2010; Ciannelli et al. 2013; Hughes et al. 2015). Evidence of complex spatial structure indicates that the spatial scale of management and monitoring needs to be reassessed for many exploited species, considering the potential for demographic structuring at relatively fine spatial scales (Cadrin & Secor 2009; Cadrin 2020). There is a clear need for increased research to enhance our understanding of population structure of exploited species.

4.3 Future research directions

The results of this thesis have highlighted some critical areas for future research. The restricted connectivity evident in this thesis warrants further research into the movement patterns of *A. australis*. Further research might focus on exploring population structure across the entire species distribution, incorporating samples from QLD and VIC, and would benefit from greater representative sampling across both locations and years. In addition, other lines of evidence may be incorporated into an integrated approach to improve the certainty of inferred stock structuring i.e. parasite diversity, age & growth rates, catch rates and composition (Cadrin et al. 2013). Broad scale acoustic telemetry networks are increasingly being established worldwide, such as the Australian Integrated Marine Observing Systems (IMOS) Animal Tracking Facility (Steckenreuter et al. 2016; Taylor et al. 2017b; Hoenner et al. 2018). Future research could utilise this Australian network to further refine our understanding of levels of exchange of *A. australis* among regions. Acoustic gates on all estuaries would be an effective way to record movement among estuaries for estuary associated species.

Future research on other fished species may benefit from adopting similar approaches to those employed in this thesis. Opportunistic use of archived samples and data in this thesis revealed some of the benefits and challenges of their utility for future research. Large government collections of archived otoliths and recreational tag-recapture databases may allow for cost effective, large scale and long-term analyses of unresolved questions relating to stock structure of exploited species. Nonetheless, there are challenges of using such sources, for instance restricted control over sampling design, variability in sample sizes, potential temporal discontinuities in samples and occasionally missing corresponding biological data.

The restricted control over sampling design when using archived otolith collections in this thesis resulted in certain assumptions having to be made. For instance, we were not able to control for fish age. Juvenile signatures were thus obtained from individuals of different year classes, and although this diminished the likelihood of identifying any connection among individuals due to temporal variability in water chemistry, we still identified differences among estuaries. The efficacy of using juvenile signatures from adult otoliths in conjunction with edge signatures has been demonstrated in this thesis, and may be a useful approach for future researchers. Additionally, as tag-recapture data provide an indirect measure of movement, the location of each individual is only available at two points in time, with no information of where an individual has been between these times. It is therefore possible that individuals may have moved considerable distances following tagging, only to be recaptured near there approximate location of tagging. Nonetheless, the long-term nature of the data used in this thesis diminishes the likelihood that any consistent patterns of migration or movement would have gone unnoticed.

The processes influencing fish population structure and connectivity are complicated, and for numerous species an improved understanding of the factors regulating the exchange of individuals is necessary (Kerr et al. 2017). The restricted movement of juvenile and adult *A. australis* indicates subpopulation structure, however it is not known what role larval dispersal plays in the connectivity and population structure of *A. australis*. There hasn't been extensive research into larval dispersal of *A. australis* (Leis et al. 2006), so it is not known whether dispersal may potentially enhance or offset the subpopulation structuring identified in this thesis. The pelagic larvae of *A. australis* may be dispersed over a wide area, as they are thought to spend a sizable time period in the coastal ocean plankton influenced by the Eastern Australian Current (EAC) (Roberts & Ayre 2010). While larval dispersal may assist in connecting and replenishing areas along the NSW coast, it may not be sufficient to offset differential fishing pressure among regions. In relatively long-lived species like *A. australis*, larval additions may not suffice in providing functional connectivity (Cowen & Sponugle 2009). Overfishing may lead to truncation of length and age structures with the loss of older and larger individuals, with larval replenishment unable to remedy this loss. Further research into the extent of dispersal of *A. australis* larvae would assist in advancing our understanding of this species connectivity and subpopulation structuring.

Additionally, there is a need to explore the potential for multiple behavioural types of *A. australis*, and the environmental and/or physiological mechanisms underlying whether individuals become resident or migratory. In a broader context, increased research is necessary to further develop our understanding of the strategy of partial migration, with intraspecific diversity in movement patterns increasingly being recognised in numerous fish taxa (Kerr et al. 2009; Parsons et al. 2011; Kerr & Secor 2012; Gillanders et al. 2015). Such research is necessary to develop a complete understanding of how the east coast population of *A. australis* is structured spatially, and how environmental perturbations and

anthropogenic pressures may influence whether individuals become resident or migratory contingents. Future research into multiple behavioural types within *A. australis* could utilise otolith chemistry transects, from the juvenile core of the otolith to the adult edge, to further investigate the possibility of partial migration in this species. Otolith transects may potentially yield the proportion of individuals that migrate, and the timing in their life history that such behaviour begins (Fowler et al. 2016).

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