# MOVEMENT, CONNECTIVITY AND POPULATION STRUCTURE OF A LARGE, NON-DIADROMOUS, TROPICAL ESTUARINE TELEOST

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Thesis submitted by

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## ABSTRACT

Understanding the degree of exchange between groups of a species, or connectivity, is fundamental to the effective management and conservation of aquatic species and ecosystems, yet remains poorly understood for tropical estuarine fishes. With anthropogenic pressures in the form of increased fishing pressure, habitat modification and climate change on this group projected to increase, understanding patterns of connectivity becomes increasingly important so that effective management can be implemented. This thesis sought to provide one of the first empirical assessments of connectivity of a tropical, non-diadromous estuarine teleost, using the king threadfin, *Polydactylus macrochir*, as a focal species. Uniquely, this thesis provides the first use of a multidisciplinary approach to discern patterns of connectivity of a tropical estuarine teleost, incorporating data from multiple complementary techniques to assess connectivity at a range of spatial, temporal and ontogenetic scales across the species' Australian distribution.

In Chapter 3, life history parameters of *P. macrochir* were examined to provide preliminary information on the connectivity and population structure of the study species across northern Australia. Specifically, the timing of annuli deposition and spawning, and patterns in growth, mortality, length and age at maturity, and length and age at sex change of *P. macrochir* were examined at up to 18 locations. Considerable variation in life history parameters was observed among locations. Both unconstrained and constrained ($t_0$=0) estimates of von Bertalanffy growth function parameters differed significantly among all neighboring locations, with the exception of two locations in Queensland's east coast and two in Queensland's Gulf of Carpentaria waters, respectively. Comparisons of back-calculated length-at-age 2 provided additional evidence for growth differences among some locations but were not significantly different among locations in the south-eastern Gulf of Carpentaria or on Queensland's east coast. Total mortality rates varied among locations, and were highest for estuaries within the Gulf of Carpentaria. The length and age at sex change differed markedly among locations, with fish from the east coast of Australia changing sex from males to females at significantly greater lengths and ages than elsewhere. Sex change occurred earliest at locations within Queensland's Gulf of Carpentaria, where a large proportion of small, young females were recorded. While it is unclear whether the spatial differences reflect genetic relationships, or result from differing environmental conditions amongst locations, the differences in life history parameters indicate limited mixing of at least post-larval fish, suggesting the probable existence of a number of spatially distinct groups of adult *P. macrochir* assemblages across northern Australia. These results suggest that future studies

examining connectivity and geographic population structure of estuarine fishes will likely benefit from the inclusion of comparisons of life history parameters.

In Chapter 4, temporal and spatial patterns in parasite assemblages were examined to further assess the degree of movement and connectivity of *P. macrochir* collected from the same 18 locations examined in Chapter 3. Ten parasites types (juvenile stages of two nematodes and seven cestodes, and adults of an acanthocephalan) were deemed to be suitable for use as biological tags, in that they were considered to have a long residence time in the fish, were relatively easy to find and were morphologically very different to each other which aided discrimination. Discriminant function analysis of these parasites revealed little difference in temporal replicates collected from five locations, suggesting that the parasite communities were stable over the timeframes explored. Univariate, discriminant function, and Bray-Curtis similarity analyses indicated significant spatial heterogeneity, with classification accuracies ranging from 55–100% for locations in north-western and northern Australia, 24–88% in the Gulf of Carpentaria, and 39–88% on the east coast of Queensland. Few differences were observed among locations separated by < 200 km. The observed patterns of parasite infection support earlier examination of life history and suggest a complex population structure of *P. macrochir* in northern Australia, with post-larval populations generally undergoing limited movement and connectivity.

In Chapter 5, age-related trends in otolith elemental chemistry were examined to provide an indication of the degree of larval dispersal of *P. macrochir*, and to provide an additional measure of connectivity in post-larval fish. Elemental signatures ($^{7}$Li, $^{24}$Mg, $^{55}$Mn, $^{59}$Co, $^{88}$Sr and $^{138}$Ba) of transverse sections of otoliths of 3+ year fish from the 2005 year class collected from 17 of the 18 locations examined in Chapters 3 and 4 were sampled using laser ablation inductively coupled plasma mass spectrometry, providing age-related elemental profiles from the otolith core through the first three years of a fish's life. Univariate and discriminant function analyses demonstrated little similarity in age-related average elemental concentrations among locations. Elemental signatures of the otolith core appeared different among most locations, although some similarities were evident among locations in the eastern Gulf of Carpentaria and among two neighbouring locations in Western Australia. Differences were evident in elemental signatures of post-larval otolith material among locations separated by as little as 50 km, suggesting fine-scale spatial structuring of juvenile and adult assemblages of *P. macrochir*. In the analyses, average $^{138}$Ba concentration provided the most discrimination among locations. The spatial structuring evident here is largely consistent with examination of parasite assemblages and life history data and suggests that *P. macrochir* populations are highly susceptible to local depletion in most locations, with limited opportunity for replenishment from neighbouring populations. In addition, the results add to

the growing body of literature that demonstrates limited connectivity of estuarine species and suggest that the age-related approach adopted here provides a viable, albeit indirect, alternative to assessing patterns of connectivity, particularly for studies in which collection of larvae or juveniles is not feasible.

Finally, in Chapter 6, data from 3,718 *P. macrochir* tagged by members of the Australian National Sportfishing Association and state fisheries researchers were analysed to provide additional information on the movement and connectivity of juvenile and adult fish in Queensland's east coast and Gulf of Carpentaria waters. Recapture information was available for 182 individuals tagged on the east coast and 40 individuals tagged in the Gulf of Carpentaria. No difference was observed between recapture rates of dart and anchor tagged fish in either region, suggesting the performance of these tags were similar. Connectivity among estuaries on the east coast of Queensland was limited, with 96% of all recaptures occurring in the same estuary in which fish were tagged. Movements outside of tagging estuaries on Queensland's east coast ranged from 1 km to 23 km. In the Gulf of Carpentaria, 70% of all recaptures occurred in the same estuary in which fish were tagged. Twelve individuals were recaptured outside of their tagging estuaries in this region. While four of these individuals were recaptured within 10 km from the mouth of their tagging estuary, eight individuals moved greater than 80 km outside of their tagging estuaries, including one individual that moved approximately 570 km. The limited connectivity among spatially-distinct estuaries is consistent with results of previous chapters and indicates that *P. macrochir* form a number of demographically-isolated populations in Queensland waters.

The findings of this study have a number of important implications for the management of *P. macrochir*, and for future research into the connectivity of estuarine fishes and fish populations in general. The limited connectivity evident for *P. macrochir* suggests that populations are susceptible to over-fishing, with limited opportunity of replenishment from neighbouring populations. These results indicate that *P. macrochir*, and other tropical estuarine species that exhibit similar patterns of restricted connectivity, should ideally be managed on a local scale to avoid localised depletion, and may be suitable candidates for protection by marine protected areas. More broadly, the findings of this thesis reinforce that a number of complementary techniques are required to accurately determine connectivity of fish populations and suggest that future studies examining connectivity of tropical estuarine fishes, and fishes in general, will greatly benefit from the inclusion of multiple, complementary approaches. Given the paucity of studies examining connectivity of non-diadromous tropical estuarine fishes, the findings of this thesis provide fundamental information from which more specific hypotheses of connectivity, population structure and gene flow of such species can be tested.

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# Chapter 1 General Introduction

There is growing consensus that life within the world's oceans is under considerable and increasing stress from anthropogenic activities (Hutchings 2000; Cowen et al. 2007). Nowhere is this stress more evident than in estuarine environments, where the cumulative impacts of over-fishing, habitat destruction and pollution contribute to make estuaries one of the world's most degraded aquatic ecosystems (Jackson et al. 2001). Fishing is one of the major anthropogenic impacts affecting estuarine ecosystems, and most estuarine fisheries are considered either fully exploited or over-exploited (Blaber et al. 2000). In addition to over-fishing, coastal development practices such as dredging, construction, deforestation, farming and the construction of dams and weirs increase the destruction, modification and fragmentation of estuarine habitats, further exacerbating the pressures on estuarine fishes (Jackson et al. 2001; Valiela et al. 2001). Anthropogenic releases of carbon dioxide and other greenhouse gases largely considered responsible for climate change will likely bring additional stresses to estuarine ecosystems, through warmer temperatures, alteration of weather patterns, rising sea levels, more severe storm events, and ocean acidification (Field 1995; Roessig et al. 2004; Sheaves et al. 2007).

Currently, an estimated 60% of the world's total human population, or approximately 3.6 billion people, live within 100 km of the coast (Vitousek et al. 1997). This figure is projected to increase to around 75%, or approximately 6.4 billion people, living within 60 km of the coast by the year 2020, with the majority of this growth expected in the tropics (Blaber 2000; DeMaster et al. 2001). Due to increasing human populations in coastal areas, it is likely that estuarine environments will be subject to ever-increasing levels of anthropogenic pressure. With increased pressure, it becomes progressively more important to understand the biology and ecology of estuarine fishes in order to implement effective management and conservation strategies. Central to this is an understanding of the degree of connectivity between spatially segregated groups of a species. Although this knowledge is considered fundamental to the effective management and conservation of estuarine-dependant fishes, it is still poorly understood for many species, particularly in tropical systems (Secor and Rooker 2005; Jones 2006; Gillanders 2009).

This thesis examines patterns and processes of connectivity of a large, tropical, non-diadromous estuarine teleost. It begins with a review outlining and discussing (1) the importance of understanding patterns of connectivity of aquatic organisms, (2) patterns of, and factors influencing, connectivity of estuarine fishes, and (3) the approaches for assessing connectivity in aquatic environments. For the purpose of this review, discussion is limited to

species that reside in estuaries for the majority of the lives, including those that may undertake seasonal and/or ontogenetic movements into adjacent coastal waters. Species that use estuaries solely as nursery habitats, although considered estuarine-dependant for a portion of their lives, or occasional visitors, such as those termed estuarine-opportunists by Potter and Hyndes (1999), are not considered.

### 1.1 Importance of understanding connectivity of fishes

Over the past decade there has been a growing interest in the subject of population connectivity of aquatic organisms (Cowen and Sponaugle 2009). Connectivity, or the exchange of individuals between spatially isolated groups of a species, influences the distribution and abundance of organisms, rates of local adaption and speciation, the dynamics and persistence of populations, and the ability of ecosystems and species to recover from disturbance (Slatkin 1987; Cowen et al. 2000; Swearer et al. 2002; Hastings and Botsford 2006; Cowen and Sponaugle 2009). Accordingly, understanding patterns of connectivity is considered fundamental to the effective management and conservation of ecological systems and marine resources (Cowen et al. 2007; Fogarty and Botsford 2007).

Historically, fish populations were largely considered as 'open', with large scale dispersal (Warner and Cowen 2002). However, there is a growing realisation that the spatial and temporal complexity of many fish species has not been considered appropriately in fisheries management and conservation measures, with many recent studies suggesting fish populations may operate on much smaller spatial scales (Swearer et al. 1999; Thorrold et al. 2001). Such evidence has led to the call for increased understanding of the patterns of connectivity and population structure of marine resources (Cowen et al. 2006).

Central to effective fisheries management is an understanding of the spatial scale at which exploited species should be managed (Begg et al. 1999a). Fisheries management models typically rely on the assumption that the group of individuals investigated form a single, well-mixed entity, with its own origin, demographics, and fate, and that each group has a closed life cycle, in which young fish in the group are produced by previous generations of the same group (Begg et al. 1999a; Cadrin et al. 2005; Waldman et al. 2005). Undertaking modeling on several closed populations, or a portion of a population, however, may produce misleading results if a single population is assumed (Begg et al. 1999a; Cadrin and Friedland 1999). The application of management measures that fail to accurately define the degree of exchange or opportunity for replenishment to local populations may lead to over-fishing (Begg et al. 1999a), resulting in dramatic changes in demography, productivity and genetic diversity of isolated groups (Ricker 1981; Smith et al. 1991; Law 2000; Dominguez-Petit et al. 2008), and ultimately localised depletion or extinction (Pauly 1988; Hilborn and Walters 1992;

Blaber et al. 1996; Hutchings 1996; Clark et al. 2000). Numerous cases have been documented where a lack of information on how populations are spatially structured, coupled with heavy exploitation and ineffective management, has resulted in the depletion of local populations to the point of collapse, and include anchovy *Engraulis ringens* (see Hilborn and Walters 1992), Atlantic cod *Gadus morhua* (see Hutchings 1996; Myers et al. 1996) and orange roughy *Hoplostethus atlanticus* (see Clark et al. 2000).

Accounting for connectivity is also an integral component in the design of marine reserves or no-take marine protected areas (MPAs). Marine protected areas are now routinely established as an effective tool for protecting biodiversity, sustaining productivity of exploited species, and allowing for continued extractive uses of the marine environment (Jones et al. 2007; Botsford et al. 2009). Marine protected areas are regarded as viable alternative management tools for tropical fisheries, particularly given the multispecies nature of these fisheries, and that many developing nations that occur in tropical regions lack the human resources, infrastructure, and financial capacity to obtain accurate catch data required to implement more conventional Maximum Sustainable Yield (MSY) or Maximum Economic Yield (MSE) based management approaches utilised by developed nations for managing temperate fisheries (Adams 1998; Blaber 2002; Sale 2002). In order for MPAs to provide benefits to fisheries, they must meet one of two conditions: (1) there must be an increase in reproductive capacity and biomass within the MPA, and (2) the export of eggs and/or larval stages and/or the movement of juveniles or adults into areas open to harvest, or 'spillover', must be sufficient enough to increase yield or at least sustainability in fished areas (Fogarty and Botsford 2007). There is ample evidence to suggest that MPAs can provide a host of benefits to exploited populations within their boundaries across a variety of ecosystems, including estuaries (e.g. Babcock et al. 1999; Johnson et al. 1999; Ley et al. 2002; Pande et al. 2008). In contrast, the extent that fish protected inside reserves contribute to areas open to harvest is poorly understood. The lack of empirical data on movement and connectivity is regarded by many authors as the greatest source of uncertainty in understanding the potential efficacy of MPAs in management scenarios (Botsford et al. 2003; Fogarty and Botsford 2007; Botsford et al. 2009; Christie et al. 2010).

**Patterns of connectivity of estuarine fishes**

Most of our understanding of connectivity of estuarine fishes comes from studies undertaken in temperate systems. Across these inherently patchy and fragmented seascapes, estuarine fishes fall on a spectrum from 'open' populations, in which the persistence of a population is decoupled from its own production of recruits, to 'closed' populations, in which the persistence of a population is solely reliant on its own production of recruits (Jones 2006). A

wide range of factors have been implicated in facilitating or impeding connectivity in these systems, which can be broadly placed into two categories: (1) species-specific life history traits, including the location and timing of spawning (Hare and Cowen 1993; Sponaugle et al. 2002), larval behaviour and dispersal capabilities (Bilton et al. 2002; Clark et al. 2005), and philopatry, or the return of individuals to their natal area to spawn (Thorrold et al. 2001; Patterson et al. 2004), and (2) physical factors, such as salinity (Loneragan et al. 1987), turbidity (Cyrus and Blaber 1987; Cyrus and Blaber 1992), water currents (Epifanio and Garvine 2001; Watson et al. 2011), or geographical landforms (Baker et al. 2007; Lindley et al. 2011). The relative importance of these factors may vary among species, or with age (Gold and Richardson 1998; Tobin et al. 2010), and may be intrinsically and complexly interconnected. For example, in north-eastern South Africa, riverbream, *Acanthopagrus berda*, spawns at the mouths of estuaries on night-time ebb tides (Garratt 1993), which Garratt (1993) suggested gave eggs and larvae the greatest chance of being washed from the estuary and therefore aiding dispersal among estuaries. In contrast, spawning in southern blue-spotted flathead, *Platycephalus speculator*, across south-western Australia occurs in late austral spring and summer, at a time when water movement is low, reducing the chances of eggs or larvae being flushed from natal estuaries (Potter and Hyndes 1999). Regional differences in movement and the degree of connectivity have also been reported for several estuarine fishes. Chaplin et al. (1998) found significant genetic heterogeneity in the estuarine-spawning black bream, *Acanthopagrus butcheri*, among estuaries separated by approximately 100 km in south-western Australia. Conversely, using the same three loci examined by Chaplin et al. (1998), Farrington et al. (2000) reported genetic homogeneity in *A. butcheri* among three estuaries separated by a similar spatial scale in south-eastern Australia. Such differential patterns of connectivity highlight the need to examine species connectivity across multiple geographical locales.

Most estuarine fishes have bipartite lifecycle, consisting of a pelagic larval stage followed by more recognisable juvenile and adult stages (Clark et al. 2005). Although population connectivity may be achieved through movement and dispersal of all life history stages (Gillanders 2009), in recent times considerable focus has been placed on the pelagic larval stage, and the processes that affect it, in addressing issues of connectivity (Cowen and Sponaugle 2009). This focus has largely been driven by the recognition of the importance of this stage in moderating connectivity of reef fishes, in which adult fish are regarded as being largely sedentary (Jones et al. 2009). However, many recent studies have documented local larval retention, or fine-scale genetic differentiation, in estuarine organisms (e.g. Sponaugle et al. 2002; Botton and Loveland 2003; North and Houde 2006; Tilburg et al. 2007; Bradbury et al. 2008a; Braverman et al. 2009; Tilburg et al. 2010), suggesting dispersal of larval stages

may be more limited than previously thought. Strong selection for local larval retention has recently been hypothesised for fishes that live in spatially-fragmented seascapes such as estuaries, as the chances of finding suitable settlement habitat are greatly reduced if larvae disperse away from the parental population (Swearer et al. 2002). Furthermore, a number of estuarine fish species have been shown to be more sedentary as juveniles than adults. For example, many estuarine-associated species of Sciaenidae often remain in close proximity to their natal habitats for the first years of life and migrate extensively thereafter (Gold and Richardson 1998). These results suggest that movement of late juvenile and adult life history stages may be an important alternative means of maintaining connectivity for some estuarine fish species. Ultimately, as movements of any one life-history stage may not necessarily be representative of connectivity throughout the life cycle (Miller and Able 2002; Tobin et al. 2010), it is important that connectivity is examined across a species' entire life history.

**Patterns of connectivity of tropical estuarine fishes**

In contrast to temperate systems, few studies have examined patterns of connectivity and population structure of tropical estuarine fishes, with the majority of studies conducted in tropical systems focusing on diadromous species, such as barramundi, *Lates calcarifer* (see Russell and Garrett 1988; Shaklee et al. 1993), hilsa, *Tenualosa ilisha* (see Milton and Chenery 2001a; Salini et al. 2004) or common snook, *Centropomus undecimalis* (see Adams et al. 2009). As with diadromous fishes in temperate systems, philopatry appears to be an important mechanism determining connectivity of these species (Jones 2006).

By comparison, there is a paucity of empirical data on the connectivity of non-diadromous species in tropical estuaries, with the majority of studies in these systems focusing on movements within estuaries (e.g. Sheaves 1993; Dantas et al. 2010). However, several features of tropical and subtropical coastal areas may facilitate greater connectivity between tropical estuarine populations than those observed in temperate systems. For example, salinity is largely considered to be a significant factor affecting the distribution, and hence movements and connectivity, of a number of temperate estuarine species (Loneragan et al. 1987; Blaber 2000; Ubeda et al. 2009). Tropical estuaries, however, regularly experience large fluctuations in salinity, often ranging from almost 0 to beyond 35‰, and as such, species that inhabit these systems have typically evolved a considerable degree of euryhalinity (Blaber 2000). Furthermore, the worldwide extent of tropical and subtropical estuaries approximately follows the distribution of mangroves (Duke 1992). Mangrove coastlines play an important role in facilitating sediment deposition, and may effectively extend estuarine conditions in coastal areas (Blaber 2000). Decreases in salinity and increases in turbidity during the tropical monsoon season may further increase the 'estuarisation' of tropical coastal areas (Longhurst

and Pauly 1987). Such phenomena may effectively increase the extent of suitable habitat for movement and dispersal, and potentially result in greater connectivity of tropical and subtropical estuarine fishes than their temperate counterparts. Irrespective of the scenario, with anthropogenic pressures on tropical estuarine fishes projected to increase (Blaber 2000; Blaber et al. 2000; Roessig et al. 2004), it becomes progressively more important to understand patterns of connectivity so that effective management practices can be implemented.

### 1.2 Methodological approaches in estimating population connectivity

The most direct evidence for population connectivity comes through the observation of tagged individuals moving from one group to another (Gillanders and Kingsford 1996). However, quantifying rates of connectivity through the use of artificial tags may be limited by a number of factors, including the proportion of the population that the tagged individuals represent, the rate of recapture of marked individuals, and length of time at liberty of those individuals. In addition, tag returns are often related to fishing effort (Ward and Caton 1992; Begg et al. 1997). While telemetric methods alleviate some of the issues relating to re-sampling, like the majority of tagging techniques they may be unsuitable for delicate species that have low survival rates following initial capture, and for use on early life history stages (Ward and Caton 1992; Gillanders 2002a).

In response to these limitations, a number of alternate techniques have been used to determine patterns of movement and connectivity of aquatic organisms, including larval transport models (Paris et al. 2005; Christensen et al. 2007), comparisons of life history (Begg et al. 1999b; Abaunza et al. 2008a; Silva et al. 2008), population genetics (Salini et al. 2004), otolith chemical signatures (Milton and Chenery 2001a; Gillanders 2002a) or shape indices (Begg and Brown 2000; Stransky et al. 2008), parasite assemblages (Lester et al. 1985; Lester et al. 2001; Moore et al. 2003; Moore et al. 2011a), or morphological or meristic characters (Kinsey et al. 1994; Salini et al. 2004). The selection of methodology employed to assess connectivity may vary depending on the type of data available, the life history stage for which connectivity is being assessed, or the questions being addressed (Begg and Waldman 1999).

There are, however, inherent limitations to each of these methodologies, and their efficacy can vary across different spatial and temporal scales, and between species. Larval transport models provide little information on connectivity of non-larval life history stages. Analyses of life history parameters typically do not enable classification of individual fish to a specific population owing to the wide natural variability that occurs within life history parameters between individual fish (Begg et al. 1999b). Genetic markers are extremely sensitive to the movement of genes between populations, and just one migrant per generation is sufficient to mask genetic differentiation (Slatkin 1987). Furthermore, genetic techniques

may be unable to identify differences between recently isolated groups, and frequently do not provide information at demographically-relevant spatial and temporal scales required for fisheries management and conservation purposes (Grosberg and Cunningham 2001; Hellberg et al. 2002; Botsford et al. 2009). Analysis of otolith chemistry and parasite assemblages, which typically relies on differences in environmental conditions, may be unable to differentiate populations within a homogeneous environment (Elsdon et al. 2008; Lester and MacKenzie 2009).

Combining the results obtained from several complementary techniques (i.e. a multidisciplinary approach (sensu Begg and Waldman 1999)) may provide considerable insight to the population connectivity of a species. The application of a multidisciplinary approach is generally regarded as more effective in determining movements than any one technique alone, as it not only gives greater confidence to the results of any one technique where consistent results are obtained, but also allows for the limitations of each technique to be resolved, effectively increasing the chances of identifying differences between spatially distinct populations in these instances (Begg and Waldman 1999). While multidisciplinary approaches are being increasingly adopted by fish biologists for the purposes of stock identification (e.g. Ayvazian et al. 2004; Buckworth et al. 2007; Abaunza et al. 2008b), such approaches have been largely overlooked by ecologists for addressing patterns of population connectivity (Thorrold et al. 2002), with most studies employing a single method to determine connectivity of a study species. However, the limited number of cases in which connectivity patterns have been examined by multiple techniques, used either concurrently or in succession, demonstrate the benefits of this approach. In one carefully designed application, Bradbury et al. (2008b) used a combination of otolith elemental data and adult tagging to examine homing and spawning site fidelity of rainbow smelt, *Osmerus mordax*, among estuaries in Newfoundland. The high degree of consistency observed between the two techniques allowed these authors to delineate the movements and connectivity to a greater degree of confidence than that resulting from either technique used in isolation. In an example of an unplanned, sequential approach, Thorrold et al. (2001) used otolith elemental signatures to examine population connectivity through natal homing in weakfish, *Cynoscion regalis*. These authors observed natal homing rates of up to 81%, with most strays going to adjacent estuaries, even though earlier genetic analyses detected no significant structure (Cordes 2000, cited in Thorrold et al. 2001). Thorrold et al. (2001) concluded that although there was significant demographic structuring among estuaries, the movement of only a few fish per generation was sufficient to prevent genetic differentiation. Such examples highlight the power in using a multidisciplinary approach to estimating connectivity.

### 1.3 Objectives and thesis structure

The broad objective of this thesis was to provide empirical data on the connectivity of a large, non-diadromous tropical estuarine teleost, using the king threadfin, *Polydactylus macrochir* Günther, 1867, as a study species. Specific aims, objectives and hypotheses are given in each chapter. Significantly, this project uses a multidisciplinary approach to discern patterns of connectivity of *P. macrochir*, incorporating data from multiple complementary techniques, including examination of life history, parasite assemblages, otolith elemental signatures, and conventional tagging data. Critically, connectivity is assessed across larval, juvenile and adult life history stages, and is examined at multiple spatial and temporal scales across the species geographical distribution.

This thesis is based upon findings presented in five research chapters. The chapters are structured as a progression of independent, yet complementary, studies, followed by a general discussion. The research chapters form the basis for stand-alone manuscripts that have been published, submitted or are being prepared for publication in peer-reviewed scientific journals. Accordingly, this approach has eventuated in some necessary and unavoidable repetition.

Chapter Two introduces the focal species of this study: the king threadfin, *P. macrochir*. The biology and ecology of the species, and its significance to fisheries, are discussed. Additionally, concurrent research into the movements and connectivity of the species are introduced. Chapter Three examines spatial patterns in life history of *P. macrochir* from 18 locations across northern Australia. Specifically, patterns in the timing of annuli deposition and spawning, longevity, growth, mortality, length and age at maturity, and length and age at sex change are assessed. Chapter Four examines the use of parasites as biological tags to examine connectivity of *P. macrochir* across these 18 locations. Spatial and temporal patterns in parasite assemblages are assessed. Chapter Five examines age-related patterns of otolith elemental signatures to provide information on the movement patterns of *P. macrochir*, including larval dispersal. In Chapter Six data from a collaborative tagging program is analysed to provide an additional measure of connectivity of *P. macrochir* in Queensland's waters. Chapter Seven consists of a general discussion, integrating the results of the various techniques and highlighting the significance and implications of the findings. Finally, key areas for future research are discussed.

# Chapter 2 Study species: king threadfin, *Polydactylus macrochir*

The king threadfin, *Polydactylus macrochir* Günther, 1867, was chosen as the focal species for this study. Several features of the biology and ecology of *P. macrochir*, outlined below, and its ecological significance and pertinence to fisheries, make the species a particularly suitable candidate in which to explore patterns and processes of connectivity.

## 2.1 Biology and ecology

*Polydactylus macrochir* is a member of the family Polynemidae, a percoid family of which eight genera and 42 species are currently recognised (Motomura 2004; Lim et al. 2010). The species is endemic to tropical and sub-tropical northern Australia, southern Papua New Guinea and Irian Jaya (Motomura et al. 2000; Motomura 2004), and is one of seven polynemid species found in Australian waters (Motomura 2004). In Australia, the distribution of *P. macrochir* extends across tropical and sub-tropical northern Australia from the Ashburton River in Western Australia to Brisbane in southeast Queensland, where it occurs in estuaries and turbid coastal waters typically less than 5 m in depth (Blaber et al. 1995; Motomura et al. 2000; Pember et al. 2005). *Polydactylus macrochir* does not use freshwater during any life history stage (Halliday et al. 2008), and was not encountered in surveys of temporary supra-littoral pools in the Gulf of Carpentaria (Russell and Garrett 1983), suggesting that the species likely limits its use of estuarine habitats to permanent water areas of the main channels and tributaries of creeks and rivers (Halliday et al. 2008).

*Polydactylus macrochir* has a life span of at least 22 years and an estimated maximum attainable size of approximately 40 kg and 170 cm fork length (Kailola et al. 1993; Moore et al. 2011b). They are protandrous hermaphrodites, changing from males to females, and form an important component of estuarine and coastal ecosystems, with dietary studies showing they are a significant predator of crustaceans and small fishes (Brewer et al. 1995; Salini et al. 1998). Both eggs and larvae of *P. macrochir* are pelagic (Motomura 2004), suggesting a high dispersal potential for these life history stages. Young-of-the-year juveniles (30–100 mm FL) have been observed in north Queensland estuaries in salinities ranging from 2.0 to 37.8 (Ian Halliday, pers. comm.), suggesting a high due of euryhalinity of these life history stages. In the Gulf of Carpentaria, adult *P. macrochir* have been observed in waters with salinities of 35‰ (Blaber et al. 1989). As such, it is unlikely that areas of high salinity, considered a key driver in the distribution patterns and connectivity of many estuarine-associated organisms in temperate systems (Loneragan et al. 1987; Ubeda et al. 2009), form a barrier to dispersal and exchange of *P. macrochir* among the estuaries of northern Australia.

Differences in growth and spawning time have been documented among *P. macrochir* populations in Australian waters, suggesting the species may exhibit significant geographical structuring. For example, Pember et al. (2005) reported populations in Western Australia attained approximate total lengths of 322, 520 and 945 mm by the end of years 1, 2 and 5, respectively, whereas Garrett (1997) reported populations of *P. macrochir* in Queensland's Gulf of Carpentaria waters attained approximate total lengths of 345, 490 and 790 mm by the end of years 1, 2 and 5, respectively. Peak spawning along the Pilbara and Kimberly coasts of Western Australia occurs from October to December (Pember et al. 2005), while in the Gulf of Carpentaria peak spawning occurs between August and September (Garrett 1997).

## 2.2 Significance to fisheries

Not only is *P. macrochir* an ecologically important component of tropical ecosystems, the species is also an important component of commercial, recreational and artisanal fisheries across its distribution. *Polydactylus macrochir* support valuable commercial and recreational fisheries across northern Australia, and form the second most important target species for northern Australia's inshore net fisheries after the barramundi, *Lates calcarifer* Bloch, 1790, with a reported 883 t harvested commercially across Australia in 2008. Of this, approximately 331 t were taken from the waters of the Northern Territory, 295 t from Queensland's Gulf of Carpentaria, 156 t from Queensland's east coast, and 101 t from Western Australia (Northern Territory Government 2009; Newman et al. 2009; A. Roelofs, Fisheries Queensland, pers. comm.). The species is also targeted by recreational anglers throughout its distribution, and is highly regarded as both a table and sport fish (Kailola et al. 1993). In 2000–01 it was estimated that the total recreational catch of threadfins (all species combined) across northern Australia was 185,000 individuals while a further 118,000 individuals were released (Henry and Lyle 2003).

Despite the species' ecological and economic importance, the degree of connectivity among spatially-distinct groups of *P. macrochir* is poorly understood. For purposes of fisheries management, single, intermixing populations, or stocks, are assumed in the waters of each of Western Australia, the Northern Territory, Queensland's Gulf of Carpentaria, and Queensland's east coast. However, these management arrangements for *P. macrochir* make no allowance for movement of fish between jurisdictions, or for the occurrence localised populations. Given its high level of association with estuarine and turbid water habitats, it is likely *P. macrochir* form a number of discrete, non-mixing populations across northern Australia, and as such may be highly susceptible to local depletion or environmental perturbation. There is growing concern over the status of *P. macrochir* across northern Australia, with populations in Western Australia considered to be over-exploited (Pember et al. 2005). As such, an understanding of the patterns

of connectivity is urgently required to implement effective management strategies for the species.

### 2.3 Concurrent research into connectivity of *Polydactylus macrochir*

In addition to the research themes presented in this thesis, two concurrent and complementary studies into the movement and connectivity of the species have been conducted. Horne et al. (2012) examined spatial patterns in mitochondrial DNA (mtDNA) haplotypes of *P. macrochir* from 10 locations across northern Australia (Figure 2.1). Their results suggest genetic homogeneity among *P. macrochir* from Eighty Mile Beach and Roebuck Bay in Western Australia, and between the Albert, Flinders and Kendall Rivers in the Gulf of Carpentaria, whereas all other locations (Chambers Bay, Blue Mud Bay, Cleveland Bay (Townsville), and the Fitzroy and Brisbane Rivers) appeared distinct.

Newman et al. (2010) examined whole otolith oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) stable isotope ratios from nine of the 10 locations examined by Horne et al. (2012), including two locations in Western Australia, two in the Northern Territory, three in Queensland's Gulf of Carpentaria and two on Queensland's east coast (Figure 2.1). These author's results largely corroborate those of Horne et al. (2012), with similarities observed among fish from Eighty Mile Beach and Roebuck Bay in Western Australia, and the Albert, Flinders and Kendall Rivers in the Gulf of Carpentaria, whereas distinct isotopic signatures were observed among fish from Chambers Bay and Blue Mud Bay in the Northern Territory, and Townsville and the Fitzroy River on Queensland's east coast. While the broad spatial scale at which these studies were conducted limits the conclusions that can be derived from these results, they nevertheless provide complementary evidence for the locations examined, further strengthening the multidisciplinary approach employed in this thesis.

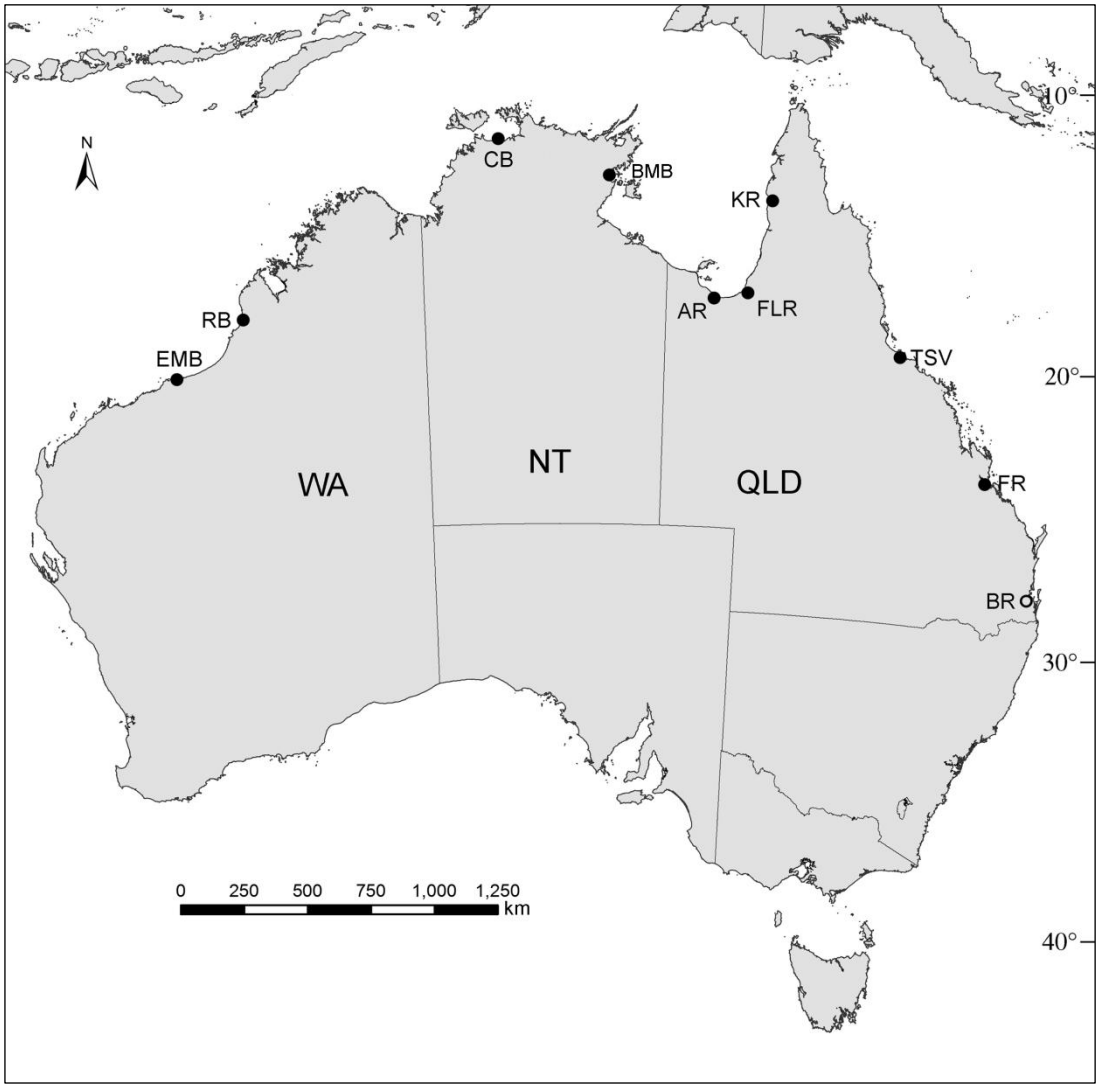


Figure 2.1 Sampling locations used in the examination of mitochondrial DNA haplotypes (Horne et al. 2012) (all circles) and whole otolith stable isotope ratios (Newman et al. 2010) (closed circles) of *Polydactylus macrochir*. Clockwise from left: EMB, Eighty Mile Beach; RB, Roebuck Bay; CB, Chambers Bay; BMB, Blue Mud Bay; AR, Albert River; FLR, Flinders River; KR, Kendall River; TSV, Cleveland Bay, Townsville; FR, Fitzroy River; BR, Brisbane River

# Chapter 3 Spatial patterns in life history reveals insight into connectivity and geographical population structure of a tropical estuarine teleost: king threadfin, *Polydactylus macrochir*

## 3.1 Introduction

Understanding the degree of exchange between geographically isolated groups of a species, or connectivity, is fundamental to the effective management of marine organisms (Begg et al. 1999a; Thorrold et al. 2001). Connectivity, which may occur through the movement of all life history stages (Gillanders 2009), influences the distribution and abundance of organisms, rates of local adaption and speciation, the dynamics and persistence of populations, and the ability of ecosystems and species to recover from disturbance (Slatkin 1987; Cowen et al. 2000). As such, an understanding of the connectivity is vital for determining the appropriate spatial scale at which a species should be managed (Begg et al. 1999a; Fogarty and Botsford 2007). For exploited species, the application of management measures that fail to accurately define the degree of exchange or opportunity for replenishment to local populations may lead to over-fishing, resulting in dramatic changes in the biological attributes and productivity rates of a species, as well as changes in genetic diversity (Ricker 1981; Smith et al. 1991; Dominguez-Petit et al. 2008), and localised depletion or extinction (Hilborn and Walters 1992; Hutchings 1996; Clark et al. 2000). Despite such critical importance, patterns of movement and connectivity are poorly understood for many species, particularly in tropical systems (Secor and Rooker 2005; Jones 2006; Gillanders 2009).

In addition to being critical components in the development of stock assessments and productivity models, life history parameters, such as age and growth relationships, mortality rates, reproductive profiles, fecundity, distribution and abundance, have been used to provide preliminary data on the connectivity and geographical population structure of fish populations (Jennings and Beverton 1991; Begg et al. 1999b; Abaunza et al. 2008a; Silva et al. 2008). The principle of the technique is that where the life histories of fish are the same, the fish either have grown in a similar environment or have a common history. Where different, it suggests that fish have spent at least part of their lives growing under different conditions and therefore may be geographically and/or reproductively isolated (Ihssen et al. 1981; Begg 2005; Caselle et al. 2011). Patterns of growth, reproductive schedules and mortality rates also provide important data for biological monitoring, and may provide an indication of a species or population's vulnerability to over-exploitation (Ricker 1975; Haddon 2001).

To date, the application of life history parameters as a tool to delineate fish movement and geographical population structure has largely focused on pelagic or groundfish species

(Begg et al. 1999b; Abaunza et al. 2008a; Silva et al. 2008). Although a number of studies have explored spatial patterns in life histories of estuarine fishes (Sarre and Potter 2000; Bedee et al. 2002; Gray et al. 2010), few studies have examined life history parameters in the context of delineating connectivity and geographical population structure in these environments. As a growing body of evidence suggests that the biology of estuarine fish is strongly linked to the environment in which they reside (Staunton-Smith et al. 2004; Robins et al. 2006; Halliday et al. 2008; Dolbeth et al. 2010), spatially isolated groups of estuarine fishes would be expected to exhibit significantly different life history parameters, particularly where differences in environmental conditions between locations are pronounced.

In this chapter, patterns in life history of *P. macrochir* are examined across the species' greater Australian distribution, as part of a multidisciplinary approach to determining connectivity of *P. macrochir* in Australian waters. Specifically, spatial patterns in age, growth, mortality rates and length and age at sex change are examined. It was hypothesised that as an estuarine species with a typically fragmented distribution, *P. macrochir* would show limited movement and exchange among locations that would manifest as differences in life history parameters.

## 3.2 Materials and methods

### Sample collection

*Polydactylus macrochir* were collected from 18 locations (lower estuarine stretches of rivers and coastal sites) across northern Australia between July 2007 and March 2010 (Figure 3.1; Table 3.1). Monthly samples were generally available for the Fitzroy, Mary and Brisbane Rivers on Queensland's east coast (Figure 3.1), allowing for quantification and comparison of the timing of annuli deposition and spawning season among these locations. At each of the 18 locations (with the exception of the Brisbane River and Lucinda), whole fish or fish frames (whole skeleton remaining after filleting) were obtained directly from commercial fishers, fish processors or by fisheries-independent sampling that generally used the same gear used by commercial fishers (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh). Brisbane River samples were collected through a fishery-independent sampling program using gillnets of 150 mm (6 in.) to 165 mm (6.5 in.) stretched mesh ($n$ = 34), by opportunistic collections from recreational fishers ($n$ = 42), and by research line-fishing ($n$ = 9), whereas Lucinda samples were obtained from recreational fishers. For each fish collected, the total length (TL), length to caudal fork (FL) and upper jaw length (UJL) was measured to the nearest millimetre unless damaged. Although whole weights ($W_w$) were generally unavailable from fishery-processor sourced samples as these had been filleted prior to biological processing, whole weights, measured to the nearest 1 g, were available for the

majority of Brisbane River specimens. Sex and maturity stage was determined from a macroscopic examination of the gonads, based on the criteria adapted from Pember et al. (2005) (Table 3.2). As some samples were eviscerated at sea it was not possible to determine sex and maturity stage for all specimens. Sagittal otoliths (hereafter referred to as otoliths) were removed for all specimens, cleaned, dried and stored in paper envelopes until processing in the laboratory. Although fishery regulations for this species is based on TL, I have generally analysed and presented FL data, as the fishery-sourced samples frequently had damage to the distal margins of the tail, precluding accurate TL measurements for some specimens. Total lengths were estimated using the equation of Moore et al. (2011b), where TL = 1.1737FL + 22.083. Missing fork lengths were estimated using the relationship between FL and UJL, where FL = 8.1501UJL + 4.7413 ($r^2$ = 0.95, $n$ = 2132).

**Age determination**

A comparison of whole and sectioned otolith reads was conducted to assess which structure would be used for ageing. Whole otoliths from a total of 460 individuals, taken from fish samples across all locations and length classes (including an additional 242 samples collected from the Fitzroy River between 2000 and 2005), were immersed in oil and examined microscopically under a reflected light against a black background and the number of opaque zones was counted. For otoliths from larger individuals, it was necessary to rotate the otolith to observe the annuli towards the otolith margin.

The same otoliths were mounted in resin and up to four transverse sections 300 μm thick were taken with a slow-speed diamond-edged saw (Buehler Isomet, Lake Bluff, IL, USA). Care was taken to ensure the primordium of the otolith was included in at least one section. All sections were cleaned and mounted on glass microscope slides with polyester resin. Otolith sections were examined under a stereo dissecting microscope with reflected light against a black background.

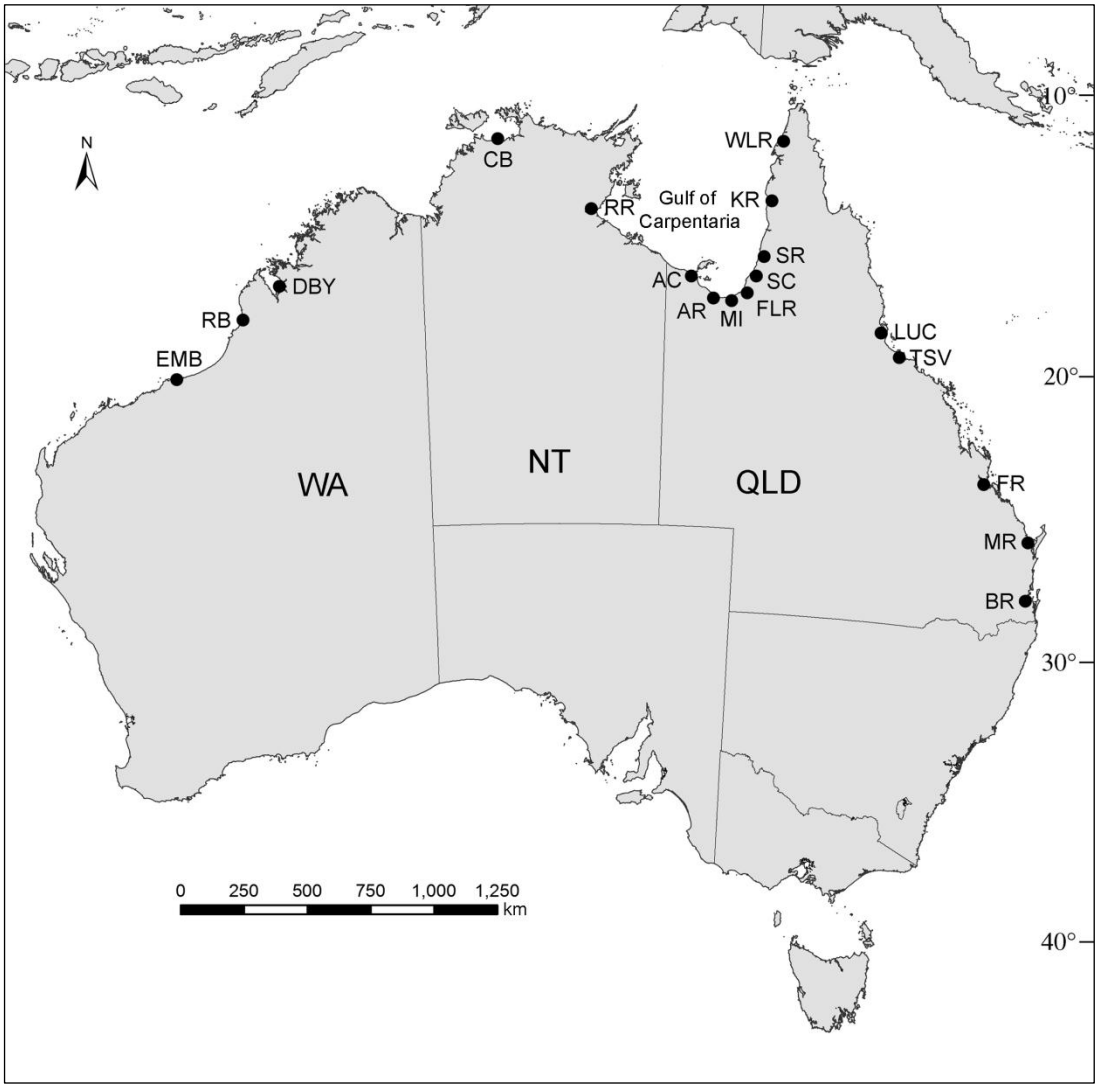


Figure 3.1 Locations where *Polydactylus macrochir* were sampled for examination of life history. From left: EMB, Eighty Mile Beach; RB, Roebuck Bay; DBY, Derby; CB, Chambers Bay; RR, Roper River; AC, Arthurs Creek; AR, Albert River; MI, Morning Inlet; FLR, Flinders River; SC, Spring Creek; SR, Staaten River; KR, Kendall River; WLR, Wenlock River; LUC, Lucinda; TSV, Cleveland Bay, Townsville; FR, Fitzroy River; MR, Mary River; BR, Brisbane River.

