Movements and activity patterns of luderick (*Girella tricuspidata*): drivers and spatial scales

by

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CERTIFICATE OF AUTHORSHIP/ORIGINALITY

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TABLE OF CONTENT

LIST OF TABLES

LIST OF FIGURES

Figure 2.5 Daily mean temperature in C° (dashed line) and conductivity in mS cm^{-1} (grey line) on the left Y-axis) and daily river discharge in m^3 s^{-1} (dotted line) on the right Y-axis monitored from 1/11/2010 to 30/09/2013 in three estuaries in SE Australia in which luderick were tagged. Black diamonds indicate the date of the last detection of the fish that had left each system. GR: Georges River (tagging period: 01/02 and 01/03/2012, Fig. 2.5a); SR: Shoalhaven River (tagging periods: 06/02-16/02/2012 and 02/10/2012, Fig. 2.5b); CR: Clyde River (tagging period: 03/04-17/04/2012, Fig. 2.5c). The horizontal solid line marks the high flow threshold for each estuary.

Figure 3.1 Maps of the three estuaries studied (GR: Georges River, SR: Shoalhaven River and CR: Clyde River), showing the linear arrays of receivers, the position of data loggers, and the tagging sites.

Figure 3.2 Histograms of the daily average fish distribution along the length of the three studied estuaries.

Figure 3.3 Modal distance-to-sea (*Modal_Dist*) (a) (black line: significant simple linear regression) and linear distance (km) along the estuary containing the 50^{th} (b) and the 90^{th} (c) percentile of the kernel density distribution (KDE 50% and KDE 90%, respectively), according to the fish length (FL, mm).

Figure 3.4 Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line) on the left Y-axis, and mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis, between January 2011 and October 2013, for each estuary (GR: Georges River (a), SR: Shoalhaven River (b) and CR: Clyde River (c)).

Figure 3.5 Frequencies of detection of luderick (daily averages per fish) according to the temperature (°C) (a) and conductivity (mS cm^{-1}) (b) recorded by the data loggers deployed mid-water (three estuaries combined).

Figure 3.6a Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line), and mean daily distance-to-sea on (km) of Fish #9, #10 and #13 on the left

Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Georges River.

Figure 3.6b Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line), and mean daily distance-to-sea on (km) of Fish #21, #23 and #30 on the left Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Shoalhaven River. (*): fish redetected outside the tagging estuary.

Figure 3.6c Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line) and mean daily distance-to-sea on (km) of Fish #50, #58 and #61 on the left Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Clyde River. (*): fish redetected outside the tagging estuary.

Figure 4.1 Map of the study area showing the two VPS networks, the estuarine array, tagging sites and the distribution of the main habitats (seagrass, saltmarshes and mangroves).

Figure 4.2 Acceleration (top) and depth (bottom) across diel period (day and night) and tidal phase (error bars correspond to the S.E.).

Figure 4.3 Number of detections per depth categories. The fish were detected in reference to the bottom (percentage of the difference between depth obtained by the AP tags and the river bathymetry divided by the river bathymetry at the point of detection).

Figure 4.4 Fish depths expressed in percentages and divided into 4 categories (Cat 1=bottom (<10%), Cat 2=10-30%, Cat 3=30-90% and Cat 4=surface (>90%), % relative depths) across diel (day and night) and tidal (high and low) periods.

Figure 4.5 Fourier analysis of detection periodicity for activity (a) and pressure (b). (FFT based on 1024 frequencies but truncated at 205 and 512 for activity and pressure, respectively, for visualisation purposes).

GENERAL ABSTRACT

A thorough knowledge of fish movements and the factors influencing them is essential to understanding the ecology of a species, and underpins effective management actions and planning. This thesis aims to understand the movement patterns of the temperate fish species luderick (*Girella tricuspidata*), which inhabits estuaries and near coastal shallow rocky reefs of New South Wales (NSW; SE Australia) and is of high commercial and recreational fishing interest. Although the biology and ecology of this primarily herbivorous teleost fish are already documented, movements and their drivers are poorly known.

I used acoustic telemetry to address different aspects of the movements of mature luderick at various spatio-temporal scales. Using an extensive collaborative network of acoustic receivers spread along the NSW coast and in selected estuaries, I identified that large freshwater inflows resulting from heavy rainfalls were the main drivers of luderick estuarine movements: (i) they triggered fish departure from the systems and coastal migrations; (i) these events and associated changes in conductivity drove movements along estuaries; (i) and luderick decreased swimming activity and shifted in depth during high flow events.