Table 3.1 Summary of *Polydactylus macrochir* collected from 18 locations across Australia. Undetermined indicates fish were eviscerated at sea.

| **Location** | ***n*** | **Mean age (years)** | **Age class range (years)** | **Mean FL (mm)** | **FL range (mm)** | ***n* males** | ***n* females** | ***n* transitionals** | ***n* undetermined** |
|---|---|---|---|---|---|---|---|---|---|
| Eighty Mile Beach | 150 | 4.9 | 1–12 | 687 | 228–1080 | 41 | 99 | 10 | 0 |
| Roebuck Bay | 319 | 2.8 | 1–10 | 635 | 451–919 | 260 | 55 | 4 | 0 |
| Derby | 61 | 4.0 | 1–10 | 698 | 210–1040 | 28 | 26 | 7 | 0 |
| Chambers Bay | 126 | 6.3 | 2–12 | 816 | 505–1030 | 73 | 52 | 1 | 0 |
| Roper River | 126 | 4.9 | 2–11 | 864 | 480–1090 | 20 | 6 | 1 | 99 |
| Arthurs Creek | 44 | 3.5 | 2–6 | 565 | 415–835 | 38 | 5 | 1 | 0 |
| Albert River | 36 | 3.7 | 3–5 | 599 | 520–715 | 31 | 5 | 0 | 0 |
| Morning Inlet | 54 | 3.6 | 2–7 | 567 | 325–1130 | 29 | 24 | 1 | 0 |
| Flinders River | 138 | 3.6 | 2–8 | 655 | 325–930 | 83 | 49 | 5 | 1 |
| Spring Creek | 103 | 3.5 | 2–9 | 611 | 295–1020 | 55 | 45 | 2 | 1 |
| Staaten River | 31 | 2.4 | 2–4 | 495 | 320–595 | 9 | 21 | 1 | 0 |
| Kendall River | 63 | 2.1 | 1–3 | 528 | 315–810 | 57 | 6 | 0 | 0 |
| Wenlock River | 33 | 2.7 | 2–5 | 679 | 442–960 | 29 | 3 | 0 | 1 |
| Lucinda | 25 | 3.6 | 3–4 | 801 | 645–895 | 18 | 0 | 4 | 3 |
| Townsville | 84 | 2.8 | 1–4 | 701 | 450–886 | 67 | 2 | 1 | 14 |
| Fitzroy River | 699 | 4.7 | 2–22 | 801 | 430–1354 | 241 | 29 | 6 | 423 |
| Mary River | 61 | 5.3 | 2–11 | 806 | 440–1016 | 47 | 8 | 1 | 5 |
| Brisbane River | 85 | 5.6 | 2–14 | 828 | 493–1062 | 58 | 18 | 2 | 7 |

Table 3.2 Descriptions used to macroscopically stage the development of *Polydactylus macrochir* gonads (adapted from Pember et al. 2005).

| Stage | Description | Testes | Ovaries |
|---|---|---|---|
| I/II | Immature/resting | Small, grey and strand-like (Stage I) to white and ribbon-like (Stage II). | Small and transparent. Yellowish-orange. Oocytes not visible through ovarian wall. |
| III | Developing | White and occupy approximately half the length of body cavity. | Slightly larger than Stage II. Oocytes visible through ovarian wall. |
| IV | Maturing | No milt appears when pressure is applied to trunk of males. Occupy more than half the length of the body cavity. | Larger than stage III, occupying half of body cavity. Creamy orange. Large oocytes visible through ovarian wall. |
| V/VI | Ripe/running ripe | One-third to filling body cavity. Milt exuded with firm pressure to abdominal cavity (Stage VI). | Large, occupying half to two thirds of body cavity. Extensive capillaries visible in ovarian wall. Hydrated oocytes sometimes visible ovarian wall in Stage VI ovaries. Ovaries typically with anterior lateral undulations. |
| VII | Spent | Smaller than Stage V or VI. Gonads flaccid but not totally empty. | Smaller than Stages V and VI and flaccid. Some large oocytes visible through ovarian wall. |
| VIII | Recovering | Red to brown, small and flaccid. | Small, flaccid and dark red. |

An image of each whole and sectioned otolith was taken with a Leica DC 300 digital camera (Leica, Wetzlar, Germany) connected to the dissecting microscope. Ages of both whole and sectioned otoliths were assigned on the basis of counts of alternating opaque and translucent bands, verified as annuli by Pember et al. (2005). To assess the timing of annuli formation of fish from the Fitzroy, Mary and Brisbane Rivers, the margin of each otolith was classified into one of the following four categories: (0) continuous opaque band formed around the edge of otolith, with no translucent material beyond the last opaque band; (1) translucent band laid onto the outer edge comprising less than half the width of the previous translucent band; (2) translucent band laid onto the outer edge comprising roughly half or more the width of the previous translucent band; and (3) opaque band on the edge of the otolith, however band is not continuous.

The precision of annuli estimates from whole and sectioned otoliths was calculated using the coefficient of variation (CV) (Chang 1982). Greater precision is achieved when CV is minimised (Campana et al. 1995). Once the method of reading was established (see Results), each otolith was read twice. When counts did not agree, a third reading was taken, and if two counts agreed they were accepted as the number of annuli. When all three counts differed, the otolith was rejected from further analysis. All otoliths were read by a single, experienced reader (BRM) whose reading accuracy was tested against a reference set of *P. macrochir* otoliths. Otoliths used in the reference set were collected from the Fitzroy River between October 2000 and February 2005. Counts from this reader were considered valid on the basis of a consistent agreement with counts of the reference otoliths.

The absolute age of each fish was estimated from the number of annuli, the assumed birth date, the estimated date of annuli deposition, and the date of capture. Birth dates were estimated from the middle of the peak spawning period for each major water body. A birth date of 1 November was assumed for *P. macrochir* collected from the northwest coast of Western Australia (Pember et al. 2005) and Queensland's east coast (see Results; Russell 1988), whereas a birth date of the 1 September was assumed for fish collected from the Gulf of Carpentaria (Garrett 1997). Although little is known about the timing of spawning of *P. macrochir* along the northern coast of the Northern Territory, a birth date of 1 November was assumed in these waters, consistent with observations of peak spawning reported by fishers (Ian Halliday, pers. comm.). A common date of annuli completion of 31 October was assumed for fish from all locations, years and age classes (see Results; Pember et al. 2005). There was no evidence to suggest that Gulf of Carpentaria populations laid down a visible opaque zone in their first October of life (i.e. when they were 1 month old). The ageing algorithm took the form:

$$age_{\mathrm{m}} = \big((n-1) \times 12\big) + m_{\mathrm{b}} + m_{\mathrm{c}}$$

where $age_{\mathrm{m}}$ is the age in months, n is the number of annuli, $m_{\mathrm{b}}$ is the number of months for the assigned birth date to the date of annuli completion, and $m_{\mathrm{c}}$ is the number of months from the date of annuli completion to the date of capture. Ages were then converted to a yearly fraction by dividing the age in months by 12. Adjusted age estimates were rounded to the nearest year for estimation of age frequency distributions and age at sex change. Year classes were assigned on the basis of the peak spawning period (i.e. fish from the Fitzroy River spawned between October 2005 and January 2006 are considered to be from the 2005 year class).

**Data analysis**

*Growth comparisons*

Growth was compared among locations using two methods. In the first method, the von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of FL on age of *P. macrochir*. The form of the VBGF used to model length-at-age data was:

$$L_{\mathrm{t}} = L_{\infty}[1 - \mathrm{e}^{-K(t-t_0)}]$$

where $L_{\mathrm{t}}$ is the length mean of fish at age t, $L_{\infty}$ is the hypothetical asymptotic length, $K$ is the growth coefficient, and $t_0$ is the hypothetical age at which fish would have zero growth. To examine the effect of the low numbers of fish < 2 years in the samples a second set of analyses was conducted on data with the $t_0$ constrained to zero. Unconstrained and constrained VBGFs were compared among locations using likelihood ratio tests. A common range of ages was used in the analyses to ensure validity of the comparisons (Haddon 2001).

Due to the lack of older individuals in some of the samples, biologically meaningful comparisons of VBGF parameters could not be conducted for all locations. As such, a second analysis of growth, based on comparisons of back-calculated FL at age 2, was conducted. To establish the relationship between FL and otolith radius at the time of capture (OR), the distance from the nucleus of the otolith to its periphery was measured in 1430 randomly selected individuals covering a range of ages and locations, using the Image ProPlus image analysis system. Measurements were always taken at the furthest point of the structure (Figure 3.2). The relationship between FL and OR was then determined by ordinary least-squares regression. Between-location differences in the FL-OR relationship could not be examined at all locations due to the unreliability of comparing regressions based on small sample sizes at some locations. However, ANCOVA revealed no significant difference in the FL-OR relationship between 11 locations covering the geographical distribution of the sampling program, that all had relatively large sample sizes ($F = 1.68$, d.f. = 10, 1032, $P = 0.08$).

Combined with the propinquity of the data points from the overall regression (Figure 3.3), this suggests that any between-location differences in the FL-OR relationship may be negligible. Thus, data were pooled across locations to establish the relationship between fork length and otolith radius.

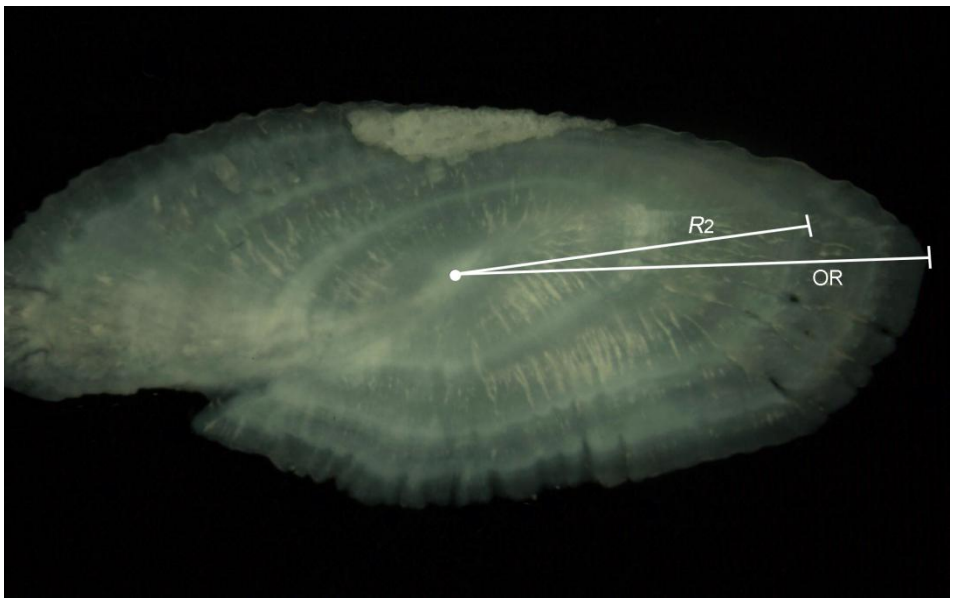


Figure 3.2 Sagittal otolith of a 3 year-old *Polydactylus macrochir* collected from the Fitzroy River showing measurements made for back-calculation of length-at-age 2. OR is the radius of the otolith at capture and $R_2$ is the radius of the otolith at 2 years.

To establish the back-calculated length-at-age 2, a second measurement from the otolith nucleus to the furthest point of the second annuli was taken for each fish from the 2005 year class (Figure 3.2). The 2005 year class was selected to reduce the effect of temporal variation in growth. Back-calculated length-at-age 2 was then determined by substituting this measurement into a body proportional equation (Francis 1990). The length of an individual fish when the second annulus was laid down ($FL_2$) was calculated as:

$$FL_2 = (R_2|OR)^{\nu}FL$$

where $R_2$ is the distance from the otolith nucleus to the furthest point of the second annuli, FL is the fork length at capture and $\nu$ is the constant derived from the power function that best described the relationship between FL and OR (Figure 3.3). Shapiro-Wilk tests revealed that the derived length-at-age 2 data were non-normally distributed ($P < 0.05$), so to satisfy assumptions of normality and homogeneity of variances the data were log-transformed prior to analysis. One-way analysis of variance (ANOVA) was used to test for differences in back-

calculated lengths-at-age 2 among locations using location as a fixed factor. Significant results were examined using Tukey-Kramer post-hoc pairwise comparisons. Only locations that had at least 10 individuals were considered in the analysis, which is similar to the samples sizes used by Erzini (1994) and Abaunza et al. (2008a) in their respective studies of variability of length-at-age of marine fishes.

*Mortality*

Total instantaneous mortality rates (*Z*) were estimated using age-based catch curves (Ricker 1975), where the frequency of fish in each age class was log-transformed (ln x+1) and regressed against the corresponding age. Total mortality was estimated as the absolute value of the regression slope, *b*. Regressions were fitted from the first modal age class, presumed to be the first age class fully selected by the sampling gear, through to the oldest age class that was preceded by no more than two zero frequencies. Estimates of *Z* were compared among locations by analysis of covariance (ANCOVA), with age as the covariate. Due to low sample sizes and a general lack of older individuals for some locations mortality rates were calculated only for those locations where comparisons of VBGF parameters were conducted.

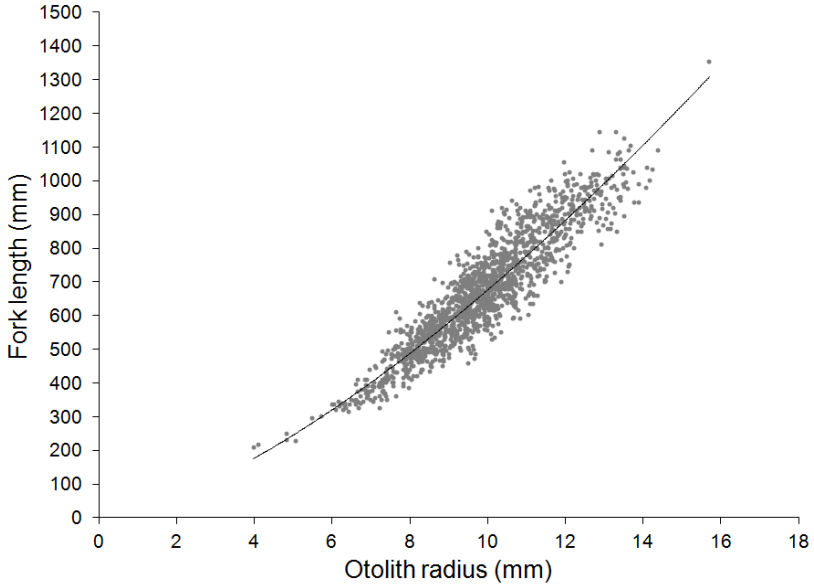


Figure 3.3 Plot of fork length on otolith radius for *Polydactylus macrochir* and the power relationship ($FL = 23.271OR^{1.463}$, $r^2 = 0.864$, $n = 1490$).

*Spawning season*

The spawning season for *P. macrochir* at the Fitzroy, Mary and Brisbane Rivers on Queensland east coast was estimated on the basis of macroscopic staging of reproductive

tissue samples and by the gonado-somatic index (GSI). The GSI was calculated for each male fish with a FL greater than the estimated length at 50% maturity ($L_{m50}$) and for each mature female fish (Stage III or above) using the following equation:

$$GSI = (W\mathrm{g}|W\mathrm{w}) \times 100$$

where $W_g$ is gonad weight and $W_w$ is the whole-fish weight. For several individuals, only one complete gonad lobe was available, as a result of damage during capture and processing. Analysis of 50 randomly sampled gonads revealed no statistically significant difference between the weight of the left and right lobe (one way ANOVA, $P < 0.05$). Consequently, $W_g$ was estimated by multiplying the weight of the single complete lobe by two. Because measurements of $W_w$ were generally unavailable from the Fitzroy or Mary River samples, $W_w$ was estimated for these individuals using the length-weight relationship established on the basis of samples predominately from the Brisbane River. It was assumed that estimates of $W_w$ derived from this relationship would suffice for use in estimating GSI values because only the temporal patterns in GSI, rather than absolute values, were examined to determine spawning season. Mean monthly GSI values and the proportion of individuals in each macroscopically determined reproductive stage were plotted separately for males and females to determine the seasonality of spawning in *P. macrochir* from the Fitzroy, Mary and Brisbane Rivers. Because preliminary results revealed no significant difference in the peak or duration of spawning among the three locations, the GSI and staging data were pooled across locations to maximise samples sizes for each month.

*Length and age at maturity*

The length and age at maturity was determined for samples of male fish on the basis of the macroscopic stage assessments (Table 3.2). Fish with gonads staged III–VIII were defined as mature. Individuals assigned a gonad stage of I or II were defined as immature, because they were considered incapable of spawning during the upcoming spawning season. To reduce the probability of mis-identifying post-spawning gonads as immature, only fish collected immediately prior to or during the spawning season, or those that were obviously mature (i.e. milt present), were used to calculate the length and age at sexual maturity. This limited comparison of length and age at maturity to three locations: the Fitzroy, Mary and Brisbane Rivers.

The length and age at which 50% of the *P. macrochir* population attains maturity for each of the locations was then determined by logistic regression analysis, using the following equation:

$$Pm = 1/[1 + \exp(-\ln(19)\,(m - m_{50})/(m_{95} - m_{50}))]$$

where *Pm* = the proportion of mature fish in each age or 50 mm FL class *m*, $m_{50}$ and $m_{95}$ are the lengths or ages at which 50% and 95% of the population is mature, respectively. The data (immature or mature) were randomly re-sampled and analysed to create 500 sets of bootstrap estimates for the parameters of the logistic equation and estimates of the probability of maturity within the recorded lengths and ages. The point estimates for each parameter and of each probability of maturity were taken as the medians of the bootstrap estimates. Approximate 95% confidence limits of the parameters were calculated as the 2.5 and 97.5 percentiles of the parameter estimates obtained from the re-sampling technique. Non-overlapping confidence intervals were used to indicate significant differences in maturity profiles among locations.

*Length and age at sex change*

The length and age at which 50% of *P. macrochir* changed sex at each location was determined by logistic regression analysis, using the equation:

$$Ps = 1/[1 + \exp(-\ln(19)\,(s - s_{50})(s_{95} - s_{50}))]$$

where *Ps* = the proportion of females in each 50 mm length or age class *s*, $s_{50}$ and $s_{95}$ are the ages or lengths at which 50% and 95% of the population have changed to females, respectively. Due to low numbers, transitional individuals were excluded from the analysis. As with maturity estimates, the data (male or female) for individual fish were randomly re-sampled and analysed to create 500 sets of bootstrap estimates for the parameters of the logistic equation and estimates of the probability of maturity within the recorded lengths and ages. Approximate 95% confidence limits of the parameters were calculated as the 2.5 and 97.5 percentiles of the parameter estimates obtained from the re-sampling technique. The point estimates for each parameter and of the probability of fish being female at each specified length or age were taken as the medians of the bootstrap estimates. Non-overlapping confidence intervals were used to indicate significant differences in sex change profiles among locations.

## 3.3 Results

### Age determination

The CV of age estimates between whole and sectioned otoliths was 1.22% (averaged across all ages), indicating a high degree of precision between whole- and sectioned-otolith age estimates. However, when analysed against age, there was an increasing divergence in age estimation between whole and sectioned otoliths as the number of annuli increased, particularly for otoliths with 7–17 annuli, with whole otoliths providing an underestimation of

age compared to sectioned otoliths (Figure 3.4). The apparent increase in accuracy in whole reads of fish with 18 or more annuli is likely to be due to the small sample sizes in the age classes, and an awareness of the maximum age of the species. Based on these results, all otoliths were initially read whole. Otoliths in which six or fewer annuli were counted in the initial read were read whole again, whereas otoliths in which more than six annuli were counted in the initial read were sectioned before being read again.

Examination of the otolith marginal increment revealed consistent trends in the timing of annuli deposition among the Fitzroy, Mary and Brisbane Rivers (Figure 3.5). Otoliths collected between December and July from all locations had translucent margins. Non-continuous bands were generally observed in samples collected between August and October, whereas newly formed completed bands were observed in fish collected in October and November. These results suggest that annuli deposition is completed by the beginning of November at each of these locations.

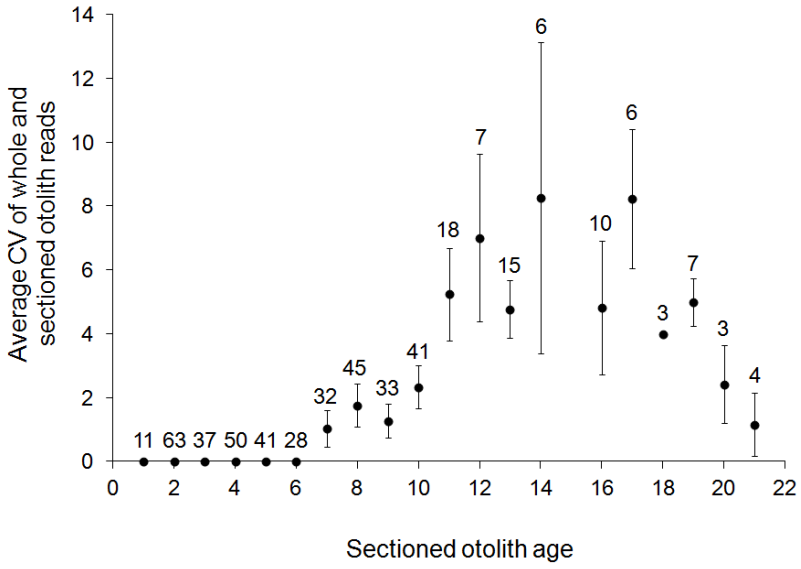


Figure 3.4 Coefficient of variation (CV) (± 1 s.e.) for annuli estimates between whole and sectioned otoliths plotted against counts of annuli from sectioned otoliths of *Polydactylus macrochir*. Numbers above error bars indicate sample size.

**Age and growth**

Considerable differences were observed in the maximum age of *P. macrochir* between locations. Fish aged eight years or older were recorded at only 10 of the 18 locations (Table 3.1). The oldest fish (21.9 years) was recorded from the Fitzroy River, whereas the maximum

age of fish from locations in Western Australia and the Queensland's Gulf of Carpentaria was 11.5 and 8.5 years, respectively

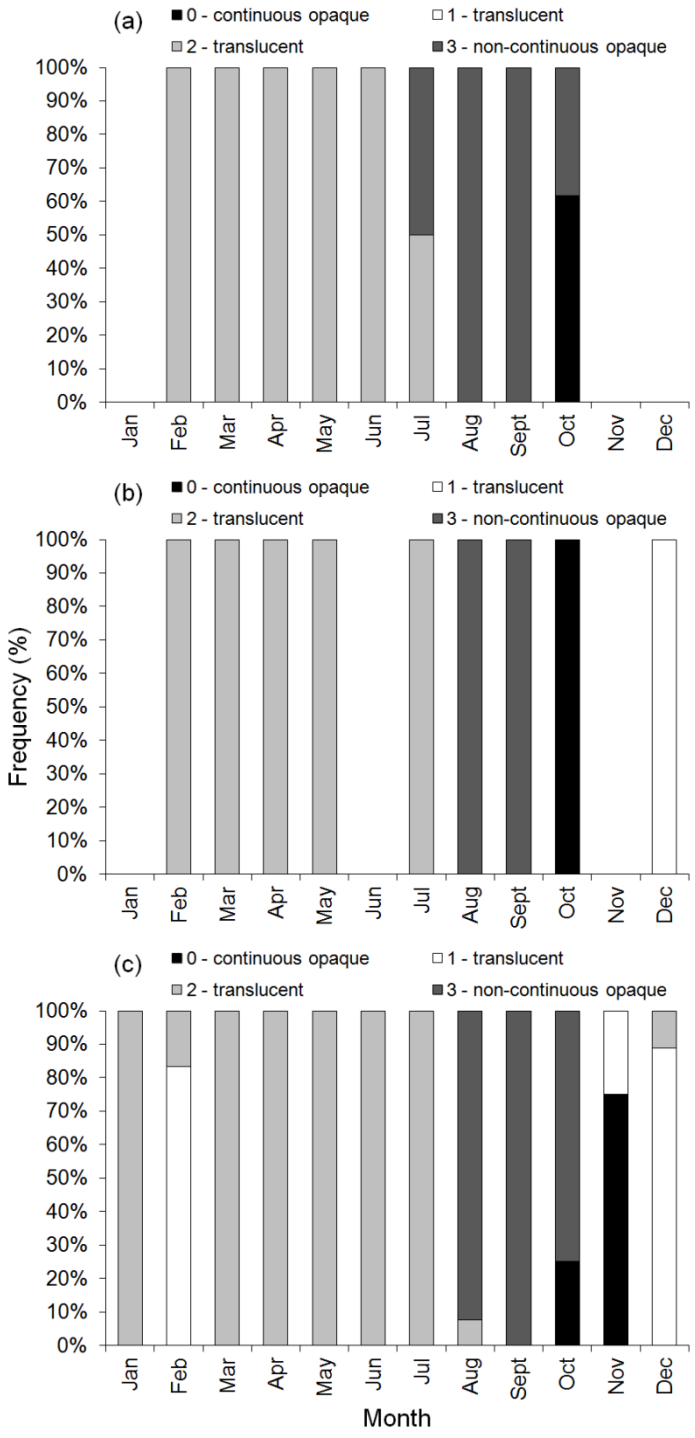


Figure 3.5 Percentage of *Polydactylus macrochir* otoliths in each marginal edge category from the (a) Fitzroy, (b) Mary, and (c) Brisbane Rivers on the east coast of Queensland, Australia. See text for a full description of the margin category codes.

*Comparisons of von Bertalanffy growth parameters*

Due to the lack of older individuals at some locations, estimation and comparison of the VBGF parameters were considered appropriate for only the 10 locations that contained fish that were eight years of age or older (Table 3.3). In general, the constrained fit of the VGBF typically resulted in slightly lower estimates of $L_\infty$ and slightly higher estimates of $K$ than the unconstrained fit (with the exception of samples from Derby, the Flinders River, Spring Creek and the Mary River) (Table 3.4). Differences between the constrained and unconstrained fits, however, were generally minimal (Figure 3.6), suggesting that a sufficiently wide range of length and age classes were sampled to establish biologically reasonable estimates of growth without the need to constrain $t_0$.

Both constrained and unconstrained VBGF parameters estimates showed considerable difference among locations. Likelihood ratio tests of unconstrained VBGFs of fish across common age classes indicated that growth differed amongst most locations at $P = 0.05$, with the exception of Derby and the Mary River ($\chi^2 = 6.576$, $P = 0.087$), the Flinders River and Spring Creek ($\chi^2 = 5.211$, $P = 0.157$) and the Mary and Brisbane Rivers ($\chi^2 = 6.191$, $P = 0.103$). Likelihood ratio tests of constrained VBGFs confirmed the similarity observed in the comparisons of the unconstrained growth estimates of fish from the Flinders River and Spring Creek ($\chi^2 = 6.679$, $P = 0.083$) and the Mary and Brisbane Rivers ($\chi^2 = 0.759$, $P = 0.684$). With the exception of Eighty Mile Beach and Spring Creek ($\chi^2 = 1.366$, $P = 0.505$), Roebuck Bay and Chambers Bay ($\chi^2 = 5.289$, $P = 0.071$), and the Roper River and Fitzroy River ($\chi^2 = 5.227$, $P = 0.073$), other comparisons were significantly different at $P = 0.05$.

Table 3.3 Summary of locations where biologically meaningful comparisons of *Polydactylus macrochir* life history were possible.

| Location | Marginal increments | VBGF parameters | Back-calculated length-at-age 2 | Total mortality | Spawning season | Length and age at maturity | Length and age at sex change |
|---|---|---|---|---|---|---|---|
| Eighty Mile Beach | - | ✓ | ✓ | ✓ | - | - | ✓ |
| Roebuck Bay | - | ✓ | ✓ | ✓ | - | - | ✓ |
| Derby | - | ✓ | ✓ | ✓ | - | - | ✓ |
| Chambers Bay | - | ✓ | ✓ | - | - | - | ✓ |
| Roper River | - | ✓ | ✓ | - | - | - | - |
| Arthurs Creek | - | - | ✓ | - | - | - | - |
| Albert River | - | - | ✓ | - | - | - | - |
| Morning Inlet | - | - | ✓ | - | - | - | - |
| Flinders River | - | ✓ | ✓ | ✓ | - | - | - |
| Spring Creek | - | ✓ | ✓ | ✓ | - | - | - |
| Staaten River | - | - | - | - | - | - | - |
| Kendall River | - | - | ✓ | - | - | - | - |
| Wenlock River | - | - | ✓ | - | - | - | - |
| Lucinda | - | - | ✓ | - | - | - | - |
| Townsville | - | - | ✓ | - | - | - | - |
| Fitzroy River | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Mary River | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Brisbane River | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |

Table 3.4 von Bertalanffy growth parameters and rates of total mortality for *Polydactylus macrochir* from ten locations across northern Australia.

| **Location** | **Unconstrained VBGF** | | | **Constrained ($t_0$ = 0) VBGF** | | **Total mortality** | |
|---|---|---|---|---|---|---|---|
| | $L_\infty$ **(mm)** | $K$ | $t_0$ | $L_\infty$ **(mm)** | $K$ | $Z$ | $r^2$ |
| Eighty Mile Beach | 1108 | 0.23 | -0.26 | 1074 | 0.26 | 0.162 | 0.42 |
| Roebuck Bay | 888 | 0.46 | -0.33 | 869 | 0.55 | 0.372 | 0.51 |
| Derby | 1176 | 0.26 | 0.10 | 1199 | 0.24 | 0.373 | 0.68 |
| Chambers Bay | 965 | 0.32 | -1.05 | 942 | 0.46 | 0.120 | 0.20 |
| Roper River | 1094 | 0.33 | -0.04 | 1091 | 0.34 | 0.626 | 0.89 |
| Flinders River | 835 | 0.53 | 0.53 | 1094 | 0.38 | 0.887 | 0.94 |
| Spring Creek | 978 | 0.35 | 0.48 | 1096 | 0.25 | 0.642 | 0.64 |
| Fitzroy River | 1222 | 0.24 | -0.34 | 1201 | 0.27 | 0.119 | 0.49 |
| Mary River | 975 | 0.46 | 0.79 | 1018 | 0.33 | 0.311 | 0.46 |
| Brisbane River | 1047 | 0.30 | -0.25 | 1034 | 0.33 | 0.298 | 0.55 |

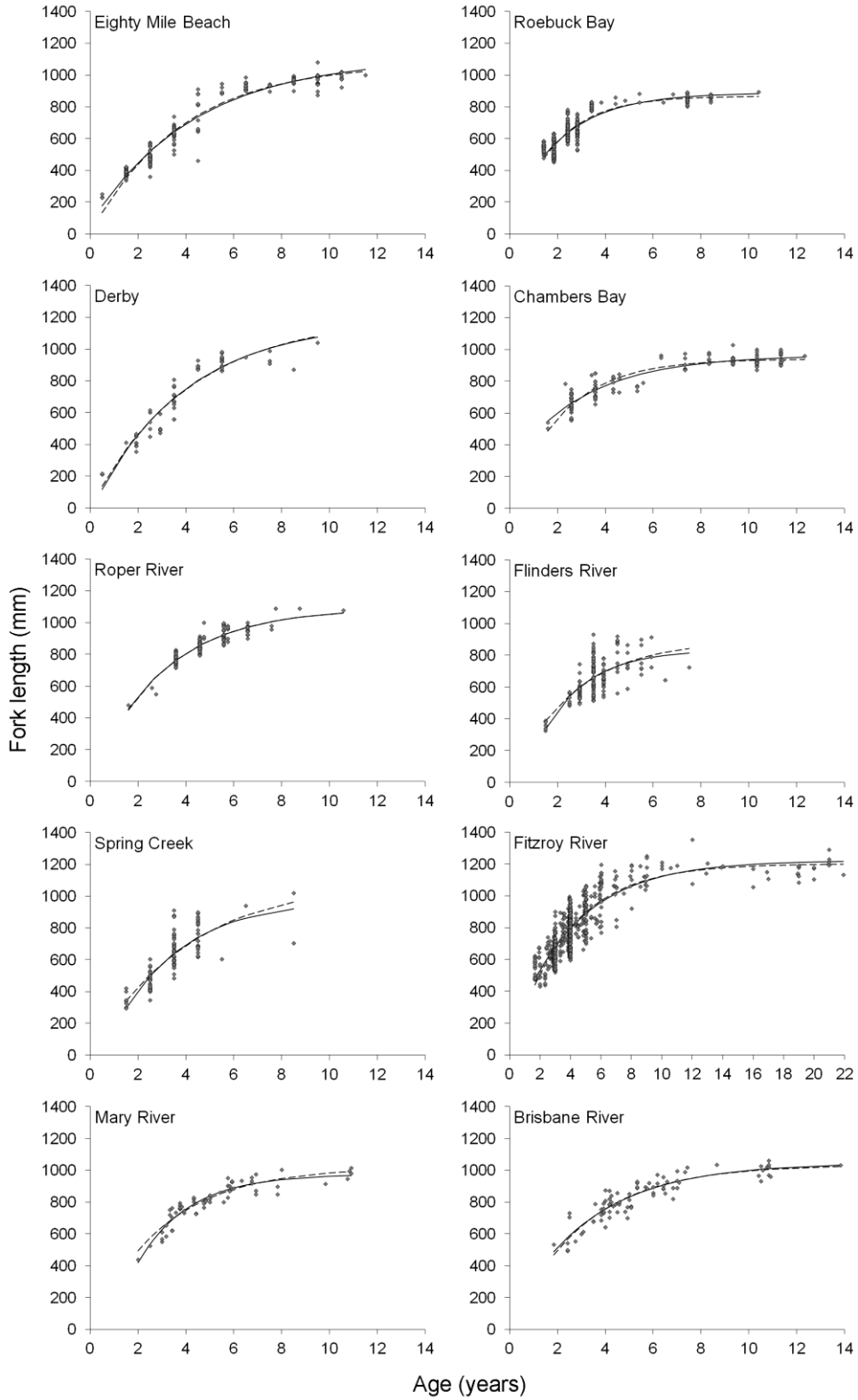


Figure 3.6 Length at age data, unconstrained (solid lines) and constrained ($t_0 = 0$) (dashed lines) and von Bertalanffy growth function curves for *Polydactylus macrochir* in Australian waters. See Table 3.4 for parameter estimates.

*Comparisons of back-calculated length-at-age*

One-way ANOVA revealed that the mean back-calculated length-at-age 2 estimates differed significantly among locations ($F = 18.6$, d.f. = 16, 389, $P < 0.01$). Tukey-Kramer pair-wise comparisons gave an indication of the similarity between the spatially distinct samples (Table 3.5). Samples from Eighty Mile Beach and Roebuck Bay differed significantly, with Roebuck Bay samples generally being larger than those from Eighty Mile Beach (Figure 3.7). Samples from Derby differed to those of neighbouring Roebuck Bay and Chambers Bay. No difference was observed between Chambers Bay, Roper River, Kendall River or Wenlock River samples. Samples from Arthurs Creek, the Albert and Flinders Rivers, Morning Inlet, and Spring Creek in Queensland's south-eastern Gulf of Carpentaria waters appeared similar, suggesting that these fish had either grown in a similar environment or moved between locations. Samples from these locations were generally smaller than those from all other Gulf of Carpentaria locations (Figure 3.7). No significant difference was observed between the five locations on the east coast of Queensland (Lucinda, Townsville, and the Fitzroy, Mary and Brisbane Rivers).

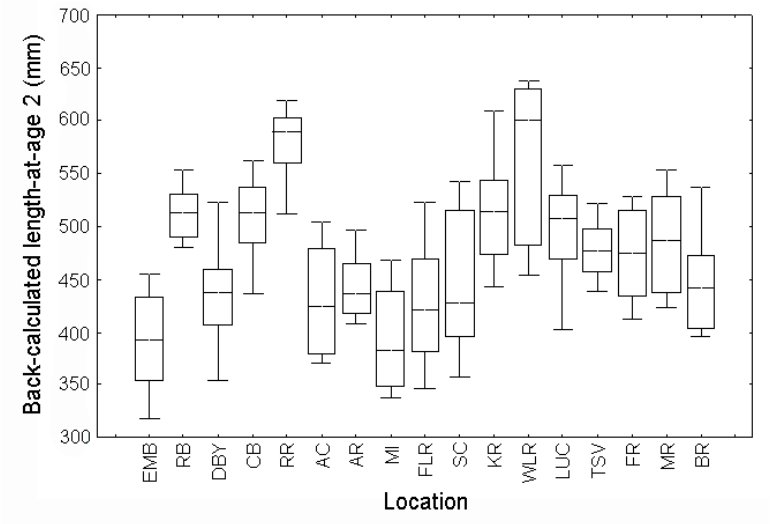


Figure 3.7 Back-calculated fork length-at-age 2 for *Polydactylus macrochir* from 17 locations across northern Australia. The mean, 25$^{th}$ and 75$^{th}$ percentiles (boxes) and 90$^{th}$ percentiles (whiskers) are represented in the boxplots. See Figure 3.1 for location codes.

Table 3.5 *P*-values from Tukey-Kramer pair-wise comparisons of back-calculated length-at-age 2 for *Polydactylus macrochir* from the 2005 year class collected from 17 locations across northern Australia (bold indicates significant difference).

| Location | EMB | RB | DBY | CB | RR | AC | AR | MI | FLR | SC | KR | WLR | LUC | TSV | FR | MR | BR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EMB | – | **<0.001** | 0.459 | **<0.001** | **<0.001** | 0.518 | 0.072 | 1.000 | 0.509 | **0.025** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **0.026** |
| RB | | – | **<0.001** | 1.000 | 0.056 | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | 1.000 | 0.652 | 0.998 | 0.194 | **0.013** | 0.972 | **0.004** |
| DBY | | | – | **0.017** | **<0.001** | 1.000 | 1.000 | 0.637 | 1.000 | 1.000 | **0.012** | **<0.001** | 0.209 | 0.419 | 0.668 | 0.528 | 1.000 |
| CB | | | | – | 0.060 | **<0.001** | **0.017** | **<0.001** | **<0.001** | **0.003** | 1.000 | 0.541 | 1.000 | 0.899 | 0.513 | 1.000 | 0.098 |
| RR | | | | | – | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | 0.161 | 1.000 | **0.012** | **<0.001** | **<0.001** | **0.006** | **<0.001** |
| AC | | | | | | – | 1.000 | 0.740 | 1.000 | 0.999 | **<0.001** | **<0.001** | **0.006** | **0.006** | **0.021** | 0.061 | 0.990 |
| AR | | | | | | | – | 0.173 | 0.996 | 1.000 | **0.012** | **<0.001** | 0.271 | 0.509 | 0.782 | 0.660 | 1.000 |
| MI | | | | | | | | – | 0.756 | 0.087 | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | 0.074 |
| FLR | | | | | | | | | – | 0.987 | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **<0.001** | **0.016** | 0.943 |
| SC | | | | | | | | | | – | **0.002** | **<0.001** | 0.127 | 0.223 | 0.482 | 0.485 | 1.000 |
| KR | | | | | | | | | | | – | 0.732 | 1.000 | 0.813 | 0.407 | 0.998 | 0.071 |
| WLR | | | | | | | | | | | | – | 0.220 | **0.005** | **<0.001** | 0.130 | **<0.001** |
| LUC | | | | | | | | | | | | | – | 1.000 | 0.994 | 1.000 | 0.607 |
| TSV | | | | | | | | | | | | | | – | 1.000 | 1.000 | 0.888 |
| FR | | | | | | | | | | | | | | | – | 1.000 | 0.984 |
| MR | | | | | | | | | | | | | | | | – | 0.910 |

**Total mortality**

Total mortality (*Z*) estimates differed significantly among the ten locations where comparisons were possible (ANCOVA, F = 3.97, d.f. = 9, 81, $P < 0.001$) (Table 3.4). Locations in the Gulf of Carpentaria (Flinders River, Spring Creek and the Roper River) had the highest estimates of *Z*, whereas *Z* was lowest for the Fitzroy River, Chambers Bay and Eighty Mile Beach (Table 3.4).

**Spawning season**

The mean monthly GSIs for male *P. macrochir* collected from the Fitzroy, Mary and Brisbane Rivers rose gradually from a low in June and July to reach a maximum in November, and then declined over the ensuing four months (Figure 3.8). Ripe (Stage V) males were present in samples collected from September to February, and running ripe (Stage VI) males were observed in samples collected from October to January. The majority of spent males were observed in December, February and March, although a few spent males were observed in April (Figure 3.8), suggesting that spawning activity may have continued until at least March.

The mean monthly GSI for females rose sharply from a low in July to high levels in October and December (Figure 3.8). In addition, most females with ripe and running ripe ovaries were present in samples collected from August-October and December (Figure 3.8). Females with ovaries containing hydrated oocytes, indicative of active spawning, were sampled only in October and December. There were no females collected in November or January from any of the three locations, precluding the verification of whether females spawned in these months. However, because of the elevated GSI values in the preceding and following months, it is likely that female GSI values remained high during these months. On the basis of these trends in GSI and monthly frequencies of ovarian and testicular stages, it was concluded that *P. macrochir* spawns between October and March at each location on the eastern coast of Queensland, with peak spawning occurring between October and December.

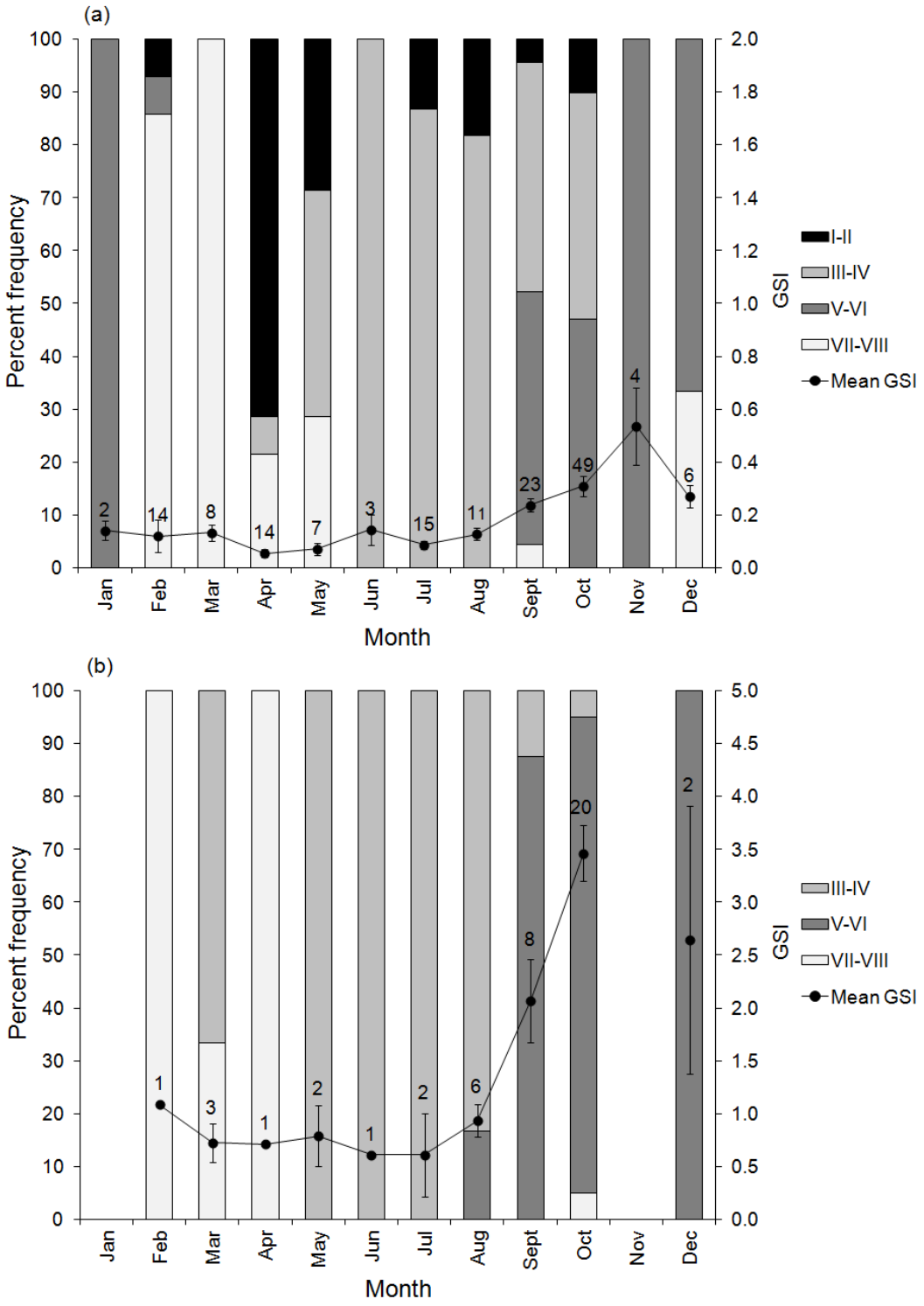


Figure 3.8 Monthly macroscopic gonad stages and mean gonado-somatic index (GSI) values (± s.e.) for (a) male and (b) female *Polydactylus macrochir* from the Fitzroy, Mary and Brisbane Rivers on the east coast of Queensland, Australia. Numbers above error bars indicate sample size.

**Length and age at maturity**

The estimated length and age at which 50% of male fish are mature (i.e. $L_{m50}$ and $A_{m50}$) were lowest for the Brisbane River, intermediate for the Mary River and highest for the Fitzroy River (Table 3.6). Although overlapping confidence intervals indicated that there were no significant differences in length at 50% maturity between the Fitzroy and Mary Rivers, or the Mary and Brisbane Rivers, the length at 50% maturity of fish from the Brisbane River was significantly lower than that from the Fitzroy River (Table 3.6). Estimates of the length at 50% maturity from all locations were considerably greater than the current minimum legal size of 49 cm FL (converted from 60 cm TL). Age at 50% maturity was significantly higher for Fitzroy River fish than for fish from the Mary or Brisbane Rivers (Table 3.6). Mary and Brisbane River fish did not differ, as evidenced by the overlapping confidence intervals.

Table 3.6 Estimates of length and age (and upper and lower 95% confidence intervals) at which 50% of male *Polydactylus macrochir* mature at three locations on the east coast of Queensland, Australia.

| Location | Fork length (mm) | | | Age (years) | | |
|---|---|---|---|---|---|---|
| | $L_{50}$ | Lower 95% CI | Upper 95% CI | $A_{50}$ | Lower 95% CI | Upper 95% CI |
| Fitzroy River | 765 | 743 | 788 | 4.4 | 4.2 | 4.7 |
| Mary River | 755 | 723 | 785 | 3.9 | 3.2 | 4.1 |
| Brisbane River | 710 | 677 | 740 | 3.3 | 2.7 | 3.8 |

**Length and age at sex change**

In general, there was a large overlap in the length distributions of males and females (Figure 3.9). As expected for a protandrous hermaphrodite, males typically dominated the smaller length classes and females dominated the larger length classes for samples from Eighty Mile Beach, Roebuck Bay, Derby, Chambers Bay, and the Roper, Fitzroy, Mary and Brisbane Rivers. In contrast, there were a large proportion of small, young females from the seven locations in the south-eastern Gulf of Carpentaria (Arthurs Creek, Albert River, Morning Inlet, Flinders River, Spring Creek, Staaten River and the Kendall River) (Figure 3.9). A general lack of increase in the proportion of females with both length and age was observed at these locations, precluding any estimates of the length and age at which 50% of the population changed sex, even when data for these locations were pooled. The general absence of young females at locations outside of the Gulf of Carpentaria (Figure 3.9) suggests little movement, at least of smaller females, to these locations from those within the Gulf.

Due to low numbers of females at some locations and the lack of increase in proportion of females with length or age for locations in the south-east Gulf of Carpentaria, estimates of the length and age at which 50% of the population changed sex were possible for only seven of the 18 locations sampled (Table 3.3). Considerable variation was observed in both the length and age at sex change among the seven locations (Table 3.7). The estimated length at which 50% of the population was female (i.e. $L_{50}$) was lowest for Eighty Mile Beach (450 mm FL) and highest for the Fitzroy River (1140 mm FL) (Table 3.7). The $L_{50}$ of fish from Eighty Mile Beach, Chambers Bay and the Fitzroy River each appeared significantly different to all other locations. Overlapping confidence intervals indicated no significant difference in the $L_{50}$ estimates between Roebuck Bay and Derby, or the Mary and Brisbane Rivers (Table 3.7). The estimated age at which 50% of the population was female (i.e. $A_{50}$) was lowest for Eighty Mile Beach (2.0 years) and highest for the Fitzroy River (9.7 years) (Table 3.7). The $A_{50}$ of fish from Eighty Mile Beach was significantly lower than all other locations. Overlapping confidence intervals indicated no significant differences in the $A_{50}$ estimates between Roebuck Bay and Derby, the Fitzroy, Mary and Brisbane Rivers, and Chambers Bay and the Mary and Brisbane Rivers (Table 3.7). All other comparisons were significantly different, as indicated by non-overlapping 95% confidence intervals.

Table 3.7 Estimates of length and age (and upper and lower 95% confidence intervals) at which 50% of *Polydactylus macrochir* change sex at seven locations across northern Australia.

| **Location** | **Fork length (mm)** | | | **Age (years)** | | |
|---|---|---|---|---|---|---|
| | $L_{50}$ | **Lower 95% CI** | **Upper 95% CI** | $A_{50}$ | **Lower 95% CI** | **Upper 95% CI** |
| Eighty Mile Beach | 450 | 308 | 541 | 2.0 | 0.0 | 3.3 |
| Roebuck Bay | 779 | 757 | 799 | 5.1 | 4.3 | 6.1 |
| Derby | 707 | 614 | 804 | 4.2 | 3.6 | 5.0 |
| Chambers Bay | 882 | 868 | 893 | 7.0 | 6.4 | 7.6 |
| Fitzroy River | 1140 | 1082 | 1234 | 9.7 | 8.4 | 12.6 |
| Mary River | 960 | 925 | 1053 | 8.3 | 7.1 | 9.8 |
| Brisbane River | 932 | 912 | 959 | 7.5 | 6.5 | 8.9 |

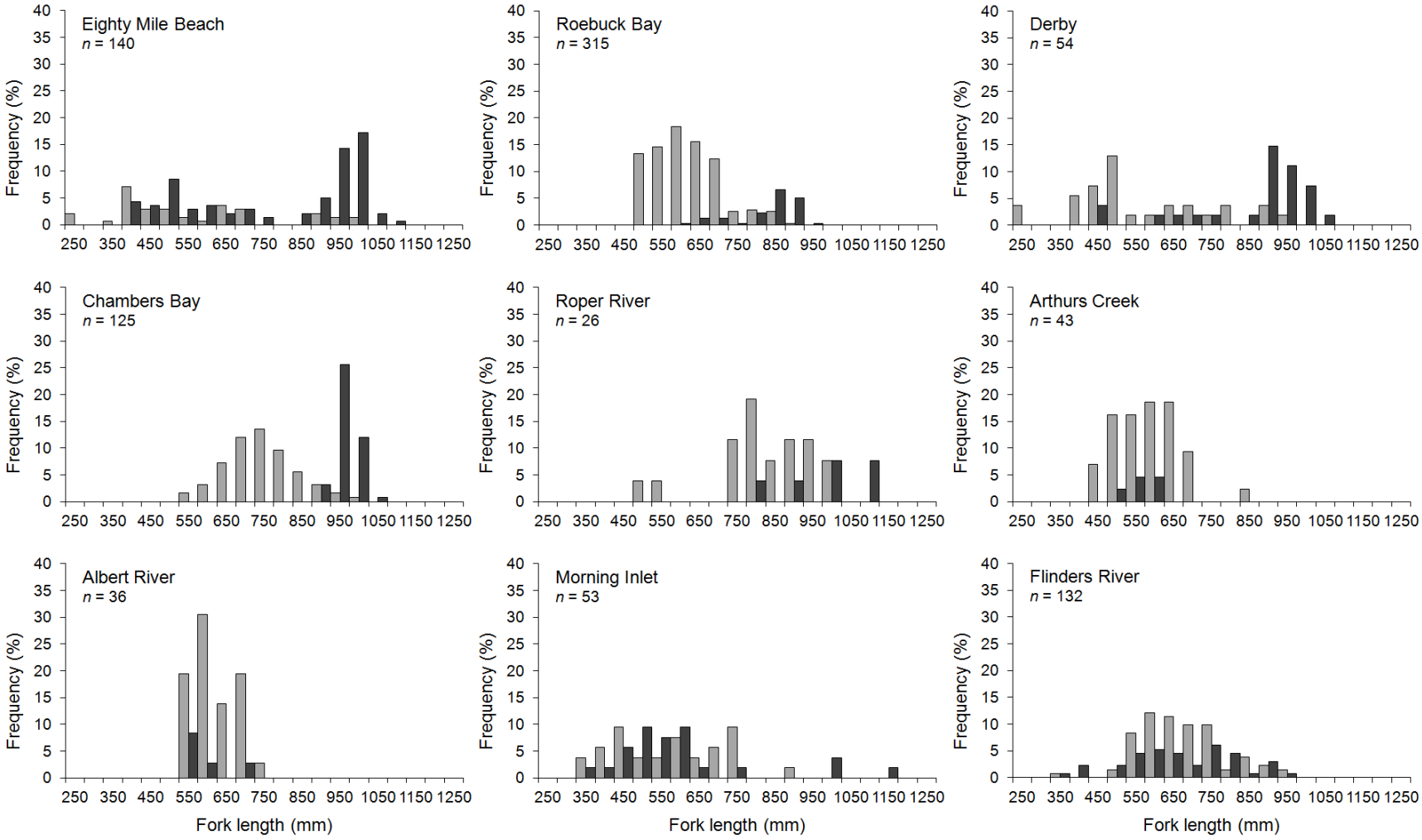


Figure 3.9 Length frequency distributions for male (light grey) and female (dark grey) *Polydactylus macrochir* from 18 locations in Australian waters.

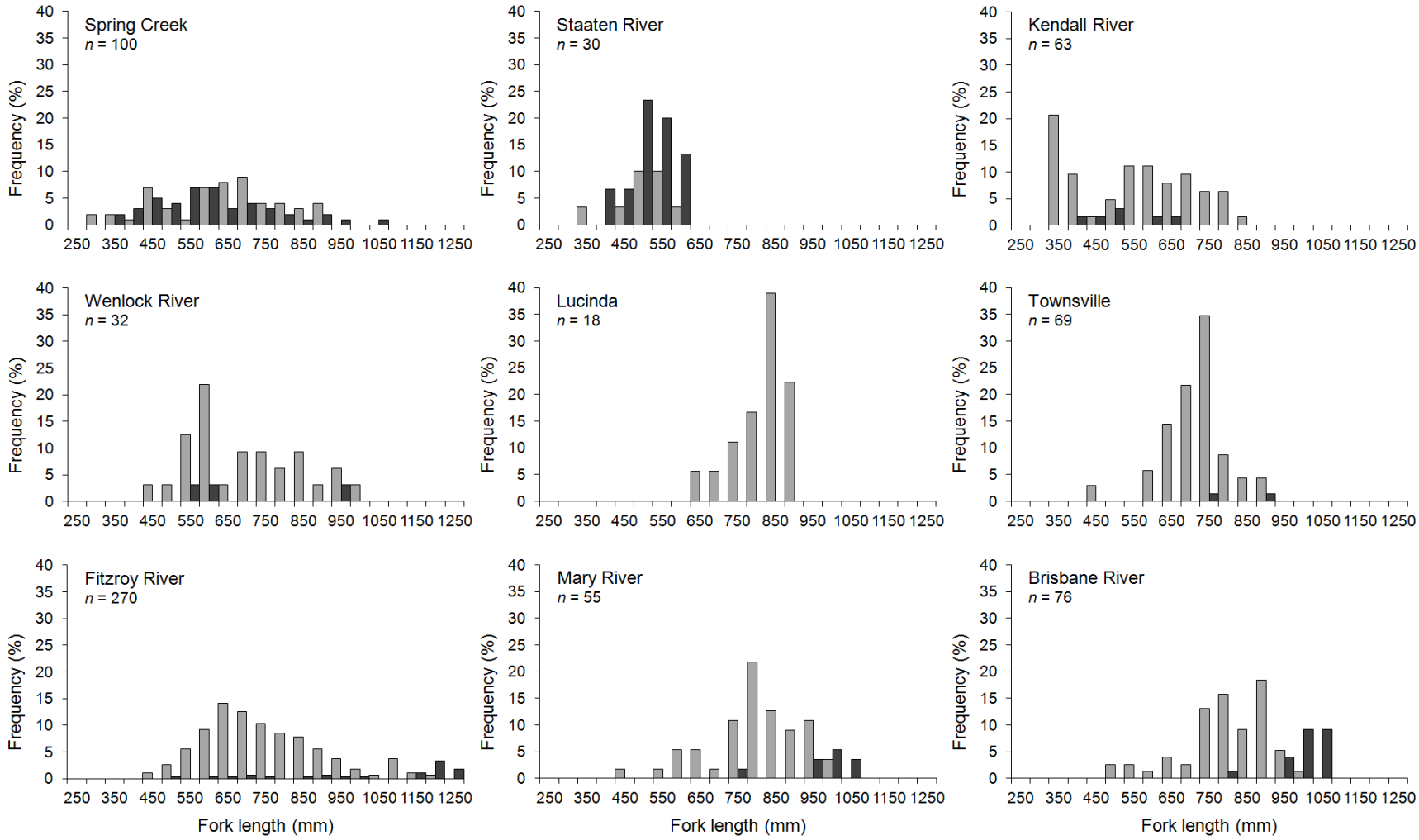


Figure 3.9 (cont.). Length frequency distributions for male (light grey) and female (dark grey) *Polydactylus macrochir* from 18 locations in Australian waters.

## 3.4 Discussion

The use of life history parameters to provide information on the movement, connectivity and geographical population structure of fishes relies on differences in one or more biological parameter between locations (Begg et al. 1999b). In the present study, significant variation was observed in growth patterns, rates of total mortality and length- and/or age-at-sex change profiles of post-recruitment assemblages of *P. macrochir*, at a range of spatial scales in Australian waters. Differences in life history parameters over similar spatial scales as those observed here have been reported for several estuarine species, including black bream, *Acanthopagrus butcheri* (see Sarre and Potter 2000), spotted sea trout, C*ynoscion nebulosus* (see Bedee et al. 2002), and luderick, *Girella tricuspidata* (see Gray et al. 2010).

A key limitation of using life history data to comment on connectivity of fishes is that the technique seldom provides information the genetic relationships amongst groups. Although potentially mediated by both genetic and environmental factors, life history parameters are frequently predominantly characterised by the environment or exploitation rates a fish experiences over its life history, because of their sensitivity to extrinsic variables (Beacham 1982; Begg 2005). Accordingly, the approach provides little information on dispersal and connectivity of egg and larval life history stages. In the case of *P. macrochir*, it may be that recruits originate from a single common source, or number of common sources, that export individuals to locations with different environmental conditions or exploitation rates which ultimately generate the different life history patterns observed. Under this scenario, *P. macrochir* may conform to a metapopulation structure, at least for some locations. While this possibility cannot be ruled out from the life history data, the observed spatial differences in life history parameters suggests limited movement and connectivity of at least post-recruitment fish. If there was broadscale mixing of post-recruitment fish among locations, the life histories amongst locations would be similar (Ihssen et al. 1981; Begg et al. 1999b). Given that connectivity may be achieved through the movement of all life history stages (Gillanders 2009), and movement of adult life history stages has been proposed as a means of maintaining connectivity for some estuarine fishes, such as many species of Sciaenidae (Gold and Richardson 1998; Thorrold et al. 2001), the identification of spatially-distinct post-recruitment populations of *P. macrochir* has important implications for management of the species.

The spatial structure of juvenile and adult *P. macrochir* evident from the life history data is generally consistent with concurrent research into the movements and stock structure of the species, suggesting comparisons of life history data may provide a reliable method of identifying spatially-discrete adult assemblages of *P. macrochir*. For example, the similarities observed among locations in growth and length and age at sex change for *P. macrochir* in the south-eastern Gulf of Carpentaria is in accordance with recent investigations of mitochondrial

DNA haplotypes (Horne et al. 2012) and whole otolith oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) stable isotope ratios (Newman et al. 2010), which suggests the occurrence of a single demographic population in this region, with extensive mixing of post-larval stages of *P. macrochir*. Nevertheless, some discrepancies are evident between these complementary techniques. Newman et al. (2010) found no difference in otolith stable isotope ratios of fish from Eighty Mile Beach and Roebuck Bay, whereas significant variation was observed in VBGF parameters, mean back-calculated length-at age 2 estimates and length and age at sex change among these locations in the present study, suggesting fish from these locations may form spatially discrete groups, or stocks. These apparently conflicting results among methodologies highlight the importance and value in using multiple techniques to determine the movement and connectivity of fishes. Begg et al. (1999b) suggest that life history parameters should be used as a preliminary technique to identifying stock structure of fishes, before applying more refined methods, such as analyses of parasite assemblages or otolith elemental signatures. Such an approach may further corroborate and refine the spatial patterns observed here.

As locations were generally sampled with similar gear (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh at each location), it is unlikely that the differences in life history parameters reflect differences in sampling methods between locations. However, samples from Lucinda and some Brisbane River fish were collected from recreational fishers, which may have confounded comparisons against net-caught fish. Several studies have identified differences in length-at-age of fish collected by gillnets compared to other sampling methods, with gillnets generally capturing the larger individuals of a particular age class (Hilborn and Walters 1992; Begg and Sellin 1998; Lucena and O'Brien 2001). Conversely, Moore et al. (2011b) found no significant differences in length-at-age between gillnet- and recreationally-caught *P. macrochir* from the Brisbane River, suggesting negligible effects of any size-selectivity between netting and recreational fishing methods in this case. Furthermore, although the sample sizes varied markedly among locations, it is unlikely that these differences affected the comparisons of VBGF parameters, because these analyses were conducted on common age classes across the locations. Similarly, the unequal sample sizes are factored into the comparisons of back-calculated length-at-age and the development of the 95% confidence intervals for the comparisons of length and age at maturity and sex change, and thus are unlikely to confound these comparisons.

It is unclear what effect temporal differences in life history parameters had on the spatial comparisons. Numerous studies have documented temporal variation in life history parameters that have occurred in response to changing environmental conditions and/or exploitation patterns (e.g. DeVries and Grimes 1997; Begg et al. 1999b). In the present study, it was necessary to pool location-specific collections within or among years for comparisons

of VBGF, length and age at maturity, and length and age at sex change estimates, due to small sample sizes, which may have potentially confounded spatial patterns among locations. However, comparisons of growth of Fitzroy River fish between 2007 and 2009 revealed that whilst growth varied slightly from year to year, these differences were of a much reduced magnitude compared with those observed between the Fitzroy River and other locations (B. Moore, unpublished data). Further sampling and analysis is required to accurately quantify the degree of temporal variation in life history parameters of *P. macrochir*, and its effect on the spatial comparisons.

There was a conspicuous absence of fish < 2 years old in the samples. This is most likely a result of selectivity of the sampling gear used, rather than the existence of separate juvenile and adult habitats. Juveniles of *P. macrochir* have been observed to be broadly distributed in estuaries, and are commonly observed in the stomachs of adult fish (Pember 2006; B. Moore, pers. obs.), suggesting overlap in their distributions. The exclusion of fish < 2 years old from estimates of growth using the VBGF may result in an underestimation of $K$ and a corresponding overestimation of $L_\infty$ (Ferreira and Russ 1994; Williams et al. 2007). Nevertheless, it is likely that the absence of fish < 2 years old had little effect on the growth comparisons, particularly given the lack of differences observed from the constrained and unconstrained VBGF data and the similarity in the range of age classes sampled among estuaries.

Although a slight difference in mortality was observed among locations, the catch curves generally provided a poor fit to the data. The poor relationship observed for some locations most likely results from variability in recruitment patterns and the persistence of a few strong year classes, and highlights the sensitivity of catch-curve analysis to violations of the underlying assumptions of constant recruitment and constant mortality among cohorts. Variability in recruitment biases estimates of mortality using catch curves (Ricker 1975). The variable year-class strength observed for all locations suggests that recruitment may not be constant for populations of *P. macrochir*. Halliday et al. (2008) reported a positive association between year-class strength and the timing and duration of freshwater flow events for *P. macrochir* in the Fitzroy River, with high flow events in spring and summer leading to increased survivorship. Such variability in recruitment may be responsible for the few strong year-classes and subsequent poor correlations of the catch curves observed here.

**Causal mechanisms for the spatial patterns in life histories**

A number of factors may be responsible for the differences observed in life history parameters of *P. macrochir*. In general, there was a positive association between longevity, growth and length and age at sex change, suggesting that these parameters are strongly correlated. For

example, fish from the Fitzroy River were generally found to live longer, obtain larger observed and hypothetical asymptotic lengths, and change sex at greater lengths and ages than elsewhere. The positive association of longevity, growth and sex change implies that size plays an important role in the timing of sex change in *P. macrochir,* a result that is consistent with the size advantage hypothesis of sex-allocation theory (Ghiselin 1969; Warner 1988).

It is unclear whether the spatial patterns reflect genetic differences between locations. Recent genetic examination of nine of the 18 locations examined in the present study (Eighty Mile Beach, Roebuck Bay, Chambers Bay, Albert River, Flinders River, Kendall River, Townsville, Fitzroy River and the Brisbane River), suggest that, with the exception of Eighty Mile Beach and Roebuck Bay, and the Albert, Kendall and Flinders Rivers, fish at each location constitute a genetically-discrete population (Horne et al. 2012), however sampling locations in this study were widely separated. Further fine-scale genetic examination, conducted across all locations examined here, is warranted to determine whether the spatial differences in life history parameters reflect genetic patterns.

Geographical differences in fishing pressure are also likely to play a significant role in the observed spatial patterns in life histories. Worldwide, fishing pressure has been demonstrated to cause significant biological change in fish populations, and has been implicated as the most likely cause of biological change in a variety of exploited species (e.g. Millner and Whiting 1996; Hidalgo et al. 2009; Silberschneider et al. 2009). Size-selective fishing gear such as gillnets may favor the survival of smaller individuals, leading to overall decreases in length-at-age (Ricker 1981), or conversely may result in a reduction in population density, resulting in lower levels of competition and increased availability of food, leading to faster growth and an increase in length-at-age (Millner and Whiting 1996; Hidalgo et al. 2009). In hermaphroditic species, the removal of larger, older individuals (typically those of the secondary sex) of a population through size-selective harvest practices has been documented to result in decreases in the length and age at sex change (Platten et al. 2002; Hawkins and Roberts 2003). Such changes may have subsequent effects on growth rates, with individuals allocating energy to reproduction rather than to growth (de Roos et al. 2006).

Although it is difficult to elucidate the effect of fishing pressure from genetic and environmental influences, there is indirect evidence to suggest that fishing is an important causal mechanism of the observed spatial patterns in life histories of *P. macrochir*. Populations on Queensland's east coast, and along the north coast of the Northern Territory, where fishing pressure has historically been light and total mortality was generally lowest, were found to live longer and change sex at greater lengths and ages than elsewhere. Conversely, populations in the south-eastern Gulf of Carpentaria, where fishing pressure has historically been the highest and total mortality was greatest, exhibited the smallest back-

calculated lengths, youngest maximum ages and changed sex much earlier than at other locations. Further evidence for fishing being an important determinant of life history parameters in *P. macrochir*, particularly within in the south-eastern Gulf of Carpentaria, is discussed below.

Environmental conditions may play an important role in the observed patterns in life history parameters. Water temperature has been shown to be an important influence on fish growth and subsequent reproductive schedules (Conover 1992; Durieux et al. 2009; Tolan and Fisher 2009). In the present study, *P. macrochir* from lower latitudes (as a proxy for water temperature) were generally found to grow significantly faster and reached greater back-calculated lengths-at-age 2 than those from higher latitudes for comparable coastlines. For example, along the Western Australian coastline, fish from Roebuck Bay generally grew faster and reach a greater length-at-age 2 than those from Eighty Mile Beach. Fish from the Wenlock River, in the north-eastern Gulf of Carpentaria, obtained a significantly greater back-calculated length-at-age 2 than those from the south-eastern Gulf. As is typical of poikilotherms (Atkinson and Sibly 1997), fish from higher latitudes (e.g. the Fitzroy and Brisbane Rivers) were generally found to live longer, grow slower (based on constrained estimates) and reach greater maximum sizes than those in warmer waters. Such observations suggest that growth of *P. macrochir* may be, at least partly, related to water temperature. However, significant variation was observed among locations occupying similar latitudes, such as Lucinda on Queensland's east coast, Queensland's southern Gulf of Carpentaria, and Derby, suggesting that temperature is unlikely to be the sole driver of the observed spatial patterns.

In addition to temperature, freshwater flow is considered an important environmental influence on growth in estuarine fish (Robins et al. 2006; Davidson et al. 2010), and may also play an important role in the observed patterns. Increases in freshwater flow has been suggested to affect growth of estuarine fishes via increased prey availability due to increases in nutrient availability and primary productivity (Whitfield 2005; Robins et al. 2006), or by increased foraging opportunity under the protection of higher turbidities (Hecht and van der Lingen 1992). Increases in freshwater flow have been documented to result in increased growth and trigger downstream movement of banana prawns *Penaeus merguiensis* (see Vance et al. 1985; Vance et al. 1998), one of the dominant prey items for *P. macrochir* (see Salini et al. 1998), which may make them more susceptible to predation. As such the spatial differences in life history parameters among locations may in part reflect differences in freshwater flow, however a general lack of flow data for most of the locations examined here precludes examination of the influence of freshwater flow on the observed spatial patterns in *P. macrochir* life histories.

In addition, factors such as duration of spawning season (Choat et al. 2003; Robertson et al. 2005), parasite loadings (Adlard and Lester 1994), or spatial differences in predator abundances or predation rates (Hixon 1991; Hixon and Webster 2002; Jones and McCormick 2002) can also influence the life histories of fishes, and may have an influence here. It is likely that a combination of several of the above factors is responsible for the observed spatial patterns in life history parameters.

**Evidence for temporal changes in life history parameters of *P. macrochir* in the Gulf of Carpentaria**

There are a number of differences in life history parameters of *P. macrochir* in the south-eastern Gulf of Carpentaria between the results of the present study and that of previous research in these waters. The maximum age observed for fish from the south-eastern Gulf of Carpentaria in the present study (8.5 years) is considerably lower than previous estimates of the maximum age reported for *P. macrochir* in these waters, and those observed elsewhere across northern Australia in the present study. Despite lower sample sizes, Garrett (1997) reported a maximum age for *P. macrochir* of 14 years in Queensland's Gulf of Carpentaria waters, whereas fish up to 22 years old were observed on the east coast in the present study. Additionally, there has been an apparent decrease in the length frequency of fish caught, with a reduction in the number of large fish caught through the commercial fishery (Figure 3.10). Although it is likely that small *P. macrochir* were discarded in the historical catch to make room for larger, more profitable individuals or the more valuable *Lates calcarifer*, which may partially explain the lack of small fish in the historical data, the lack of large individuals in the present study is considered to be indicative of a general reduction in the size and age of *P. macrochir* in these waters.

The pattern of sex change observed for populations within the south-eastern Gulf of Carpentaria in the present study is in stark contrast to that reported by Garrett (in Kailola et al. 1993) in these waters, who observed the typical pattern of increasing proportion of females with length expected for protandrous species (Figure 3.10), resulting in an estimated $L_{50}$ of 923 mm FL (B. Moore, unpublished data). The large overlap in the length and age distributions of males and females observed for all locations, and the lack of previous observations of small females in the Gulf of Carpentaria (Figure 3.10) suggests that sex change in *P. macrochir* is a social and phenotypically plastic response to local conditions, rather than being fixed at a particular length or age. For species in which sex change is under social control, sex allocation theory predicts that individuals should change sex whenever their net future reproductive success would be higher for the opposite sex than for the existing sex (Charnov 1982; Munday et al. 2006). Although individuals generally refrain from changing

sex when small or young in populations with many large individuals of the secondary sex, sex change can occur at smaller sizes and younger ages when a population contains few individuals of the secondary sex (Munday et al. 2006; Hamilton et al. 2007). The removal of larger, older *P. macrochir* by size-selective fishing methods such as gillnets from the waters of Queensland's south-eastern Gulf of Carpentaria, as indicated by the truncation of ages and lack of old fish in these waters, may result in males changing sex to females at smaller lengths (and younger ages) than historically documented in order to increase their reproductive success, and potentially explains the large number of small, young female *P. macrochir* in this region.

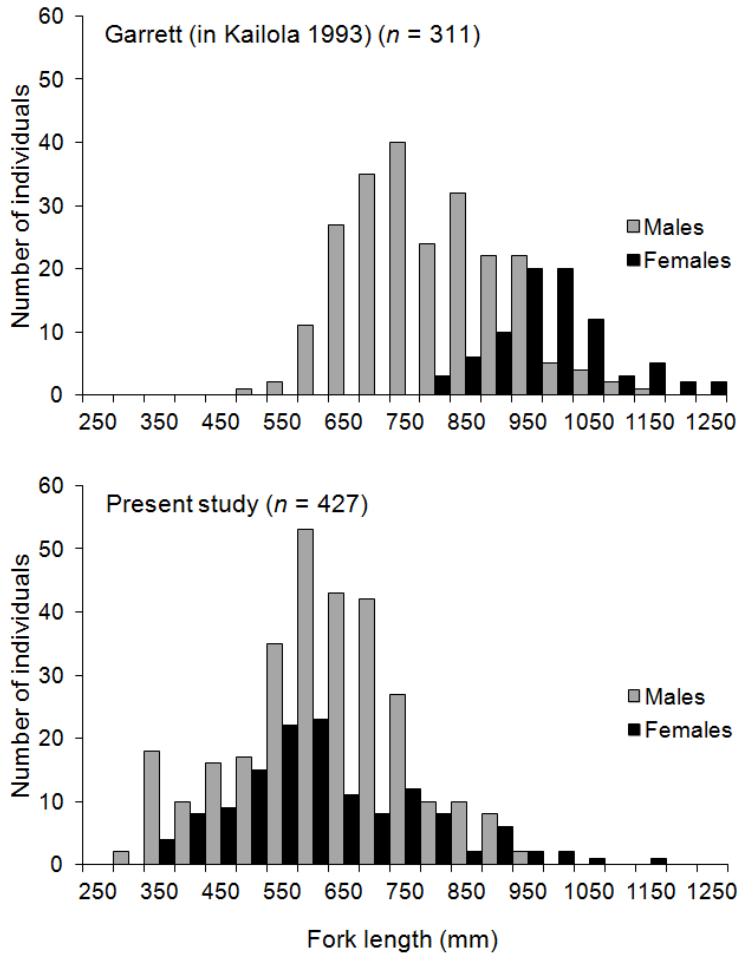


Figure 3.10 Number of male and female *Polydactylus macrochir* in each 50 mm length class collected from Queensland's south-eastern Gulf of Carpentaria waters based on data of Garrett (in Kailola et al. 1993) and the present study.

Gear selectivity patterns and size-selective fishing practices can have a considerable effect on demographic comparisons (Sinclair et al. 2002; Taylor et al. 2005). Gillnets are highly selective, and generally capture the larger individuals of a particular age class (Hilborn and Walters 1992). Although the samples of Garrett (in Kailola et al. 1993), and Garrett (1997) were obtained using gillnets of 100 mm to 200 mm (4 to 8 in.) stretched mesh (c.f. 100 mm to 165 mm in the present study), it is unlikely that the observed differences in age class structure, length frequency and length at sex change between the historical data and the present study is a artifact of differences in sampling gears. Despite using nets of a smaller maximum size than previous studies, a number of large, old fish were collected at locations outside of the Gulf of Carpentaria during the present study, including fish up to 22 years of age and 1354 mm FL (1612 mm TL) from the Fitzroy River. The observation of these fish in the samples suggest that they would have been collected by the sampling gear in the south-eastern Gulf of Carpentaria during the present study had they occurred in these waters.

Despite the apparent decreases in length and age at sex change of *P. macrochir* in the south-eastern Gulf of Carpentaria, there has been no decline in catch-per-unit effort (CPUE) in these waters. In other teleosts it has been shown that smaller and younger individuals have lower fecundity (Sadovy 1996), and also produce offspring that are less viable with a lower probability of survivorship than larger, older females (Kjesbu et al. 1996; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004). As such, reductions in the length at sex change as observed for populations in the south-eastern Gulf may be expected to ultimately lead to a decrease in recruitment, and should thus result in a decrease in CPUE. However, the CPUE of *P. macrochir*, as measured by kg/day, has generally remained steady over recent years (DPI&F 2007). Stability in CPUE in the fishery may reflect that the observed biological change could be relatively recent, and may have not yet manifested in changes in CPUE. Conversely, stability in CPUE may be attributed to effort creep, with technological advances in fishing methods (e.g. the increased use of net reels), hyperstability, whereby declines in abundance may not be reflected in changes in CPUE due to the efficiency of targeting individual schools (Welch et al. 2002), or recruitment from less heavily fished populations into the south-eastern Gulf. The lack of decline in CPUE, in the face of the observed biological change, suggests that analysis of fisheries-dependent patterns in CPUE in isolation may be a poor monitoring strategy for the species, and highlights the importance of continual monitoring of the life histories of exploited species in addition to catch trends.

**Implications and future directions**

The life history parameters examined in this study have shown distinct spatial signatures, suggesting the probable existence of a number of spatially distinct groups of at least post-

larval *P. macrochir* assemblages across northern Australia. This is in contrast to the current management arrangements for the species, whereby post-recruitment *P. macrochir* are managed as separate, independent populations in the waters of Western Australia, the Northern Territory, Queensland's Gulf of Carpentaria and Queensland's east coast, respectively. While further techniques are required to accurately define the connectivity and population structure of *P. macrochir*, the limited connectivity evident between most locations from the spatial differences in life history of post-recruitment *P. macrochir* suggests that management practices within each jurisdiction, such as the development of monitoring and assessment programs, harvest strategies and establishment of suitable fishery regulations, need to be reviewed to recognise the potential for localised depletion of adult *P. macrochir* assemblages. Furthermore, the observed variation in life history parameters within jurisdictional boundaries suggests that the spatially segregated populations of *P. macrochir* will likely respond differently to fishing pressure if managed as a single entity. Failure to take account of such differences in stock assessments and subsequent management arrangements may lead to less productive populations being over-fished, whereas potential yields may not be realised for more productive components (Williams et al. 2006). The spatial differences in life history of *P. macrochir* should ideally be incorporated into fisheries assessment models for this species, to obtain reliable model outputs and to optimise management.

This chapter has demonstrated the effectiveness of using life history parameters as a tool for assessing movement and connectivity of a large, tropical estuarine teleost, and suggests that future studies examining connectivity and geographical structure of estuarine fishes will likely benefit from the inclusion of comparisons of life history parameters. Holistic approaches, that integrate multiple techniques, have been advocated as the preferred approach to delineating patterns of movement, connectivity and stock structure of fishes (Begg and Waldman 1999). Additional techniques, such as comparisons of parasite assemblages or otolith elemental signatures, used in synergy with the life history parameters analysed here, will likely shed additional light on the movements of *P. macrochir*, including connectivity of larval stages to post-recruitment assemblages, to provide a comprehensive understanding of patterns of movement and connectivity and the appropriate spatial scales for management, monitoring and assessment.

# Chapter 4 Parasites as indicators of movement and population connectivity of a non-diadromous, tropical estuarine teleost: king threadfin, *Polydactylus macrochir*

## 4.1 Introduction

Understanding patterns of connectivity, or the exchange of individuals between spatially-distinct groups, is fundamental to the effective management and conservation of marine organisms and ecological systems (Cowen et al. 2007). Knowledge of the degree of connectivity is critical for establishing the spatial scale at which species should be managed, and in the design of marine protected areas (Thorrold et al. 2001; Fogarty and Botsford 2007). Such knowledge is also fundamental to understanding the population dynamics and ecology of species, which will lead to a greater comprehension of their resilience, and possible responses, when faced with environmental change. For exploited species, failure to accurately define the degree of connectivity between spatially-distinct groups can lead to over-fishing (Begg et al. 1999a), resulting in dramatic changes in demography, productivity and genetic diversity of isolated groups (Ricker 1981; Smith et al. 1991; Dominguez-Petit et al. 2008), and ultimately localised depletion or extinction (Hilborn and Walters 1992; Hutchings 1996; Clark et al. 2000).

Estuarine fishes are generally regarded to be particularly vulnerable to localised depletion, given their typically patchy distributions, and close proximity to human populations where fishing pressure is typically high (Blaber 2000; Blaber 2002; Secor and Rooker 2005). As estuarine species worldwide continue to face added pressures of habitat degradation and fragmentation, it becomes increasingly important to identify patterns of movement and exchange between groups. Although such information is considered fundamental to managing estuarine fishes, the degree of connectivity is still poorly understood for many species, particularly in tropical systems (Secor and Rooker 2005; Jones 2006; Gillanders 2009). With anthropogenic pressures on tropical estuarine-dependent fishes projected to increase (Blaber 2000; Roessig et al. 2004), it becomes increasingly important to understand patterns of connectivity so that effective management can be implemented.

While population connectivity may be achieved through movement and dispersal of larvae, juvenile, and/or adult life history stages, in recent times considerable focus has been placed on the pelagic larval stage, and the processes that affect it, in addressing issues of connectivity. This focus has largely been driven by the recognition of the importance of this stage in moderating connectivity of reef fishes, in which adult fish are regarded as being largely sedentary (Jones et al. 2009). However, many recent studies have documented local

larval retention in fishes, and a number of estuarine fish species have been shown to be more sedentary as juveniles than adults (Gold and Richardson 1998; Swearer et al. 2002; Braverman et al. 2009; Tilburg et al. 2010). For example, many estuarine-associated species of Sciaenidae often remain in close proximity to their natal habitats for the first years of life and migrate extensively thereafter (Gold and Richardson 1998). These results suggest that movement of late juvenile and adult life history stages may be an important alternative means of maintaining connectivity for some estuarine fish species.

The use of parasites as biological tags offers a powerful technique to provide information of movement and connectivity between spatially distinct groups of fish. Analysis of individual parasite species or community assemblages have been used successfully to determine stock structure (Lester et al. 1988; Timi et al. 2008; Moore et al. 2011a), determine sources of recruitment (MacKenzie 1985), and to quantify schooling integrity (Lester et al. 1985; Moore et al. 2003). Studies on marine species have found variation in parasite faunas over scales of hundreds of kilometers (Lester et al. 1985) to as little as tens of metres (Cribb et al. 2000). The principle is that where the parasite fauna of fish from two areas is the same, the fish either have grown in a similar environment or have a common history. Where the parasite fauna is different, the history of the fish is different according to the residence time of the parasite counted in or on the fish, with parasites with short residence times, such as many species of gill monogeneans and copepods, providing information on recent history, and parasites with long residence times, such as encysted juvenile stages of cestodes and nematodes, providing information on long-term history (Lester 1990; Lester and MacKenzie 2009).

In this chapter, patterns in parasite community assemblages were examined to provide information on the movements and connectivity of post-recruitment assemblages of *P. macrochir*, as part of a multidisciplinary study into the stock structure and population connectivity of the species in Australian waters. The specific objectives were to (1) document the spatial patterns in parasite assemblages of *P. macrochir* in Australian waters, (2) assess whether these patterns are stable over time, and (3) use these estimates to determine movement, connectivity and appropriate management strategies for the species.

## 4.2 Materials and methods

### Sample collection

*Polydactylus macrochir* were collected from 18 locations (lower estuarine stretches of rivers and coastal sites) in Australian waters between winter 2007 and winter 2009; four locations in north-west and northern Australia, nine in the Gulf of Carpentaria and five on the east coast (Figure 4.1; Table 4.1). These locations were selected as they cover the geographical

distribution of *P. macrochir* in Australian waters and constitute important commercial and recreational fishing areas for the species. Roebuck Bay (RB) and the Roper (RR), Flinders (FLR) and Wenlock (WLR) Rivers were sampled twice across the sampling period, and the Fitzroy River (FR) was sampled three times, to examine temporal patterns in abundance of the parasites encountered. Where possible, sampling was generally conducted during the protracted spawning season of *P. macrochir*, which typically extends from September-March for locations across north-west and northern Australia and the east coast of Queensland, with a peak in October-December (Pember et al. 2005; Chapter 3), and August-March, with a peak of August-September, for the Gulf of Carpentaria (Garrett 1997) (Table 4.1). At each location (with the exception of the Brisbane River and Lucinda), whole fish or fish frames (whole skeleton remaining after filleting) were obtained directly from commercial fishers, fish processors or by fisheries-independent sampling that generally used the same gear used by commercial fishers (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh). Brisbane River samples were collected through a fishery-independent sampling program using the same gear as used by commercial fishers as outlined above, by opportunistic collections from recreational fishers, and by research line-fishing, whereas Lucinda samples were obtained from recreational fishers. For each fish collected, the location, date of capture, sex, maturity stage, total length (TL), fork length (FL) and upper jaw length (UJL) were recorded. Missing fork lengths were estimated using the relationship between FL and UJL, where FL = 8.1501UJL + 4.7413 ($r^2$ = 0.95, $n$ = 2132). Whole weight ($W_w$) was recorded to the nearest 1 g, where possible. Where unavailable, $W_w$ was estimated using the equation $W_w = 2.00\text{x}10^{-5}$ x $FL^{2.9156}$ ($r^2$ = 0.99), based on the relationship between FL and $W_w$ measured for 73 whole individuals collected across the sampling locations. Heads and viscera were frozen in individually labeled plastic bags for later laboratory examination. Sagittal otoliths (hereafter referred to as otoliths) were removed from all fish for later ageing.

**Sample processing**

In the laboratory, samples were defrosted in water, and the head and viscera were examined for parasites, including those encysted within the stomach wall. Parasites encountered were extracted, identified, enumerated and categorised as temporary or permanent, based on their probable residence time in or on the fish. All dissections were performed by a single examiner (BRM), which removed any potential effect of difference between examiners.

To facilitate parasite identification, fresh samples were taken from the Fitzroy, Mary and Brisbane Rivers on Queensland's east coast. Live trypanorhynchs were placed in fresh water to facilitate the tentacle eversion required for accurate identification. Representative specimens were stained in Mayer's haematoxylin, dehydrated in a graded ethanol series,

cleared in methyl salicylate and mounted in Canada balsam. Once identified, the morphology of the scolex, bothridia and blastocyst were considered adequate to separate trypanorhynch species. Parasites were identified according to descriptions in Podder (1937), Cannon (1977), Pillai (1985), Lom and Dykova (1992), Campbell and Beveridge (1996), Chambers et al. (2000), Amin et al. (2003), and Palm (2004).

Ages of *P. macrochir* were estimated from examination of whole and sectioned otoliths, following the procedures outlined in Chapter 3. Briefly, all otoliths were initially read whole. Otoliths in which six or fewer annuli were counted in the initial read were read whole again, whereas otoliths in which more than six annuli were counted in the initial read were sectioned before being read again. Once the method of reading was established each otolith was read twice. When annuli counts between the two reads did not agree, a third reading was taken, and the two concurrent readings being accepted as the number of annuli. When all three counts differed, the otolith was rejected from further analysis. The absolute age of each fish was estimated from the number of annuli, the assumed birth date (1 September for Gulf of Carpentaria fish, and 1 November for other locations, corresponding to the middle of the peak spawning period), the estimated date of annuli deposition (31 October for all locations), and the date of capture. Age classes were assigned by rounding the fractional age estimates to the nearest year. All otoliths were read by a single, experienced reader (BRM), whose reading accuracy was tested against a set of *P. macrochir* otoliths.

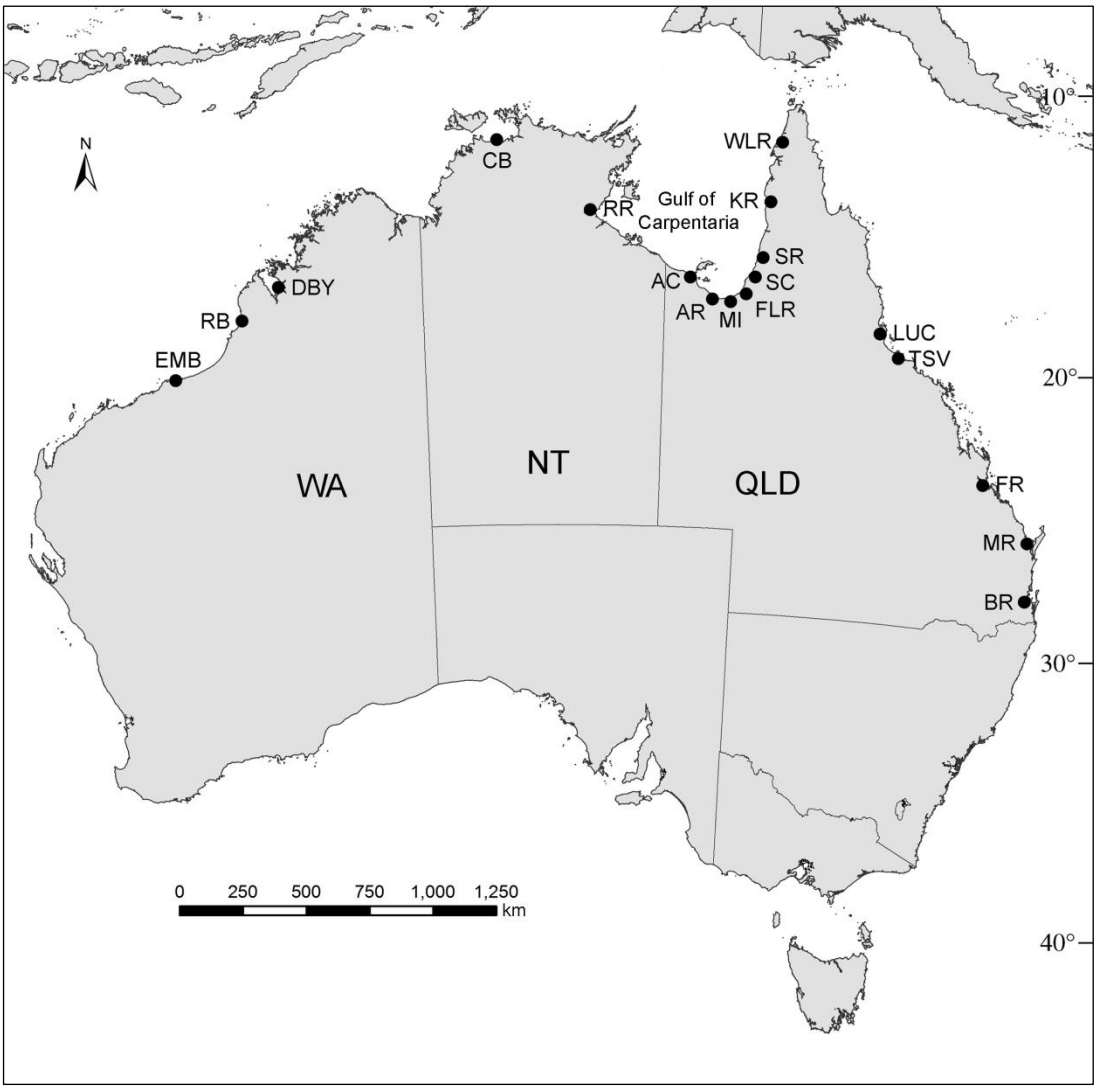


Figure 4.1 Locations where *Polydactylus macrochir* were sampled for examination of parasite assemblages. From left: EMB, Eighty Mile Beach; RB, Roebuck Bay; DBY, Doctors Creek, Derby; CB, Chambers Bay; RR, Roper River; AC, Arthurs Creek; AR, Albert River; MI, Morning Inlet; FLR, Flinders River; SC, Spring Creek; SR, Staaten River; KR, Kendall River; LUC, Lucinda; TSV, Cleveland Bay, Townsville; FR, Fitzroy River; MR, Mary River; BR, Brisbane River.

Table 4.1 Sampling details of *Polydactylus macrochir* examined for parasites

| Sample code | Location | *n* | Months collected | Mean age (years) | Age class range (years) | Mean $L_F$ (mm) | $L_F$ range (mm) |
|---|---|---|---|---|---|---|---|
| EMB | Eighty Mile Beach | 53 | Apr 2009 | 4.7 | 1–11 | 658 | 228–1021 |
| RB a | Roebuck Bay | 56 | Mar 2008 | 3.1 | 1–7 | 685 | 495–892 |
| RB b | Roebuck Bay | 55 | Aug 2008 | 2.3 | 2–7 | 575 | 463–881 |
| DBY | Doctors Creek, Derby | 35 | Apr 2009 | 4.6 | 2–10 | 780 | 413–1040 |
| CB | Pt Stuart, Chambers Bay | 52 | May 2009 | 3.2 | 2–6 | 709 | 505–850 |
| RR a | Roper River | 8 | May 2008 | 5.9 | 3–9 | 918 | 550–1090 |
| RR b | Roper River | 17 | Mar 2009 | 4.3 | 2–7 | 811 | 480–1000 |
| AC | Arthurs Creek | 42 | Aug 2008 | 3.5 | 2–6 | 568 | 415–835 |
| AR | Albert River | 35 | Oct 2008 | 3.7 | 3–5 | 597 | 520–715 |
| MI | Morning Inlet | 50 | Sept 2008 | 3.6 | 2–7 | 561 | 350–980 |
| FLR a | Flinders River | 50 | July 2007 | 3.7 | 3–6 | 642 | 495–915 |
| FLR b | Flinders River | 50 | Feb 2009 | 3.8 | 3–8 | 664 | 495–880 |
| SC | Spring Creek | 50 | Feb 2009 | 3.8 | 3–9 | 663 | 500–880 |
| SR | Staaten River | 25 | Feb 2009 | 2.6 | 3–4 | 519 | 470–595 |
| KR | Kendall River | 63 | Sept 2008 | 2.1 | 1–3 | 535 | 315–906 |
| WLR a | Wenlock River | 21 | Mar 2009 | 2.5 | 2–4 | 642 | 442–890 |
| WLR b | Wenlock River | 11 | Nov 2009 | 3.2 | 2–5 | 766 | 570–960 |
| LUC | Lucinda | 18 | Jun – July 2009 | 3.6 | 3–4 | 799 | 645–895 |
| TSV | Cleveland Bay, Townsville | 54 | Jun – Sept 2008 | 2.7 | 3 | 687 | 568–810 |
| FR a | Fitzroy River | 51 | Sept – Oct 2007 | 4.1 | 2–17 | 708 | 446–1126 |
| FR b | Fitzroy River | 53 | Oct 2008 | 4.5 | 2–21 | 750 | 515–1290 |
| FR c | Fitzroy River | 45 | Sept – Oct 2009 | 5.0 | 2–9 | 884 | 485–1250 |
| MR | Mary River | 43 | Mar – Oct 2009 | 5.5 | 3–11 | 832 | 552–995 |
| BR | Brisbane River | 53 | Mar – Nov 2009 | 5.8 | 3–14 | 840 | 601–1062 |

**Data analysis**

Summary statistics were compiled for each sample, and included mean abundance (total number of individuals of a particular parasite per sample divided by the total number of hosts examined, including uninfected hosts) and prevalence (number of hosts infected with a particular parasite divided by number of hosts examined, expressed as a percentage) for each parasite species deemed suitable for use as a biological tag, following the terminology of Bush et al. (1997). Only parasite species with a prevalence $\geq$ 10 % in at least one of the samples were used in the analysis (component species; Bush et al. 1990). Shapiro-Wilk tests revealed that the frequency distributions of the parasite species were not normal ($P < 0.05$). In general, the abundance data for each parasite had two components: one which could be approximated by a negative binomial distribution and a second component consisting of a large zero category, presumably arising because some fish had not been exposed to infection. The natural log of the parasite + 1 (Ln[x + 1]) was used to minimise the variance of the abundance data. These transformed data were used throughout the analyses.

Parasites with long residence times in fish tend to accumulate with host age (Rohde 1982), which may obscure differences in parasite fauna between areas if samples contain hosts of different ages. To reduce the effect of fish age on the analyses, only fish in age classes 2–11 were used in the analyses. These age classes constituted approximately 95% of the fish collected through the sampling program. As an added safeguard, individual parasite species were examined for correlation with fish age. Where significant, the abundances of the correlated species were adjusted to the mean host age following the method of Moore et al. (2003). Mean fish age was used to adjust parasite abundances as opposed to $W_w$ or FL as preliminary analysis revealed parasite abundances were generally more strongly correlated with age rather than $W_w$ or FL. Adjusting the parasite counts to median fish age (3.5 years) was also done but this gave the same results, hence only mean-adjusted resulted are displayed here. No adjustment was made if the parasite abundance was zero.

*Patterns of individual parasite species*

A combination of univariate and multivariate analyses were used to examine both temporal and spatial patterns in the parasite abundances. One-way ANOVA was applied to identify differences in abundance of individual parasite species among each of the temporal replicates and among the 18 spatial locations. Temporal replicates were pooled for the spatial univariate comparisons. The assumption of homogeneity of variance was tested prior to each analysis using Cochran's C test. Although Shapiro-Wilk tests revealed the frequency distributions of the transformed counts of most parasite species were not normal, analyses were still performed, as ANOVA is robust to departures from assumptions of normality and

homogeneity of variances where sample sizes are relatively large (Underwood 1997). Significant results were examined using Tukey-Kramer post-hoc pair-wise comparisons (Sokal and Rohlf 1995).

*Patterns of parasite community assemblages*

Because of the non-normality and heterogeneity of variances, multivariate analysis of variance (MANOVA) was not used to examine patterns in parasite community assemblages, as this method is known to be particularly sensitive to departures to the assumptions of multivariate normality and equal variance-covariance matrices (Clarke 1993). Similarly, non-parametric permutational multivariate analysis of variance (PERMANOVA), commonly used to examine non-normally distributed datasets, could not be reliably used, as the assumptions of homogeneity of dispersions required by this test (Anderson et al. 2008) were not met (PERMDISP, $P < 0.01$).