Tagged luderick detected outside their tagging estuary (13 out 61 individuals) migrated predominantly in a northward direction, suggesting spawning migrations. Luderick travelled up to 492 km, and at speeds exceeding 57 km d^{-1}. This swimming velocity corresponds to the optimal metabolic speed estimated in laboratory experiments. Migrating luderick could visit multiple estuaries, and individuals from different estuaries converged to similar coastal areas, providing further understanding of luderick estuarine connectivity. Partial population migration may explain the inter-individual variability in estuarine residency and large-scale movements of luderick. This behaviour may provide further resilience to harvesting and changing environments.

Strong diel and sub-diel rhythms in activity were found, with luderick being more active during the day compared to the night. Luderick field metabolic rates increased from dawn and throughout the day, until they declined after dusk, which could be related to diurnal foraging activity and nocturnal sheltering behaviour.

Swimming activity decreased with temperature, and while effects of seasonality could not be fully addressed in this study, it is predicted that movement patterns of luderick would vary across seasons and years, driven by fluctuations in temperatures and rainfall regimes.

This thesis provides an understanding of luderick movement patterns and their drivers, and shows that luderick respond to changing environment by adopting a range of behavioural responses. These findings will improve the management of this species and its fishery.

CHAPTER 1: General introduction

1.1 Animal movement

The mechanisms governing animal movements and their motivations have inspired researchers for more than 2000 years. In the 4th century B.C., the Greek philosopher Aristotle, in his *De Motu Animalium*, discussed the general principles of motion in animals. More recently, with the aim of unifying the research related to the movement of organisms, a group of researchers developed a new field of research, called "movement ecology" (Holden, 2006; Nathan et al., 2008). Animal movement can be defined as a change of location at the individual level. Starting from this broad and simple definition, movement can then be considered through a much more complex approach. For instance, the framework of "movement ecology" consists of four components contributing to the movement of organisms: (i) the internal state (motivation, physiology), (ii) the motion (ability to move); (iii) navigation capacities (ability to orient and to locate) and (iv) the external environmental factors (abiotic and biotic) that influence (i) and (ii) (Nathan et al., 2008). Understanding animal movements requires the observation of patterns and the search for explanations regarding what causes the observed movements. The literature dealing with movement of organisms is extensive; however, in most of the studies, the movements are only described and measured and are not often linked to ecological and physiological factors (Holyoak et al., 2008).

Animal movement is an important ecological process that determines the spatial distribution and the genetic structure of populations and also plays a role in trophic interactions (Pittman and McAlpine, 2001). It is well recognised that animal movements, especially migration and dispersal, have an important role in the distribution and the persistence of biodiversity (Trakhtenbrot et al., 2005; Jeltsch et al., 2013). Therefore, a thorough knowledge of animal movement is important in the study of species' ecology and also an essential component to take into account when making decisions concerning species management and biodiversity conservation (Driscoll et al., 2014).

1.2 Types of fish movements

Marine fish taxa show a large variation in movement patterns in space and time during their lifetime. Therefore, a thorough understanding of fish movements at different spatio-temporal scales is essential for appropriate design and location of Marine Protected Areas (MPAs) and the management of fish stocks (Zeller and Russ, 1998; Pittman and McAlpine, 2001; Palumbi, 2004; Gaines et al., 2010). The selection of adequate spatial and time scales with regard to the questions addressed is important (Schneider, 2001) and the study of fish movements at these different scales require the use of appropriate methods.

Many fish species have a multi-phase life cycle. Specific movements are related to the ontogenetic phases and can be classified into five categories: (i) movements of eggs and larvae; (ii) ontogenetic shifts; (iii) home range movements; (iv) relocation of home range and (v) migrations (Pittman and McAlpine, 2001).

Movements of eggs and larvae and ontogenetic shifts

The movements of eggs and larvae result from a combination of passive transport by hydrodynamic processes (e.g. currents) and active larval behaviour (e.g. swimming and orientation) (Boehlert and Mundy, 1988; Leis et al., 1996). These movements play an important role in dispersal of individuals and population structure (Cowen and Sponaugle, 2009; Jones et al., 2009; Planes et al., 2009).

Ontogenetic shifts in movement behaviours are an important ecological process to understand for species conservation and management, as well as population structure. During their life cycle, organisms change morphologically and physiologically (Ebenman, 1992). The increase in body size with age is often associated with changes in refuge requirements, predation pressure, mobility, diet, reproductive condition and therefore, the response to these pressures involve modifications in movement patterns and shifts in habitats (Dahlgren and Eggleston, 2000).