Instead, discriminant function analysis (DFA, SYSTAT v 13.0) was conducted to provide a visual indication of the similarities of the permanent parasite assemblages between samples. Results of the DFA were plotted as graphs of the first and second discriminant axes, with 95% confidence intervals established around the mean canonical score of each sample. Due to the non-normality and heterogeneity of variance of the dataset, no further interpretation, such as the calculation of Wilk's Lambda values to assess parasite species contributions, or classification scores of individual fish, was conducted on the results of the DFA, as these tests are highly sensitive to departures of normality and homogeneity of variances (Clarke 1993). To provide an indication of classification success of the samples, the fauna abundance profiles of individual fish were compared against the sample means using the Bray-Curtis similarity coefficient (Primer v 6.1.13). A random number between zero and +0.001 was added to the age-adjusted data to allow for inversion in the Bray-Curtis similarity matrix. The resulting scores were used to classify fish to the location of 'best-fit'. This method allowed for a semi-metric estimate of classification that was not subject to the assumptions of multivariate normality that confines parametric designs (Anderson et al. 2008). Preliminary analysis suggested that some samples separated by thousands of kilometers of coastline were similar (e.g. FLR vs. FR; Figure 4.1), with very different locations in between. To avoid these locations being forced together in the results, locations were separated into three regions for the multivariate analyses: north-west and northern Australia (comprising locations EMB, RB, DBY and CB), the Gulf of Carpentaria (RR, AC, AR, MI, FLR, SC, SR, KR, WLR), and Queensland's east coast (LUC, TSV, FR, MR, and BR) (see Figure 4.1). To ensure that the classification results of the Bray-Curtis comparisons in the Gulf of Carpentaria were not a function of the greater number of possible locations an individual fish could be classified to

relative to the other regions, this grouping was further divided into southern and eastern regions. At least one location was repeated between neighbouring regions in the Bray-Curtis analysis to link the analyses between groups, and the Flinders River (FLR) was included in the DFA for both the southern and eastern Gulf of Carpentaria for the same purpose. As the DFA revealed no significant differences in parasite community assemblages between temporal replicates for any of the five locations that were sampled on multiple occasions (see Results), the replicates were pooled in the Bray-Curtis classification analysis.

### 4.3 Results

A total of 990 *P. macrochir* were examined for parasites. From these, 22 different types of parasites were found (Table 4.2). Seven types were identified to species: the copepod *Thysanote eleutheronemi* Rangnekar, 1961, the acanthocephalan *Neoechinorhynchus topseyi* Podder, 1937, and the cestodes *Callitetrarhynchus gracilis* Pinter, 1931, *Parotobothrium balli* (Southwell, 1929), *Pseudotobothrium dipsacum* (Linton, 1897), *Pterobothrium australiense* Campbell & Beveridge, 1996, and *Pterobothrium pearsoni* Southwell, 1929. Ten parasites were considered as suitable markers to investigate long-term movements, in that they were considered to have a long residence time in the fish, were relatively easy to find and were morphologically very different to each other which aided discrimination. They were juvenile stages of the nematodes *Anisakis* spp. and *Terranova* (type II), juveniles of the cestodes *C. gracilis*, *Nybelinia* sp., *Proemotobothrium* sp., *P. dipsacum*, *P. australiense, P. pearsoni*, and *Pterobothrium* sp. B, and adults of the acanthocephalan *Pomphorhynchus* sp.. Although evidence suggests that acanthocephalans generally have short residence times in fish (Moller 1976; Lester et al. 1985), encapsulated bulbs of dead *Pomphorhynchus* sp. were readily observed on the intestinal wall, suggesting that this species may be a suitable indicator of long-term movement. Some fish contained many thousands of nematodes throughout the viscera and body cavity. To speed up the dissections the two nematode species were counted only if encysted on the liver. Due to the frozen nature of most samples, representatives of the genus *Anisakis* could not be accurately identified to 'type' or species level, and thus were grouped as *Anisakis* spp. in the analyses.

The distributions and abundances of the 10 parasites varied markedly across the sampling locations (Table 4.3). *Nybelinia* sp. was common in fish from the east coast, less prevalent in the Gulf of Carpentaria and absent from the north-west and northern locations. In contrast, *Proemotobothrium* sp. was prevalent in fish from the north-west and northern locations, less common in fish from the Gulf of Carpentaria and absent from east coast fish. *P. australiense* was observed in fish from all locations except for the Mary (MR) and Brisbane (BR) Rivers, whereas *P. dipsacum* was observed in only the Mary and Brisbane Rivers. Of the 10 types,

transformed counts of five species, *Anisakis* spp., *C. gracilis*, *Nybelinia* sp., *Proemotobothrium* sp. and *Terranova* (type II) were significantly correlated with fish age at $P < 0.05$, and were thus adjusted to the mean age of the fish sampled (3.76 years).

**Patterns of individual parasite species**

*Temporal patterns in individual parasite species*

Comparisons of individual parasite species found little difference among temporal replicates. Abundances of *Proemotobothrium* sp. differed significantly among replicates from Roebuck Bay (RB) ($F = 10.560$, d.f. = 1, 100, $P = 0.002$), while abundances of *Pterobothrium australiense* differed among replicates from the Wenlock River (WLR) ($F = 4.798$, d.f. = 1, 30, $P = 0.036$). In the Fitzroy River (FR), only abundances of *Anisakis* spp. differed among the three temporal replicates ($F = 3.949$, d.f. = 2, 142, $P = 0.021$). No difference was observed in the abundance of any individual parasite species among temporal replicates from the Roper (RR) and Flinders (FLR) Rivers.

*Spatial patterns in individual parasite species*

One-way ANOVA indicated that the abundance of all parasite species was significantly different across the 18 locations. Tukey-Kramer pair-wise comparisons indicated which species contributed to the differences (Table 4.4). Samples from Eighty Mile Beach (EMB) had significantly higher abundances of *Proemotobothrium* sp., *P. pearsoni* and *Terranova* (type II) than those from neighbouring Roebuck Bay (RB). Derby (DBY) fish appeared distinct, with no less than three parasite species being significantly different to all other locations. Fish from Chambers Bay (CB), on the north coast of the Northern Territory, and the Roper River (RR), in the western Gulf of Carpentaria, appeared distinct. Fewer differences were observed within the south-eastern Gulf of Carpentaria, with no more than three parasite species being significantly different between any two locations. Samples from the Wenlock River (WLR), in the north-eastern Gulf of Carpentaria, appeared distinct to all other locations. On the east coast, samples from Lucinda (LUC) and Townsville (TSV) appeared homogeneous, with no significant differences apparent for any parasite species. Fish from the Fitzroy (FR), Mary (MR) and Brisbane (BR) Rivers appeared distinct, with the abundances of no fewer than three parasite species differing between these locations.

Table 4.2 Parasites found infecting *Polydactylus macrochir*. [1]New host record. *Species used as biological tags.

| Parasite group | Taxon | Site of infection |
|---|---|---|
| Copepoda | *Caligus* sp. | Inside operculum |
| | *Thysanote eleutheronemi*[1] | Inside operculum |
| Acanthocephala | *Neoechinorhynchus topseyi*[1] | Intestine |
| | *Raosentis* sp. | Intestine |
| | *Pomphorhynchus* sp.* | Intestine |
| Cestoda | *Callitetrarhynchus gracilis*[1]* | Body cavity |
| | *Nybelinia* sp.* | Body cavity |
| | *Parotobothrium balli*[1] | Body cavity |
| | *Proemotobothrium* sp.* | Body cavity |
| | *Pseudotobothrium dipsacum*[1]* | Body cavity |
| | *Pterobothrium australiense*[1]* | Body cavity |
| | *Pterobothrium pearsoni*[1]* | Body cavity |
| | *Pterobothrium* sp. B* | Body cavity |
| | Trypanorhynch type A | Body cavity |
| | Trypanorhynch type B | Body cavity |
| | Tetraphyllidean type 4 | Body cavity |
| Myxozoa | *Myxidium* sp. | Gall bladder |
| | *Unicapsula* sp. | Muscle |
| Nematoda | *Anisakis* spp.* | Body cavity |
| | *Terranova* (type II)* | Body cavity |
| | Ascaridoid type | Intestine |
| Trematoda | Bucephalid type | Stomach |

Queensland Museum accession codes for species used as biological tags: *Anisakis* spp., G232644–232645; *C. gracilis*, G232648–232650; *Nybelinia* sp., G232651–232653, *Pomphorhynchus* sp. G232669–232673; *Proemotobothrium* sp., G232666–668; *P. dipsacum*, G232664–232665; *P. australiense*, G232661–232663; *P. pearsoni*, G232654–232657; *Pterobothrium* sp. B, G232658–232660; *Terranova* (type II), 232646–232647.

**Patterns in parasite community assemblages**

Results of the DFA and the Bray-Curtis similarity analyses were generally in close agreement (Figure 4.2; Tables 4.5–4.8). Differences in parasite community assemblages among temporal replicates at any of the five locations were not considered significant because of the overlapping confidence intervals in the DFA plots (Figure 4.2). Samples from Eighty Mile Beach (EMB) and Roebuck Bay (RB), in the north-west and northern region, appeared similar, evidenced by the overlapping confidence ellipses in the DFA (Figure 4.2). Whilst fish from Roebuck Bay had a relatively high classification success (79%) in the Bray-Curtis similarity analysis, those from Eighty Mile Beach had a poor overall classification success, with only 55% correctly classified (Table 4.5). The remaining 23 individuals (45%) aligned with those from Roebuck Bay, suggesting that these fish moved from Roebuck Bay to Eighty Mile Beach. Fish from both Derby (DBY) and Chambers Bay (CB) appeared distinct from all locations, with 100% of individuals correctly classified at each of these locations (Figure 4.2; Table 4.5). Samples from the Roper River (RR), in the Gulf of Carpentaria, appeared distinct from the north-west and northern locations, with 96% of fish correctly classified (Table 4.5). When compared against other locations in the southern Gulf however, samples from the Roper River appeared similar, with 8 of 25 individuals (32%) classified to locations in Queensland waters. Samples from Arthurs Creek (AC), the Albert River (AR), Morning Inlet (MI), the Flinders River (FLR), Spring Creek (SC) and the Staaten River (SR) appeared similar in the discriminant function analysis, evidenced by the tightly overlapping confidence intervals (Figure 4.2). Bray-Curtis similarity indices further demonstrated the similarities between these locations (Tables 4.6; Table 4.7). A number of fish caught from the Flinders River and Spring Creek aligned with those from the Kendall River (KR), suggesting southward movement of fish from the Kendall River to these estuaries. Conversely, there appeared to be little evidence of movement into the Kendall River from other estuaries, evidence by a high classification success (88%) of fish caught in this river. There was little evidence of movement between the Wenlock River (WLR) and locations in the south-east Gulf of Carpentaria or east coast, with 84% of individuals correctly classified from this location (Table 4.7; Table 4.8). Samples from Lucinda (LUC) and Townsville (TSV), on Queensland's east coast, appeared similar, evidenced by the overlapping confidence ellipses in the DFA and the relatively high number of fish cross-classified between these locations in the Bray-Curtis matrix (Figure 4.2; Table 4.8). Fish from the Fitzroy (FR), Mary (MR) and Brisbane (BR) Rivers each appeared distinct to other east coast locations, with 88%, 84% and 88% of individuals correctly classified, respectively.

Table 4.3 Mean abundance (± 1 s.e.) of parasites per fish in king threadfin, *Polydactylus macrochir*, sampled from 18 locations across northern Australia (see Figure 4.1; to 1 decimal place; fish age classes 2-11; untransformed data). Prevalence is given in parentheses.

| **Region** | **North-western and northern Australia** | | | | |
|---|---|---|---|---|---|
| **Location ID** | **EMB** | **RB a** | **RB b** | **DBY** | **CB** |
| **Sample size** | **51** | **47** | **55** | **35** | **52** |
| **Mean age (years)** | **4.8** | **3.4** | **2.3** | **4.6** | **3.2** |
| **Age class range (years)** | **2–11** | **2–7** | **2–7** | **2–10** | **2–6** |
| **Mean $L_F$ (mm)** | **675** | **711** | **575** | **780** | **709** |
| *Anisakis* spp. | 0.1 ± 0.1 (6) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.3 ± 0.1 (21) |
| *Callitetrarhynchus gracilis* | 1.1 ± 0.2 (39) | 1.3 ± 0.3 (43) | 0.8 ± 0.2 (31) | 1.2 ± 0.3 (40) | 8.1 ± 0.7 (100) |
| *Nybelinia* sp. | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pomphorhynchus* sp. | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (3) | 2.4 ± 0.9 (23) |
| *Proemotobothrium* sp. | 74.9 ± 14.2 (100) | 12.6 ± 2.0 (96) | 4.2 ± 1.0 (87) | 6834.7 ± 833.2 (100) | 274.3 ± 41.3 (100) |
| *Pseudotobothrium dipsacum* | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pterobothrium australiense* | 0.6 ± 0.2 (25) | 0.3 ± 0.1 (17) | 0.1 ± 0.0 (7) | 1.8 ± 0.4 (57) | 0.8 ± 0.2 (40) |
| *Pterobothrium pearsoni* | 0.7 ± 0.2 (35) | 0.1 ± 0.1 (9) | 0.1 ± 0.0 (7) | 0.5 ± 0.3 (17) | 0.5 ± 0.1 (29) |
| *Pterobothrium* sp. B | 0.1 ± 0.1 (8) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.7 ± 0.2 (37) | 0.4 ± 0.1 (29) |
| *Terranova* (type II) | 3.6 ± 0.7 (49) | 0.6 ± 0.3 (17) | 0.1 ± 0.1 (11) | 1.4 ± 0.5 (31) | 1.1 ± 0.4 (21) |

Table 4.3 (cont.) Mean abundance (± 1 s.e.) of parasites per fish in king threadfin, *Polydactylus macrochir*, sampled from 18 locations across northern Australia (see Figure 4.1; to 1 decimal place; fish age classes 2-11; untransformed data). Prevalence is given in parentheses.

| **Region** | **Gulf of Carpentaria** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Location ID** | **RR a** | **RR b** | **AC** | **AR** | **MI** | **FLR a** | **FLR b** | **SC** | **SR** | **KR** | **WLR a** | **WLR b** |
| **Sample size** | **8** | **17** | **42** | **35** | **50** | **50** | **50** | **50** | **25** | **41** | **21** | **11** |
| **Mean age (years)** | **5.9** | **4.3** | **3.5** | **3.7** | **3.6** | **3.7** | **3.8** | **3.8** | **2.6** | **2.6** | **2.5** | **3.2** |
| **Age class range (years)** | **3–9** | **2–7** | **2–6** | **3–5** | **2–7** | **3–6** | **3–8** | **3–9** | **3–4** | **2–3** | **2–4** | **2–5** |
| **Mean $L_F$ (mm)** | **918** | **811** | **568** | **597** | **561** | **642** | **664** | **663** | **519** | **629** | **642** | **766** |
| *Anisakis* spp. | 0.3 ± 0.3 (13) | 0.7 ± 0.3 (47) | 0.1 ± 0.1 (5) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (2) | 0.0 ± 0.0 (0) | 0.1 ± 0.0 (6) | 0.0 ± 0.0 (4) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.1 ± 0.1 (10) | 0.2 ± 0.1 (18) |
| *Callitetrarhynchus gracilis* | 10.9 ± 3.9 (100) | 11.4 ± 3.4 (88) | 10.1 ± 1.3 (100) | 18.5 ± 1.6 (100) | 14.7 ± 1.9 (94) | 5.5 ± 0.6 (94) | 8.8 ± 1.2 (90) | 7.7 ± 1.0 (88) | 3.9 ± 0.5 (100) | 15.9 ± 1.7 (100) | 0.8 ± 0.2 (48) | 0.8 ± 0.4 (45) |
| *Nybelinia* sp. | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (2) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (4) | 0.1 ± 0.1 (8) | 0.7 ± 0.4 (12) | 0.2 ± 0.2 (8) | 0.1 ± 0.0 (7) | 0.0 ± 0.0 (5) | 0.0 ± 0.0 (0) |
| *Pomphorhynchus* sp. | 0.5 ± 0.5 (13) | 0.3 ± 0.2 (18) | 0.2 ± 0.1 (10) | 0.0 ± 0.0 (0) | 0.2 ± 0.1 (12) | 0.4 ± 0.2 (18) | 0.2 ± 0.1 (10) | 1.5 ± 0.4 (26) | 0.4 ± 0.1 (28) | 0.2 ± 0.1 (10) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Proemotobothrium* sp. | 0.1 ± 0.3 (13) | 0.1 ± 0.1 (6) | 0.1 ± 0.1 (10) | 0.4 ± 0.1 (26) | 0.6 ± 0.2 (34) | 0.8 ± 0.2 (26) | 1.0 ± 0.2 (52) | 2.8 ± 0.5 (78) | 0.5 ± 0.2 (40) | 0.9 ± 0.2 (44) | 0.1 ± 0.1 (14) | 0.2 ± 0.2 (9) |
| *Pseudotobothrium dipsacum* | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pterobothrium australiense* | 2.1 ± 0.6 (75) | 2.1 ± 0.4 (76) | 5.8 ± 0.5 (98) | 7.8 ± 0.9 (97) | 7.7 ± 0.9 (94) | 7.7 ± 0.8 (96) | 6.5 ± 1.0 (94) | 6.3 ± 1.0 (96) | 4.4 ± 0.7 (92) | 4.1 ± 0.5 (100) | 1.5 ± 0.6 (71) | 3.5 ± 1.2 (91) |
| *Pterobothrium pearsoni* | 0.1 ± 0.1 (13) | 0.2 ± 0.1 (18) | 1.4 ± 0.4 (38) | 0.9 ± 0.2 (40) | 0.2 ± 0.1 (12) | 0.2 ± 0.1 (16) | 0.2 ± 0.1 (14) | 0.2 ± 0.1 (16) | 0.1 ± 0.1 (8) | 2.2 ± 0.3 (73) | 1.0 ± 0.2 (62) | 0.9 ± 0.3 (55) |
| *Pterobothrium* sp. B | 0.6 ± 0.3 (50) | 0.5 ± 0.2 (47) | 0.1 ± 0.1 (5) | 0.1 ± 0.0 (6) | 0.0 ± 0.0 (2) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (4) | 0.1 ± 0.0 (6) | 0.0 ± 0.0 (4) | 0.0 ± 0.0 (2) | 0.9 ± 0.2 (71) | 1.2 ± 0.3 (73) |
| *Terranova* (type II) | 1.1 ± 0.4 (75) | 1.2 ± 0.2 (71) | 0.1 ± 0.0 (7) | 0.0 ± 0.0 (0) | 0.1 ± 0.0 (8) | 0.0 ± 0.0 (0) | 0.1 ± 0.0 (4) | 0.1 ± 0.0 (4) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (2) | 0.1 ± 0.1 (10) | 0.6 ± 0.3 (27) |

Table 4.3 (cont.) Mean abundance (± 1 s.e.) of parasites per fish in king threadfin, *Polydactylus macrochir*, sampled from 18 locations across northern Australia (see Figure 4.1; to 1 decimal place; fish age classes 2-11; untransformed data). Prevalence is given in parentheses.

| **Region** | **East coast** | | | | | | |
|---|---|---|---|---|---|---|---|
| **Location ID** | **LUC** | **TSV** | **FR a** | **FR b** | **FR c** | **MR** | **BR** |
| **Sample size** | **18** | **54** | **50** | **50** | **45** | **43** | **50** |
| **Mean age (years)** | **3.6** | **2.7** | **3.9** | **3.7** | **5.0** | **5.5** | **5.4** |
| **Age class range (years)** | **3–4** | **3** | **2–9** | **2–8** | **2–9** | **3–11** | **3–11** |
| **Mean $L_F$ (mm)** | **799** | **687** | **700** | **721** | **884** | **832** | **828** |
| *Anisakis* spp. | 0.1 ± 0.1 (6) | 0.0 ± 0.0 (4) | 0.1 ± 0.1 (8) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Callitetrarhynchus gracilis* | 1.1 ± 0.2 (67) | 0.9 ± 0.1 (54) | 22.1 ± 2.8 (100) | 18.4 ± 3.2 (100) | 21.4 ± 2.7 (96) | 0.5 ± 0.1 (28) | 11.2 ± 1.8 (92) |
| *Nybelinia* sp. | 0.8 ± 0.3 (39) | 0.3 ± 0.1 (22) | 1.4 ± 0.3 (44) | 1.7 ± 0.3 (64) | 2.0 ± 0.6 (67) | 0.0 ± 0.0 (0) | 2.0 ± 0.4 (72) |
| *Pomphorhynchus* sp. | 0.1 ± 0.1 (6) | 0.0 ± 0.0 (2) | 0.1 ± 0.1 (6) | 0.1 ± 0.0 (4) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Proemotobothrium* sp. | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pseudotobothrium dipsacum* | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.6 ± 0.2 (37) | 0.4 ± 0.1 (22) |
| *Pterobothrium australiense* | 9.2 ± 1.9 (100) | 6.2 ± 0.7 (81) | 4.7 ± 0.6 (94) | 4.6 ± 0.5 (92) | 5.8 ± 0.7 (98) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pterobothrium pearsoni* | 0.2 ± 0.1 (17) | 0.1 ± 0.1 (11) | 0.3 ± 0.1 (24) | 0.4 ± 0.1 (30) | 0.3 ± 0.1 (24) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Pterobothrium* sp. B | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) | 0.0 ± 0.0 (0) |
| *Terranova* (type II) | 0.4 ± 0.1 (39) | 0.1 ± 0.1 (11) | 0.2 ± 0.1 (4) | 0.1 ± 0.0 (6) | 0.1 ± 0.1 (9) | 0.3 ± 0.1 (16) | 0.0 ± 0.0 (4) |

Table 4.4 Tukey-Kramer pair-wise comparisons of parasite species infecting *Polydactylus macrochir*. The number in the table corresponds to the parasite species that is significantly different at 95% CI. (1) *Anisakis* spp.; (2) *C. gracilis*; (3) *Nybelinia* sp.; (4) *Pomphorhynchus* sp.; (5) *Proemotobothrium* sp., (6) *P. dipsacum*; (7) *P. australiense*; (8) *P. pearsoni*; (9) *Pterobothrium* sp. B; (10) *Terranova* sp.

| Location | RB | DBY | CB | RR | AC | AR | MI | FLR | SC | SR | KR | WLR | LUC | TSV | FR | MR | BR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **EMB** | 5,8,10 | 5,9,10 | 1,2,4,5, 9,10 | 1,2,5,7, 9 | 2,5,7, 10 | 2,5,7, 10 | 2,5,7, 10 | 2,5,7,8, 10 | 2,4,5,7, 10 | 2,5,7,10 | 2,5,7,8, 10 | 5,7,9, 10 | 3,5,7, 10 | 5,7,8, 10 | 2,3,5,7, 10 | 5,6,8, 10 | 2,3,5,6, 8,10 |
| **RB** | | 5,7,9 | 1,2,4,5, 9 | 1,2,5,7, 9,10 | 2,5,7,8 | 2,5,7,8 | 2,5,7 | 2,5,7 | 2,4,5,7 | 2,5,7 | 2,5,7,8 | 5,7,8,9, | 3,5,7 | 5,7 | 2,3,5,7 | 5,6 | 2,3,5,6 |
| **DBY** | | | 1,2,4,5 | 1,2,5 | 2,5,7,8, 9,10 | 2,5,7,9, 10 | 2,5,7,9, 10 | 2,5,7,9, 10 | 2,4,5,7, 9,10 | 2,5,7,9, 10 | 2,5,7,8, 9,10 | 5,8,9 | 3,5,7,9 | 5,7,9 | 2,3,5,7, 9,10 | 5,6,7,9 | 2,3,5,6, 7,9,10 |
| **CB** | | | | 5,7 | 1,4,5,7, 9,10 | 1,2,4,5, 7,9,10 | 1,4,5,7, 9,10 | 1,4,5,7, 9,10 | 1,5,7,9, 10 | 1,5,7,9, 10 | 1,2,4,5, 7,8,9,10 | 2,4,5,9 | 2,3,4,5, 7,9 | 1,2,4,5, 7,9 | 1,2,3,4, 5,7,9,10 | 1,2,4,5, 6,9 | 1,3,4,5, 6,8,9,10 |
| **RR** | | | | | 1,7,8,9, 10 | 1,2,7,9, 10 | 1,7,9, 10 | 1,7,9, 10 | 1,5,7,9, 10 | 1,5,9, 10 | 1,2,5,8, 9,10 | 1,2,8,9, 10 | 1,2,3,7, 9 | 1,2,7,9 | 1,2,3,7, 9,10 | 1,2,6,7, 9,10 | 1,3,6,7, 9,10 |
| **AC** | | | | | | 2 | 8 | 2,5,8 | 4,5,8 | 5,8 | 2,5,8 | 2,7,9 | 2,3,8 | 2,8 | 3,8 | 2,6,7,8 | 3,6,7,8 |
| **AR** | | | | | | | 8 | 2,8 | 2,4,5 | 2 | 5,8 | 2,7,9 | 2,3 | 2,8 | 3,7 | 2,6,7,8 | 2,3,6,7, 8 |
| **MI** | | | | | | | | 2 | 2,4,5 | 2 | 5,8 | 2,7,8,9 | 2,3 | 2 | 3 | 2,6,7 | 2,3,6,7 |
| **FLR** | | | | | | | | | 4,5 | | 2,8 | 2,7,8,9 | 2,3 | 2,5 | 2,3,5 | 2,5,6,7 | 3,5,6,7 |
| **SC** | | | | | | | | | | 5 | 2,4,8 | 2,4,5,7, 8,9 | 2,4,5 | 2,4,5 | 2,3,4,5 | 2,4,5,6, 7 | 3,4,5,6, 7 |
| **SR** | | | | | | | | | | | 2,8 | 2,7,8,9 | 2,5 | 2,5 | 2,3,5 | 2,5,6,7 | 3,5,6,7 |
| **KR** | | | | | | | | | | | | 2,5,7,8, 9 | 2,3,5,8 | 2,5,8 | 3,5,8 | 2,5,6,7, 8 | 2,3,5,6, 7,8 |
| **WLR** | | | | | | | | | | | | | 3,7,9 | 7,8,9 | 2,3,7,8, 9 | 6,7,8,9 | 2,3,6,7, 8,9 |
| **LUC** | | | | | | | | | | | | | | | 2 | 3,6,7 | 2,6,7 |
| **TSV** | | | | | | | | | | | | | | | 2,3 | 6,7 | 2,3,6,7 |
| **FR** | | | | | | | | | | | | | | | | 2,3,6,7 | 2,6,7 |
| **MR** | | | | | | | | | | | | | | | | | 2,3,6 |

Table 4.5 Results of Bray-Curtis similarity classification success of 10 permanent parasite species infecting *Polydactylus macrochir* from locations across north-west and northern Australia. Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Location | % correct | EMB | RB | DBY | CB | RR |
|---|---|---|---|---|---|---|
| **EMB** | **55** | **28** | 23 | 0 | 0 | 0 |
| **RB** | **79** | 18 | **81** | 0 | 1 | 2 |
| **DBY** | **100** | 0 | 0 | **35** | 0 | 0 |
| **CB** | **100** | 0 | 0 | 0 | **52** | 0 |
| **RR** | **96** | 1 | 0 | 0 | 0 | **24** |

Table 4.6 Results of Bray-Curtis similarity classification success of 10 permanent parasite species infecting *Polydactylus macrochir* from locations in the southern Gulf of Carpentaria, Australia. Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Location | % correct | RR | AC | AR | MI | FLR |
|---|---|---|---|---|---|---|
| **RR** | **68** | **17** | 3 | 3 | 1 | 1 |
| **AC** | **29** | 2 | **12** | 12 | 8 | 8 |
| **AR** | **71** | 0 | 3 | **25** | 7 | 0 |
| **MI** | **30** | 2 | 1 | 22 | **15** | 10 |
| **FLR** | **43** | 6 | 9 | 15 | 27 | **43** |

Table 4.7 Results of Bray-Curtis similarity classification success of 10 permanent parasite species infecting *Polydactylus macrochir* from locations in the eastern Gulf of Carpentaria, Australia. Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Location | % correct | FLR | SC | SR | KR | WLR |
|---|---|---|---|---|---|---|
| **FLR** | **48** | **48** | 15 | 13 | 20 | 4 |
| **SC** | **52** | 3 | **26** | 6 | 12 | 3 |
| **SR** | **24** | 9 | 10 | **5** | 1 | 0 |
| **KR** | **88** | 2 | 2 | 1 | **36** | 0 |
| **WLR** | **84** | 2 | 0 | 2 | 1 | **27** |

Table 4.8 Results of Bray-Curtis similarity classification success of 10 permanent parasite species infecting *Polydactylus macrochir* from locations on the east coast of Queensland, Australia. Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Location | % correct | WLR | LUC | TSV | FR | MR | BR |
|---|---|---|---|---|---|---|---|
| **WLR** | **84** | **27** | 2 | 2 | 0 | 0 | 1 |
| **LUC** | **67** | 0 | **12** | 5 | 1 | 0 | 0 |
| **TSV** | **39** | 0 | 22 | **21** | 1 | 2 | 8 |
| **FR** | **88** | 1 | 1 | 6 | **128** | 0 | 9 |
| **MR** | **84** | 0 | 0 | 1 | 0 | **36** | 6 |
| **BR** | **88** | 0 | 0 | 0 | 5 | 1 | **44** |

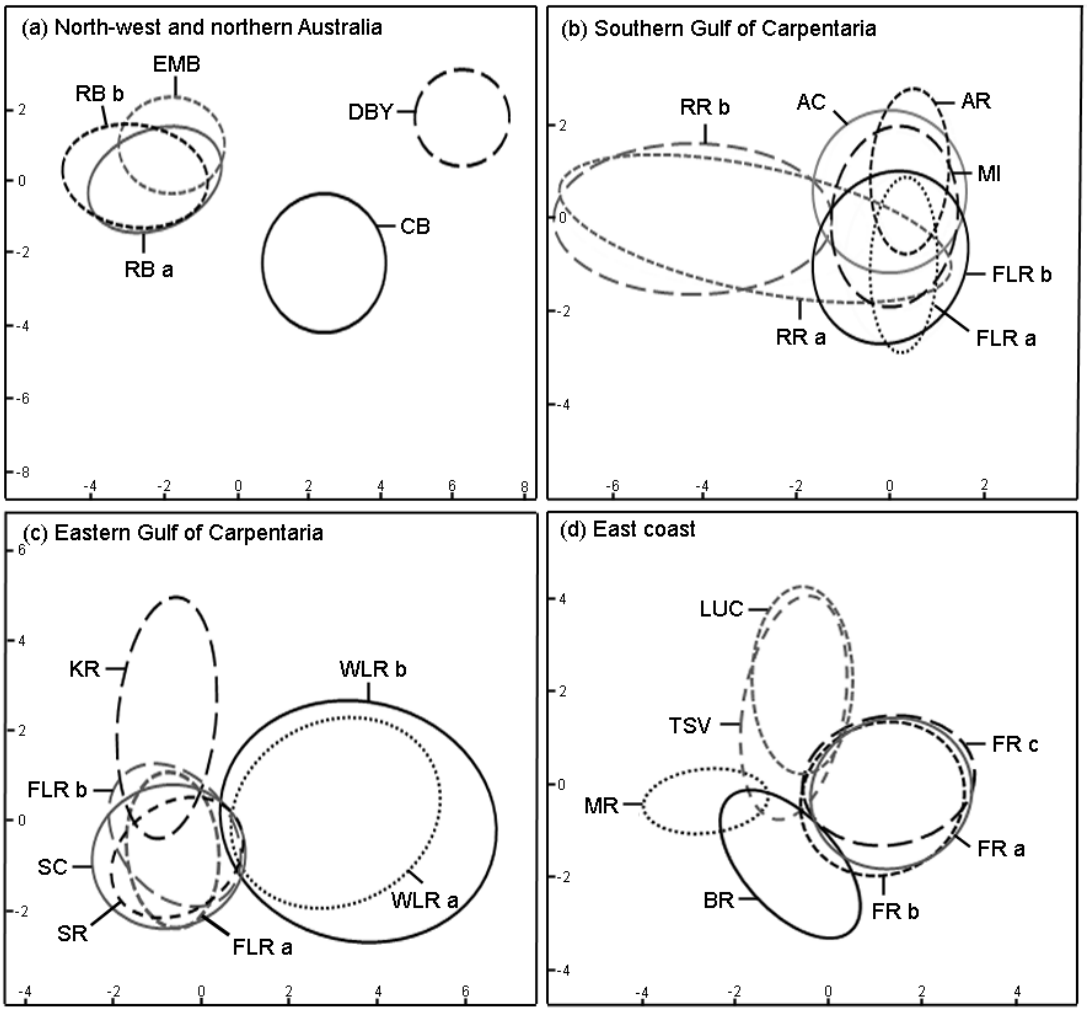


Figure 4.2 95% confidence ellipses from discriminant function analysis (DFA) of 10 parasites species infecting *Polydactylus macrochir* in Australian waters (see Figure 4.1). Axes 1 vs. 2. A separate DFA was run for each region.

## 4.4 Discussion

*Polydactylus macrochir* harboured a varied and abundant parasite fauna, with no fewer than 22 species recorded. Many of the same species, and a similar parasite diversity, have been recorded in the closely related blue threadfin, *Eleutheronema tetradactylum* Shaw, 1804 (see Zischke et al. 2009; Moore et al. 2011a). Given the low host specificity of the juvenile stages of the parasites examined (Palm 2004), the similarities in parasite faunas between *P. macrochir* and *E. tetradactylum* suggests that many aspects of their ecology, in particular diet and habitat, are similar (Moran et al. 1996; Poulin and Rohde 1997; Marques et al. 2011); a hypothesis that is consistent with surveys of the diet and distribution of the two species (Blaber et al. 1989; Brewer et al. 1995; Salini et al. 1998).

**Temporal patterns in parasite assemblages**

Understanding temporal patterns of parasite assemblages is critical when using parasites as biological tags, as temporal changes in parasite assemblages may confound differences between locations if sampling is conducted across different seasons and/or years (MacKenzie 1987; Campbell et al. 2007; Timi et al. 2009). Although it was not possible to examine the temporal stability of the parasites infecting *P. macrochir* at all locations in the present study due to the remoteness of the sampling locations and the variable nature of fishing activities, examination of temporal stability in parasite community assemblages was possible for five locations covering the majority of the sampling region. In this analysis, parasite community assemblages showed strong similarities between temporal replicates collected between five months to three years apart. While the relatively small sample sizes for the Roper and Wenlock Rivers may have confounded analyses at these locations, the similarities observed among temporal replicate samples from Roebuck Bay and the Flinders and Fitzroy River suggests that the parasite communities at these locations were stable over the timeframes explored. Several studies have reported similar results over comparable timeframes. Campbell et al. (2007) found no difference in the prevalence or abundance of the nematode *Anisakis simplex* and the larval cestode *Lacistorhynchus tenuis* infecting herring, *Clupea harengus*, in the Irish Sea over a two year period from 2003 and 2004. Similarly, Charters et al. (2010) observed no significant difference in the abundances of *P. pearsoni*, *C. gracilis*, *Terranova* (type II) and *A. simplex* infecting grey mackerel, *Scomberomorus semifasciatus*, collected from multiple locations across northern Australia between 2005 and 2006. However, the lack of temporal variation reported in these studies should not be taken as evidence that parasite communities are stable over these timeframes in general. Rather, given the potential of temporal difference to confound results, temporal patterns in parasite assemblages should be examined on a study-specific basis, particularly for cases where spatial sampling is conducted over large temporal periods.

**Spatial patterns in parasite assemblages**

The parasite assemblages of *P. macrochir* were found to be significantly different among locations at a range of spatial scales, indicating that juvenile and adult assemblages of *P. macrochir* undergo limited broadscale connectivity and remain resident in areas that reflect the different environmental or ecological conditions they experience in their life. Samples from Derby, Chambers Bay, and the Wenlock, Fitzroy, Mary and Brisbane Rivers each appeared distinct to all other samples, consistent with spatial isolation of fish from these locations. Differences in parasite assemblages over similar spatial scales have been observed for several teleost species in Australian waters, including blue threadfin, *E. tetradactylum* (see Moore et

al. 2011a), southern garfish, *Hyporhamphus melanochir* (see Hutson et al. 2011), and narrow-barred Spanish mackerel, *Scomberomorus commerson* (see Moore et al. 2003).

Similar parasite assemblages, however, were observed among locations separated by approximately 500 km in Queensland's Gulf of Carpentaria, and among Eighty Mile Beach and Roebuck Bay in Western Australia, and Lucinda and Townsville on Queensland's east coast. These similarities suggest that either fish are moving among locations, or the environmental and ecological conditions affecting parasite infection, such as the distribution of the definitive or suitable alternate intermediate hosts, are similar among locations. For Lucinda and Townsville, and the south-eastern Gulf of Carpentaria, the similarities in parasite assemblages are largely consistent with concurrent studies into the connectivity of *P. macrochir*, suggesting fish from these locations may form single, intermixing populations. Newman et al. (2010) and Horne et al. (2012) found no significant difference in whole otolith stable isotope ratios and mtDNA signatures, respectively, among fish from the south-eastern Gulf of Carpentaria, supporting the hypothesis of movement within this region. Life history parameters, including back-calculated length-at-age 2, total mortality rates and patterns of length and age at sex change were also largely similar among locations in this region (Chapter 3), further corroborating the hypothesis of a single population. Although not included in the studies of Newman et al. (2010) or Horne et al. (2012), fish from Lucinda were found to exhibit similar growth patterns to those from Townsville (Chapter 3). While the consistency of these results imparts a greater degree of confidence to those of any one technique used in isolation, it is important to note that it cannot be unequivocally concluded that such similarities prove the existence of a single, intermixing, population in each of these regions. Rather, the results of these techniques merely fail to falsify a null hypothesis of a single population (Waldman 1999).

The pattern of connectivity of post-larval assemblages of *P. macrochir* between Eighty Mile Beach and Roebuck Bay is slightly less clear. In accordance with the parasite data, comparisons of mtDNA haplotypes (Horne et al. 2012) and whole otolith stable isotopes (Newman et al. 2010) found no difference between these locations. In contrast, patterns in life history parameters, in particular growth and length and age at sex change, differed significantly among these locations (Chapter 3). The greater net movement of *P. macrochir* from Roebuck Bay to Eighty Mile Beach, as suggested by the parasite assemblages, may account for the differences observed in life history parameters. Alternately, the similarities observed in otolith isotopes and parasites assemblages may reflect similarities in the environmental and ecological conditions between locations, while the similarities in mtDNA haplotypes may result from larval mixing and/or movement of low numbers of adults. Additional techniques, such as analyses of otolith element signatures, may provide further

insight into the movement and connectivity of *P. macrochir* across the species' Australian distribution.

Using the qualitative criteria listed by Lester (1990) and MacKenzie and Abaunza (1998), ten parasite types were considered suitable for use as biological tags. Seven of the 10 parasites species were larval stages of trypanorhynch cestodes, the adults of which occur in elasmobranchs. The availability of definitive hosts is regarded as more important in regulating the distribution of cestodes than that of intermediate hosts due to the higher host-specificity of the parasitic adult stages (Rohde 1982; Palm 2004). As such, movements of fish may be deduced by examining the occurrence of these parasites in relation to the distribution of their elasmobranch definitive hosts. For example, in the present study, metacestodes of *P. australiense* were observed at all locations except for the Mary and Brisbane Rivers in south-east Queensland. Adults of this parasite have been recorded from the green sawfish, *Pristis zijsron* (see Campbell and Beveridge 1996). *Pristis zijsron* occur in coastal waters as far south as Perth in Western Australia across northern Australia to the east coast of Queensland (Last and Stevens 2009). Once reported to occur as far south as Jervis Bay, New South Wales (approximately 35ºS), *P. zijsron* are considered to be extinct in south-east Queensland and New South Wales waters (Stevens et al. 2005). Although it is conceivable that *P. australiense* may mature in other sawfish species, no sawfish species occur in south-east Queensland waters. The absence of this parasite in fish from the Mary or Brisbane Rivers thus suggests that no post-larval *P. macrochir* move from northern or central Queensland waters to the south-east. Although a lack of fresh material required for species-level identification for some of the parasites examined (e.g. *Proemotobothrium* sp., *Pterobothrium* sp. B), or lack of knowledge of the definitive host of others (e.g. *P. dipsacum*), precluded similar assessments for all species used as biological tags, the differences in abundances observed among locations nevertheless suggests limited connectivity of post-larval *P. macrochir* assemblages.

**Management implications and future directions**

The results of this study have important implications for the management of *P. macrochir*. The parasite assemblages examined suggest that post-larval *P. macrochir* form a number of discrete populations, with limited movement and connectivity between areas. These results suggest that *P. macrochir* is vulnerable to localised depletion, either through over-fishing or environmental perturbation, with reduction in any one area unlikely to be compensated for by immigration from other locations, at least of late juvenile and adult life history stages. The presence of fine-scale population structuring evident for juvenile and adult assemblages of *P. macrochir* suggests that the spatial scale of management, including the development of

monitoring and assessment programs, harvest strategies and establishment of suitable fishery regulations, needs to be reviewed in order to recognise the potential for localised depletion.

However, while the parasite data suggest limited exchange among post-recruitment *P. macrochir*, they provide little data on the connectivity of larval fish to adult assemblages. For at least some locations, the discrete adult assemblages observed in the present study may be interconnected by larval dispersal. Under this scenario, *P. macrochir* may conform to a metapopulation structure. Alternately, the spatially-discrete assemblages of *P. macrochir* evident from the parasite data may represent closed populations, with limited larval dispersal, or local larval retention, occurring among locations. Recently, strong selection for local larval retention has been hypothesised for fishes that live in spatially-fragmented seascapes such as estuaries, as the chances of finding suitable settlement habitat are greatly reduced if larvae disperse away from the parental population (Swearer et al. 2002). Understanding patterns of larval dispersal and recruitment to adult assemblages is considered critical to gaining a full understanding of the population structure of *P. macrochir*. Additional techniques, such as comparisons of otolith elemental signatures, may shed additional light on the movements and exchange of *P. macrochir*, including connectivity of larval life history stages to adult populations.

Recently, holistic approaches, that integrate multiple, complementary techniques, have been advocated as the preferred method for delineating patterns of movement and connectivity of fishes, as they effectively maximise the likelihood of identifying spatially-discrete groups (sensu Begg and Waldman 1999). This chapter forms a significant contribution to the holistic study into the movements and connectivity of *P. macrochir*, and, given the paucity of studies examining connectivity of non-diadromous tropical estuarine fishes, provides fundamental information from which more specific hypotheses of connectivity, population structure and gene flow of such species can be tested.

# Chapter 5 Connectivity and population structure of a non-diadromous, tropical estuarine teleost as determined by otolith microchemistry

## 5.1 Introduction

Understanding the population structure and degree of exchange between groups of a species, or connectivity, is fundamental to the effective management and conservation of aquatic species and ecosystems (Cowen et al. 2007). Information on connectivity, achieved through the dispersal of individuals as larvae, juveniles, or adults, helps to identify which groups are susceptible to localised depletion and potential sources of replenishment and recruitment to local populations (Thorrold et al. 2001; Cowen and Sponaugle 2009). Such knowledge is fundamental for determining the spatial scale at which a species should be managed and in the design of protected areas such as marine reserves or marine protected areas (MPAs). If managed inappropriately, spatially discrete populations could be inadvertently subject to localised depletion or extinction through over-fishing or environmental perturbation, as there would be limited opportunity for replenishment from neighbouring populations (Hilborn and Walters 1992). Furthermore, there is the potential to reduce local productivity, alter biological or ecological processes, and reduce genetic diversity (Ricker 1981; Smith et al. 1991).

Analysis of elemental signatures of otoliths offers a powerful approach to examining patterns of connectivity of fishes (Thorrold et al. 2001; Gillanders 2002a; Gillanders 2005; Elsdon et al. 2008). Resolution of such methods has been demonstrated to be fine enough to distinguish differences in elemental signatures among sites separated by as little as several metres (e.g. Kingsford and Gillanders 2000). Otoliths are crystalline structures composed of calcium carbonate located in the membranous labyrinth of the inner ear of teleosts. Three pairs of otoliths occur in teleosts; the sagittae, the asteriscii, and the lapilli. Of these, the sagittae are most commonly used in studies of otolith chemistry, owing to their larger size and ease of extraction (Thresher 1999). As an otolith grows, elements are incorporated into its calcium carbonate structure at rates largely mediated by both environmental and endogenous factors, including ambient concentration, water temperature, salinity and diet (Fowler et al. 1995; Bath et al. 2000; Milton and Chenery 2001b). For example, strontium (Sr) typically occurs at high, uniform concentrations in marine environments, while barium (Ba) shows the opposite pattern and is enriched in freshwater or in the low salinity region of freshwater plumes during flood events (McCulloch et al. 2005; Walther and Thorrold 2006). As otoliths are metabolically inert (i.e. they are not subject to resorption, remodelling or regeneration), the deposition of elements and resulting chemical signature remains unaltered through time (Campana and Neilson 1985).

Consequently, otoliths retain a chronological record of the environments experienced by a fish throughout its life (Secor and Rooker 2000; Elsdon and Gillanders 2003). Correlating patterns of elemental signatures with temporal references within otoliths, such as the annual or daily growth increments, can facilitate examination of age-related patterns of movement and connectivity (Fowler et al. 2005; McCulloch et al. 2005; Steer et al. 2009).

Examination of life history parameters (Chapter 3) and parasite assemblages (Chapter 4) suggest that post-larval *P. macrochir* generally undergo limited movement and thus form a number of spatially distinct assemblages. Broadscale differences in otolith stable isotope ratios (Newman et al. 2010), and mitochondrial DNA haplotypes (Horne et al. 2012) have also been reported. However, these studies were largely based on late juvenile and adult fish, which may not necessarily be representative of the dispersal capabilities and connectivity of larval or early juvenile life history stages (Tobin et al. 2010). As connectivity may be achieved through dispersal of all life history stages (Palumbi 2004; Fogarty and Botsford 2007), understanding the degree of movement and dispersal of pre-recruitment stages of *P. macrochir* is of critical importance in order to implement effective management strategies for the species. In this chapter, patterns in otolith elemental signatures of *P. macrochir* were investigated to determine movement and connectivity of the species across northern Australia. The specific aim of this study was to examine age-related elemental signatures from the otolith core (reflecting larval/early juvenile life history) through to material laid down during adult life, to assess whether the connectivity and population structure observed in adult fish reflects dispersal and movement of early life history stages.

## 5.2 Materials and methods

### Sample collection

*Polydactylus macrochir* were collected from commercial net fishers, fisheries-independent sampling and from recreational anglers from 17 locations (lower estuarine stretches of rivers and coastal sites) across northern Australia between July 2007 and February 2010 (Figure 5.1). Locations were separated by 10s to 100s of kilometers and were centered on the important commercial and recreational fishing areas for *P. macrochir* across northern Australia. At each location (with the exception of the Brisbane River and Lucinda), whole fish or fish frames (whole skeleton remaining after filleting) were obtained directly from commercial fishers, fish processors or by fisheries-independent sampling that generally used the same gear used by commercial fishers (i.e. a combination of gillnets of 100 mm (4 in.) to 165 mm (6.5 in.) stretched mesh). Brisbane River samples were collected through a fishery-independent sampling program using the same gear as used by commercial fishers as outlined above, by opportunistic collections from recreational fishers, and by research line-fishing, whereas

Lucinda samples were obtained from recreational fishers. The location, date of capture, sex, maturity stage, total length (TL), fork length (FL) and upper jaw length (UJL) were recorded for each fish collected, unless damaged. Sagittal otoliths (hereafter referred to as otoliths) were removed from all fish. Otoliths were rinsed in deionised (Milli-Q) water, cleaned of adhering tissue and stored to dry for later ageing. Each fish was aged following the protocol in Chapter 3 and assigned to a year class on the basis of spawning year. To minimise any confounding temporal influences on the spatial comparisons due to differences in collection time, examination of elemental profiles was conducted on 3+ year fish that originated from the 2005 year class. Up to 18 otoliths were randomly selected from those available from each of the 17 locations for the analyses. After ageing, a single otolith from each fish was rinsed with ultra-pure water and air-dried overnight for processing.

**Otolith preparation**

Each otolith was embedded in epoxy resin and a transverse section of 400 μm thickness was taken through the primordium removed from the core region using a low speed diamond-edged circular saw continuously lubricated with ultra-pure water. Each otolith section was polished down to the inner core on both sides using 1500 grit-size abrasive paper that was wet with Milli-Q water. Each polished section was triple rinsed with Milli-Q water and air-dried. Four randomly selected sections were fixed on an acid-washed 50 mm x 25 mm microscope slide with resin. Each slide was wiped with a paper towel that had been wet with 0.5 M $HNO_3$ to remove any surface contamination, rinsed with Milli-Q water and air-dried before being stored in an individual plastic bag for transportation to the laser ablation facility.

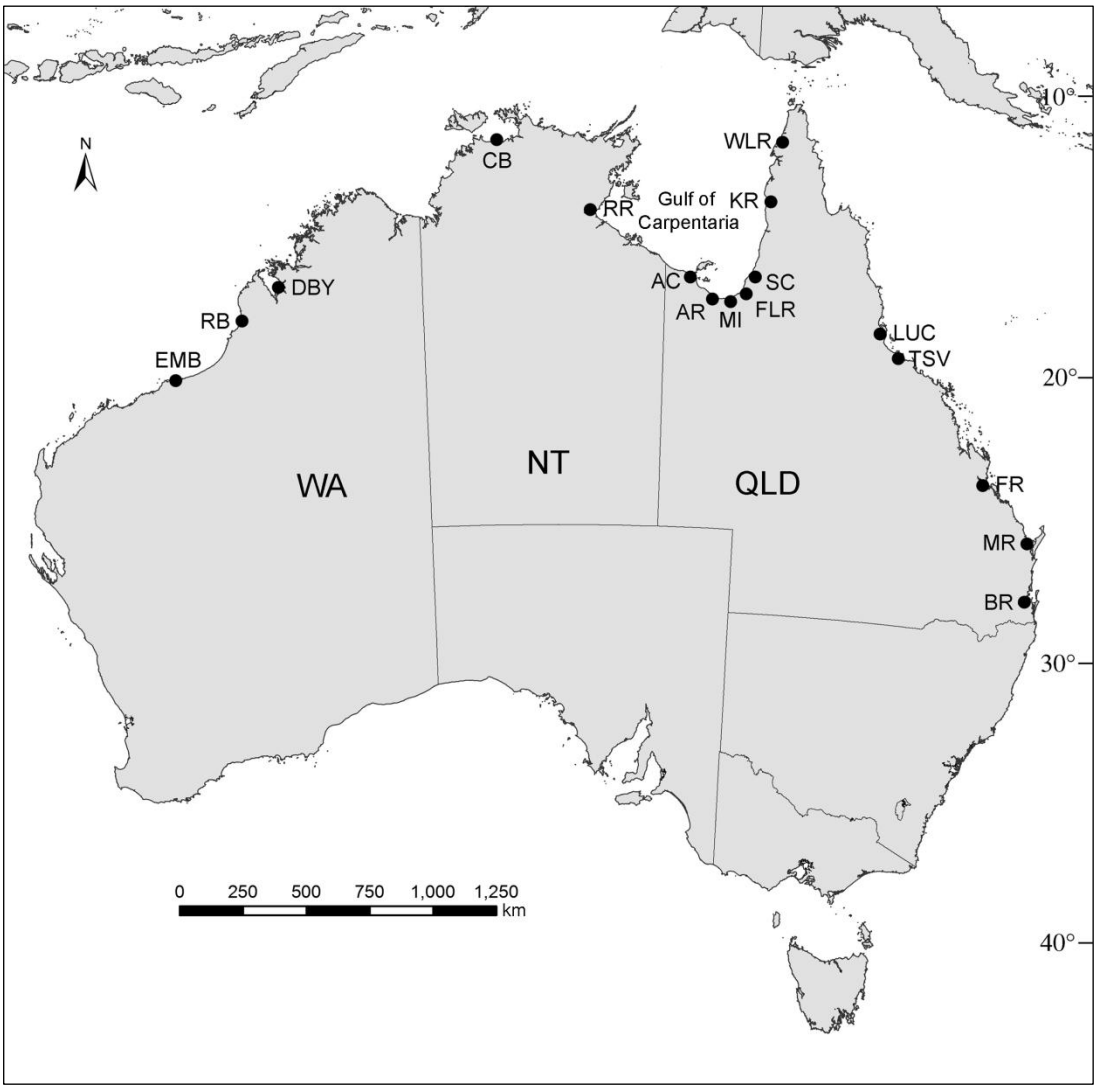


Figure 5.1 Locations where *Polydactylus macrochir* were sampled for examination of otolith elemental signatures (sample sizes in parentheses). From left: EMB, Eighty Mile Beach (15); RB, Roebuck Bay (16); DBY, Doctor's Creek, Derby (10); CB, Chambers Bay (11); RR, Roper River (14); AC, Arthurs Creek (14); AR, Albert River (15); MI, Morning Inlet (14); FLR, Flinders River (18); SC, Spring Creek (14); KR, Kendall River (10); WLR, Wenlock River (8); LUC, Lucinda (6); TSV, Cleveland Bay, Townsville (10); FR, Fitzroy River (12); MR, Mary River (10); BR, Brisbane River (10).

**Elemental analysis**

The otolith sections were analysed by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Environmental Analytical Chemistry Laboratory, Charles Darwin University, Darwin, Australia. The system consisted of a New Wave UP-213 high performance ultraviolet laser ablation system connected to an Agilent 7500ce ICP-MS. Each

slide was placed in a sealed perspex ablation chamber with helium atmosphere (1.10 L $min^{-1}$) and viewed remotely via a computer monitor. The laser was programmed to follow a transect from the core to the outer edge of the otolith section (Figure 5.2). This sampling axis was chosen as it generally provided well defined opaque annuli. Examination of the elemental profiles revealed a distinct peak of Mn in the otolith core of most samples (see Results). Accordingly, the presence of these Mn peaks was used to confirm that each transect sampled the otolith core and to allow identification of the position of the core along each transect. Transects were ablated using an 80 μm diameter laser beam, at a pulse rate of 5 Hz, a laser energy of 80% and a scan speed of 10 μm $s^{-1}$. A pilot study revealed concentrations of $^{7}$Li, $^{24}$Mg, $^{43}$Ca, $^{55}$Mn, $^{59}$Co, $^{86}$Sr, $^{88}$Sr, $^{137}$Ba and $^{138}$Ba were generally measured above detection limits and showed no evidence of surface contamination, based on comparisons of pre-ablated and non pre-ablated otoliths. As these isotopes are thought to be metabolically inert, not under significant physiological control, and not subject to interference from other isotopes (Campana 1999), they were recorded for all transects. As previous studies have shown Sr and Ba to be particularly useful for discriminating groups of estuarine fishes (Gillanders 2002a; Milton and Chenery 2003), two isotopes of Sr and Ba were read in order to cross-check the occurrence of any possible interference of these elements.

Prior to each ablation, background counts of each elemental isotope were measured in the blank sample gas for 20 seconds. This provided average background counts of the analysed isotopes, which were subtracted from the sample counts for each ablation. After each ablation the chamber was purged with Argon gas for approximately 2–3 minutes to eliminate any background gases that may have contained contaminants. Otolith sections were analysed in random order to eliminate any possible biases associated with instrument drift. Counts of elemental isotopes were calibrated against the National Institute of Standards (NIST) 612 glass standard. This standard was analysed once at the beginning and completion of each slide (4 ablations) to further eliminate short-term instrument drift by linear interpolation. The minimum detection limit at the 99% confidence level was calculated using GLITTER software (Van Achterbergh et al. 2001). Average detection limits (in p.p.m.) for each isotope were estimated as: $^{7}$Li 0.01, $^{24}$Mg 0.02, $^{43}$Ca 20.62, $^{55}$Mn 0.05, $^{59}$Co 0.01, $^{86}$Sr 0.76, $^{88}$Sr 0.05, $^{137}$Ba 0.02, $^{138}$Ba 0.01. Estimates of precision (% relative standard deviation (RSD)) based on the repeated analysis of the NIST 612 standard for each isotope were: $^{7}$Li 7.80%, $^{24}$Mg 5.16%, $^{55}$Mn 3.18%, $^{59}$Co 4.84%, $^{86}$Sr 4.94%, $^{88}$Sr 2.81%, $^{137}$Ba 3.26%, $^{138}$Ba 3.01%.

Calcium ($^{43}$Ca) was used as an internal standard to correct for variations in ablation yield. Calcium concentration was assumed to be constant at 388 000 μg $g^{-1}$ based on published values for certified otolith reference material (Yoshinaga et al. 2000). All elemental data were

expressed as molar ratios to $^{43}Ca$. Elemental values in the NIST 612 standard were derived from Pearce et al. (1997).

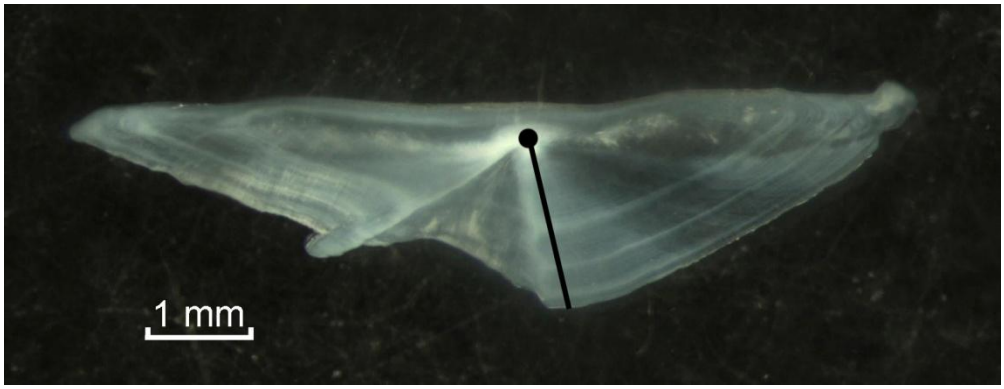


Figure 5.2 Transverse section of an otolith from a 3+ year old *Polydactylus macrochir* from the 2005 year class. The black line indicates the ablation transect.

**Relating elemental signatures to fish age**

The elemental signatures were related to fish age using the annuli of the otolith as a temporal reference, following Fowler et al. (2005) After each otolith was ablated using LA-ICP-MS, a digital image of the section was recorded using a Leica DC 300 digital camera mounted to a dissecting microscope. Using this image, a transect was drawn adjacent to the ablation scar, and the width of each annual increment was measured along this transect from the outer edges of the consecutive opaque zones. The elemental profiles were then divided into up to four life-history stages according to the measured distances along this transect: larval/early juvenile (first 100 μm of the transect, comprising the otolith core, consistent with measurements of this structure for the species), and years 1, 2 and 3. Only the chemical signatures from the core to the third opaque zone were used in the analyses. Although fish were collected from the different locations over a 12-month period, no analyses were conducted on the elemental signatures within the marginal increment.

**Data analysis**

To reduce the noise in the data, concentrations of each element were averaged using a nine-point running median, and then further smoothed using a nine-point running mean as described by Sinclair et al. (1998). The elemental profiles for each element were plotted against fish age, to examine age-related variation of elemental signatures within and among locations. For each otolith an age group mean was then calculated from the elemental readings that were assigned to each age group, based on the annuli measurements. This provided four

age group means for each otolith: one for the core (larval/early juvenile portion), and the three for each consecutive year of the fish's life.

A combination of univariate and multivariate analyses were used to examine spatial patterns in the otolith elemental signatures. As Shapiro Wilk tests revealed the data for some elements were non-normal ($P < 0.05$), concentrations were ln(x+1) transformed prior to analysis, to normalise and minimise the variance of the data. One-way ANOVA was applied to identify differences in abundance of the individual elements among the 17 locations, using location as a fixed factor in the univariate design. Significant results were examined using Tukey-Kramer post-hoc pair-wise comparisons (Sokal and Rohlf 1995).

Differences in multi-element signatures among locations were examined by multiple analysis of variance (MANOVA), followed by forward step-wise discriminant function analysis (DFA). Canonical discriminant plots were constructed to visualise differences in multi-element signatures among locations and age groups. To assess how accurately individuals could be assigned to location using multi-element signatures, cross-validation classifications were performed using jackknife 'leave one out' procedures. Preliminary analysis suggested that some samples separated by thousands of kilometers of coastline were similar (e.g. EMB vs. TSV; Figure 5.1), with very different locations in between. To avoid these locations being forced together in the results, locations were separated into the same four regions used in Chapter 4 for multivariate analyses; north-western and northern Australia, southern Gulf of Carpentaria, eastern Gulf of Carpentaria and Queensland's east coast. A single MANOVA and DFA were run on the elemental signatures assigned to each age group (larval/early juvenile, age 1, age 2 and age 3), and for each region (north-western and northern, southern Gulf of Carpentaria, eastern Gulf of Carpentaria and east coast). Partial Wilk's lambda values were used to identify the elements that contributed the most discriminatory power to the overall DFA models, ranging from zero (total discriminatory power) to 1 (no discriminatory power) (McGarigal et al. 2000).

## 5.3 Results

### Single element analyses

Concentrations of $^{7}$Li, $^{24}$Mg, $^{55}$Mn and $^{59}$Co were highest in the otolith cores and generally decreased throughout the first three years of a fish's life (Figure 5.3). As average $^{55}$Mn concentrations generally dropped below detection levels with increasing distance from the core (Figure 5.3), data for this element were included only in the analyses of otolith cores (larval/early juvenile portion). Whilst concentrations of $^{7}$Li, $^{24}$Mg, and, to a lesser extent, $^{59}$Co, showed similar patterns, concentrations of these elements consistently exceeded the detection limits throughout a fish's life, and as such their data were included for analyses of all age

groups. The two isotopes recorded for Sr ($^{86}$Sr and $^{88}$Sr) and Ba ($^{137}$Ba and $^{138}$Ba) showed similar trends across the otoliths, suggesting that variation in their profiles represent real trends in chemical composition. Of the two isotopes, $^{88}$Sr and $^{138}$Ba showed the lowest variance, and were therefore considered more reliable for analysis.

One-way ANOVA detected significant variation in the age-related mean concentration of all elements for at least one age group ($P < 0.05$). In some cases, however, differences were inconsistent among locations and age groups, with an element differing among locations for one age group but not the next. Little overall variation was evident among locations for average concentrations of $^{24}$Mg or $^{59}$Co (Figure 5.3). Average $^{7}$Li concentrations were lower for samples from the Fitzroy, Mary and Brisbane Rivers relative to other locations for the core region and ages 1 and 2. Average $^{55}$Mn concentrations were lowest in the core region of samples from Eighty Mile Beach and Roebuck Bay, and highest in fish from the Fitzroy River. Sr concentrations varied considerably over the life of an individual fish, with age-related Sr profiles showing numerous peaks and troughs. Average $^{88}$Sr concentrations exhibited a slight decrease from the western locations to the eastern locations, and were generally lowest for Brisbane River fish (Figure 5.3).

Of the six elements analysed, $^{138}$Ba showed the most variation among locations (Figure 5.3). Average $^{138}$Ba concentration showed little correlation with age for most locations, however, average $^{138}$Ba concentrations increased with age for fish from the Roper River, Flinders River and Spring Creek locales in the Gulf of Carpentaria, and decreased with age for fish from the Fitzroy, Mary and Brisbane Rivers on the east coast. Average $^{138}$Ba concentrations were highest for samples from Derby and the Fitzroy and Brisbane Rivers for the north-western and northern and east coast regions, respectively. In the Gulf of Carpentaria, average $^{138}$Ba signatures were highest for the Roper River, in the Northern Territory, and Flinders River and Spring Creek, in Queensland's south-eastern Gulf of Carpentaria waters. Examination of age-related plots of $^{138}$Ba profiles for locations within Queensland's Gulf waters revealed further trends in this region. Three general $^{138}$Ba signature types were evident: fish with 'high' $^{138}$Ba (consistently exceeding 25 μmol mol$^{-1}$ throughout a fish's life after the first austral wet season (Oct-March)), fish with 'variable' $^{138}$Ba (one or more peaks and troughs, with peaks exceeding 25 μmol mol$^{-1}$), and those with 'low' $^{138}$Ba (not exceeding 25 μmol mol$^{-1}$ at any point of a fish's life) (Figure 5.4). Fish with 'high' $^{138}$Ba signatures were only observed at the Flinders River and Spring Creek locations. All fish from the Morning Inlet, and the Kendall and Wenlock Rivers, had 'low' $^{138}$Ba signatures. A single fish from Arthurs Creek and the Albert River had a 'variable' $^{138}$Ba signature, while the remaining fish had 'low' $^{138}$Ba signatures (Table 5.1).

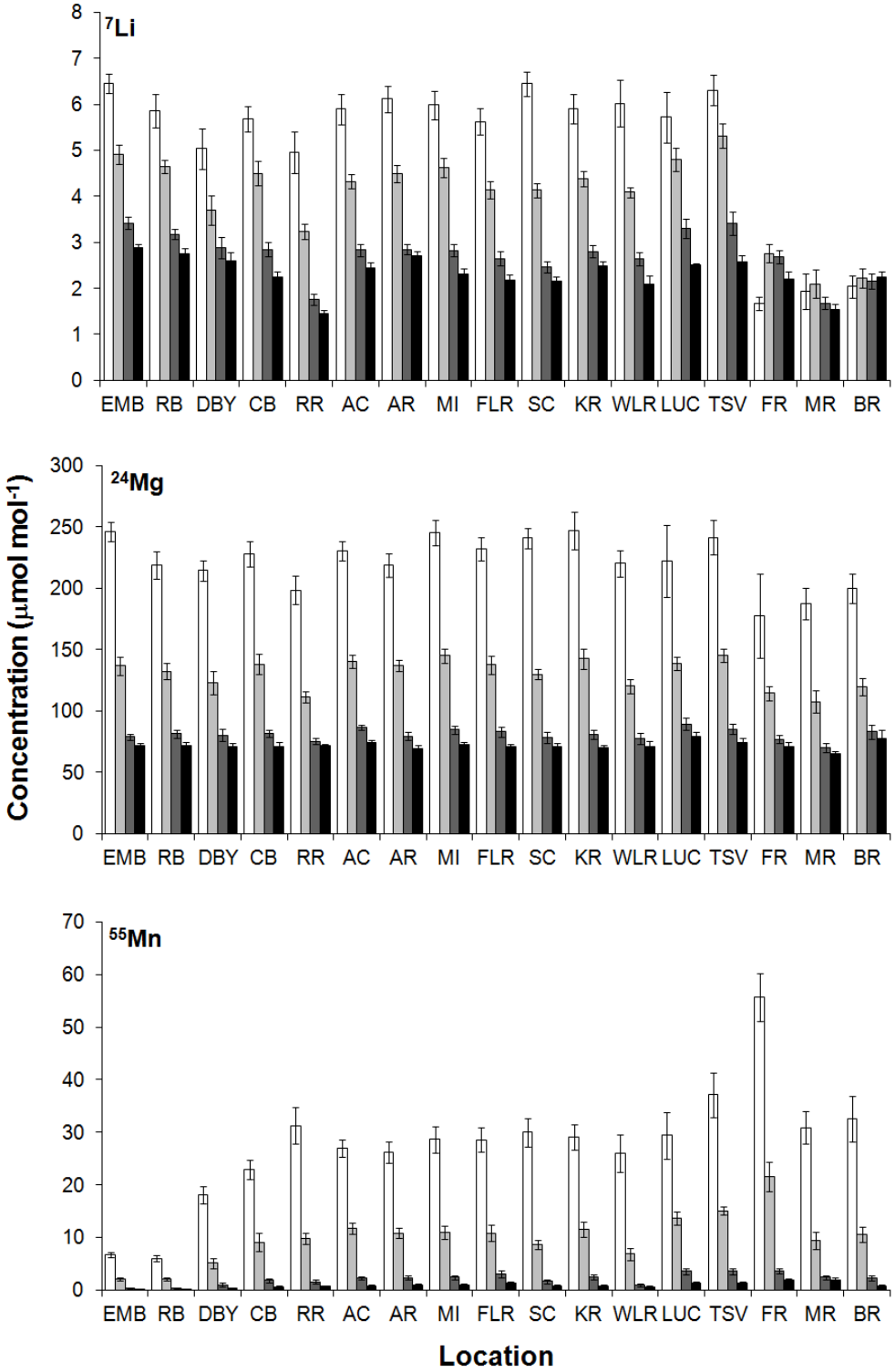


Figure 5.3 Age-related mean concentrations (µmol mol$^{-1}$relative to $^{43}$Ca) of $^{7}$Li, $^{24}$Mg and $^{55}$Mn in *Polydactylus macrochir* otoliths collected from 17 locations across northern Australia (± 1 s.e.). Juvenile = white, age 0–1 = light grey, age 1–2 = dark grey, age 2–3 = black. See Figure 5.1 for location codes.

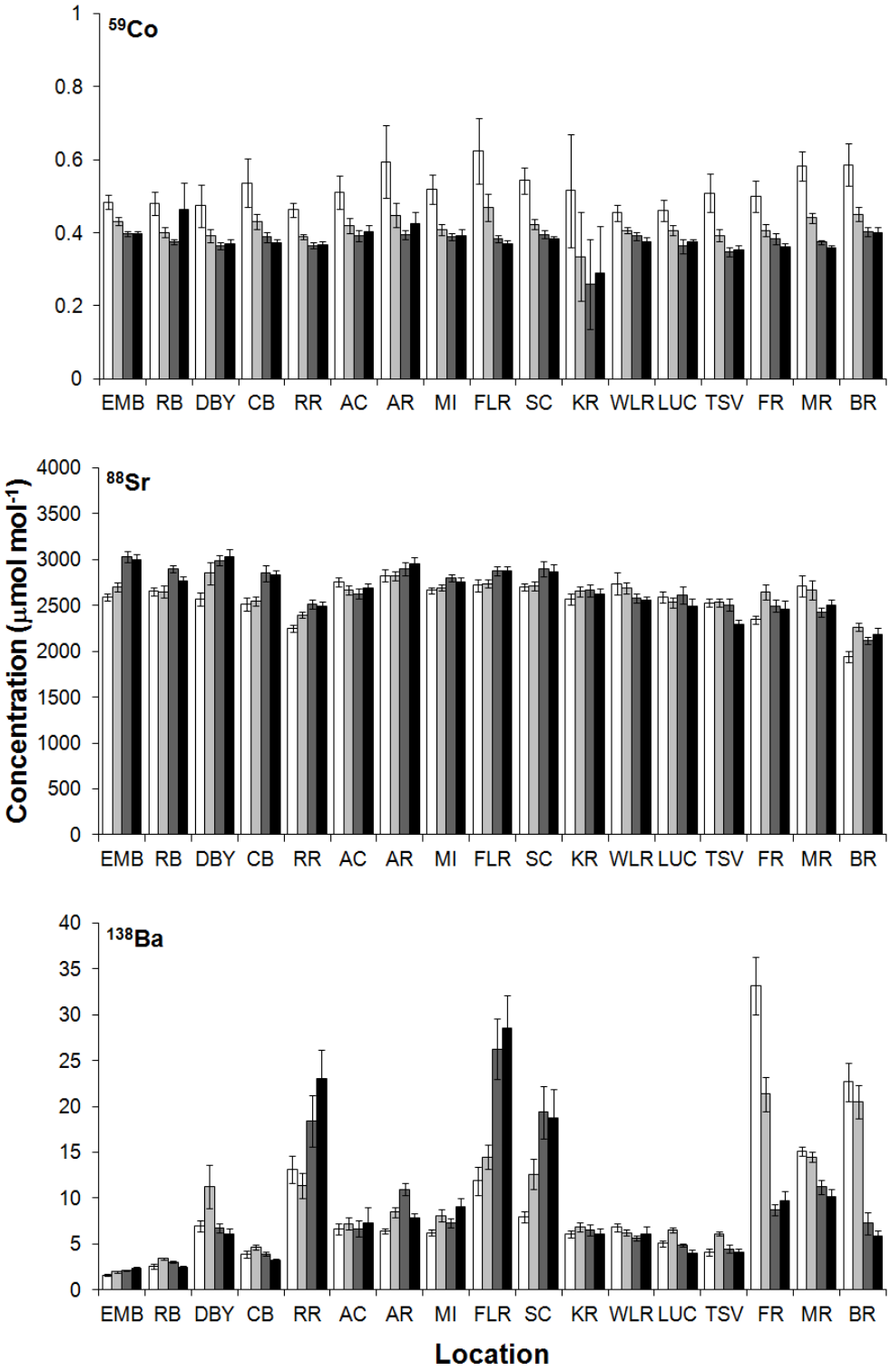


Figure 5.3 (cont.) Age-related mean concentrations (µmol mol$^{-1}$relative to $^{43}$Ca) of $^{59}$Co, $^{88}$Sr and $^{138}$Ba in *Polydactylus macrochir* otoliths collected from 17 locations across northern Australia (± 1 s.e.). Juvenile = white, age 0–1 = light grey, age 1–2 = dark grey, age 2–3 = black. See Figure 5.1 for location codes.

Table 5.1 Numbers of *Polydactylus macrochir* in each $^{138}$Ba otolith signature category for locations in Queensland's Gulf of Carpentaria waters (see text for criteria).

| Location | Barium signature | | |
|---|---|---|---|
| | **High Ba** | **Variable Ba** | **Low Ba** |
| Arthurs Creek | 0 | 1 | 13 |
| Albert River | 0 | 1 | 14 |
| Morning Inlet | 0 | 0 | 14 |
| Flinders River | 6 | 7 | 5 |
| Spring Creek | 2 | 7 | 5 |
| Kendall River | 0 | 0 | 10 |
| Wenlock River | 0 | 0 | 8 |

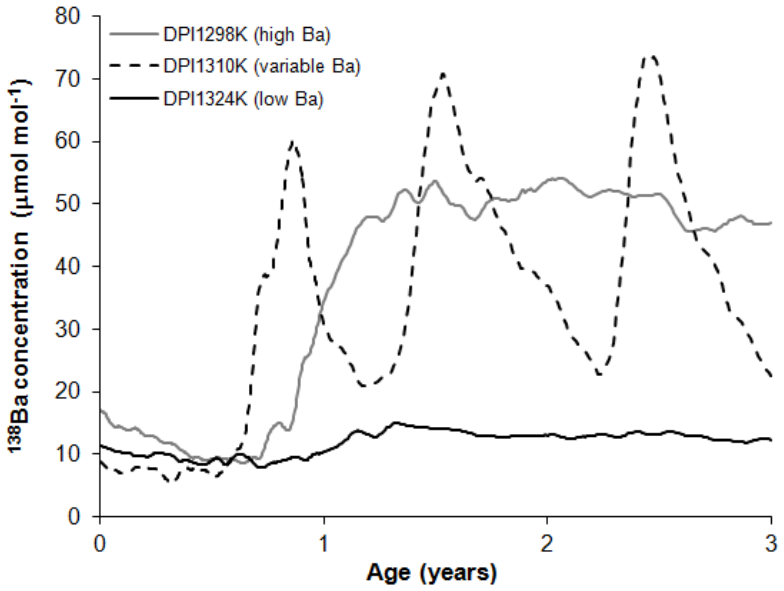


Figure 5.4 Examples of age-related variability in $^{138}$Ba concentration of three *Polydactylus macrochir* caught from the Flinders River from the Gulf of Carpentaria.

**Multi-element analyses**

*North-west and northern Australia*

Otolith elemental signatures differed significantly for all age groups among the four locations across north-western and northern Australia (MANOVA, $P < 0.001$) (Figure 5.5; Table 5.2). Fish from Eighty Mile Beach generally had high classification success (ranging from 73–100%). In contrast, fish from Roebuck Bay were poorly classified (≤ 56% for all age groups), with incorrectly classified fish aligning with those from Eighty Mile Beach and Chambers

Bay. Similarly, most incorrectly classified individuals caught at Chambers Bay were assigned to Roebuck Bay. Given that fish from Roebuck and Chambers Bays are genetically distinct (Horne et al. 2012), the similarity observed in the elemental data likely reflects a lack of heterogeneity in the factors affecting elemental deposition among these locations, rather than movement between locations. Fish from Derby appeared largely distinct for all age groups, with classification rates ranging from 80–100% (Table 5.3). Chambers Bay fish generally had poor classification success for ages 1, 2 and 3, with 50%, 33% and 67% of fish correctly classified in the age groups, respectively. In the analysis, average $^{55}$Mn concentration was identified as the main element responsible for the discrimination among locations for the early juvenile portion, whereas average $^{138}$Ba accounted for the majority of discrimination among locations for ages 1–3 (Table 5.2).

*Gulf of Carpentaria*

Multi-element signatures were significantly different among locations for all age groups for both regions of the Gulf of Carpentaria (MANOVA, $P \leq 0.012$) (Table 5.2). Discriminant function analysis further demonstrated the differences among locations (Figure 5.5). In the southern Gulf, samples from the Roper River appeared distinct to all other locations, with jackknifed classification success of 93%, 93%, 79% and 86% for the larval/early juvenile portion and ages 1, 2 and 3, respectively (Table 5.4). Classification success of Arthurs Creek, Albert River and Morning Inlet samples was poor for all age groups (Table 5.4), with many fish incorrectly classified among these three locations. Samples from the Flinders River were similar to all other locations for the larval/early juvenile and age 1 material, but appeared largely distinct for age 2 onwards, reaching classification success of 89% (16 of 18 individuals correctly classified) for age 3.

When compared against locations in the eastern Gulf, classification success of Flinders River fish similarly increased with age, with 50% of individuals correctly classified for the larval/early juvenile portion and 56%, 72% and 78% for ages 1, 2 and 3, respectively (Table 5.5). Spring Creek samples showed poor classification throughout, with classification success $\leq$ 29% for each of the four age groups examined. The majority of individuals that were incorrectly classified from Spring Creek were allocated to the Flinders River for all age groups. Samples from the Kendall and Wenlock Rivers were similarly poorly classified (Table 5.5). In the analyses, $^{88}$Sr and $^{138}$Ba were responsible for the majority of discrimination among locations for all age groups in the southern Gulf, and $^{138}$Ba had the most discriminating properties for all age groups in the eastern Gulf (Table 5.2).

*East coast*

Differences were apparent among locations for all age groups on the east coast (MANOVA, $P < 0.001$) (Table 5.2; Table 5.6). Samples from Lucinda and Townsville appeared similar in the DFA plots for all age groups (Figure 5.5). While Townsville fish generally had moderate classification success (ranging from 50–60%), fish from Lucinda were poorly classified ($\leq$ 67% for all age groups), with all incorrectly classified fish aligning with those from Townsville (Table 5.6). There appeared to be little evidence for dispersal of larval/early juvenile fish among the Fitzroy, Mary and Brisbane Rivers, with jackknifed classification success of 80–100% for the early juvenile signature of fish caught at each of these locations (Table 5.6). Despite their apparent convergence in the DFA plot (Figure 5.5), classification successes for these locations for ages 1–3 were high (Table 5.6), indicating that fish remained spatially distinct throughout their life. In the analysis, average $^{88}Sr$ and average $^{138}Ba$ were the main elements responsible for the discrimination of the early juvenile signatures, whereas average $^{138}Ba$ concentration typically accounted for the majority of discrimination among locations for ages 1–3 (Table 5.2).

Table 5.2 Summary of MANOVA and discriminant function analyses for elemental signatures of *Polydactylus macrochir* otoliths from four regions across northern Australia. Core analyses were based on $^{7}$Li, $^{24}$Mg, $^{55}$Mn, $^{59}$Co, $^{88}$Sr and $^{138}$Ba whereas all other age groups based on $^{7}$Li, $^{24}$Mg, $^{59}$Co, $^{88}$Sr and $^{138}$Ba. GoC = Gulf of Carpentaria.

| Region | Age group | MANOVA | | | Discriminant function analysis | |
|---|---|---|---|---|---|---|
| | | ***P*** | **F** | **d.f** | **Discriminant functions** | **Contributing elements (Partial Wilk's lambda)** |
| **NW & northern** | Core | <0.001 | 15.04 | 18, 124 | DF1 = 89%; DF2 = 10%; DF3 = 1% | $^{55}$Mn (0.24), $^{138}$Ba (0.51), $^{24}$Mg (0.70), $^{88}$Sr (0.88) |
| | 1 | <0.001 | 8.20 | 15, 124 | DF1 = 88%; DF2 = 10%; DF3 = 2% | $^{138}$Ba (0.34), $^{88}$Sr (0.73), $^{7}$Li (0.82), $^{24}$Mg (0.86), $^{59}$Co (0.93) |
| | 2 | <0.001 | 17.64 | 9, 114 | DF1 = 97%, DF2 = 2%, DF3 = 1% | $^{138}$Ba (0.16), $^{88}$Sr (0.85), $^{59}$Co (0.93) |
| | 3 | <0.001 | 12.41 | 12, 121 | DF1 = 89%, DF2 = 7%, DF3 = 4% | $^{138}$Ba (0.22), $^{88}$Sr (0.68), $^{7}$Li (0.85), $^{59}$Co (0.87) |
| **Southern GoC** | Core | <0.001 | 7.39 | 16, 205 | DF1 = 82%, DF2 = 14%, DF3 = 3.9%, DF4 = 0.1% | $^{88}$Sr (0.58), $^{138}$Ba (0.65), $^{24}$Mg (0.89), $^{59}$Co (0.93) |
| | 1 | <0.001 | 9.84 | 12, 180 | DF1 = 68%, DF2 = 30%, DF3 = 2% | $^{88}$Sr (0.55), $^{138}$Ba (0.64), $^{24}$Mg (0.77) |
| | 2 | <0.001 | 10.44 | 16, 205 | DF1 = 59%, DF2 = 38%, DF3 = 2%, DF4 = 1% | $^{138}$Ba (0.43), $^{7}$Li (0.68), $^{88}$Sr (0.86), $^{24}$Mg (0.87) |
| | 3 | <0.001 | 12.87 | 16, 205 | DF1 = 56%, DF2 = 43%, DF3 = 0.9% DF4 = 0.1% | $^{138}$Ba (0.44), $^{7}$Li (0.58), $^{24}$Mg (0.68), $^{88}$Sr (0.82) |
| **Eastern GoC** | Core | 0.012 | 2.28 | 12, 114 | DF1 = 71%, DF2 = 20%, DF3 = 9% | $^{138}$Ba (0.73), $^{88}$Sr (0.91), $^{24}$Mg (0.92), $^{7}$Li (0.92) |
| | 1 | <0.001 | 6.72 | 6, 90 | DF1 = 91%, DF2 = 9% | $^{138}$Ba (0.53), $^{24}$Mg (0.90) |
| | 2 | <0.001 | 5.33 | 12, 114 | DF1 = 95%, DF2 = 4%, DF3 = 1% | $^{138}$Ba (0.37), $^{7}$Li (0.81), $^{59}$Co (0.91), $^{24}$Mg (0.92) |
| | 3 | <0.001 | 8.38 | 9, 107 | DF1 = 96%, DF2 = 3.9%, DF3 = 0.1% | $^{138}$Ba (0.31), $^{7}$Li (0.67), $^{24}$Mg (0.93) |
| **East coast** | Core | <0.001 | 18.43 | 20, 130 | DF1 = 86%, DF2 = 9%, DF3 = 4%, DF4 = 1% | $^{88}$Sr (0.34), $^{138}$Ba (0.35), $^{7}$Li (0.56), $^{55}$Mn (0.66), $^{59}$Co (0.85) |
| | 1 | <0.001 | 12.04 | 20, 130 | DF1 = 83%, DF2 = 12%, DF3 = 4.9%, DF4 = 0.1% | $^{138}$Ba (0.24), $^{88}$Sr (0.65), $^{59}$Co (0.66), $^{7}$Li (0.67), $^{24}$Mg (0.87) |
| | 2 | <0.001 | 8.70 | 20, 130 | DF1 = 68%, DF2 = 26%, DF3 = 5%, DF4 = 1% | $^{59}$Co (0.53), $^{88}$Sr (0.53), $^{138}$Ba (0.60), $^{7}$Li (0.69), $^{24}$Mg (0.76) |
| | 3 | <0.001 | 7.29 | 20, 130 | DF1 = 58%, DF2 = 29%, DF3 = 11%, DF4 = 2% | $^{138}$Ba (0.45), $^{88}$Sr (0.48), $^{7}$Li (0.51), $^{59}$Co (0.63), $^{24}$Mg (0.77) |

Table 5.3 Jackknifed classification success of discriminant function analyses of trace element concentrations of *Polydactylus macrochir* otoliths from locations across north-western and northern Australia (see Figure 5.1). Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Age group | Location | % correct | EMB | RB | DBY | CB |
|---|---|---|---|---|---|---|
| **Juvenile** | **EMB** | **87** | **13** | 2 | 0 | 0 |
| | **RB** | **56** | 7 | **9** | 0 | 0 |
| | **DBY** | **80** | 0 | 0 | **8** | 2 |
| | **CB** | **83** | 0 | 0 | 2 | **10** |
| **Age 1** | **EMB** | **93** | **14** | 0 | 0 | 1 |
| | **RB** | **44** | 5 | **7** | 0 | 4 |
| | **DBY** | **80** | 0 | 0 | **8** | 2 |
| | **CB** | **50** | 0 | 6 | 0 | **6** |
| **Age 2** | **EMB** | **100** | **15** | 0 | 0 | 0 |
| | **RB** | **50** | 4 | **8** | 0 | 4 |
| | **DBY** | **100** | 0 | 0 | **10** | 0 |
| | **CB** | **33** | 0 | 5 | 3 | **4** |
| **Age 3** | **EMB** | **73** | **11** | 4 | 0 | 0 |
| | **RB** | **56** | 3 | **9** | 0 | 4 |
| | **DBY** | **100** | 0 | 0 | **10** | 0 |
| | **CB** | **67** | 1 | 3 | 0 | **8** |

Table 5.4 Jackknifed classification success of discriminant function analyses of trace element concentrations of *Polydactylus macrochir* otoliths from locations in the southern Gulf of Carpentaria, Australia (see Figure 5.1). Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Age group | Location | % correct | RR | AC | AR | MI | FLR |
|---|---|---|---|---|---|---|---|
| **Juvenile** | **RR** | **93** | **13** | 0 | 0 | 0 | 1 |
| | **AC** | **0** | 0 | **0** | 9 | 3 | 2 |
| | **AR** | **47** | 1 | 4 | **7** | 3 | 0 |
| | **MI** | **43** | 0 | 3 | 4 | **6** | 1 |
| | **FLR** | **39** | 3 | 4 | 1 | 3 | **7** |
| **Age 1** | **RR** | **93** | **13** | 1 | 0 | 0 | 0 |
| | **AC** | **36** | 0 | **5** | 3 | 4 | 2 |
| | **AR** | **40** | 0 | 3 | **6** | 3 | 3 |
| | **MI** | **21** | 2 | 5 | 2 | **3** | 2 |
| | **FLR** | **56** | 1 | 2 | 4 | 1 | **10** |
| **Age 2** | **RR** | **79** | **11** | 0 | 0 | 2 | 1 |
| | **AC** | **43** | 1 | **6** | 1 | 6 | 0 |
| | **AR** | **47** | 0 | 3 | **7** | 2 | 3 |
| | **MI** | **21** | 0 | 7 | 4 | **3** | 0 |
| | **FLR** | **72** | 0 | 0 | 5 | 0 | **13** |
| **Age 3** | **RR** | **86** | **12** | 0 | 0 | 2 | 0 |
| | **AC** | **57** | 1 | **8** | 1 | 3 | 1 |
| | **AR** | **60** | 0 | 0 | **9** | 6 | 0 |
| | **MI** | **29** | 2 | 3 | 5 | **4** | 0 |
| | **FLR** | **89** | 0 | 0 | 1 | 1 | **16** |

Table 5.5 Jackknifed classification success of discriminant function analyses of trace element concentrations of *Polydactylus macrochir* otoliths from locations in the eastern Gulf of Carpentaria, Australia (see Figure 5.1). Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Age group | Location | % correct | FLR | SC | KR | WLR |
|---|---|---|---|---|---|---|
| **Juvenile** | **FLR** | **50** | **9** | 5 | 3 | 1 |
| | **SC** | **29** | 7 | **4** | 2 | 1 |
| | **KR** | **40** | 1 | 4 | **4** | 1 |
| | **WLR** | **0** | 1 | 5 | 2 | **0** |
| **Age 1** | **FLR** | **56** | **10** | 5 | 2 | 1 |
| | **SC** | **14** | 7 | **2** | 4 | 1 |
| | **KR** | **10** | 2 | 3 | **1** | 4 |
| | **WLR** | **50** | 0 | 1 | 3 | **4** |
| **Age 2** | **FLR** | **72** | **13** | 5 | 0 | 0 |
| | **SC** | **14** | 9 | **2** | 2 | 1 |
| | **KR** | **20** | 1 | 2 | **2** | 5 |
| | **WLR** | **38** | 0 | 0 | 5 | **3** |
| **Age 3** | **FLR** | **78** | **14** | 4 | 0 | 0 |
| | **SC** | **29** | 6 | **4** | 1 | 3 |
| | **KR** | **50** | 1 | 2 | **5** | 2 |
| | **WLR** | **50** | 0 | 0 | 4 | **4** |

Table 5.6 Jackknifed classification success of discriminant function analyses of trace element concentrations of *Polydactylus macrochir* otoliths from locations on the east coast of Queensland, Australia (see Figure 5.1). Listed in the table is the percent of fish correctly classified and the number of fish classified to each location.

| Age group | Location | % correct | LUC | TSV | FR | MR | BR |
|---|---|---|---|---|---|---|---|
| **Juvenile** | **LUC** | **17** | **1** | 5 | 0 | 0 | 0 |
| | **TSV** | **60** | 4 | **6** | 0 | 0 | 0 |
| | **FR** | **92** | 0 | 0 | **11** | 0 | 1 |
| | **MR** | **80** | 0 | 0 | 2 | **8** | 0 |
| | **BR** | **100** | 0 | 0 | 0 | 0 | **10** |
| **Age 1** | **LUC** | **0** | **0** | 6 | 0 | 0 | 0 |
| | **TSV** | **60** | 4 | **6** | 0 | 0 | 0 |
| | **FR** | **83** | 0 | 0 | **10** | 2 | 0 |
| | **MR** | **80** | 0 | 0 | 0 | **8** | 2 |
| | **BR** | **70** | 0 | 0 | | 2 | **8** |
| **Age 2** | **LUC** | **0** | **0** | 6 | 0 | 0 | 0 |
| | **TSV** | **50** | 5 | **5** | 0 | 0 | 0 |
| | **FR** | **83** | 0 | 1 | **10** | 0 | 1 |
| | **MR** | **70** | 0 | 0 | 3 | **7** | 0 |
| | **BR** | **80** | 0 | 0 | 1 | 1 | **8** |
| **Age 3** | **LUC** | **67** | **4** | 2 | 0 | 0 | 0 |
| | **TSV** | **60** | 2 | **6** | 1 | 0 | 1 |
| | **FR** | **75** | 0 | 0 | **9** | 1 | 2 |
| | **MR** | **90** | 0 | 0 | 1 | **9** | 0 |
| | **BR** | **80** | 1 | 0 | 1 | 0 | **8** |

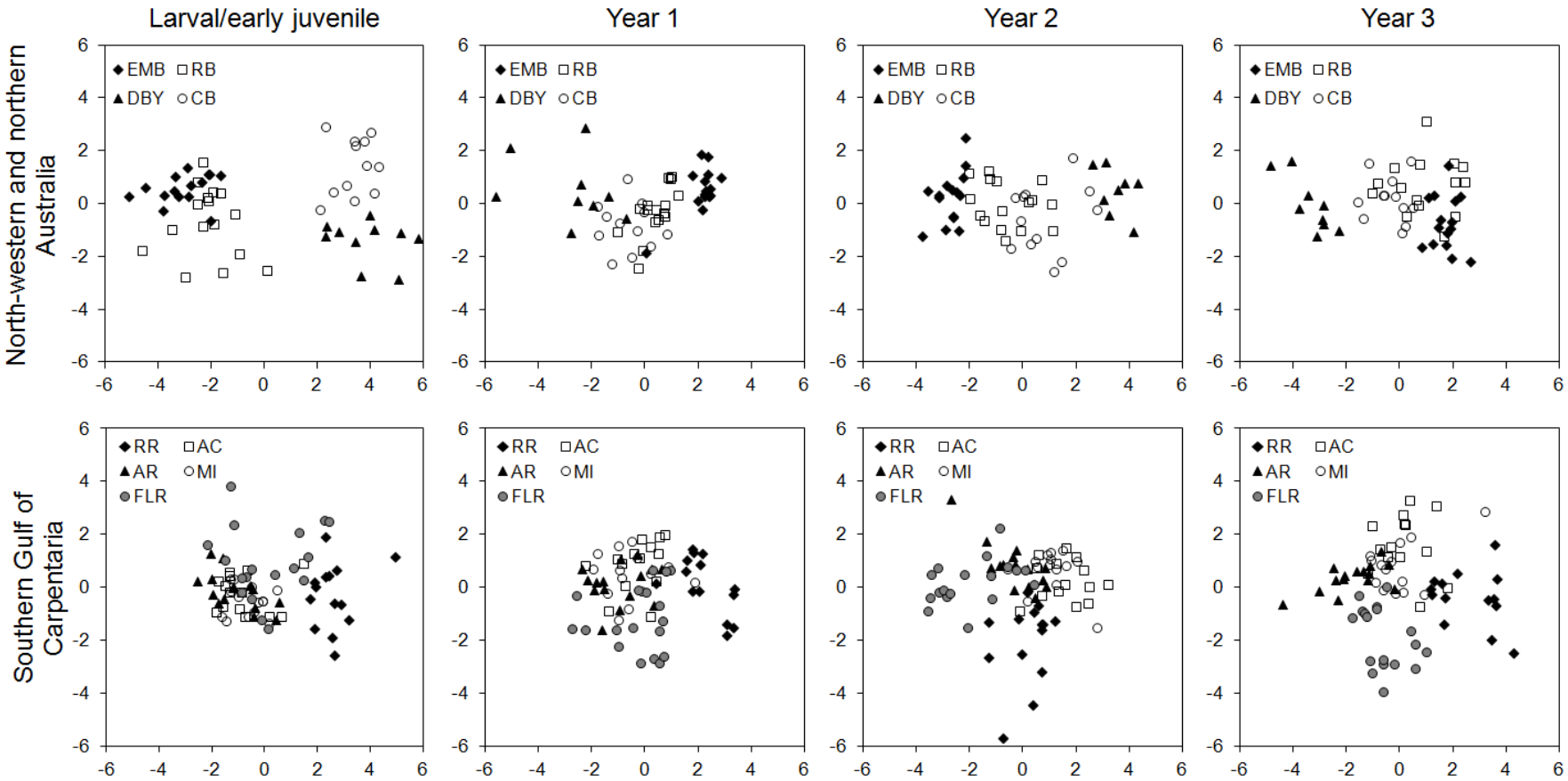


Figure 5.5 Canonical scores of discriminant function analyses (DFA) of age-related otolith elemental signatures of *Polydactylus macrochir* (axes 1 vs. 2). See Figure 5.1 for location codes. A separate DFA was run for each age group and region.

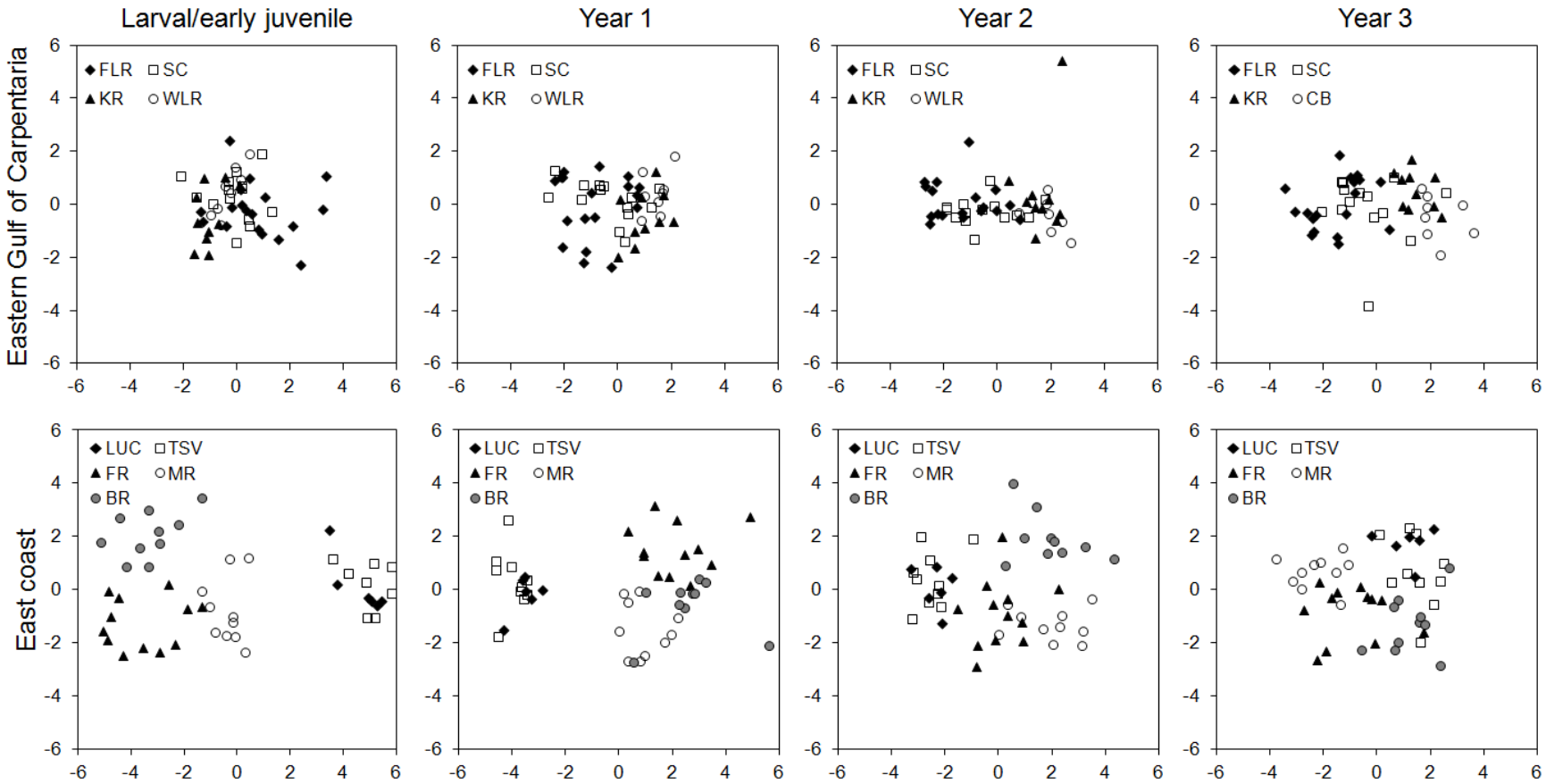


Figure 5.5 (cont.) Canonical scores of discriminant function analyses (DFA) of age-related otolith elemental signatures of *Polydactylus macrochir* (axes 1 vs. 2). See Figure 5.1 for location codes. A separate DFA was run for each age group and region.

## 5.4 Discussion

The elemental composition of *P. macrochir* otoliths varied considerably across northern Australia. Significantly, differences in elemental composition among locations were largely consistent throughout the life of an individual fish. This result is consistent with the hypothesis of limited connectivity of both larval/early juvenile and adult life history stages among spatially isolated groups of *P. macrochir*. Although differences in otolith elemental signatures over similar spatial scales have been observed for a number of estuarine-associated fishes in temperate and sub-tropical systems (e.g. Gillanders 2002a; Vasconcelos et al. 2007; Bradbury et al. 2008b), this study is the first to use otolith elemental signatures to examine connectivity in a tropical, non-diadromous, estuarine fish species.

In the analysis, Ba generally provided the most discrimination among locations, particularly for ages 1, 2 and 3. Otolith Ba concentration is considered to be closely associated with ambient Ba concentration (Bath et al. 2000; Elsdon and Gillanders 2003), which in turn is negatively correlated with salinity, with Ba typically enriched in low salinity environments such as freshwater or flood plumes, where it is desorbed from fine-grained suspended particles (Elsdon and Gillanders 2005; McCulloch et al. 2005). As such, the differences observed in Ba concentrations in *P. macrochir* otoliths were likely a reflection of differences in terrestrial runoff and freshwater flow among locations. For example, otolith $^{138}$Ba signatures of fish from the Flinders River increased dramatically relative to other locations shortly before the deposition of the first annual band, which is typically completed by the start of November in *P. macrochir* (Pember et al. 2005; Chapter 3). The enrichment of $^{138}$Ba in otoliths from this location coincided with the timing of a large and persistent flood in this system, which peaked at a mean daily flow rate of 100,520 ML/day in April 2006 (measured at Walker's Bend, approximately 103 km adopted middle thread distance (AMTD) from the mouth of the river) (DERM 2010). In contrast, mean daily flow rates of the Gregory River, approximately 15 km to the west of the sampling location at the mouth of the Albert River, and Alligator Creek, one of the main river systems that run into the Cleveland Bay sampling location at Townsville, ranged from approximately 141–2,977 ML/day and 0–1,120 ML/day over the study period, respectively (DERM 2010).

Relative to Ba, Sr offered little discrimination among locations. This was surprising, given that Sr has been used successfully to discriminate among estuaries for a number of estuarine and coastal fish species in temperate waters (Gillanders et al. 2003). It is generally assumed that there is a positive relationship between otolith Sr and ambient salinity; however, recent studies suggest that Sr may additionally be influenced by ambient Sr (Bath et al. 2000; Milton and Chenery 2001b) and temperature (Elsdon and Gillanders 2002). In the present study, Sr concentrations were found to vary considerably over the life of an individual fish,

with age-related Sr profiles showing numerous peaks and troughs that exhibited little temporal consistency, suggesting they were not related to season. Such variation may reflect movement of fish between differing salinities profiles, or episodic changes in salinity or ambient temperature at a particular location.

Concentrations of $^{7}$Li, $^{24}$Mg, and $^{55}$Mn, and, to a lesser extent, $^{59}$Co, were found to be elevated in the otolith core relative to the surrounding material. Although several studies have reported similar patterns of core enrichment in fish otoliths across a number of phylogenetically distinct species (Brophy et al. 2004; Ruttenberg et al. 2005; Warner et al. 2005), the mechanisms responsible for the elevated concentrations and spatial variation are largely unknown. The consistent occurrence of core enrichment among locations over such large spatial distances indicates that this phenomenon in *P. macrochir* may be attributed to similar physiological or maternal effects, rather than ambient concentrations or dietary influences. Furthermore, the spatial patterns in core enrichment of some elements were in agreement with results of recent genetic comparisons, suggesting that, for these elements, this phenomenon may be mediated at a genetic level. For example, Horne et al. (2012) found no difference in mtDNA haplotypes among fish from Eighty Mile Beach and Roebuck Bay, however these locations differed to all other locations examined; a result that is consistent with spatial patterns in otolith $^{55}$Mn concentration observed in the present study. Similarly, fish from the Fitzroy and Brisbane Rivers are genetically distinct (Horne et al. 2012), and differed significantly in average Mn concentration in their otolith cores. However, this pattern was not consistent for all elements examined in this study (e.g. Li), suggesting other mediating factors are also likely.

The pattern of connectivity and population structure evident from the elemental data presented here largely agrees with concurrent investigations of mtDNA haplotypes (Horne et al. 2012), otolith stable isotope ratios (Newman et al. 2010), life history parameters (Chapter 3) and parasite assemblages (Chapter 4), which suggest limited connectivity of post-larval (i.e. juvenile and adult) *P. macrochir* assemblages. However, in contrast to the elemental data, these complementary studies failed to detect any differences in post-larval fish among locations within the south-eastern Gulf of Carpentaria. Although not apparent among all locations within this region, the differences evident in the otolith elemental data, in particular Ba, among fish from the Flinders River and the other Gulf samples, for example, suggest that post-larval fish in this region are not a homogenous group, and that movement of juvenile and adult life history stages may be more restricted than previously thought. Given the fine spatial scale between the Flinders River and neighbouring locations (i.e. approximately 50 km), it is likely that similarities in elemental signatures observed elsewhere in this region reflect a lack of environmental heterogeneity in the factors affecting elemental deposition, rather than

movement of fish, among locations. The apparent contradiction between the results of the present study and those of earlier research highlights the importance of using complementary approaches to discern connectivity and population structure of fishes, in that they effectively increase the chances of identifying differences between spatially distinct populations (sensu Begg and Waldman 1999).

In contrast to the difference observed for post-recruitment fish, it is unclear whether the similarity observed in the larval/early juvenile elemental signatures among samples from Queensland's Gulf of Carpentaria results from mixing of these life history stages, or regional homogeneity in the factors affecting elemental deposition (e.g. ambient concentration, temperature, salinity, diet), among locations. Spawning in *P. macrochir* in Queensland's Gulf waters occurs between August and September (Garrett 1997), immediately prior to the beginning of the austral wet season and at a time when the amount of freshwater flowing into the Gulf of Carpentaria estuaries is typically low (DERM 2010). As a consequence, the otolith cores showed little Ba enrichment that discriminated the later life history stages. Although little is known of the dispersal capabilities of *P. macrochir* larvae, Horne et al. (2011) concluded that the fine-scale genetic structuring observed for the closely related blue threadfin, *Eleutheronema tetradactylum*, resulted from a high rate of self-recruitment in this species, in addition to limited adult movement. A similar scenario may be likely for *P. macrochir*, and requires further research. Alternately, transgenerational marking techniques, whereby gravid female fish are injected with an enriched isotope (e.g. Ba), which is eventually incorporated into the otolith of the embryonic fish (Thorrold et al. 2006; Almany et al. 2007), have been used to provide direct evidence of larval connectivity on coral reefs, and could potentially be used to provide unique direct empirical evidence of both the scaling of larval dispersal and level of population exchange within the Gulf of Carpentaria, although the feasibility of conducting such an approach on the scale of even an individual estuary remains untested.

In addition to movements among estuaries, the results of this study provide information on movement within estuaries. Despite having high overall classification success, suggesting little movement into other estuaries, fish from the Flinders River exhibited considerable variation in elemental profiles, in particular Ba, indicating that they had differing life histories and had occupied different parts of the estuary over the course of their lives. In this estuary, some fish appeared resident to areas with high ambient Ba, exhibiting consistently high (> 30 μmol $mol^{-1}$) otolith Ba signatures throughout their lifetime, others appeared transient, moving in and out of high Ba environments, and some had low Ba signatures, suggesting that they had spent these years in areas with low ambient Ba, most likely the downstream, polyhaline reaches of the estuary or adjacent coastal foreshores. Flexibility in movement patterns has

been reported in other studies examining otolith elemental data of estuarine and inshore fishes. Using a combination of Sr/Ba ratios and Sr isotopic composition, McCulloch et al. (2005) observed considerable flexibility in the movement of barramundi, *Lates calcarifer*, caught in freshwater, estuarine and marine environments near Townsville. Some barramundi exhibited an early-natal estuarine phase, with freshwater signatures apparent in the juvenile portion of their otoliths that gave way to a marine signature as they matured and migrated into marine environments, whereas others exhibited purely marine and estuarine signatures, suggesting that these fish had not entered freshwater at any stage of their life history (McCulloch et al. 2005).

In contrast to the variation observed in the Flinders River, otoliths of *P. macrochir* collected from the Fitzroy, Mary and Brisbane Rivers, on the east coast of Queensland, were found to have a consistent pattern of a relatively high Ba signature for their larval/early juvenile portion that decreased with ontogeny. Given the consistency of these results between estuaries, and considering Ba concentrations are generally higher in the mesohaline reaches of estuarine systems (Elsdon and Gillanders 2005), these data suggest that these fish likely moved from mesohaline estuarine conditions to more polyhaline conditions as they grew and matured. This hypothesis is consistent with fisheries independent sampling (B. Moore, unpublished data) in these systems, which indicate that smaller fish generally inhabit the upper reaches, while large adult fish are typically captured in the lower reaches. A similar downstream pattern of movement has been documented for another non-diadromous estuarine teleost, red drum, *Sciaenops ocellatus*, in estuaries along the Gulf of Mexico and Atlantic coast of Florida. Juvenile red drum are largely considered to occupy upper estuarine reaches, and move downstream into the coastal environment as they approach maturity at around three years of age (Beckman et al. 1988; Bacheler et al. 2009a; Bacheler et al. 2009b), with such movement considered to reflect changing salinity tolerances and/or diet and habitat preferences with age (Bacheler et al. 2009a).

It is unlikely the observed spatial patterns in otolith elemental signatures were confounded by temporal differences. Inter-annual variation in otolith elemental signatures has been documented in a number of studies, and may potentially confound spatial comparisons among sites that are sampled across different years. For example, Gillanders and Kingsford (2000) reported inter-annual differences in Mn, Sr and Ba signatures of trumpeter, *Pelates sexlineatus*, in estuaries in New South Wales. Similarly, Patterson et al. (1999) observed significant differences in Ba in otoliths of the Nassau grouper, *Epinephelus striatus*, among samples collected in two consecutive years. To reduce the effect of inter-annual differences in the present study, only fish from the 2005 year class were examined, and the same time period (i.e. juvenile to three years old) was considered for all otoliths, ensuring any differences

among otoliths could not be attributed to temporal differences in the time period when fish were alive or fish age.

In addition to inter-annual variability, intra-annual variability in otolith elemental signatures may also confound spatial comparisons, particularly for species with protracted spawning seasons, as has been suggested for *P. macrochir* on both the western and eastern coasts of Australia (Pember et al. 2005; Chapter 3). Cook (2011) observed significant increases in the concentrations of Mg, Pb, and U and significant decreases in Mn, Sr and Ba across the protracted spawning season of the garibaldi, *Hypsypops rubicundus*. Hamer et al. (2003) observed significant differences in the concentrations of Ba, Mn and Sr in otoliths of juvenile snapper, *Pagrus auratus*, across the February to March recruitment season in south-eastern Australia, yet found that such variability did not influence the classification accuracy of adult snapper to their juvenile origin. In the present study, considerable within-location variation was observed for otolith elemental signatures of the cores of fish from some locations, particularly the Fitzroy River, which may reflect intra-annual variation in ambient chemistry over the species' protracted spawning period. Additionally, the variability in otolith core signatures of fish from the Fitzroy River may be due in part to within-estuary variation. Elemental variation among sites within estuaries has been reported for several studies (Thorrold et al. 1998; Gillanders and Kingsford 2000). The estuarine reaches of the Fitzroy River contains numerous drainages of varying size (Long and McKinnon 2002), that may be expected to have different anthropogenic and terrigenous inputs of trace elements. However, regardless of the cause of such variation, a high classification success was observed for the core signatures of fish from this location (100%), suggesting that any differences within locations were of a much reduced magnitude compared to those observed among locations.

Although informative, the age-related approach used here places limitations on the interpretations that can be made regarding the timing of movement and exchange between spatially distinct groups, where apparent, and the connectivity of larval *P. macrochir* to adult populations. Although considerable similarity was observed in the elemental signatures of the core regions of fish from Eighty Mile Beach and Roebuck Bay, Lucinda and Townsville, and in Queensland's Gulf of Carpentaria, this does not necessarily indicate larval dispersal, but may reflect regional homogeneity in the factors affecting elemental deposition, or result from movement and mixing of fish at some point before capture. It may be that larval life history stages recruit to the nearest estuary to which they were spawned, and that homogeneity in core elemental signatures is facilitated by late juvenile or adult fish moving among locations.

Furthermore, despite the high classification success observed for the core region, particularly for some locations on the north-western and east coasts, it cannot be unequivocally concluded using the age-related profile approach that each fish caught at a

particular location originated from that specific location. Rather, the results suggest that fish caught at each location in these regions have a different natal origin to those caught from the other locations examined. Given the high degree of self-recruitment proposed for *E. tetradactylum*, and the increasing number of studies that have documented self-recruitment in estuarine species (North and Houde 2006; Tilburg et al. 2007; Braverman et al. 2009; Tilburg et al. 2010), it is considered likely that the natal origins of each population are proximate to the respective collection locations and result from self-recruitment of adult populations. Although more direct approaches, such as those in which otolith elemental signatures of larvae or early juveniles, which represent natal origins, are compared with those of adults of the same cohort (e.g. Gillanders 2002a), are required to identify the natal origins of the adults, the age-related approach employed in the present study nevertheless suggests limited exchange of *P. macrochir* among locations. The success of the age-related approach suggests that it provides a viable, albeit indirect, alternative to assessing patterns of connectivity, particularly for species in which collection of larval or early juveniles life history stages is not feasible, such as those that occur in geographically remote environments or for species whose larval and/or juvenile habitats are unknown.

The limited connectivity evident for *P. macrochir* suggests that the species is vulnerable to localised depletion, either through over-fishing or environmental perturbation, with reduction in any one area unlikely to be compensated for by immigration from other locations. The presence of fine-scale population structuring evident for all life history stages of *P. macrochir* should be considered when reviewing the management arrangements for this species, including the development of monitoring and assessment programs, and establishment of suitable fishery regulations.

# Chapter 6 Movement and connectivity of king threadfin, *Polydactylus macrochir*, in Queensland waters inferred from conventional tagging data

## 6.1 Introduction

Understanding patterns of movement and the degree of exchange of groups of marine species, or connectivity, is vital for managing harvested stocks, designing marine protected areas, and determining whether populations are open or closed (Begg et al. 1999a; Gillanders 2002a). Such knowledge is also fundamental to understanding the population dynamics and ecology of species, which will lead to a greater comprehension of their resilience, and possible responses, when faced with environmental change. However, for many estuarine fishes, the degree of connectivity is still poorly understood. With anthropogenic pressures on estuarine fishes projected to increase (Blaber 2000; Roessig et al. 2004), such knowledge becomes increasingly important so that effective management can be implemented.

Conventional tag-recapture methods can provide a powerful approach of determining connectivity. Recoveries of tagged individuals through time give point locations, from which an individual's range and movement, and subsequent population mixing and connectivity, can be inferred (Ihssen et al. 1981; Begg et al. 1997). These methods, however, can typically be constrained by cost and effort limitations, including the proportion of the population that the tagged individuals represent, the number of recaptures, and length of time at liberty of those individuals, and the distribution of tagging and recapture effort (Ward and Caton 1992). Such limitations are particularly relevant for species with wide-ranging distributions or those that undertake broadscale movements (Begg et al. 1997).

Cooperative tagging programs, whereby recreational anglers tag fish in collaboration with scientific researchers, offer an opportunity to reduce some of these limitations, by providing an efficient and cost-effective means of tagging large numbers of fish over a wide geographic area (Saul and Holdsworth 1992). In addition, data from cooperative tagging programs have been used to provide key information on growth and longevity, exploitation rates and mortality, and population or stock size (Francis and Francis 1992; Morton et al. 1993; Myers et al. 1997; Gillanders et al. 2001). Involving recreational fishers in tagging programs can also provide a number of additional community benefits and may promote responsible fishing and conservation ethics among anglers by encouraging the release of tagged fish (Matthews and Deguara 1992). In Australia, data from collaborative tagging studies conducted by researchers and members of recreational fishing organizations such as the Australian Sport Fishing Association (ANSA) have been used to provide valuable biological information for management for a number of species, including school mackerel,

*Scomberomorus queenslandicus*, and spotted mackerel, *S. munroi* (see Begg et al. 1997), swallowtail dart, *Trachinotus coppingeri* (see McPhee et al. 1999), and snapper, *Pagrus auratus* (see Sumpton et al. 2003).

In this chapter, tag-recapture data, obtained from the SUNTAG program of ANSA, were examined to explore the usefulness of cooperative tagging data to further test the hypothesis of limited connectivity of post-recruitment *P. macrochir* in Queensland waters. The information supplied in this chapter in compared against, and builds upon, that provided by other techniques, to thus achieve a more complete understanding of the species' ecology and population structure.

## 6.2 Materials and methods

### Tagging

A total of 3,718 *P. macrochir* were tagged by ANSA members and state fisheries researchers between January 1986 and September 2011. Tagging operations were undertaken in estuaries across Queensland's east coast and Gulf of Carpentaria waters (Figure 6.1). Fish were captured by anglers using rod and reel, and were tagged using predominantly dart or anchor tags, with a small number of individuals ($n$ = 18) tagged with loop tags. Tagging was conducted according to methods outlined in the AusTag Manual (www.info-fish.net). Tags contained a message requesting fishers to measure the fish and report the recapture to a freecall phone number. Length (TL and FL), date, location (SUNTAG grid reference) and fishers name were recorded both when fish were tagged, and when fish were recaptured. Recaptures were reported by both recreational anglers and commercial fishers. In cases where only one length variable was recorded (i.e. TL or FL), missing lengths were estimated from the relationship of TL and FL of Moore et al. (2011b), where TL = 1.1737FL + 22.083. Length information was typically not provided for *P. macrochir* recaptured by commercial fishers.

### Data analysis

To visualise movement patterns, maps of tagging and recovery locations were constructed using Google Earth (version 6.0.3). Movements were measured in Google Earth using the path tool and were delineated by the shortest water distance between the tagging and recapture locations. Movement paths were categorised into three types: no movement (i.e. fish remained within tagging grid), within-estuary movement (i.e. movement outside of tagging grid but within tagging estuary), and ex-estuary movement (including movements among estuaries). As the overall objective of this thesis was to examine connectivity among estuaries, the distance moved outside of the tagging estuary was measured from the estuary mouth for all individuals categorised as having undertaken 'ex-estuary' movements, as determined by Google Earth

imagery. As the tagging and recapture location data were provided as a SUNTAG grid reference (typically a 1 $km^2$ grid), measurements commenced and terminated at the closest water point to the middle of the tag/recapture grid and were rounded to the nearest km.

Recapture data were grouped into two regions: Gulf of Carpentaria and east coast, to examine regional patterns in movement. Lengths at tagging of recaptured fish were compared with lengths at tagging of all fish using unpaired *t*-tests to determine whether recaptured fish were representative of the total tagged population in each region. Length data were log transformed prior to analysis to correct for unequal variances. Recapture rates of dart and anchor tagged fish were compared for each region using a chi-squared ($\chi^2$) test.

The percentage of fish deemed to have undertaken each of the three movement types was calculated for each region, and were compared among regions using a 3x2 contingency table and $\chi^2$ test. Regression analysis was used to examine relationships between total distance moved, TL at tagging, and time at liberty for each region. Each dependant variable was log transformed prior to analysis, to normalise and minimise the variance of the data. The time at liberty and TL at tagging of fish deemed to have undertaken 'ex-estuary' movements were compared against those recaptured within their tagging estuary (i.e. including those categorised as having undertaken no movement) for each region using one-way analysis of variance (ANOVA). All data analyses were conducted using Statistica (v. 7.0).

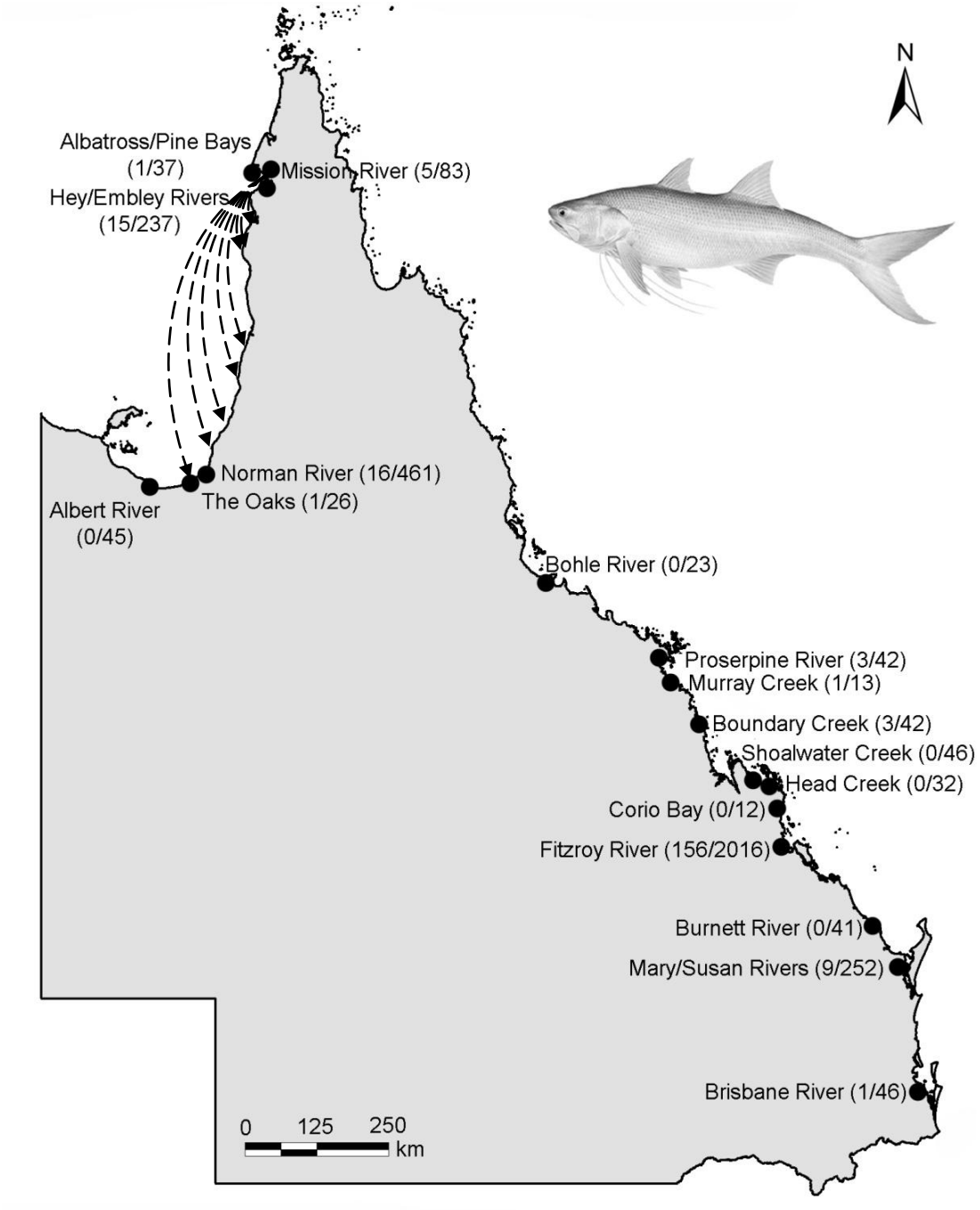


Figure 6.1 Locations where > 10 *Polydactylus macrochir* were tagged on the Queensland coast. Numbers in parentheses indicate number recaptured (regardless of recapture location) / total number tagged at location. Dashed lines represent movement paths of recaptured individuals that travelled ≥ 80 km from their point of release. *Polydactylus macrochir* image © R. Swainston http://anima.net.au

## 6.3 Results

### Summary statistics

A total of 239 tagged *P. macrochir* were recaptured, with 194 recaptures made on the east coast and 45 in the Gulf of Carpentaria. Recaptures were made between September 1986 and February 2011 on the east coast, and February 1990 and May 2010 in the Gulf of Carpentaria, and were made by both recreational anglers and commercial inshore net fishers. Recapture rates were 7.0% and 4.8% for the east coast and Gulf of Carpentaria regions, respectively. No significant difference was observed between recaptures rates of dart and anchor tagged fish on the east coast ($\chi^2 = 0.362$, d.f. = 1, $P = 0.548$), or Gulf of Carpentaria ($\chi^2 = 0.069$, d.f. = 1, $P = 0.793$), suggesting that recapture rates were not influenced by the type of tag used. There was insufficient information on the tagging or recapture location for 17 individuals, including 12 from the east coast and five from the Gulf of Carpentaria; hence these fish were removed from the dataset prior to analysis.

On the east coast, recaptured *P. macrochir* were significantly larger when they were initially tagged (542 $\pm$ 130 mm TL, mean $\pm$ s.d.) than were tagged fish that were not recaptured (518 $\pm$ 164 mm TL, mean $\pm$ s.d.) ($t = 2.768$, d.f. = 2828, $P = 0.006$). In the Gulf of Carpentaria, no difference was observed between the length of recaptured fish when they were initially tagged (666 $\pm$ 165 mm TL, mean $\pm$ s.d.) and tagged fish that were not recaptured (623 $\pm$ 158 mm TL, mean $\pm$ s.d.) ($t = 1.611$, d.f. = 884, $P = 0.108$).

The percentage frequency of fish that undertook each of the three movement types differed significantly among regions ($\chi^2 = 42.334$, d.f. = 2, $P < 0.05$). On Queensland's east coast, movements of *P. macrochir* were limited, with 96% of recaptures occurring within the same estuary in which fish were tagged. Of these, approximately 31% of fish were recaptured in the same grid where they were tagged, while a further 65% of fish were recaptured within the same estuary system in which they were tagged (Figure 6.2; Table 6.1). Only 4% of recaptures were made outside of the estuary in which fish were tagged. Movements within east coast estuaries ranged from 0 km to 65 km. There was a significant correlation between total distance moved and time at liberty ($r^2 = 0.83$, F = 16.147, d.f. = 1, 179, $P < 0.001$), and total distance moved and TL at tagging ($r^2 = 0.04$, F = 8.270, d.f. = 1, 178, $P = 0.005$) for *P. macrochir* tagged on the east coast (Figure 6.3; Figure 6.4). No relationship existed between time at liberty and TL at tagging in this region ($r^2 = 0.01$, F = 1.158, d.f. = 1, 178, $P = 0.283$).

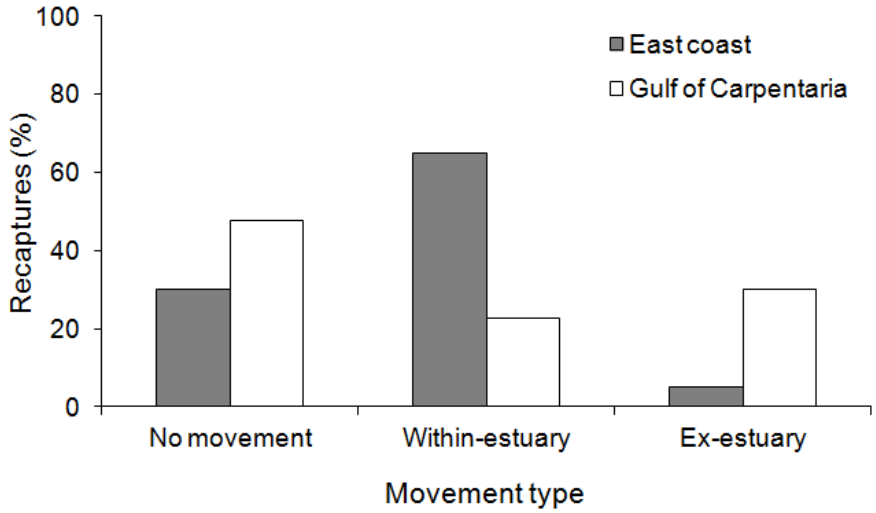


Figure 6.2 Percentage frequency of movement types of *Polydactylus macrochir* based on tag-recapture data.

In the Gulf of Carpentaria, the majority of recaptured individuals (70%) were recaptured within the same estuary in which they were tagged (Figure 6.2; Table 6.1). There was no relationship between total distance moved and time at liberty ($r^2 = 0.05$, F = 0.194, d.f. = 1, 38, $P = 0.662$) (Figure 6.3), with one individual being recaptured only 1 km away from its tagging location, despite being at liberty for 2,599 days. There was a significant relationship between total distance moved and TL at tagging ($r^2 = 0.31$, F = 17.149, d.f. = 1, 38, $P < 0.001$) (Figure 6.4). A significant negative relationship was observed between time at liberty and TL at tagging ($r^2 = 0.32$, F = 17.574, d.f. = 1, 38, $P < 0.001$), with larger fish being at liberty for fewer days than smaller individuals in this region.

Table 6.1 Distribution of distances moved by recaptured *Polydactylus macrochir* tagged in Queensland's east coast and Gulf of Carpentaria waters.

| **Distance moved (km)** | **Percentage of returns** | |
|---|---|---|
| | **East coast** | **Gulf of Carpentaria** |
| 0–10 | 76.4 | 70.0 |
| 11–20 | 7.1 | 5.0 |
| 21–40 | 11.0 | 5.0 |
| 41–100 | 5.5 | 2.5 |
| 101–300 | 0 | 5.0 |
| >300 | 0 | 12.5 |

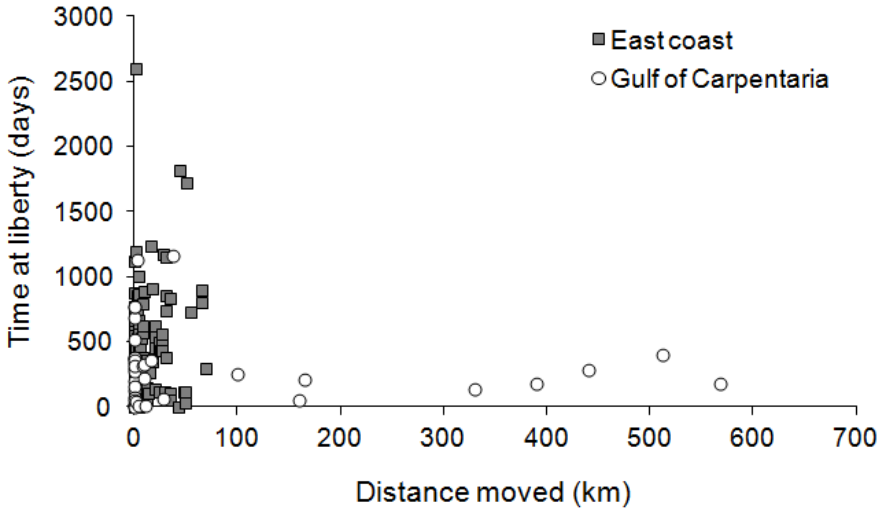


Figure 6.3 Distance moved and time of liberty of recaptured *Polydactylus macrochir* in Queensland's east coast and Gulf of Carpentaria waters.

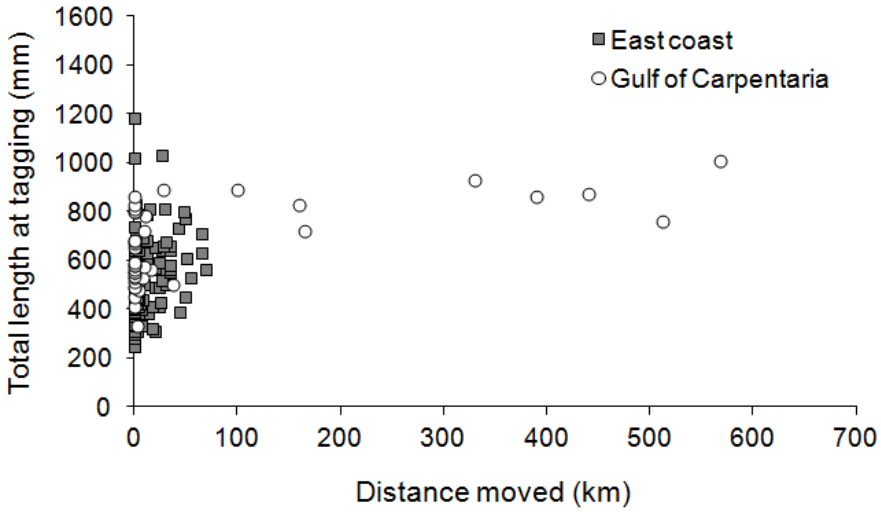


Figure 6.4 Distance moved and total length at tagging for recaptured *Polydactylus macrochir* in Queensland's east coast and Gulf of Carpentaria waters.

**Movement outside of estuaries**

A total of nine (4% of recaptures) and 12 fish (30% of recaptures) were deemed to have moved outside of their tagging estuary for the east coast and Gulf of Carpentaria regions, respectively. On the east coast, movements outside of tagging estuaries were limited, ranging from 1 km to 23 km from the estuary mouths (8.0 $\pm$ 7.2 km, mean $\pm$ s.d.), and were generally restricted to the associated coastal foreshores of the tagging estuaries. A slight, yet significant difference was observed between the time at liberty of fish that undertook 'ex-estuary' movements compared to those that were recaptured within the estuary in which they were

tagged, with fish recaptured in their tagging estuary being at liberty for a longer period (F = 4.099. d.f. = 1, 179, $P = 0.044$). No significant difference was observed between TL at tagging of fish that undertook 'ex-estuary' movements compared to those that were recaptured within the estuary in which they were tagged (F = 0.204, d.f. = 1, 180, $P = 0.652$).

Movements outside of tagging estuaries were more extensive in the Gulf of Carpentaria. While four of the 12 individuals moved $\leq$ 10 km from the mouth of their tagging estuary, eight individuals (20% of all Gulf of Carpentaria recaptures) undertook broad-scale movement, including one individual that moved from its tagging site in the Hey River in the north-eastern Gulf to 'The Oaks', at the mouth of the Flinders River in the south-eastern Gulf, a total distance of approximately 568 km (Figure 6.1). All eight individuals that undertook broadscale movements were tagged in the Hey/Embley and Mission River systems in the north-eastern Gulf and travelled in a southerly direction (Figure 6.1). Distances moved outside of tagging estuaries in this region ranged from 4 km to 552 km from the tagging estuary mouths (215.4 $\pm$ 207.6, mean $\pm$ s.d.). No significant difference was observed between time at liberty of fish that undertook 'ex-estuary' movements compared to those that were recaptured within the estuary in which they were tagged (F = 0.121, d.f. = 1, 38, $P = 0.730$). The mean TL of fish that moved outside of their tagging estuary was significantly larger than that of fish that were recaptured within their tagging estuary (F = 13.080, d.f. = 1, 38, $P < 0.001$).

## 6.4 Discussion

### Movement patterns

Movements of *P. macrochir* in Queensland's east coast and Gulf of Carpentaria waters were generally restricted, with the majority of recaptures occurring in the same estuary in which fish were tagged. These results support the notion that *P. macrochir* form a number of demographically-isolated populations, with limited dispersal of juvenile and adult fish among spatially-distinct estuaries.

While movement of *P. macrochir* outside of tagging estuaries was generally limited, particularly for individuals tagged on the east coast, a few individuals tagged in the Gulf of Carpentaria undertook large-scale movements, including one individual that moved approximately 570 km. A similar pattern of movement has been observed for *P. macrochir* in north-western Western Australia. In these waters, although approximately 80% of tagged *P. macrochir* were recaptured in the same location as they were tagged, five individuals moved greater than 400 km from their tagging location, including one individual that moved approximately 640 km (Sawynok 2005).

The differences in observed maximum movement outside of tagging estuaries between fish tagged on the east coast and the Gulf of Carpentaria likely reflect regional differences in

the occurrence of physical or physiological barriers to movement. The Gulf of Carpentaria is a largely continuous stretch of estuarine and coastal habitat characterised by turbid waters and sandy sediments (Somers 1994; Somers and Long 1994). Such features may facilitate the broadscale movement of individual *P. macrochir* observed in this region. In contrast, the east coast features a number of prominent rocky headlands and expanses of relatively clear waters and high energy beaches, which may form a barrier to movement of *P. macrochir*. Zischke et al. (2009) proposed a similar scenario for blue threadfin, *Eleutheronema tetradactylum*, on the east coast of Queensland, with parasite and conventional tagging data suggesting population structuring on the scale of individual embayments separated by rocky promontories.

The use of water currents for movement is well documented in fishes, and there is evidence to suggest that in addition to a lack of physical barriers, water currents may play a role in facilitating the broadscale movement observed for several tagged fish in the Gulf of Carpentaria. Notably, all of the tagged individuals that moved greater than 10 km outside of their tagging estuary in the Gulf of Carpentaria travelled in a southerly direction. Whilst fishing effort is typically higher in the south-eastern Gulf (DPI&F 2007), which may have biased the results, the directionality of these movements is consistent with summer water current patterns, which typically flow in a clockwise direction (Church and Forbes 1983; Forbes and Church 1983; Wolanski 1993). The clockwise summer current may facilitate the movement of *P. macrochir* throughout these waters, either directly, by minimising energy expenditure (Childs et al. 2008), or indirectly, through the movement of highly turbid waters. Campbell et al. (2010) report a similar pattern of movement for estuarine crocodiles, *Crocodylus porosus*, in the eastern Gulf of Carpentaria. Using acoustic tagging, these authors observed several individuals moving southwards with the prevailing long-shore current in the Gulf of Carpentaria. Further research into the timing of such broadscale movements are required to test this hypothesis for *P. macrochir*.

A positive relationship was observed between overall distance moved and TL at tagging, with greater movement generally undertaken by larger individuals, particularly in the Gulf of Carpentaria. Using estimates of length at sex change based on data of Garrett (1997) (B. Moore, unpublished data), it is likely that the largest movements were undertaken by female fish. Whether these reflect size-related influences such as decreased energetic costs of movement associated with larger size, increasing resource needs, or sex-specific differences in movement, is unclear. Ontogenetic increases in movement have been reported for a number of estuarine-associated species. Using conventional tagging data, Bacheler et al. (2009b) observed an increase in movement of red drum, *Sciaenops ocellatus*, in North Carolina waters, with larger age 4+ fish undertaking greater movements than smaller, younger individuals. Similarly, Knip et al. (2011) observed an increase in home range size with age class among

juvenile pigeye sharks, *Carcharhinus amboinensis*, in the nearshore waters of Cleveland Bay, Townsville. These authors hypothesised that the differences in home range were due to age classes being affected by different selective pressures, with younger, smaller juveniles potentially more influenced by predation risk, and older, larger juveniles more driven by resource acquisition.

Alternately, the greater movement observed for larger *P. macrochir* individuals may reflect sex-specific differences in movement. Like *P. macrochir*, many species of estuarine fishes are hermaphrodites, changing sex at some point in their lives (Sadovy de Mitcheson and Liu 2008). Although not empirically examined for any hermaphroditic estuarine fishes, gender-specific movements have been reported in other sex-changing species, and may play an important role in mediating patterns of movement and connectivity. For example, patterns of movement were found to differ between sexes in the protogynous California sheephead, *Semicossyphus pulcher*, with terminal phase females displaying less site fidelity and greater movement than initial phase males (Lindholm et al. 2010).

The limited movement evident for populations in the south-eastern Gulf of Carpentaria is consistent with investigations of otolith elemental signatures of fish in this region, which indicated limited movement among neighbouring estuaries (Chapter 5). In contrast to these results, analyses of mitochondrial DNA haplotypes (Horne et al. 2012), otolith stable isotope ratios (Newman et al. 2010), life history parameters (Chapter 3) and parasite assemblages (Chapter 4) found no evidence of spatial segregation of *P. macrochir* in this region. Whilst the small amount of broad-scale movement evident from the tagging data is likely sufficient to maintain genetic homogeneity in *P. macrochir* in this region, the limited movement evident from the tagging and otolith elemental data suggests that the observed similarities in otolith stable isotope ratios, life history parameters, and parasite assemblages likely reflect geographical similarities in the causal ecological and/or environmental mechanisms underlying each of these techniques, rather than broadscale mixing in this region. The apparent contradiction between the tagging and otolith elemental data and that of earlier research highlights the importance of using complementary approaches to discern the connectivity and population structure of fishes (sensu Begg and Waldman 1999).

In contrast to the limited movement outside of tagging estuaries, movements within tagging estuaries were extensive, with one individual tagged in the Fitzroy River moving 65 km within this system. These data suggest that *P. macrochir* form single, well-mixed populations within individual estuarine systems.

**Recapture rates, data assumptions and limitations**

The recaptures rates of *P. macrochir* are consistent with those of other collaborative tagging studies of teleost fishes conducted in Queensland's waters. McPhee et al. (1999) reported a recapture rate of 5.3% in their study into the movements of swallowtail dart, *Trachinotus coppingeri*, on the east coast of Queensland. Sumpton et al. (2003) reported an overall recapture rate of 7.7% in their study into the movements of snapper, *Pagrus auratus*, in Moreton Bay in south-east Queensland.

The non-reporting of recaptures is one of the major uncertainties and potential sources of error in collaborative tagging studies (Hilborn 1988). Despite the comparable recapture rates relative to other studies, there was a suggestion that non-reporting occurred from both the commercial and recreational fishing sectors in the present study. Some commercial and recreational fishers operating on the east coast claimed to discard recaptured tags owing to the belief that the ensuing information would benefit other fishers or a sector other than their own, or to their personal resentment of fisheries management or research. A similar scenario was observed by Begg et al. (1997) in their study into the movements of school mackerel, *Scomberomorus queenslandicus*, and spotted mackerel, *S. munroi*, in Queensland's east coast waters. Similarly, in their study on the movements and growth of monkfish, *Lophius piscatorius*, Laurenson et al. (2005) reported that approximately one-third of tag returns were reported by fish processors, indicating that fishers were either not observing the tags or not reporting tag recaptures. However, it is unlikely that the suggested non-reporting of tag returns in any one location influenced the results of the present study, given the general limited degree of movement consistently observed among all tagging locations.

Because tag returns came from the commercial and recreational fishing sectors, the limited movement of *P. macrochir* outside of tagging estuaries could potentially have been confounded by spatially heterogeneous fishing effort, with the distribution of recoveries more reflective of the spatial distribution of fishing, rather than being indicative of the true extent of movement. Furthermore, as data from conventional tagging is based on point locations of tagging and recapture, it may be that the pattern of movement is an under-representation of the total movement of *P. macrochir*, with fish travelling further between tagging and recapture than was evident from the data. Integrating the conventional tagging data with telemetric methods could be used to determine whether these issues confounded the results of the present study. For example, Bolle et al. (2005) used electronic transmitters to show that conventional tagging provided a reliable representation of movement of European plaice, *Pleuronectes platessa*, in the North Sea. Similarly, Bacheler et al. (2009b) observed consistencies in the timing and direction of movement of *S. ocellatus* tracked with ultrasonic transmitters and those tagged with conventional methods in a North Carolina creek. However, given the

consistency between the results of the present study data and the limited movement of *P. macrochir* evident from complementary approaches such as analyses of otolith elemental signatures (Chapter 5), it is considered that the tagging data offers a reliable representation of patterns of movement and connectivity of *P. macrochir*, and provides ideal baseline from which more specific hypotheses of movement can be tested using telemetric methods.

**Management implications**

The results of this study have important implications for the management of *P. macrochir*. The restricted movements and limited connectivity among estuaries suggests that the species is vulnerable to localised depletion, either through over-fishing or environmental perturbation, with reduction in any one area unlikely to be compensated for by immigration from other locations. These results contrast the current management arrangements for the species in Queensland's waters, whereby *P. macrochir* are managed as single, intermixing populations in the waters of each of the east coast and Gulf of Carpentaria regions. The presence of fine-scale population structuring suggests that the spatial scale of management, including the development of monitoring and assessment programs, harvest strategies and establishment of suitable fishery regulations, needs to be reviewed in order to recognise the potential for localised depletion.

Marine protected areas are now routinely established as an effective tool for protecting biodiversity, sustaining productivity of exploited species, and allowing for continued extractive uses of the marine environment (Jones et al. 2007; Botsford et al. 2009). Marine protected areas are particularly advocated for tropical systems, largely due to the fact that many of the developing nations that occur in tropical regions lack the human resources, infrastructure, and financial capacity to obtain accurate catch data required to implement more conventional management approaches used in the management of temperate fisheries (Adams 1998; Blaber 2002; Sale 2002). Fogarty and Botsford (2007) suggest that in order for MPAs to provide benefits to fisheries, they must meet one of two conditions: (1) there must be an increase in reproductive capacity and biomass within the MPA, and (2) the export of eggs and/or larval stages and/or the movement of juveniles or adults into areas open to harvest must be sufficient enough to increase yield or at least sustainability in fished areas. The limited movement outside of, and extensive movement within, individual river systems observed in the present study suggests that MPAs on the scale of individual estuaries will likely have a positive effect on local populations. Additionally, the moderate straying, or 'spill-over', of individual *P. macrochir* in the Gulf of Carpentaria could enhance fisheries in adjacent systems.

# Chapter 7 General Discussion

## 7.1 Overview

Understanding the degree of exchange between groups of a species, or connectivity, is fundamental to the effective management and conservation of aquatic species and ecosystems (Cowen et al. 2007). Connectivity, which may occur through the movement of all life history stages (Gillanders 2009), influences the distribution and abundance of organisms, rates of local adaption and speciation, the dynamics and persistence of populations, and the ability of ecosystems and species to recover from disturbance (Slatkin 1987; Cowen et al. 2000; Swearer et al. 2002; Hastings and Botsford 2006; Cowen and Sponaugle 2009). As such, knowledge of patterns of connectivity of a species is critically important in establishing effective harvest regimes and in the design of alternative management tools such as marine reserves or marine protected areas (MPAs). However, despite this fundamental requirement, the degree of connectivity of many estuarine fishes is poorly understood, particularly in tropical systems (Secor and Rooker 2005; Jones 2006; Gillanders 2009). With anthropogenic pressures in the form of increased fishing pressure, habitat modification and climate change on tropical estuarine-dependent fishes projected to increase (Blaber 2000; Roessig et al. 2004), understanding patterns of connectivity becomes increasingly important so that effective management can be implemented.

This thesis sought to fill this void by providing one of the first empirical assessments of connectivity of a tropical, non-diadromous estuarine teleost, using the king threadfin, *Polydactylus macrochir*, as a focal species. By adopting a multidisciplinary approach, incorporating analyses of life histories, parasite assemblages, otolith elemental signatures, and conventional tagging data, combined with concurrent research examining population genetics and otolith stable isotopic ratios, it provides empirical evidence of the patterns of connectivity of the focal species across multiple spatial, temporal and ontogenetic scales. Ultimately, the findings of this thesis contribute to global literature to further our understanding of the general patterns and processes governing dispersal and connectivity of estuarine fishes, and fishes in general. A synthesis and discussion of this research, and its implications for future studies of connectivity and management of tropical estuarine fishes and fishes in general, is provided in the next section, followed by a discussion of specific management implications and key future research priorities that have arisen as a result.

## 7.2 Integration of the methodological approaches

In general, there was a high degree of concordance among the results of the different methodological approaches, with the pattern evident in one technique largely repeated by another. For example, samples from Derby, Chambers Bay and the Fitzroy River had distinct life histories (Chapter 3), parasite assemblages (Chapter 4) and otolith elemental signatures for all life history stages examined (Chapter 5) compared to all other locations, indicating they form discrete populations, with limited exchange of either larval or post-larval life history stages to other locations. Tagging studies in Queensland (Chapter 6) and Western Australia (Sawynok 2005) corroborate these results, with *P. macrochir* undertaking limited movement outside of estuaries in which they were tagged. By direct contrast, samples from Lucinda and Townsville, although not included in the otolith isotope or genetic analyses of Newman et al. (2010) and Horne et al. (2012), exhibited similar life histories, parasite assemblages and otolith elemental signatures for all age groups. While the consistency of these results imparts a greater degree of confidence to a single population hypothesis than any one technique used in isolation, it is important to note that such similarities do not unequivocally prove the existence of a single, intermixing, population between these locations, but rather fail to falsify a null hypothesis of a single population (Waldman 1999). Indeed, tagging data for the east coast suggest it is unlikely there is extensive movement of post-larval fish over this spatial scale (approximately 100 km), although it is noted that there were only low numbers of tag returns from this region.

Minor inconsistencies among techniques were observed among several other locations that warrant discussion. Fish from the Mary and Brisbane Rivers were found to have a similar life history, yet differed in parasite assemblages and otolith elemental signatures across all ages, suggesting that they are geographically isolated throughout their life history, a result that was supported by the tagging data, at least for post-larval life history stages. Although no difference was observed in parasite assemblages between samples from the Roper River and estuaries within Queensland's Gulf of Carpentaria, these locations differed in life history parameters and otolith elemental signatures for all life history stages examined, suggesting little mixing of any life history stage among these locations. Samples from Eighty Mile Beach and Roebuck Bay differed in life history traits, yet exhibited similar parasite assemblages, otolith elemental profiles, otolith isotope ratios (Newman et al. 2010) and mtDNA haplotypes (Horne et al. 2012), suggesting a degree of connectivity among these locations.

A more complex population structure was observed for samples from Queensland's Gulf of Carpentaria. In this region, no difference was observed in otolith larval elemental signatures among any locations. With respect to post-larval fish, samples from the Wenlock River, in the north-eastern Gulf, exhibited different back-calculated mean length-at-age 2

estimates and parasite assemblages, suggesting limited exchange of post-larval life history stages to other Queensland Gulf locations. Although no difference was observed in parasite assemblages, otolith isotopic ratios (Newman et al. 2010) or mtDNA haplotypes (Horne et al. 2012) of post-larval fish from locations within the south-eastern Gulf of Carpentaria, the life history data and otolith elemental data of age groups 1–3 showed some differences among locations, with fish from the Kendall River exhibiting larger back-calculated mean length-at-age estimates than elsewhere, and Flinders River fish exhibiting significantly different otolith elemental signatures to those from nearby estuaries. The spatial separation of post-larval fish within these regions was further supported by the tagging data in Chapter 6, which indicated few post-larval fish moved out of the estuary in which they were tagged. These contrasting results observed among techniques highlights the benefits of using complementary approaches to discern population structure and connectivity of fishes, in that it effectively maximises the likelihood of identifying spatially-discrete groups (sensu Begg and Waldman 1999).

While the general lack of differences observed in the parasite and otolith elemental and isotopic ratio data among samples from Queensland's Gulf of Carpentaria may reflect homogeneity in the environmental (e.g. temperature, salinity) and ecological (e.g. diet) conditions experienced within this region, several possible explanations occur for the homogeneity in mtDNA haplotypes observed for the region by Horne et al. (2012). First, the differences observed may be a function of the different intrinsic time scales of the techniques employed. Genetic markers typically reflect patterns of connectivity over broad temporal scales, whereas otolith elemental signatures typically provide information over an individual fish's entire life history or part thereof (Begg and Waldman 1999; Gillanders 2002b). As such, it may be that fish from these estuaries have had insufficient time to develop sufficient genetic differentiation. The present-day Gulf of Carpentaria is a relatively young body of salt water that only became marine approximately 9,000 years ago (Harris et al. 2008). Given the relatively recent colonisation of this region it may be that spatially-isolated populations have had insufficient time to diverge into monophyletic assemblages. This would seem unlikely, however, as genetic heterogeneity has been observed in several other teleost species within these waters, including the confamilial blue threadfin, *Eleutheronema tetradactylum* (see Horne et al. 2011), and barramundi, *Lates calcarifer* (see Salini and Shaklee 1988; Shaklee et al. 1993).

More likely is that the genetic homogeneity in this region results from the dispersal of egg and larval stages, and/or from the few individuals that were observed to undertake large-scale movements from the tagging data. While the similarities observed in the larval/early juvenile otolith elemental signatures evident among locations in Queensland's Gulf of Carpentaria do not necessarily reflect larval mixing, for reasons discussed in Chapter 5, the

broadscale movement of a few individuals from the tagging data in this region (Chapter 6), is likely sufficient to maintain genetic homogeneity (Slatkin 1987). Under this scenario, it is likely that *P. macrochir* assemblages in this region operate as a metapopulation, or series of largely discrete, local populations, connected by a degree of non-trivial movement that is neither so low as to negate significant demographic connectivity, nor so high as to eliminate independence of local population dynamics (Kritzer and Sale 2004; Sale et al. 2006). Given the differences observed in life history among fish from Eighty Mile Beach and Roebuck Bay, a similar scenario is likely among these locations. In further support of a metapopulation structure for *P. macrochir* in Queensland's Gulf waters, Horne et al. (2012) observed deep genetic variation between their samples and those examined by Chenoweth and Hughes (2003) collected approximately 10 years earlier, but found little variation amongst spatially-distinct samples collected in consecutive years. Horne et al. (2012) suggests that the occurrence of temporal, but not spatial, genetic structuring in *P. macrochir* across locations in Queensland's Gulf of Carpentaria indicates that the change in genetic signature in these populations has occurred as a unit over time, suggesting demographic interdependence among locations.

## 7.3 Factors influencing population connectivity in tropical estuarine fishes

The spatial scale at which sampling was conducted in this thesis allows insight into the general mechanisms that facilitate or impede connectivity of *P. macrochir*, thus furthering discussion and evaluation of the key factors influencing dispersal and connectivity in tropical estuarine fishes, and estuarine fishes in general. It is likely both biological and physical processes, acting on both larval and post-larval (i.e. juvenile and adult) life history stages, play a role in mediating the observed patterns of connectivity of *P. macrochir* across northern Australia.

### Processes affecting larval life history stages

Historically, the timing and location of spawning have been considered to play a fundamental role in mediating patterns of dispersal or retention of larvae of fishes, and hence connectivity of these life history stages, by affecting their initial spatial and temporal placement (Hare and Cowen 1993; Begg et al. 1999b). Although spawning at estuary mouths, as observed for *P. macrochir* on the east coast of Queensland (Chapter 3), has historically been proposed to facilitate dispersal for some estuarine fishes (e.g. *Acanthopagrus berda* (see Garratt 1993)) due to passive transport of eggs and larval stages away from natal estuaries by tidal currents, a growing number of recent studies have documented local larval retention in species that similarly spawn in the lower reaches of estuaries (e.g. Sponaugle et al. 2002; Botton and Loveland 2003; North and Houde 2006; Tilburg et al. 2007; Braverman et al. 2009; Tilburg et al. 2010). It is now well recognised that larvae of many species are not passive particles, but

have strong sensory, orientation and swimming abilities (Clark et al. 2005; Gerlach et al. 2007; Leis et al. 2009), Used in conjunction with local water currents and eddies that typically form around estuaries (Brown et al. 2005), such abilities are capable of influencing dispersal trajectories to remain near natal estuaries (Leis 2006). Recently, strong selection for local larval retention has been hypothesised for fishes that live in spatially-fragmented seascapes such as estuaries, as the chances of finding suitable settlement habitat are greatly reduced if larvae disperse away from the parental population (Swearer et al. 2002). While the methodologies used in this thesis preclude conclusions regarding local larval retention of the study species, there is some evidence to suggest local larval retention may occur. The differences in larval otolith elemental signatures and mtDNA haplotypes observed for most locations across north-west and northern Australia, and on Queensland's east coast, suggest that along with limited adult movement, there is limited dispersal, and potentially local retention, of *P. macrochir* larvae at these locations. Furthermore, although little is known of the sensory and swimming abilities of *P. macrochir* larvae, these life history stages appear to settle exclusively in estuaries (Halliday et al. 2008), suggesting that they may be able to locate these systems, orientate themselves and take directed movements. Sensory-guided behaviour of pelagic larvae has been suggested for other tropical estuarine-associated fishes, namely the confamilial blue threadfin, *E. tetradactylum*, and the leioganthid *Leiognathus equulus* (Leis et al. 2009). When released in open water, larvae of these species initially swam in circles, potentially in an attempt to detect olfactory cues from settlement habitats (Leis et al. 2009). Such behaviour may indicate orientation towards estuaries, therefore facilitating larval retention in areas of suitable habitat. Supporting this hypothesis, Horne et al. (2011) observed fine-scale genetic structuring in *E. tetradactylum*, including among locations separated by as little as 15 km. For such differentiation to occur there must be limited dispersal and fine-scale retention of egg and larval stages, in addition to limited movement of juvenile and adult fish. These results suggest that local retention of larvae may be a feature of some tropical estuarine-associated fishes. Assuming that tropical estuarine fishes are able to detect olfactory cues from estuarine habitat, as suggested for *E. tetradactylum* and other estuarine-associated fishes (James et al. 2008; Leis et al. 2009), it may be that responding to generic, rather than natal, estuarine odour is adequate to facilitate their recruitment to suitable habitat, similar to that proposed for some coral reef fishes (Gerlach et al. 2007). Quantification of the behaviour of larval stages of tropical estuarine fishes, and the spatial scale at which larval dispersal/retention operates, is critical to further understanding of the patterns of connectivity of this group, and requires further research.

The duration of the pelagic larval stage has historically been considered to be a key mediator of connectivity of fishes (Roberts 1997; Cowen et al. 2006). Generally, species with

long-lived pelagic larval stages are considered to have high dispersal capabilities (Cowen and Sponaugle 2009). Although little is known of the pelagic larval duration of *P. macrochir*, young-of-the-year juveniles have been observed in estuaries on the east coast of Queensland during the peak spawning period in December (Ian Halliday, pers. comm.), suggesting the pelagic larval duration in this species may be brief, further accounting for the limited dispersal of larval *P. macrochir* evident for most locations. This hypothesis is consistent with the few estimates of pelagic larval duration available for other estuarine-associated fishes with similarly restricted patterns of connectivity. Observations of cultured *E. tetradactylum*, a species which exhibits fine-scale structuring and limited connectivity (Horne et al. 2011) suggest the species can reach approximately two-thirds of the maximum larval length of 30 mm in 16–27 days (J. Leis, pers. comm.). Similarly, metamorphosis of barramundi, *L. calcarifer*, again demonstrated to exhibit fine-scale population structuring (Shaklee et al. 1993), from larvae to juveniles has been reported to occur when fish are approximately 18 days old (Barlow et al. 1995). The consistency of these results suggests that relatively short pelagic larval durations may be a feature of some tropical estuarine fishes, potentially resulting in fine-scale dispersal and limited connectivity of these life history stages. Assessment of the duration of the pelagic larval stage in additional species is requirement to test this hypothesis.

**Processes affecting post-larval life history stages**

As discussed in Chapter 6, the greater broadscale movement of a few tagged *P. macrochir* in the Gulf of Carpentaria observed in the present study compared to those tagged on the east coast likely reflects the lack of physical barriers to movement in the Gulf. The presence of zoogeographic barriers, such as rocky headlands and promontories, has been frequently cited as a key factor affecting connectivity of estuarine and coastal fishes. For example, Schaffler et al. (2009) concluded that Cape Hatteras formed a significant barrier to latitudinal recruitment of Atlantic croaker, *Micropogonias undulatus*, to estuaries on the eastern coast of the United States. Zischke et al. (2009) proposed a similar scenario for blue threadfin, *E. tetradactylum*, on the east coast of Queensland, with parasite and conventional tagging data suggesting population structuring on the scale of individual embayments separated by rocky promontories. The consistency of the results of the present study with those of other studies further confirms the limiting influence of zoogeographic barriers on patterns of movement and connectivity of estuarine and coastal fishes.

However, while the presence of such barriers likely act to restrict connectivity of estuarine fishes, the results of the present study suggest that the absence of barriers, and, in turn, the presence of suitable habitat corridors, do not necessarily promote broadscale connectivity among tropical estuaries. The broadscale movement of a few tagged individuals

in the eastern Gulf of Carpentaria observed in Chapter 6 supports this hypothesis, in that it demonstrates that even though broadscale movement in this region is physically possible, such movements are only undertaken by a small proportion of the population. Significantly, the limited exchange among estuaries observed for post-larval *P. macrochir* is consistent with the few studies that have examined movements of tropical, non-diadromous estuarine fishes. In the study of Sheaves et al. (1999), none of the 962 *Acanthopagrus berda* tagged in creeks in the Hinchinbrook Channel, Queensland, were found to have moved to nearby creeks. Similarly, examination of mitochondrial and microsatellite loci (Horne et al. 2011), whole otolith isotope ratios (Newman et al. 2011) and parasite assemblages (Moore et al. 2011a), conducted concurrently with the present study, revealed fine-scale site fidelity in *E. tetradactylum*, with differences evident for some methods estuaries separated by as little as 15 km in the Gulf of Carpentaria. The consistency of these results suggests that limited connectivity of post-larval stages may be a feature of some tropical non-diadromous estuarine fishes, even where adjacent habitat appears conducive to movement.

The limited connectivity observed in the present study and above examples implies that rather than being mediated by factors outside of estuaries, the limited exchange of juvenile and adult fish among tropical estuaries may reflect the benefits offered by these environments, most notably food availability and greater protection from predators. Movement among spatially-discrete habitat patches, such as estuaries, is energetically expensive, and typically renders organisms more susceptible to predation (Dingle 1996; Dodson and Godin 1997). Thus to be evolutionarily advantageous, the benefits of movement, be they environmental, trophic or reproductive, must ultimately outweigh the associated costs. Tropical estuaries are inherently productive ecosystems, typically supporting greater biomass and diversity of aquatic organisms than their associated coastal foreshores or temperate counterparts (Day et al. 1981; Blaber et al. 1989; Blaber et al. 1995; Blaber 2000). In addition, tropical estuaries are typically highly turbid and thermally stable environments (Blaber 2002). As such, there may be little requirement or overall benefit for fishes to move among estuaries. In the case of *P. macrochir*, it is likely that due to the highly productive nature of tropical estuarine systems (Blaber 2002), the species' generalist diet (Brewer et al. 1995; Salini et al. 1998), high degree of euryhalinity proposed for all life history stages of the species (Chapter 2) and overlap in distribution of males and females (Chapter 3), there may be little requirement or advantage for an individual to move among estuaries once recruited to a particular estuary. Examination of additional tropical estuarine species, and the mechanisms influencing their connectivity, is required to further test this hypothesis.

The observation of a positive relationship between total distance moved and TL at tagging for *P. macrochir* tagged in the eastern Gulf of Carpentaria indicates that the

movement and home range of *P. macrochir* in this region increases with ontogeny. Similar patterns of ontogenetic increases in movement have been reported for a number of estuarine-associated species, and have been suggested to result from an increase in resource needs, or greater protection from predators, associated with a larger body size (Taylor et al. 2006; Bacheler et al. 2009b; Knip et al. 2011). To meet greater resource needs of a larger individual, larger *P. macrochir* may range further than smaller individuals to obtain larger-sized or a greater amount of prey items. Alternately, larger size may offer greater protection from predators, thus enabling greater movement (Sogard 1997; Harter and Heck 2006). As such ontogenetic patterns in movement likely have a significant influence on connectivity, these results demonstrate that consideration of life history stage and ontogenetic effects are fundamentally important in studies examining population connectivity of fish species.

An alternative explanation for the apparent increase in movement and connectivity with ontogeny observed for *P. macrochir* in the Queensland's Gulf of Carpentaria in the present study is that such increases may reflect sex-specific differences in movement. Due to the protandrous life-history of *P. macrochir*, the largest individuals are typically females. Although sex-specific differences in movement have not been empirically examined for any hermaphroditic estuarine fishes, such phenomena have been reported for sex-changing fishes in other environments, and may play an important role in mediating patterns of movement and connectivity in these instances. For example, Lindholm et al. (2010) observed sex-specific differences in movement patterns of the protogynous California sheephead, *Semicossyphus pulcher*, among rocky reefs of Anacapa Island, California, with terminal phase males undertaking greater movement than initial phase females. Whether such differences reflect true gender-mediated differences, or are merely an artifact of the larger size of the secondary-sex individuals, is unclear. However, in the present study, a similar increase in movement among estuaries with body size was not observed for tagged *P. macrochir* on Queensland's east coast, indicating that such movements are only possible where physical factors permit. Irrespective of the causal mechanisms, the observation that larger *P. macrochir* individuals undertook the greatest overall movements on both the east coast and Gulf of Carpentaria regions has important implications for connectivity and fisheries management. As fishing pressure is typically biased toward the larger, older individuals of a population (Hilborn and Walters 1992), removal of larger individuals of hermaphroditic species may decrease connectivity between spatially-distinct groups, thus limiting replenishment or gene flow among neighbouring populations, and increasing the susceptibility of local populations to depletion.

## 7.4 Implications of this study

### Implications for future studies examining connectivity of fishes

The results of this study have several important implications for future research into connectivity of both estuarine fishes and fish populations in general. While the multidisciplinary approach employed in this thesis is being increasingly adopted by fish biologists for the purposes of stock identification (e.g. Ayvazian et al. 2004; Buckworth et al. 2007; Abaunza et al. 2008b), there are few examples adopting such approaches in the connectivity literature (Thorrold et al. 2002). The ability of some techniques (e.g. comparisons of otolith elemental signatures and tagging data) to discriminate among estuaries in the south-eastern Gulf of Carpentaria in the present study while others (e.g. parasite assemblages, otolith isotope ratios) provided little spatial differentiation demonstrate the advantages of using multiple complementary methodologies to determine connectivity. By maximising the opportunity to detect differences among samples, the use of multiple complementary techniques provides greater power in the detection of connectivity patterns than any one approach used in isolation (Begg and Waldman 1999; Waldman 1999). Future studies examining connectivity in fishes will likely benefit from this approach.

Upon advocating a multidisciplinary approach to assessing connectivity, it is pertinent to discuss what techniques should be used to determine patterns of connectivity. In the present study, no one technique used in isolation provided the most complete understanding of connectivity of the study species. These results are consistent with previous studies that have used multiple complementary methods for determining the stock structure of exploited fishes (e.g. Begg 1996; Abaunza et al. 2008b). For purposes of fish stock identification, Waldman et al. (1988) concluded that the best overall discrimination occurred for a combination of techniques that vary substantially in the type of variation that is measured, while Begg and Waldman (1999) recommend the use of at least a genetic procedure and at least one phenotypic-based approach such as comparisons of otolith chemistry or parasite assemblages. Ultimately, the choice of complementary techniques used to determine connectivity largely depends on the questions being asked, and the life history stage for which connectivity is being assessed (Begg and Waldman 1999; Bergenius et al. 2005). For example, if the research objective was to examine patterns of gene flow in a species, genetic techniques, such as comparisons of nuclear and mtDNA haplotypes, should be examined. However, genetic techniques may be unable to identify differences between recently isolated groups, and frequently do not provide information at demographically-relevant scales required for fisheries management and conservation purposes, such as the design of marine protected areas (Grosberg and Cunningham 2001; Hellberg et al. 2002; Botsford et al. 2009). In these

instances, tagging approaches and examination of otolith elemental signatures or parasite assemblages may be more suitable. Similarly, while tagging methods may be suitable for examining connectivity of late juvenile or adult life history stages, they can be problematic for quantifying connectivity of larval or early juvenile life history stages to adult populations due to the small size, high abundance, delicate nature, and high rate of mortality of these life history stages (Gillanders 2002a; Thorrold et al. 2002). Alternate approaches, such as examination of otolith elemental signatures or parasite assemblages, have been shown to be particularly suitable for assessing connectivity of these life history stages (e.g. MacKenzie 1985; Swearer et al. 1999; Gillanders 2002a; Schaffler et al. 2009).

The results of this study add to the growing body of literature demonstrating that the scale and pattern of connectivity can vary significantly across a species' range. Such findings have important implications for studies of connectivity and management of aquatic species, in that they highlight the importance of assessing movement and connectivity across either a species' entire distribution, or the specific geographical location relevant to the management questions being asked of a species, rather than inferring connectivity based on studies conducted elsewhere within a species' distribution. The differential degrees of connectivity observed over similar spatial scales within the different study regions suggests that spatially-relevant management practices adopted in any one region may not be applicable across a particular species' entire distribution. For example, the metapopulation structure proposed for *P. macrochir* between Eighty Mile Beach and Roebuck Bay, or within Queensland's Gulf of Carpentaria, has different management implications to those for closed populations such as those from the Fitzroy, Mary or Brisbane Rivers on Queensland's east coast. Ultimately, inferring a degree of 'openness' for closed populations would likely over-estimate the resilience, and thus under-estimate the risk, of such populations to localised depletion.

A limiting factor of this study was a lack of standarised sampling with respect to both fish age and year of sample collection, particularly for samples collected from locations in Queensland's Gulf of Carpentaria and the Northern Territory. Samples from locations within these regions were largely collected opportunistically from commercial fishers, which resulted in samples from different locations being collected in different years, or comprising fish from different age or year classes. As temporal variation in life histories, parasite assemblages and otolith elemental signatures has the potential to confound spatial patterns among sites (MacKenzie 1987; Begg et al. 1999b; Gillanders and Kingsford 2000), considerable effort was made to reduce the influence of temporal variation on the spatial comparisons, such as examining individuals from the 2005 year class only (the year-class that was common to the greatest number of locations and provided the largest sample sizes) for comparisons of back-calculated length-at-age 2 or otolith elemental signatures. This reduced the sample sizes

available for these analyses, and resulted in some locations (e.g. Staaten River) being excluded from these comparisons, due to low sample sizes from this year class. Future studies examining connectivity would benefit from targeted and standarised sampling among locations.

**Implications of a changing climate**

Climate change will likely have a significant impact on patterns of movement and connectivity of *P. macrochir* and other tropical estuarine fishes that exhibit similar patterns of movement and connectivity. Broadly speaking, increasing ocean temperatures and changing weather patterns are projected to change the speed and direction of water currents, which has the potential to alter estuary morphologically, disrupt larval dispersal pathways, and hence influence patterns of connectivity, of tropical estuarine fishes (Cowen and Sponaugle 2009; Gillanders et al. 2011). In addition, elevated $CO_2$ levels have been shown to affect the olfactory system of some marine fishes, rendering them unable to distinguish between ecologically important chemical cues (Munday et al. 2009). Assuming that *P. macrochir* and other tropical estuarine fishes are able to detect olfactory cues from estuarine habitat, such effects may result in larvae recruiting to inappropriate habitats, greatly reducing the chances of connectivity and population replenishment (Munday et al. 2009; Pankhurst and Munday 2011).

Climate change also has the potential to influence movement of post-larval assemblages of tropical estuarine fishes. Under the current CSIRO Mk 3.5 Climate Model, a general decrease in rainfall is expected across northern Australia, with reductions particularly evident for the Gulf of Carpentaria and north-west Western Australia, where reductions in annual mean rainfall of 20–25% relative to the year 2000 are predicted (Okey and Poloczanska 2008; Gordon et al. 2010). Changes in rainfall are expected to lead to a reduction in the amount of river run-off flowing into the coastal environment (Okey and Poloczanska 2008), thus leading to reductions in inshore turbidity levels. Additionally, projected increases in land temperatures are expected to result in greater evaporation in freshwater systems thus leading to a decrease in run-off into estuarine and inshore environments, further reducing inshore turbidity levels (Hobday and Lough 2011). Given that turbidity is hypothesised to be a significant factor mediating patterns of connectivity of post-larval *P. macrochir*, reductions in turbidity in these regions will likely result in alterations to the patterns observed here, further isolating *P. macrochir* at local spatial scales.

Climate change may also significantly impact the demography of *P. macrochir*, and other tropical estuarine fishes. There is growing evidence to suggest that the demography of estuarine fishes is strongly linked to the environmental conditions of the estuaries in which

they reside, with positive associations between environmental factors such as freshwater flow and CPUE (as a proxy for population abundance), growth and year-class strength reported for several species (Staunton-Smith et al. 2004; Bonvechio and Allen 2005; Robins et al. 2006; Halliday et al. 2008; Gillson et al. 2009). Halliday et al. (2008) documented significant positive relationships between spring and summer freshwater flow and year-class strength for *P. macrochir* in Australian waters, which these authors hypothesised likely resulted from greater food availability, an alteration of energy budgets in areas of decreased salinity, and/or a reduction in predation, with turbid waters enhancing juvenile survival rates. Given this association, a reduction in rainfall, and therefore freshwater flow, particularly over spring and summer, is likely to result in reduced survivorship of juvenile *P. macrochir*. In addition, whilst not empirically examined for *P. macrochir*, body condition and growth of a number of estuarine fish species has been shown to be positively associated with freshwater flow (e.g. Robins et al. 2006; Dolbeth et al. 2010). As survival rates of fishes are generally positively associated with body condition (Hare and Cowen 1997; Holmes and McCormick 2009; Duffy and Beauchamp 2011), a reduction in flow may result in fewer *P. macrochir* surviving to maturity. Given that smaller fish produce fewer eggs, reductions in condition and growth will also likely reduce the reproductive output of mature individuals, ultimately leading to reductions in the number of *P. macrochir* that survive to recruitment. Projected sea-level rise and increased storm events are expected to considerably reduce the extent of mangrove and seagrass habitat across northern Australia, particularly where landward migration is not possible (Okey and Poloczanska 2008; Gillanders et al. 2011), further exacerbating the effects on fish growth and reproduction, due to reductions in abundance of prey items. For example, in March 1985 Cyclone Sandy destroyed approximately 20% (183 $km^2$) of the seagrass beds in the Gulf of Carpentaria (Rothlisberg et al. 1988; Poiner et al. 1989). Following the loss of these nursery habitats, there was a reduction in the offshore catch of penaeid prawns in the region (Poiner et al. 1993). As penaeid prawns represent a significant part of the diet of *P. macrochir* (see Brewer et al. 1995; Salini et al. 1998), a reduction in prawn biomass resulting from more intense cyclone events may further compromise growth and survival of *P. macrochir*.

**Management implications**

The results of this study have important implications for the management of tropical estuarine fishes and, more specifically, for the management of *P. macrochir*. Broadly, the results of the present study add to the growing body of evidence that suggest that populations of many fish species are far more structured than previously thought (Swearer et al. 1999; Thorrold et al. 2001; Clarke et al. 2009). Such findings indicate that the spatial scale of management of many

marine resources, including the development of monitoring and assessment programs, harvest strategies and establishment of suitable fishery regulations, need to be reviewed to recognise the observed fine-scale demographic population structuring, and highlight the need for more research to facilitate further understanding of population structure and connectivity of aquatic organisms.

*Implications for the management of Polydactylus macrochir*

More specifically, the results of this study have a number of important implications for the management of *P. macrochir*. The limited connectivity observed for *P. macrochir* is in contrast to that currently assumed for management purposes. *Polydactylus macrochir* are currently managed as single populations, or stocks, in the waters of each of Western Australia, the Northern Territory, Queensland's Gulf of Carpentaria and Queensland's east coast, with different management strategies adopted within each region. For example, the current minimum legal length for the retention of *P. macrochir* is 60 cm TL in Queensland, 45 cm TL Western Australia, while there is no minimum legal length in the Northern Territory. The limited connectivity evident for *P. macrochir* across most locations suggests that the species is vulnerable to localised depletion, as the size of the spawning component in each local population directly affects recruitment to that population. As such, reduction in any one area is unlikely to be compensated for by immigration from other locations. For most locations, *P. macrochir* would benefit from fine-scale management actions, to account for the limited movement and complex population structure of the species. While this would be best addressed at a local (i.e. individual estuary) level, given the limited connectivity among estuaries, implementing catch and effort controls at this scale is unlikely to be feasible, and it may be more practical to apply management practices at regional scales, providing a trade-off between the disconnect of current management arrangements and fine-scale spatial structuring observed in the present study.

Within Queensland's Gulf of Carpentaria, the identification of spatially-distinct post-larval assemblages that may be connected by larval dispersal has significant and unique management implications. Assuming larval dispersal occurs in this region, the size of the total spawning population (i.e. the combined sum of spawning individuals in each spatially-discrete post-larval assemblage) influences recruitment to the individual, spatially-discrete post-larval assemblages. Thus, over-depletion of any one post-larval assemblage could impact the recruitment to other assemblages, due to a reduction in spawning stock biomass (sensu Newman et al. 2000). More targeted research required to accurately define the degree of larval mixing in this region.

In addition to over-fishing, the limited connectivity evident for *P. macrochir* suggests that populations are susceptible to depletion through localised environmental perturbation, including alteration of freshwater flow regimes to estuarine environments. Given the significant positive relationship between spring and summer freshwater flow and year-class strength observed for *P. macrochir* by Halliday et al. (2008), and the low rates of connectivity observed in the present study, any local reduction in the number of individuals surviving to recruitment due to decreases in freshwater flow, be it natural or unnatural (i.e. through the construction of dams and weirs), would not be compensated for by movement of fish from other areas. Alterations to commercially-fished watersheds, in particular the inclusion of dams or other flow-reducing devices, and their subsequent effects on downstream populations of estuarine fishes, need to be factored in when establishing management plans for tropical estuarine species.

The results of this study suggest *P. macrochir*, and other tropical species that exhibit similar patterns of movement and connectivity, may be a good candidate for protection by marine protected areas (MPAs). Marine protected areas are now routinely established as an effective tool for protecting biodiversity, sustaining productivity of exploited species, and allowing for continued extractive uses of the marine environment (Jones et al. 2007; Botsford et al. 2009). Marine protected areas are particularly advocated for tropical systems, largely due to the fact that many of the developing nations that occur in tropical regions lack the human resources, infrastructure, and financial capacity to obtain accurate catch data required to implement more conventional management approaches used in the management of temperate fisheries (Adams 1998; Blaber 2002; Sale 2002). The limited movement and low degree of connectivity among estuaries, and extensive movement within individual river systems, observed in the present study suggests that MPAs on the scale of individual estuaries will likely have a positive effect on local populations. Preliminary results of the effect of areas closed to commercial fishing on *P. macrochir* populations by Ley et al. (2002) support this hypothesis. These authors observed greater abundances, a greater size range, and a greater number of larger *P. macrochir* in estuaries that had been closed to commercial fishing for as little as five years compared with commercially-fished estuaries (Ley et al. 2002). Accordingly, a greater number of fish may survive to spawning age within estuaries closed to fishing, resulting in greater overall egg production and recruitment success within these systems (Blaber et al. 1999; Ley et al. 2002).

However, while the moderate straying, or 'spill-over', of individual *P. macrochir* observed from the tagging data, and potential for larval dispersal, in Queensland's Gulf of Carpentaria suggest that MPAs may enhance fisheries in adjacent systems in this region, the restricted movement and limited connectivity on Queensland's east coast over similar spatial

scales indicates that protection from MPAs may offer little benefit with respect to replenishment of larval, juvenile and adult life history stages to populations in areas open to fishing. Given the relatively short time frame (five years) for MPAs to provide benefits to local populations observed by Ley et al. (2002), a series of systematic, rolling closures, whereby an individual estuary is closed to fishing for a finite duration, may be suitable to ensure localised sustainability of *P. macrochir*, and other tropical species that exhibit similar restricted patterns of movement and connectivity. Rolling closures have been used successfully in the Gulf of Maine to limit exploitation on populations of Atlantic cod, *Gadus morhua*, and harbour porpoise, *Phocoena phocoena*, which are caught by demersal gillnet fisheries in this region (Murawski et al. 2005). However, the impacts of such closures on the commercial and recreational fishing sectors, and subsequent effects on regional or local economies, would need to be assessed before such closures are implemented, particularly given that commercial netting in northern Australia's estuaries effectively ceases during the seasonal closure on the capture of *L. calcarifer* that typically occurs from November to January (inclusive).

In addition to those relating to connectivity, the results of this thesis have a number of implications for the management of *P. macrochir*, both in Australia and elsewhere across the species distribution. First, the results of the present study provide much required data on key demographic parameters required for the establishment of stock assessments and productivity models from which suitable harvest regimes and effective management strategies can be derived, including age and growth patterns, mortality rates, length and age at maturity and length and age at sex change. Furthermore, the observed variation in these parameters highlight the importance of gaining an understanding of the spatial patterns in demography of exploited fish populations. The significant spatial variation in demography suggests that spatially separated populations of *P. macrochir* will likely respond differently to fishing pressure and therefore require spatially distinct management arrangements (Begg et al. 2005; Mapstone et al. 2008). Failure to take account of such differences in stock assessments and subsequent management arrangements may lead to less productive populations being over-fished, whereas potential yields may not be realised for more productive components (Williams et al. 2006). The spatial differences in life history should ideally be incorporated into fisheries assessment models for this species in order to obtain reliable model outputs and to optimise management. Given the species' apparent over-exploitation in Western Australia (Pember et al. 2005), and the evidence of over-fishing of populations in Queensland's Gulf of Carpentaria observed in the present study (Chapter 3), a proactive approach to management is strongly recommended to ensure sustainability of *P. macrochir* across the species' distribution. While there is opportunistic monitoring of *P. macrochir* demography around the

Roebuck Bay region of Western Australia, and plans to conduct regular monitoring in this region (S. Newman, pers. comm.), there is currently no monitoring of *P. macrochir* demography in any other region across the species' distribution. In addition to mentoring trends in catch and CPUE, spatially distinct landings and demography should be monitored closely for signs of over-exploitation, including truncation of length and age classes and changes to length-at-age, maturity and sex change profiles.

The demographic analyses presented in Chapter 3 suggest that the minimum legal length of 60 cm TL currently in effect in Queensland's east coast waters is insufficient if its objective is to allow 50% of males the opportunity to spawn at least once before capture, and thus should be increased to meet this objective. The success of increasing the minimum legal length, however, is contingent on either a high survival rate of released fish, or fish not being selected for by the fishing gear. The fisheries-dependent collections on the east coast examined in this study were largely collected from fish processors, providing little information on the proportion of undersized fish captured by the commercial fleet. However, samples from the Gulf of Carpentaria were generally collected by commercial fishers working under a state fisheries collection permit. Thus, although the gear used reflects that used by the commercial fleet, these fishers were able to retain any fish smaller than the current minimum legal size that they collected, providing an indication of the proportion of the catch constituted by undersized fish that would normally be discarded. Of the 502 fish collected from Queensland's Gulf of Carpentaria, approximately 20% (115 individuals) were smaller than the current minimum legal size, indicating that undersized fish comprise a significant proportion of the catch in this region. Given that survival rates of net-caught *P. macrochir* are generally poor (Ley et al. 2002; B. Moore, pers. obs.), the majority of undersized fish would be returned to the water in a moribund state. As such, further increases in the minimum legal length, in isolation, are likely to be ineffective in reducing fishing pressure on immature *P. macrochir*. An increase in the minimum net mesh diameter may be a viable alternative in reducing fishing pressure on undersized individuals, and warrants further research.

More pertinently, the relative longevity and protandrous life history of *P. macrochir* makes the species particularly susceptible to over-fishing. As fishing pressure is typically biased toward the larger, older individuals of a population, it is the females of protandrous species that are subjected to the greatest fishing mortality, which may lead to egg limitation and recruitment overfishing (Milton et al. 1998; Blaber et al. 1999). To help mitigate these effects on sex-changing species, fisheries managers commonly implement output controls such as maximum legal lengths. There is currently no maximum legal length restriction for *P. macrochir* in any Australian jurisdiction. Given the small proportion of the population they represent (see Table 3.1), a maximum legal length should be introduced as a priority across all

jurisdictions to offer some protection for the larger females. However, the effectiveness of a maximum legal length is contingent on fish surviving long enough to reach the proposed length, and on a high survival rate of released fish should fish over the maximum legal length be caught. Further research into the survivorship of net-caught fish is warranted to fully understand the effectiveness of size limits as a management tool for *P. macrochir*. In a similar principle to increasing the minimum net mesh diameter to reduce fishing pressure on immature fish, a reduction in the maximum net mesh diameter may be a viable alternative in reducing the fishing pressure on female *P. macrochir*, by limiting the incidence of capture of these individuals.

## 7.5 Future directions for research

The findings of this research have highlighted important opportunities for future research. Ultimately, the scale of connectivity of the study species, or lack thereof, observed from the comparisons of life histories, parasite assemblages and otolith elemental signatures was largely a function of the spatial scale at which sampling was conducted, and the occurrence of spatial variation in the causal environmental and/or ecological mechanisms underlying each of these methodologies. Given the limited movement evident from the tagging data presented in Chapter 6, further fine-scale sampling will likely reveal greater spatial structuring, provided differences exist in environmental and ecological conditions between locations.

As discussed previously, the similarities observed in the larval/early juvenile otolith elemental signatures evident among locations in Queensland's Gulf of Carpentaria do not necessarily reflect larval mixing. Rather, these similarities fail to falsify the null hypothesis of a single population (Waldman 1999). Larval mixing in Queensland's Gulf waters has significant management implications, as outlined above. As such, the degree of larval mixing in this region should be quantified as a research priority. Similarly, despite the limited connectivity for larval/early juvenile life history stages among locations evident from the otolith elemental data, particularly for samples from Derby, Chambers Bay, and the Roper, Fitzroy, Mary and Brisbane Rivers, it could not be unequivocally concluded that each fish caught at a particular location originated from that specific location. Rather, the results suggested that fish caught at each location in these regions had a different natal origin to those caught from the other locations examined. More direct approaches, such as those in which otolith elemental signatures of larvae or early juveniles, which represent natal origins, are compared with those of adults of the same cohort (e.g. Gillanders 2002a), should be trialed to identify the natal origins of the adult fish. As discussed in Chapter 5, techniques such as transgenerational marking (Thorrold et al. 2006; Almany et al. 2007) could be used in future studies to provide unique direct empirical evidence of both the degree of larval dispersal in

Queensland's Gulf of Carpentaria waters, and the scaling of larval retention where otolith elemental signatures revealed differences, however the feasibility of conducting such an approach on the scale of even an individual estuary remains untested. In addition, greater knowledge of the longevity, dispersal capabilities and behaviour of *P. macrochir* larvae, and indeed of the larvae of tropical estuarine fishes in general, may assist in determining connectivity of this life history stage, although it is acknowledged that larval longevity is not necessarily an effective predictor of dispersal in fishes (Shulman and Bermingham 1995).

It was not possible to identify all parasites types used as biological tags in Chapter 4 as many species did not occur at the east coast locations where fresh (i.e. unfrozen) material that is required for successful identification was collected. Identification of these species, facilitated through the collection of fresh (i.e. unfrozen) material, coupled with identification of their elasmobranch definitive hosts, may shed further light on the distributional patterns of the parasites and thus on the movement patterns of *P. macrochir*. Given that many of the parasite types examined in the present study have been used successfully to delineate movements of other teleost species across northern Australia (Moore et al. 2003; Zischke et al. 2009; Charters et al. 2010; Moore et al. 2011a), it may ultimately be possible to establish a 'library' of parasite distributions that could be used in analyses of connectivity of other species, similar to that suggested for otolith elemental signatures (e.g. Gillanders 2002b).

The observed changes in biology between the present study and historical data for *P. macrochir* in the Queensland's south-eastern Gulf of Carpentaria reported in Chapter 3, and the small proportion of fish greater than five years old observed in this region, are indicative of a fishery that is over-exploited. More specific research and monitoring is urgently required to evaluate the status of *P. macrochir* populations in Queensland's Gulf of Carpentaria waters, and to test whether fishing is responsible for the observed temporal differences in biology, high mortality rates and truncation of ages in the region. In the meantime, a cautious management approach to *P. macrochir* fishing in Queensland's south-eastern Gulf of Carpentaria is recommended and, with confirmation of the indicators of over-fishing observed here, urgent and decisive management intervention is warranted.

## References


Abaunza P, Gordo LS, Santamaria MTG, Iversen SA, Murta AG, Gallo E (2008a) Life history parameters as basis for the initial recognition of stock management units in horse mackerel (*Trachurus trachurus*). Fisheries Research 89: 167–180

Abaunza P, Murta AG, Campbell N, Cimmaruta R, Comesana AS, Dahle G, Santamaria MTG, Gordo LS, Iversen SA, MacKenzie K, Magoulas A, Mattiucci S, Molloy J, Nascetti G, Pinto AL, Quinta R, Rarnos P, Sanjuan A, Santos AT, Stransky C, Zimmermann C (2008b) Stock identity of horse mackerel (*Trachurus trachurus*) in the Northeast Atlantic and Mediterranean Sea: integrating the results from different stock identification approaches. Fisheries Research 89: 196–209

Adams A, Wolfe RK, Barkowski N, Overcash D (2009) Fidelity to spawning grounds by a catadromous fish, *Centropomus undecimalis*. Marine Ecology Progress Series 389: 213–222

Adams T (1998) The interface between traditional and modern methods of fishery management in the Pacific Islands. Ocean and Coastal Management 40: 127–142

Adlard RD, Lester RJG (1994) Dynamics of the interaction between the parasitic isopod, *Anilocra pomacentri*, and the coral reef fish, *Chromis nitida*. Parasitology 109: 311–324

Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. Science 316: 742–744

Amin OM, Abdullah SMA, Mhaisen FT (2003) Description of *Pomphorhynchus spindletruncatus* n. sp. (Acanthocephala: Pomphorhynchidae) from freshwater fishes in northern Iraq, with the erection of a new pomphorhynchid genus, *Pyriproboscis* n. g., and keys to genera of the Pomphorhynchidae and the species of *Pomphorhynchus* Monticelli, 1905. Systematic Parasitology 54: 229–235

Anderson MJ, Gorley RN, Clarke KR (2008) *PERMANOVA+* for *PRIMER*: guide to software and statistical methods. PRIMER-E, Plymouth, UK

Atkinson D, Sibly RM (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends in Ecology & Evolution 12: 235–239

Ayvazian SG, Bastow TP, Edmonds JS, How J, Nowara GB (2004) Stock structure of Australian herring (*Arripis georgiana*) in southwestern Australia. Fisheries Research 67: 39–53

Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. Marine Ecology Progress Series 189: 125–134

Bacheler NM, Paramore LM, Buckel JA, Hightower JE (2009a) Abiotic and biotic factors influence the habitat use of an estuarine fish. Marine Ecology Progress Series 377: 263–277

Bacheler NM, Paramore LM, Burdick SM, Buckel JA, Hightower JE (2009b) Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. Fishery Bulletin 107: 405–419

Baker TG, Morand S, Wenner CA, Roumillat WA, de Buron I (2007) Stock identification of the sciaenid fish *Micropogonias undulatus* in the western North Atlantic Ocean using parasites as biological tags. Journal of Helminthology 81: 155–167

Barlow CG, Pearce MG, Rodgers LJ, Clayton P (1995) Effects of photoperiod on growth, survival and feeding periodicity of larval and juvenile barramundi *Lates calcarifer* (Bloch). Aquaculture 138: 159–168

Bath GE, Thorrold SR, Jones CM, Campana SE, McLaren JW, Lam JWH (2000) Strontium and barium uptake in aragonitic otoliths of marine fish. Geochimica et Cosmochimica Acta 64: 1705–1714

Beacham TD (1982) Some aspects of growth, Canadian exploitation, and stock identification of Atlantic cod (*Gadus morhua*) on the Scotian Shelf and Georges Bank in the northwest Atlantic Ocean. Canadian Technical Report of Fisheries and Aquatic Sciences 1069: 43

Beckman DW, Wilson CA, Stanley AL (1988) Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the Gulf of Mexico. Fishery Bulletin 87: 17–28

Bedee CD, DeVries DA, Bortone SA, Palmer CL (2002) Estuary-specific age and growth of spotted seatrout in the northern Gulf of Mexico. In: Bortone SA (ed) Biology of Spotted Sea Trout. CRC Press, Boca Raton, FL, pp 57–77

Begg GA (1996) Species coexistence, stock structure and fisheries management of school (*Scombermorus queenslandicus*) and spotted mackerel (*S. munroi*) in Queensland east coast waters. PhD thesis, Department of Zoology, The University of Queensland, Brisbane, Australia

Begg GA (2005) Life history parameters. In: Cadrin SX, Friedland KD, Waldman JR (eds) Stock Identification Methods: Applications in Fishery Science. Elsevier Academic Press, Burlington, MA, pp 119–150

Begg GA, Brown RW (2000) Stock identification of haddock *Melanogrammus aeglefinus* on Georges Bank based on otolith shape analysis. Transactions of the American Fisheries Society 129: 935–945

Begg GA, Cameron DS, Sawynok W (1997) Movements and stock structure of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in Australian east-coast waters. Marine and Freshwater Research 48: 295–301

Begg GA, Friedland KD, Pearce JB (1999a) Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research 43: 1–8

Begg GA, Hare JA, Sheehan DD (1999b) The role of life history parameters as indicators of stock structure. Fisheries Research 43: 141–163

Begg GA, Mapstone BD, Williams AJ, Adams S, Davies CR, Lou DC (2005) Multivariate life-history indices of exploited coral reef fish populations used to measure the performance of no-take zones in a marine protected area. Canadian Journal of Fisheries and Aquatic Sciences 62: 679–692

Begg GA, Sellin MJ (1998) Age and growth of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) in Queensland east-coast waters with implications for stock structure. Marine and Freshwater Research 49: 109–120

Begg GA, Waldman JR (1999) An holistic approach to fish stock identification. Fisheries Research 43: 35–44

Bergenius MAJ, Mapstone BD, Begg GA, Murchie CD (2005) The use of otolith chemistry to determine stock structure of three epinepheline serranid coral reef fishes on the Great Barrier Reef, Australia. Fisheries Research 72: 253–270

Berkeley SA, Chapman C, Sogard SM (2004) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85: 1258–1264

Bilton DT, Paula J, Bishop JDD (2002) Dispersal, genetic differentiation and speciation in estuarine organisms. Estuarine Coastal and Shelf Science 55: 937–952

Blaber SJ, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuarine Coastal and Shelf Science 29: 509–531

Blaber SJM (2000) Tropical Estuarine Fishes: Ecology, Exploitation and Conservation. Blackwell Science, Oxford, UK

Blaber SJM (2002) 'Fish in hot water': the challenges facing fish and fisheries research in tropical estuaries. Journal of Fish Biology 61: 1–20

Blaber SJM, Brewer DT, Milton DA, Merta GS, Efizon D, Fry G, van der Velde T (1999) The life history of the protandrous tropical shad *Tenualosa macrura* (Alosinae: Clupeidae): fishery implications. Estuarine Coastal and Shelf Science 49: 689–701

Blaber SJM, Brewer DT, Salini JP (1995) Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. Estuarine Coastal and Shelf Science 40: 177–193

Blaber SJM, Cyrus DP, Albaret JJ, Ching CV, Day JW, Elliott M, Fonseca MS, Hoss DE, Orensanz J, Potter IC, Silvert W (2000) Effects of fishing on the structure and

functioning of estuarine and nearshore ecosystems. ICES Journal of Marine Science 57: 590–602

Blaber SJM, Milton DA, Pang J, Wong P, BoonTeck O, Nyigo L, Lubim D (1996) The life history of the tropical shad *Tenualosa toli* from Sarawak: first evidence of protandry in the Clupeiformes? Environmental Biology of Fishes 46: 225–242

Bolle LJ, Hunter E, Rijnsdorp AD, Pastoors MA, Metcalfe JD, Reynolds JD (2005) Do tagging experiments tell the truth? Using electronic tags to evaluate conventional tagging data. ICES Journal of Marine Science 62: 236–246

Bonvechio TF, Allen MS (2005) Relations between hydrological variables and year-class strength of sportfish in eight Florida waterbodies. Hydrobiologia 532: 193–207

Botsford LW, Brumbaugh DR, Grimes C, Kellner JB, Largier J, O'Farrell MR, Ralston S, Soulanille E, Wespestad V (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Reviews in Fish Biology and Fisheries 19: 69–95

Botsford LW, Micheli F, Hastings A (2003) Principles for the design of marine reserves. Ecological Applications 13: S25–S31

Botton ML, Loveland RE (2003) Abundance and dispersal potential of horseshoe crab (*Limulus polyphemus*) larvae in the Delaware estuary. Estuaries 26: 1472–1479

Bradbury IR, Campana SE, Bentzen P (2008a) Low genetic connectivity in an estuarine fish with pelagic larvae. Canadian Journal of Fisheries and Aquatic Sciences 65: 147–158

Bradbury IR, Campana SE, Bentzen P (2008b) Otolith elemental composition and adult tagging reveal spawning site fidelity and estuarine dependency in rainbow smelt. Marine Ecology Progress Series 368: 255–268

Braverman MS, Acha EM, Gagliardini DA, Rivarossa M (2009) Distribution of whitemouth croaker (*Micropogonias furnieri*, Desmarest 1823) larvae in the Rio de la Plata estuarine front. Estuarine Coastal and Shelf Science 82: 557–565

Brewer DT, Blaber SJM, Salini JP, Farmer MJ (1995) Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. Estuarine Coastal and Shelf Science 40: 577–600

Brophy D, Jeffries TE, Danilowicz BS (2004) Elevated manganese concentrations at the cores of clupeid otoliths: possible environmental, physiological, or structural origins. Marine Biology 144: 779–786

Brown CA, Jackson GA, Holt SA, Holt GJ (2005) Spatial and temporal patterns in modeled particle transport to estuarine habitat with comparisons to larval fish settlement patterns. Estuarine Coastal and Shelf Science 64: 33–46

Buckworth RC, Newman SJ, Ovenden JR, Lester RJG, McPherson GR (2007) The Stock Structure of Northern and Western Australian Spanish Mackerel. Fisheries Research and Development Corporation Final Report No. 98/159. Department of Primary Industry, Fisheries and Mines, Northern Territory Government, Darwin, Australia

Bush AO, Aho JM, Kennedy CR (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. Evolutionary Ecology 4: 1–20

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al revisited. Journal of Parasitology 83: 575–583

Cadrin SX, Friedland KD (1999) The utility of image processing techniques for morphometric analysis and stock identification. Fisheries Research 43: 129–139

Cadrin SX, Friedland KD, Waldman JR (2005) Stock identification methods - an overview. In: Cadrin SX, Friedland KD, Waldman JR (eds) Stock Identification Methods: Applications in Fishery Science. Elsevier Academic Press, Burlington, MA, pp 3–6

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263–297

Campana SE, Annand NC, MacMillan JI (1995) Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124: 131–138

Campana SE, Neilson JD (1985) Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42: 1014–1032

Campbell HA, Watts ME, Sullivan S, Read MA, Choukroun S, Irwin SR, Franklin CE (2010) Estuarine crocodiles ride surface currents to facilitate long-distance travel. Journal of Animal Ecology 79: 955–964

Campbell N, Cross MA, Chubb JC, Cunningham CO, Hatfield EMC, MacKenzie K (2007) Spatial and temporal variations in parasite prevalence and infracommunity structure in herring (*Clupea harengus* L.) caught to the west of the British Isles and in the North and Baltic Seas: implications for fisheries science. Journal of Helminthology 81: 137–146

Campbell RA, Beveridge I (1996) Revision of the family Pterobothriidae Pintner, 1931 (Cestoda: Trypanorhyncha). Invertebrate Taxonomy 10: 617–662

Cannon LRG (1977) Some larval Ascaridoids from southeastern Queensland marine fishes. International Journal for Parasitology 7: 233–243

Caselle JE, Hamilton SL, Schroeder DM, Love MS, Standish JD, Rosales-Casian JA, Sosa-Nishizaki O (2011) Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. Canadian Journal of Fisheries and Aquatic Sciences 68: 288–303

Chambers CB, Cribb TH, Jones MK (2000) Tetraphyllidean metacestodes of teleosts of the Great Barrier Reef, and the use of in vitro cultivation to identify them. Folia Parasitologica 47: 285–292

Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39: 1208–1210

Chaplin JA, Baudains GA, Gill HS, McCulloch R, Potter IC (1998) Are assemblages of black bream (*Acanthopagrus butcheri*) in different estuaries genetically distinct? International Journal of Salt Lake Research 6: 303–321

Charnov EL (1982) The Theory of Sex Allocation. Princeton University Press, Princeton, NJ

Charters RA, Lester RJG, Buckworth RC, Newman SJ, Ovenden JR, Broderick D, Kravchuk O, Ballagh A, Welch DJ (2010) The stock structure of grey mackerel *Scomberomorus semifasciatus* in Australia as inferred from its parasite fauna. Fisheries Research 101: 94–99

Chenoweth SF, Hughes JM (2003) Oceanic interchange and nonequilibrium population structure in the estuarine dependent Indo-Pacific tasselfish, *Polynemus sheridani*. Molecular Ecology 12: 2387–2397

Childs AR, Cowley PD, Naesje TF, Booth AJ, Potts WM, Thorstad EB, Okland F (2008) Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. Estuarine Coastal and Shelf Science 78: 227–236

Choat JH, Robertson DR, Ackerman JL, Posada JM (2003) An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. Marine Ecology Progress Series 246: 265–277

Christensen A, Daewel U, Jensen H, Mosegaard H, St John M, Schrum C (2007) Hydrodynamic backtracking of fish larvae by individual-based modelling. Marine Ecology Progress Series 347: 221–232

Christie MR, Tissot BN, Albins MA, Beets JP, Jia YL, Ortiz DM, Thompson SE, Hixon MA (2010) Larval connectivity in an effective network of marine protected areas. PLoS One 5: e15715

Church JA, Forbes AMG (1983) Circulation in the Gulf of Carpentaria. 1. Direct observations of currents in the southeast corner of the Gulf of Carpentaria. Australian Journal of Marine and Freshwater Research 34: 1–10

Clark DL, Leis JM, Hay AC, Trnski T (2005) Swimming ontogeny of larvae of four temperate marine fishes. Marine Ecology Progress Series 292: 287–300

Clark MR, Anderson OF, Francis R, Tracey DM (2000) The effects of commercial exploitation on orange roughy (*Hoplostethus atlanticus*) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. Fisheries Research 45: 217–238

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143

Clarke LM, Walther BD, Munch SB, Thorrold SR, Conover DO (2009) Chemical signatures in the otoliths of a coastal marine fish, *Menidia menidia*, from the northeastern United States: spatial and temporal differences. Marine Ecology Progress Series 384: 261–271

Conover DO (1992) Seasonality and the scheduling of life history at different latitudes. Journal of Fish Biology 41 (suppl. B): 161–178

Cook GS (2011) Changes in otolith microchemistry over a protracted spawning season influence assignment of natal origin. Marine Ecology Progress Series 423: 197–209

Cowen RK, Gawarkiewicz GG, J. P, Thorrold SR, Werner FE (2007) Population connectivity in marine systems - an overview. Oceanography 20: 14–21

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287: 857–859

Cowen RK, Paris CB, Srinivasan A (2006) Scaling connectivity in marine populations. Science 311: 522–527

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annual Review of Marine Science 1: 443–466

Cribb TH, Anderson GR, Dove ADM (2000) *Pomphorhynchus heronensis* and restricted movement of *Lutjanus carponotatus* on the Great Barrier Reef. Journal of Helminthology 74: 53–56

Cyrus DP, Blaber SJM (1987) The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. Continental Shelf Research 7: 1411–1416

Cyrus DP, Blaber SJM (1992) Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Estuarine Coastal and Shelf Science 35: 545–563

Dantas DV, Barletta M, Costa MF, Barbosa-Cintra SCT, Possatto FE, Ramos JAA, Lima ARA, Saint-Paul U (2010) Movement patterns of catfishes (Ariidae) in a tropical semi-arid estuary. Journal of Fish Biology 76: 2540–2557

Davidson RS, Letcher BH, Nislow KH (2010) Drivers of growth variation in juvenile Atlantic salmon (*Salmo salar*): an elasticity analysis approach. Journal of Animal Ecology 79: 1113–1121

Day JH, Blaber SJ, Wallace JH (1981) Estuarine fishes. In: Day JH (ed) Estuarine Ecology with Particular Reference to Southern Africa. A. A. Balkema, Rotterdam, pp 197–221

de Roos AM, Boukal DS, Persson L (2006) Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proceedings of the Royal Society of London B 273: 1873–1880

DeMaster DP, Fowler CW, Perry SL, Richlen ME (2001) Predation and competition: the impact of fisheries on marine mammal populations over the next one hundred years. Journal of Mammalogy 82: 641–651

DERM (2010) Water Monitoring Data Portal http://watermonitoring.derm.qld.gov.au/host.htm Queensland Government Department of Environment and Resource Management, Brisbane, Australia

DeVries DA, Grimes CB (1997) Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla*, 1977–1992. Fishery Bulletin 95: 694-708

Dingle H (1996) Migration: the Biology of Life on the Move. Oxford University Press, Oxford, UK

Dodson JJ, Godin JGJ (1997) Fish migration: an evolutionary perspective. In: Godin JGJ (ed) Behavioural Ecology of Teleost Fishes. Oxford University Press, Oxford, UK, pp 10–36

Dolbeth M, Martinho F, Freitas V, Costa-Dias S, Campos J, Pardal MA (2010) Multi-year comparisons of fish recruitment, growth and production in two drought-affected Iberian estuaries. Marine and Freshwater Research 61: 1399–1415

Dominguez-Petit R, Korta M, Saborido-Rey F, Murua H, Sainza M, Pineiro C (2008) Changes in size at maturity of European hake Atlantic populations in relation with stock structure and environmental regimes. Journal of Marine Systems 71: 260–278

DPI&F (2007) Coastal Habitat Resource Information System (CHRISWeb) http://chrisweb.dpi.qld.gov.au/CHRIS/. Queensland Government Department of Employment, Economic Development and Innovation, Brisbane, Australia

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. Canadian Journal of Fisheries and Aquatic Sciences 68: 232–240

Duke NC (1992) Mangrove floristics and biogeography. In: Robertson AI, Alongi D (eds) Tropical Mangrove Ecosystems. American Geophysical Union, Washington DC, USA, pp 63–100

Durieux EDH, Meekan MG, Ponton D, Vigliola L (2009) Temperature, selective mortality and early growth in the short-lived clupeid *Spratelloides gracilis*. Journal of Fish Biology 74: 921–938

Elsdon TS, Gillanders BM (2002) Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. Canadian Journal of Fisheries and Aquatic Sciences 59: 1796–1808

Elsdon TS, Gillanders BM (2003) Reconstructing migratory patterns of fish based on environmental influences on otolith chemistry. Reviews in Fish Biology and Fisheries 13: 219–235

Elsdon TS, Gillanders BM (2005) Alternative life-history patterns of estuarine fish: barium in otoliths elucidates freshwater residency. Canadian Journal of Fisheries and Aquatic Sciences 62: 1143–1152

Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, Secor DH, Thorrold SR, Walther BD (2008) Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology: An Annual Review 46: 297–330

Epifanio C, Garvine R (2001) Larval transport on the Atlantic continental shelf of North America: a review. Estuarine Coastal and Shelf Science 52: 51–77

Erzini K (1994) An empirical study of variability in length-at-age of marine fishes. Journal of Applied Ichthyology 10: 17–41

Farrington LW, Austin CM, Coutin PC (2000) Allozyme variation and stock structure in the black bream, *Acanthopagrus butcheri* (Munro) (Sparidae) in southern Australia: implications for fisheries management, aquaculture and taxonomic relationship with *Acanthopagrus australis* (Günther). Fisheries Management and Ecology 7: 265–279

Ferreira BP, Russ GR (1994) Age validation and estimation of growth-rate of the coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, northern Great Barrier Reef. Fishery Bulletin 92: 46–57

Field CD (1995) Impact of expected climate change on mangroves. Hydrobiologia 295: 75–81

Fogarty MJ, Botsford LW (2007) Population connectivity and spatial management of marine fisheries. Oceanography 20: 112–123

Forbes AMG, Church JA (1983) Circulation in the Gulf of Carpentaria II. Residual currents and mean sea-level. Australian Journal of Marine and Freshwater Research 34: 11–22

Fowler AJ, Campana SE, Jones CM, Thorrold SR (1995) Experimental assessment of the effects of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. Canadian Journal of Fisheries and Aquatic Sciences 52: 1421–1430

Fowler AJ, Gillanders BM, Hall KC (2005) Relationship between elemental concentration and age from otoliths of adult snapper (*Pagrus auratus*, Sparidae): implications for movement and stock structure. Marine and Freshwater Research 56: 661–676

Francis MP, Francis RICC (1992) Growth rate estimates for New Zealand rig (*Mustelus lenticulatus*). Australian Journal of Marine and Freshwater Research 43: 1157–1176

Francis R (1990) Back calculation of fish length: a critical review. Journal of Fish Biology 36: 883–902

Garratt PA (1993) Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary. South African Journal of Zoology 28: 26–31

Garrett RN (1997) Biology and Harvest of Tropical Fishes in the Queensland Gulf of Carpentaria Gillnet Fishery. Fisheries Research and Development Corporation Final Report No. 92/145. Queensland Government Department of Primary Industries, Brisbane, Australia

Gerlach G, Atema J, Kingsford MJ, Black KP, Miller-Sims V (2007) Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 104: 858–863

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Quarterly Review of Biology 44: 189–208

Gillanders BM (2002a) Connectivity between juvenile and adult fish populations: do adults remain near their recruitment estuaries? Marine Ecology Progress Series 240: 215–223

Gillanders BM (2002b) Temporal and spatial variability in elemental composition of otoliths: implications for determining stock identity and connectivity of populations. Canadian Journal of Fisheries and Aquatic Sciences 59: 669–679

Gillanders BM (2005) Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuarine Coastal and Shelf Science 64: 47–57

Gillanders BM (2009) Tools for studying biological marine ecosystem interactions-natural and artificial tags. In: Nagelkerken I (ed) Ecological Connectivity Among Tropical Coastal Ecosystems Springer, New York, pp 457–492

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology Progress Series 247: 281–295

Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ (2011) Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Marine and Freshwater Research 62: 1115–1131

Gillanders BM, Ferrell DJ, Andrew NL (2001) Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging programme? Marine and Freshwater Research 52: 179–192

Gillanders BM, Kingsford MJ (1996) Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. Marine Ecology Progress Series 141: 13–20

Gillanders BM, Kingsford MJ (2000) Elemental fingerprints of otoliths of fish may distinguish estuarine 'nursery' habitats. Marine Ecology Progress Series 201: 273–286

Gillson J, Scandol J, Suthers I (2009) Estuarine gillnet fishery catch rates decline during drought in eastern Australia. Fisheries Research 99: 26–37

Gold JR, Richardson LR (1998) Mitochondrial DNA diversification and population structure in fishes from the Gulf of Mexico and Western Atlantic. Journal of Heredity 89: 404–414

Gordon H, O'Farrell S, Collier M, Dix M, Rotstayn L, Kowalczyk E, Hirst T, Watterson I (2010) The CSIRO Mk3.5 Climate Model. The Centre for Australian Weather and Climate Research Technical Report No. 21, Melbourne, Australia.

Gray CA, Ives MC, Macbeth WG, Kendall BW (2010) Variation in growth, mortality, length and age compositions of harvested populations of the herbivorous fish *Girella tricuspidata*. Journal of Fish Biology 76: 880–899

Grosberg R, Cunningham CW (2001) Genetic structure in the sea: from populations to communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine Community Ecology. Sinauer Associates Inc., Sunderland, UK, pp 61–84

Haddon (2001) Modelling and Quantitative Methods in Fisheries. Chapman & Hall, London

Halliday IA, Robins JB, Mayer DG, Staunton-Smith J, Sellin MJ (2008) Effects of freshwater flow on the year-class strength of a non-diadromous estuarine finfish, king threadfin (*Polydactylus macrochir*), in a dry-tropical estuary. Marine and Freshwater Research 59: 157–164

Hamer PA, Jenkins GP, Gillanders BM (2003) Otolith chemistry of juvenile snapper *Pagrus auratus* in Victorian waters: natural chemical tags and their temporal variation. Marine Ecology Progress Series 263: 261–273

Hamilton SL, Caselle JE, Standish JD, Schroeder DM, Love MS, Rosales-Casian JA, Sosa-Nishizaki O (2007) Size-selective harvesting alters life histories of a temperate sex-changing fish. Ecological Applications 17: 2268–2280

Hare JA, Cowen RK (1993) Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. Marine Ecology Progress Series 98: 1–16

Hare JA, Cowen RK (1997) Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78: 2415–2431

Harris PT, Heap AD, Marshall JE, McCulloch M (2008) A new coral reef province in the Gulf of Carpentaria Australia: colonization, growth and submergence during the early Holocene. Marine Geology 251: 85–97

Harter SL, Heck KLJ (2006) Growth rates of juvenile pinfish (*Lagodon rhomboides*): effects of habitat and predation risk. Estuaries and Coasts 29: 318–327

Hastings A, Botsford LW (2006) Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences 103: 6067–6072

Hawkins JP, Roberts CM (2003) Effects of fishing on sex-changing Caribbean parrotfishes. Biological Conservation 115: 213–226

Hecht T, van der Lingen CD (1992) Turbidity-induced changes in feeding strategies of fish in estuaries. South African Journal of Zoology 27: 95–107

Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. Bulletin of Marine Science 70: 273–290

Henry GW, Lyle JM (2003) The National Recreational and Indigenous Fishing Survey. Fisheries Research and Development Corporation Final Report No. 99/158. NSW Fisheries, Sydney, Australia

Hidalgo M, Massuti E, Guijarro B, Moranta J, Ciannelli L, Lloret J, Oliver P, Stenseth NC (2009) Population effects and changes in life history traits in relation to phase transitions induced by long-term fishery harvesting: European hake (*Merluccius merluccius*) off the Balearic Islands. Canadian Journal of Fisheries and Aquatic Sciences 66: 1355–1370

Hilborn R (1988) Determination of tag return from recaptured fish by sequential examination of tags. Transactions of the American Fisheries Society 117: 510–514

Hilborn R, Walters CJ (1992) Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty. Routledge, Chapman & Hall, Inc, New York

Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, pp 475–508

Hixon MA, Webster MS (2002) Density dependence in reef fish populations. In: Sale PF (ed) Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp 303–325

Hobday AJ, Lough JM (2011) Projected climate change in Australian marine and freshwater environments. Marine and Freshwater Research 62: 1000–1014

Holmes TH, McCormick MI (2009) Influence of prey body characteristics and performance on predator selection. Oecologia 159: 401–413

Horne JB, Momigliano P, Welch DJ, Newman SJ, van Herwerden L (2011) Limited ecological population connectivity suggests low demands on self-recruitment in a tropical inshore marine fish (*Eleutheronema tetradactylum*: Polynemidae). Molecular Ecology 20: 2291–2306

Horne JB, Momigliano P, Welch DJ, Newman SJ, van Herwerden L (2012) Searching for common threads in threadfins: phylogeography of Australian polynemids in space and time. Marine Ecology Progress Series 449: 263–276

Hutchings JA (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Sciences 53: 943–962

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406: 882–885

Hutson KS, Brock EL, Steer MA (2011) Spatial variation in parasite abundance: evidence of geographical population structuring in southern garfish *Hyporhamphus melanochir*. Journal of Fish Biology 78: 166–182

Ihssen PE, Booke HE, Casselman JM, McGlade JM, Payne NR, Utter FM (1981) Stock identification - materials and methods. Canadian Journal of Fisheries and Aquatic Sciences 38: 1838–1855

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638

James NC, Cowley PD, Whitfield AK, Kaiser H (2008) Choice chamber experiments to test the attraction of postflexion *Rhabdosargus holubi* larvae to water of estuarine and riverine origin. Estuarine Coastal and Shelf Science 77: 143–149

Jennings S, Beverton RJH (1991) Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L) stocks. ICES Journal of Marine Science 48: 117–125

Johnson DR, Funicelli NA, Bohnsack JA (1999) Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. North American Journal of Fisheries Management 19: 436–453

Jones CM (2006) Estuarine and diadromous fish metapopulations. In: Kritzer JP, Sale PF (eds) Marine Metapopulations. Elsevier Academic Press, Burlington, MA, pp 119–154

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28: 307–325

Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed) Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp 221–238

Jones GP, Srinivasan M, Almany GR (2007) Population connectivity and conservation of marine biodiversity. Oceanography 20: 100–111

Kailola PJ, Williams MJ, Stewart PC, Reichelt RE, McNee A, Grieve C (1993) Australian Fisheries Resources. Bureau of Resource Sciences, Department of Primary Industries and Energy, Canberra, Australia

Kingsford MJ, Gillanders BM (2000) Variation in concentrations of trace elements in otoliths and eye lenses of a temperate reef fish, *Parma microlepis*, as a function of depth, spatial scale, and age. Marine Biology 137: 403–414

Kinsey ST, Orsoy T, Bert TM, Mahmoudi B (1994) Population structure of the Spanish sardine *Sardinella aurita* - natural morphological variation in a genetically homogeneous population. Marine Biology 118: 309–317

Kjesbu OS, Solemdal P, Bratland P, Fonn M (1996) Variation in the annual egg production in individual captive Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 53: 610–620

Knip DM, Heupel MR, Simpfendorfer CA, Tobin AJ, Moloney J (2011) Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. Marine Ecology Progress Series 425: 233–246

Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries 5: 131–140

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

Laurenson CH, Johnson A, Priede IG (2005) Movements and growth of monkfish *Lophius piscatorius* tagged at the Shetland Islands, northeastern Atlantic. Fisheries Research 71: 185–195

Law R (2000) Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57: 659–668

Leis JM (2006) Are larvae of demersal fishes plankton or nekton? Advances in Marine Biology 51: 57–141

Leis JM, Piola RF, Hay AC, Wen C, Kan KP (2009) Ontogeny of behaviour relevant to dispersal and connectivity in the larvae of two non-reef demersal, tropical fish species. Marine and Freshwater Research 60: 211–223

Lester RJG (1990) Reappraisal of the use of parasites for fish stock identification. Australian Journal of Marine and Freshwater Research 41: 855–864

Lester RJG, Barnes A, Habib G (1985) Parasites of skipjack tuna, *Katsuwonus pelamis* - fishery implications. Fishery Bulletin 83: 343–356

Lester RJG, MacKenzie K (2009) The use and abuse of parasites as stock markers for fish. Fisheries Research 97: 1–2

Lester RJG, Sewell KB, Barnes A, Evans K (1988) Stock discrimination of orange roughy, *Hoplostethus atlanticus*, by parasite analysis. Marine Biology 99: 137–143

Lester RJG, Thompson C, Moss H, Barker SC (2001) Movement and stock structure of narrow-barred Spanish mackerel as indicated by parasites. Journal of Fish Biology 59: 833–842

Ley JA, Halliday IA, Tobin AJ, Garrett RN, Gribble NA (2002) Ecosystem effects of fishing closures in mangrove estuaries of tropical Australia. Marine Ecology Progress Series 245: 223–238

Lim PKA, Motomura H, Gambang AC (2010) *Polydactylus luparensis*, a new species of threadfin (Perciformes: Polynemidae) from the Batang Lupar River, Sarawak, Borneo, Malaysia. Zootaxa 2405: 63-68

Lindholm J, Knight A, Domeier M (2010) Gender-mediated patterns in the movement of California sheephead in the northern Channel Islands (eastern Pacific). California Fish and Game 96: 53–68

Lindley ST, Erickson DL, Moser ML, Williams G, Langness OP, McCovey BW, Belchik M, Vogel D, Pinnix W, Kelly JT, Heublein JC, Klimley AP (2011) Electronic tagging of green sturgeon reveals population structure and movement among estuaries. Transactions of the American Fisheries Society 140: 108–122

Lom J, Dykova I (1992) Protozoan Parasites of Fishes. Elsevier, New York

Loneragan NR, Potter IC, Lenanton RCJ, Caputi N (1987) Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. Marine Biology 94: 631–641

Long PE, McKinnon SG (2002) Habitats and fisheries resources of the Fitzroy River estuary (Central Queensland). Information Series QI02104, Queensland Department of Primary Industries, Brisbane, Australia

Longhurst AR, Pauly D (1987) Ecology of Tropical Oceans. Academic Press, San Diego, CA

Lucena FM, O'Brien CM (2001) Effects of gear selectivity and different calculation methods on estimating growth parameters of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), from southern Brazil. Fishery Bulletin 99: 432–442

MacKenzie K (1985) The use of parasites in population studies of herring, *Clupea harengus* L., in the North Sea and to the north and west of Scotland. Journal Du Conseil International pour l'Exploration de la Mer 42: 33–64

MacKenzie K (1987) Long-term changes in the prevalence of two helminth parasites (Cestoda: Trypanorhyncha) infecting marine fish. Journal of Fish Biology 31: 83–87

MacKenzie K, Abaunza P (1998) Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. Fisheries Research 38: 45–56

Mapstone BD, Little LR, Punt AE, Davies CR, Smith ADM, Pantus F, McDonald AD, Williams AJ, Jones A (2008) Management strategy evaluation for line fishing in the Great Barrier Reef: balancing conservation and multi-sector fishery objectives. Fisheries Research 94: 315–329

Marques JF, Santos MJ, Teixeira CM, Batista MI, Cabral HN (2011) Host-parasite relationships in flatfish (Pleuronectiformes) - the relative importance of host biology, ecology and phylogeny. Parasitology 138: 107–121

Marteinsdottir G, Steinarsson A (1998) Maternal influence on the size and viability of Icelandic cod (*Gadus morhua* L.) eggs and larvae. Journal of Fish Biology 52: 1241–1258

Matthews J, Deguara K (1992) Anglers and state fisheries join forces to tag gamefish. Australian Fisheries 51: 34–36

McCulloch M, Cappo M, Aumend J, Muller W (2005) Tracing the life history of individual barramundi using laser ablation MC-ICP-MS Sr-isotopic and Sr/Ba ratios in otoliths. Marine and Freshwater Research 56: 637–644

McGarigal K, Cushman S, Stafford S (2000) Multivariate Statistics for Wildlife and Ecology Research. Springer-Verlag, New York

McPhee DP, Sawynok W, Warburton K, Hobbs SJ (1999) Movements of the surf zone carangid *Trachinotus coppingeri* (Günther, 1884) in Queensland and northern New South Wales. Proceedings of the Royal Society of Queensland 108: 89–97

Miller MJ, Able KW (2002) Movements and growth of tagged young-of-the-year Atlantic croaker (*Micropogonias undulatus* L.) in restored and reference marsh creeks in Delaware Bay, USA. Journal of Experimental Marine Biology and Ecology 267: 15–33

Millner RS, Whiting CL (1996) Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science 53: 1185–1195

Milton DA, Chenery SR (2001a) Can otolith chemistry detect the population structure of the shad hilsa *Tenualosa ilisha*? Comparison with the results of genetic and morphological studies. Marine Ecology Progress Series 222: 239–251

Milton DA, Chenery SR (2001b) Sources and uptake of trace metals in otoliths of juvenile barramundi (*Lates calcarifer*). Journal of Experimental Marine Biology and Ecology 264: 47–65

Milton DA, Chenery SR (2003) Movement patterns of the tropical shad hilsa (*Tenualosa ilisha*) inferred from transects of 87Sr/86Sr isotope ratios in their otoliths. Canadian Journal of Fisheries and Aquatic Sciences 60: 1376–1385

Milton DA, Die D, Tenakanai C, Swales S (1998) Selectivity for barramundi (*Lates calcarifer*) in the Fly River, Papua New Guinea: implications for managing gill-net fisheries on protandrous fishes. Marine and Freshwater Research 49: 499–506

Moller H (1976) Reduction of the intestinal parasite fauna of marine fishes in captivity. Journal of the Marine Biological Association of the United Kingdom 56: 781–785

Moore BR, Buckworth RC, Moss H, Lester RJG (2003) Stock discrimination and movements of narrow-barred Spanish mackerel across northern Australia as indicated by parasites. Journal of Fish Biology 63: 765–779

Moore BR, Stapley J, Allsop Q, Newman SJ, Ballagh A, Welch DJ, Lester RJG (2011a) Stock structure of blue threadfin *Eleutheronema tetradactylum* across northern Australia, as indicated by parasites Journal of Fish Biology 78: 923–936

Moore BR, Welch DJ, Simpfendorfer CA (2011b) Spatial patterns in the demography of a large estuarine teleost: king threadfin, *Polydactylus macrochir*. Marine and Freshwater Research 62: 937–951

Moran JDW, Arthur JR, Burt MDB (1996) Parasites of sharp-beaked redfishes (*Sebastes fasciatus* and *Sebastes mentella*) collected from the Gulf of St Lawrence, Canada. Canadian Journal of Fisheries and Aquatic Sciences 53: 1821–1826

Morton RM, Halliday IA, Cameron D (1993) Movement of tagged juvenile tailor (Pomatomus saltatrix) in Moreton Bay, Queensland. Australian Journal of Marine and Freshwater Research 44: 811–816

Motomura H (2004) Threadfins of the world (family Polynemidae). An annotated and illustrated catalogue of polynemid species known to date. Food and Agriculture Organisation of the United Nations (FAO), Rome

Motomura H, Iwatsuki Y, Kimura S, Yoshino T (2000) Redescription of *Polydactylus macrochir* (Günther, 1867), a senior synonym of *P. sheridani* (Macleay, 1884) (Perciformes: Polynemidae). Ichthyological Research 47: 327–333

Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends in Ecology & Evolution 21: 89–95

Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, Devitsina GV, Doving KB (2009) Ocean acidification impairs olfactory discrimination and homing ability of a

marine fish. Proceedings of the National Academy of Sciences of the United States of America 106: 1848–1852

Murawski SA, Wigley SE, Fogarty MJ, Rago PJ, Mountain DG (2005) Effort distribution and catch patterns adjacent to temperate MPAs. ICES Journal of Marine Science 62: 1150–1167

Myers RA, Hammill MO, Stenson GB (1997) Using mark-recapture to estimate the numbers of a migrating stage-structured population. Canadian Journal of Fisheries and Aquatic Sciences: 2097–2104

Myers RA, Hutchings JA, Barrowman NJ (1996) Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series 138: 293–308

Newman SJ, Allsop Q, Ballagh AC, Garrett RN, Gribble N, Meeuwig JJ, Mitsopoulos GEA, Moore BR, Pember MB, Rome BM, Saunders T, Skepper CL, Stapley JM, van Herwerden L, Welch DJ (2010) Variation in stable isotope ($\delta^{18}O$ and $\delta^{13}C$) signatures in the sagittal otolith carbonate of king threadfin, *Polydactylus macrochir* across northern Australia reveals multifaceted stock structure. Journal of Experimental Marine Biology and Ecology 396: 53–60

Newman SJ, Pember MB, Rome BM, Mitsopoulos GEA, Skepper CL, Allsop Q, Saunders T, Ballagh AC, van Herwerden L, Garrett RN, Gribble NA, J.M. S, Meeuwig JJ, Moore BR, Welch DJ (2011) Stock structure of blue threadfin *Eleutheronema tetradactylum* across northern Australia as inferred from stable isotopes in sagittal otolith carbonate. Fisheries Management and Ecology 18: 246–257

Newman SJ, Skepper C, Mitsopoulos G, McAuley R (2009) North coast nearshore and estuarine fishery status report. In: Fletcher WJ, Santoro K (eds) State of the Fisheries Report 2008/09. Department of Fisheries, Western Australia, pp 143–149

Newman SJ, Steckis RA, Edmonds JS, Lloyd J (2000) Stock structure of the goldband snapper *Pristipomoides multidens* (Pisces: Lutjanidae) from the waters of northern and western Australia by stable isotope ratio analysis of sagittal otolith carbonate. Marine Ecology Progress Series 198: 239–247

North EW, Houde ED (2006) Retention mechanisms of white perch (*Morone americana*) and striped bass (*Morone saxatilis*) early-life stages in an estuarine turbidity maximum: an integrative fixed-location and mapping approach. Fisheries Oceanography 15: 429–450

Northern Territory Government (2009) Fishery Report No. 101. Fishery Status Reports 2008, Department of Resources, Northern Territory Government, Darwin, Australia

Okey TA, Poloczanska ES (2008) Northern fisheries. In: Hobday AJ, Poloczanska ES, Matear RJ (eds) Implications of Climate Change for Australian Fisheries and Aquaculture: A Preliminary Assessment. Report to the Department of Climate Change, Canberra, Australia

Palm HW (2004) The Trypanorhyncha Diesing, 1863. PKSPL-IPB Press, Bogor

Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annual Review of Environment and Resources 29: 31–68

Pande A, MacDiarmid AB, Smith PJ, Davidson RJ, Cole RG, Freeman D, Kelly S, Gardner JPA (2008) Marine reserves increase the abundance and size of blue cod and rock lobster. Marine Ecology Progress Series 366: 147–158

Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. Marine and Freshwater Research 62: 1015–1026

Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. Marine Ecology Progress Series 296: 93–106

Patterson HM, McBride RS, Julien N (2004) Population structure of red drum (*Sciaenops ocellatus*) as determined by otolith chemistry. Marine Biology 144: 855–862

Patterson HM, Thorrold SR, Shenker JM (1999) Analysis of otolith chemistry in Nassau grouper (*Epinephelus striatus*) from the Bahamas and Belize using solution-based ICP-MS. Coral Reefs 18: 171–178

Pauly D (1988) Fisheries research and the demersal fisheries of southeast Asia. In: Gulland JA (ed) Fish Population Dynamics. John Wiley, London, pp 329–348

Pearce NJG, Perkins WT, Westgate JA, Gorton MP, Jackson SE, Neal CR, Chenery SP (1997) A compilation of new and published major and trace element data for NIST SRM 610 and NIST SRM 612 glass reference materials. Geostandards Newsletter 21: 115–144

Pember MB (2006) Characteristics of fish communities in coastal waters of north-western Australia, including the biology of the threadfin species *Eleutheronema tetradactylum* and *Polydactylus macrochir*. PhD thesis, Murdoch University, Murdoch, Australia

Pember MB, Newman SJ, Hesp SA, Young GC, Skepper CL, Hall NG, Potter IC (2005) Biological Parameters for Managing the Fisheries for Blue and King Threadfin Salmons, Estuary Rockcod, Malabar Grouper and Mangrove Jack in North-western Australia. Fisheries Research and Development Corporation Final Report No. 02/003. Centre for Fish and Fisheries Research, Murdoch University, Murdoch, Australia

Pillai NK (1985) The Fauna of India: Copepod Parasites of Marine Fishes. Zoological Survey of India, Calcutta

Platten JR, Tibbetts IR, Sheaves MJ (2002) The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. Journal of Fish Biology 60: 301–318

Podder TN (1937) A new species of Acanthocephala, *Neoechinorhynchus topseyi* n. sp. from a Calcutta fish, *Polynemus heptadactylus* (Cuv. and Val). Parasitology 29: 365–369

Poiner I, Conacher C, Loneragan NR, Kenyon R, Somers IF (1993) Effects of Cyclones on Seagrass Communities and Penaeid Prawn Stocks of the Gulf of Carpentaria. Fisheries Research and Development Corporation Final Report No. 87/16 and 91/45. CSIRO, Cleveland, Australia

Poiner I, Walker DI, Coles RG (1989) Regional studies - seagrasses of tropical Australia. In: Larkhum AWD, McComb AJ, Shepherd SA (eds) The Biology of Seagrasses: an Australian Perspective. Elsevier, Amsterdam, pp 279–296

Potter IC, Hyndes (1999) Characteristics of the ichthyofaunas of southwestern Australian estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate Australia: a review. Australian Journal of Ecology 24: 395–421

Poulin R, Rohde K (1997) Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. Oecologia 110: 278–283

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bulletin of the Fishery Research Board of Canada 191: 1–382

Ricker WE (1981) Changes in the average size and average age of pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38: 1636–1656

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278: 1454–1457

Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. Marine Ecology Progress Series 295: 229–244

Robins JB, Mayer DG, Staunton-Smith J, Halliday IA, Sawynok W, Sellin MJ (2006) Variable growth rates of the tropical estuarine fish barramundi *Lates calcarifer* (Bloch) under different freshwater flow conditions. Journal of Fish Biology 69: 379–391

Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Reviews in Fish Biology and Fisheries 14: 251–275

Rohde K (1982) Ecology of marine parasites. University of Queensland Press, St Lucia, Brisbane, Australia

Rothlisberg P, Staples D, Poiner I, Wolanski E (1988) Possible impact of the greenhouse effect on commercial prawn populations in the Gulf of Carpentaria. In: Pearman GI (ed) Greenhouse: Planning for Climate Change. CSIRO Publications, Melbourne, Australia, pp 216–227

Russell DJ (1988) An Assessment of the East Queensland Inshore Gill Net Fishery - Information Series QI88024. Queensland Department of Primary Industries, Brisbane, Australia

Russell DJ, Garrett RN (1983) Use by juvenile barramundi, *Lates calcarifer* (Bloch), and other fishes of temporary supralittoral habitats in a tropical estuary in northern Australia. Australian Journal of Marine and Freshwater Research 34: 805–811

Russell DJ, Garrett RN (1988) Movements of juvenile barramundi, *Lates calcarifer* (Bloch), in north-eastern Queensland. Australian Journal of Marine and Freshwater Research 39: 117–123

Ruttenberg BI, Hamilton SL, Hickford MJH, Paradis GL, Sheehy MS, Standish JD, Ben-Tzvi O, Warner RR (2005) Elevated levels of trace elements in cores of otoliths and their potential for use as natural tags. Marine Ecology Progress Series 297: 273–281

Sadovy de Mitcheson Y, Liu M (2008) Functional hermaphroditism in teleosts. Fish and Fisheries 9: 1–43

Sadovy Y (1996) Reproduction of reef fishery species. In: Polunin NVC, Roberts CM (eds) Reef Fisheries. Chapman & Hall, London, pp 15–59

Sale PF (2002) The science we need to develop more effective management. In: Sale PF (ed) Coral Reef Fishes; Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp 361–376

Sale PF, Hanski I, Kritzer JP (2006) The merging of metapopulation theory and marine ecology: establishing the historical context. In: Kritzer JP, Sale PF (eds) Marine Metapopulations. Elsevier Academic Press, Burlington, MA, pp 3–28

Salini J, Shaklee JB (1988) Genetic structure of barramundi (*Lates calcarifer*) stocks from northern Australia. Australian Journal of Marine and Freshwater Research 39: 317–329

Salini JP, Brewer DT, Blaber SJM (1998) Dietary studies on the predatory fishes of the Norman River estuary, with particular reference to penaeid prawns. Estuarine Coastal and Shelf Science 46: 837–847

Salini JP, Milton DA, Rahman MJ, Hussain MG (2004) Allozyme and morphological variation throughout the geographic range of the tropical shad, hilsa *Tenualosa ilisha*. Fisheries Research 66: 53–69

Sarre GA, Potter IC (2000) Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors. Fishery Bulletin 98: 785–799

Saul P, Holdsworth J (1992) Co-operative gamefish tagging in New Zealand waters, 1975–1990. New Zealand Fisheries Technical Report No. 33.

Sawynok W (2005) Austag Research Report 2004–2005. Australian National Sportfishing Associated Ltd and Infofish Services, Frenchville, Queensland, Australia

Schaffler JJ, Reiss CS, Jones CM (2009) Spatial variation in otolith chemistry of Atlantic croaker larvae in the Mid-Atlantic Bight. Marine Ecology Progress Series 382: 185–195

Secor DH, Rooker JR (2000) Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fisheries Research 46: 359–371

Secor DH, Rooker JR (2005) Connectivity in the life histories of fishes that use estuaries. Estuarine Coastal and Shelf Science 64: 1–3

Shaklee JB, Salini J, Garrett RN (1993) Electrophoretic characterization of multiple genetic stocks of barramundi perch in Queensland, Australia. Transactions of the American Fisheries Society 122: 685–701

Sheaves MJ (1993) Patterns of movement of some fishes within an estuary in tropical Australia. Australian Journal of Marine and Freshwater Research 44: 867–880

Sheaves MJ, Brodie J, Brooke B, Dale P, Lovelock C, Waycott M, Gehrke P, Johnston R, Baker R (2007) Vulnerability of coastal and estuarine habitats in the Great Barrier Reef to climate change. In: Johnson JE, Marshall PA (eds) Climate Change and the Great Barrier Reef: A Vulnerability Assessment. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Australia, pp 593–620

Sheaves MJ, Molony BW, Tobin AJ (1999) Spawning migrations and local movements of a tropical sparid fish. Marine Biology 133: 123–128

Shulman MJ, Bermingham E (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. Evolution 49: 897–910

Silberschneider V, Gray CA, Stewart J (2009) Age, growth, maturity and the overfishing of the iconic sciaenid, *Argyrosomus japonicus*, in south-eastern, Australia. Fisheries Research 95: 220–229

Silva A, Carrera P, Masse J, Uriarte A, Santos MB, Oliveira PB, Soares E, Porteiro C, Stratoudakis Y (2008) Geographic variability of sardine growth across the northeastern Atlantic and the Mediterranean Sea. Fisheries Research 90: 56–69

Sinclair AF, Swain DP, Hanson JM (2002) Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. Canadian Journal of Fisheries and Aquatic Sciences 59: 372–382

Sinclair DJ, J. KLP, McCulloch MT (1998) High resolution analysis of trace elements in corals by laser ablation ICPMS. Geochimica et Cosmochimica Acta 62: 1889–1901

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236: 787–792

Smith PJ, Francis R, McVeagh M (1991) Loss of genetic diversity due to fishing pressure. Fisheries Research 10: 309–316

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60: 1129–1157

Sokal RR, Rohlf FJ (1995) Biometry: The Principles and Practice of Statistics in Biological Research W.H, Freeman, San Francisco

Somers IF (1994) Species composition and distribution of commercial penaeid prawn catches in the Gulf of Carpentaria, Australia, in relation to depth and sediment type. Australian Journal of Marine and Freshwater Research 45: 317–335

Somers IF, Long BG (1994) Note on the sediments and hydrology of Gulf of Carpentaria, Australia. Australian Journal of Marine and Freshwater Research 45: 283–291

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munroe JL (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70: S341–S375

Staunton-Smith J, Robins JB, Mayer DG, Sellin MJ, Halliday IA (2004) Does the quantity and timing of freshwater flowing into a dry tropical estuary affect year-class strength of barramundi (*Lates calcarifer*)? Marine and Freshwater Research 55: 787–797

Steer MA, Fowler AJ, Gillanders BM (2009) Age-related movement patterns and population structuring in southern garfish, *Hyporhamphus melanochir*, inferred from otolith chemistry. Fisheries Management and Ecology 16: 265–278

Stevens JD, Pillans RD, Salini J (2005) Conservation assessment of *Glyphis* sp. A (speartooth shark), *Glyphis* sp. C (northern river shark), *Pristis microdon* (freshwater sawfish) and *Pristis zijsron* (green sawfish). Final Report to Department of the Environment and Heritage. CSIRO, Cleveland, Queensland, Australia

Stransky C, Baumann H, Fevolden SE, Harbitz A, Hoie H, Nedreaas KH, Salberg AB, Skarstein TH (2008) Separation of Norwegian coastal cod and Northeast Arctic cod by outer otolith shape analysis. Fisheries Research 90: 26–35

Sumpton WD, Sawynok B, Carstens N (2003) Localised movement of snapper (*Pagrus auratus*, Sparidae) in a large subtropical marine embayment. Marine and Freshwater Research 54: 923–930

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402: 799–802

Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR (2002) Evidence of self-recruitment in demersal marine populations. Bulletin of Marine Science 70: 251–271

Taylor MW, Laffan SD, Fielder DS, Suthers IM (2006) Key habitat and home range of mulloway *Argyrosomus japonicus* in a south-east Australian estuary: finding the estuarine niche to optimise stocking. Marine Ecology Progress Series 328: 237–247

Taylor NG, Walters CJ, Martell SJD (2005) A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Canadian Journal of Fisheries and Aquatic Sciences 62: 215–223

Thorrold SR, Jones CM, Swart PK, Targett TE (1998) Accurate classification of juvenile weakfish *Cynoscion regalis* to estuarine nursery areas based on chemical signatures in otoliths. Marine Ecology Progress Series 173: 253–265

Thorrold SR, Jones GP, Hellberg ME, Burton RS, Swearer SE, Neigel JE, Morgan SG, Warner RR (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bulletin of Marine Science 70: 291–308

Thorrold SR, Jones GP, Planes S, Hare JA (2006) Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 63: 1193–1197

Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal homing in a marine fish metapopulation. Science 291: 297–299

Thresher RE (1999) Elemental composition of otoliths as a stock delineator in fishes. Fisheries Research 43: 165–204

Tilburg CE, Dittel AI, Epifanio CE (2007) Retention of crab larvae in a coastal null zone. Estuarine Coastal and Shelf Science 72: 570–578

Tilburg CE, Seay JE, Bishop TD, Miller HL, Meile C (2010) Distribution and retention of *Petrolisthes armatus* in a coastal plain estuary: the role of vertical movement in larval transport. Estuarine Coastal and Shelf Science 88: 260–266

Timi JT, Lanfranchi AL, Etchegoin JA (2009) Seasonal stability and spatial variability of parasites in Brazilian sandperch *Pinguipes brasilianus* from the Northern Argentine Sea: evidence for stock discrimination. Journal of Fish Biology 74: 1206–1225

Timi JT, Lanfranchi AL, Etchegoin JA, Cremonte F (2008) Parasites of the Brazilian sandperch *Pinguipes brasilianus* Cuvier: a tool for stock discrimination in the Argentine Sea. Journal of Fish Biology 72: 1332–1342

Tobin D, Wright PJ, Gibb FM, Gibb IM (2010) The importance of life stage to population connectivity in whiting (*Merlangius merlangus*) from the northern European shelf. Marine Biology 157: 1063–1073

Tolan JM, Fisher M (2009) Biological response to changes in climate patterns: population increases of gray snapper (*Lutjanus griseus*) in Texas bays and estuaries. Fishery Bulletin 107: 36–44

Trippel EA, Kjesbu OS, Solemdal P (1997) Effects of age and size structure on reproductive output in marine fishes. In: Chambers CR, Trippel EA (eds) Early Life History and Recruitment in Fish Populations. Chapman & Hall, New York, pp 31–62

Ubeda AJ, Simpfendorfer CA, Heupel MR (2009) Movements of bonnetheads, *Sphyrna tiburo*, as a response to salinity change in a Florida estuary. Environmental Biology of Fishes 84: 293–303

Underwood AJ (1997) Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge

Valiela I, Bowen JL, York JK (2001) Mangrove forests: one of the world's threatened major tropical environments. BioScience 51: 807–815

Van Achterbergh E, Ryan C, Jackson S, Griffin W (2001) Data reduction software for LA–ICPMS. In: Sylvester P (ed) Laser-Ablation–ICPMS in the Earth Sciences: Principles and Applications. Mineralogical Association of Canada, Ottawa, pp 239–243

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR (1998) Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six year study. Marine Ecology Progress Series 163: 21–36

Vance DJ, Staples DJ, Kerr JD (1985) Factors affecting year-to-year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia. Journal Du Conseil International pour l'Exploration de la Mer 42: 83–97

Vasconcelos RP, Reis-Santos P, Tanner S, Fonseca V, Latkoczy C, Gunther D, Costa MJ, Cabral H (2007) Discriminating estuarine nurseries for five fish species through otolith elemental fingerprints. Marine Ecology Progress Series 350: 117–126

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277: 494–499

Waldman JR (1999) The importance of comparative studies in stock analysis. Fisheries Research 43: 237–246

Waldman JR, Cadrin SX, Friedland KD (2005) Definition of stocks: an evolving concept. In: Cadrin SX, Friedland KD, Waldman JR (eds) Stock Identification Methods: Applications in Fishery Science. Elsevier Academic Press, Burlington, MA, pp 7–16

Waldman JR, Grossfield J, Wirgin I (1988) Review of stock discrimination techniques for striped bass. North American Journal of Fisheries Management 8: 410–425

Walther BD, Thorrold SR (2006) Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Marine Ecology Progress Series 311: 125–130

Ward P, Caton A (1992) Why tag and release tunas? Australian Fisheries 51: 6–8

Warner RR (1988) Sex change and the size-advantage model. Trends in Ecology & Evolution 3: 133–136

Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms and consequences. Bulletin of Marine Science 70: S245–S249

Warner RR, Swearer SE, Caselle JE, Sheehy M, Paradis G (2005) Natal trace-elemental signatures in the otoliths of an open-coast fish. Limnology and Oceanography 50: 1529–1542

Watson JR, Hays CG, Raimondi PT, Mitarai S, Dong C, McWilliams JC, Blanchette CA, Caselle JE, Siegel DA (2011) Currents connecting communities: nearshore community similarity and ocean circulation. Ecology 92: 1193–1200

Welch DJ, Gribble N, Garrett R (2002) Assessment of the Threadfin Salmon Fishery in Queensland - 2002. Queensland Government Department of Primary Industries and Fisheries, Cairns, Australia

Whitfield AK (2005) Fishes and freshwater in southern African estuaries - a review. Aquatic Living Resources 18: 275–289

Williams AJ, Davies CR, Mapstone BD (2006) Regional patterns in reproductive biology of *Lethrinus miniatus* on the Great Barrier Reef. Marine and Freshwater Research 57: 403–414

Williams AJ, Mapstone BD, Davies CR (2007) Spatial and interannual patterns in growth of an exploited coral-reef fish. Journal of Fish Biology 71: 970–992

Wolanski E (1993) Water circulation in the Gulf of Carpentaria. Journal of Marine Systems 4: 401–420

Yoshinaga J, Nakama A, Morita M, Edmonds JS (2000) Fish otolith reference material for quality assurance of chemical analyses. Marine Chemistry 69: 91–97

Zischke MT, Cribb TH, Welch DJ, Sawynok W, Lester RJG (2009) Stock structure of blue threadfin *Eleutheronema tetradactylum* on the Queensland east coast, as determined by parasites and conventional tagging. Journal of Fish Biology 75: 156–171