Home range and associated movements

The concept of home range has been defined and developed by terrestrial-mammal researchers. The earliest definition of home range was developed by the mammologist W.H. Burt who defined it as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). This definition has been refined as "the area over which the animal normally travels" (Hayne, 1949; Gerking, 1953). This initial concept of home range has been translated into mathematical models evaluating the probability of finding an animal in a defined area within its home range (Jennrich and Turner, 1969). Within the home range, one or several core areas can be identified, often corresponding to sites of different activities (e.g. foraging, resting).The size of a home range of a fish is usually related to the body size (see reviews by Kramer and Chapman (1999) and Pittman and McAlpine (2001)), and therefore usually increases through ontogeny. The density of predators and the resource availability are also common factors defining the size of home ranges (Hixon, 1987; Kramer and Chapman, 1999). These daily excursions within the home range can be motivated by feeding and predator avoidance. Some species such as species from the Haemulidae and Lutjanidae families forage at night, usually to avoid predation, in areas separated from their day-time refuges (Nagelkerken et al., 2000a), whereas others (e.g. bluefin trevally *Caranx melampygus*) exhibit the opposite pattern (Holland et al., 1996). Diel activity is frequently coupled to dietary needs, with for instance, herbivorous fish species being often diurnal feeders (Helfman, 1993). Therefore, in fish movement studies, it is important to consider both diurnal and nocturnal observations as a species may exhibit marked diel movements.

Migrations (non-spawning and spawning)

Migration refers mostly to highly directional and synchronized movements of populations to defined areas in relation to seasonal changes (non-spawning migrations) and to breeding requirements implicating the need to move towards areas situated outside the home range (spawning migrations) (Pittman and McAlpine, 2001).

1.3 Environmental factors influencing fish movement and importance of habitat

In general, for many species, the relationship between fish movements and the surrounding environment, including aspects of habitat use, are poorly known, and represent information gaps for effective conservation and resource management (Whitfield and Cowley, 2010; Barton et al., 2015). Understanding fish movement patterns and the factors (biotic and abiotic) influencing them is essential because they play an important role in the distribution of the fish and this has implications for the management of fisheries resources (e.g. planning and forecasting).

Fish movements are influenced by internal and external factors, with effects over a range of different spatial and temporal scales. For instance, migrations usually rely on internal (e.g. gonad development (Taylor et al., 2014)) and external (environmental) signals such as seasonal changes in temperature (Ware and Tanasichuk, 1989; Sims et al., 2004), photoperiod (Quinn and Adams, 1996) or moon phase (Meyer et al., 2007; Starr et al., 2007), and meteorological conditions altering local environmental conditions (e.g. wind regimes altering currents (Hutchings et al., 1998)).

Fluctuations in environmental parameters can be either rhythmic (e.g. seasonal, lunar, sub-lunar, diel or sub-diel; (Morgan, 2001; Pittman and McAlpine, 2001)) or arrhythmic (e.g. stochastic events), and may vary over different temporal scales, from hours to years (Cloern and Nichols, 1985). Seasonal changes in temperature can provoke non-spawning migrations whereby fishes avoid adverse conditions. For instance, the pipefish *Syngnathus fuscus* undertakes seasonal migrations between estuary and offshore waters to avoid cold water during the winter, before returning inshore when the water temperature is more clement (Lazzari and Able, 1990).

Estuaries are highly dynamic and variable systems. For many species present in these systems, the fluctuations in temperature, turbidity, and salinity (e.g. freshwater inputs), as well as the tide (and tidal currents), influence their movement ranges and directions (Pittman and McAlpine, 2001; Childs et al., 2008; Taylor et al., 2014). For euryhaline species which tolerate a wide range of salinities, fluctuations of salinity may play a limited role (Childs et al., 2008). The tide is an important factor to take into account in the study of fish movements in estuarine systems, as most species of fish move with the tidal flow and ebb. For instance, the movements of juvenile summer flounder

Paralichthys dentatus (Szedlmayer and Able, 1993) or mulloway *Argyrosomus japonicus* (Naesje et al., 2012) are in phase with the tide in terms of amplitude and direction in response to the characteristics of the tide.

Many coastal and estuarine fish species show preferences for particular habitats (Gratwicke et al., 2006; Shibuno et al., 2008). Therefore a thorough knowledge of the distribution of habitat and their use by fish species is a fundamental component in understanding fish ecology and in the management of exploited species. Alterations in quality and distribution of habitats may directly affect fish populations in terms of distribution (e.g. relocation), life cycle (e.g. nursery habitats), population connectivity (e.g. decrease of gene flow) and resilience (Beck et al., 2001; Gillanders et al., 2003; Dahlgren et al., 2006; Lipcius et al., 2008). Discontinuities in habitats (habitat fragmentation) can act as natural barriers and can consequently affect the range of fish movement (Kramer and Chapman, 1999) and the functional connectivity in a fragmented landscape (Taylor et al., 1993). Consequently, a species with a limited range of movement and a high preference for a certain type of habitat will likely be more vulnerable to habitat loss or exploitation compared to species that are habitat generalists.

1.4 Methods used to study fish movements

The challenge in subtidal studies is the limited access to the research environment, especially when the visibility conditions are poor, as often occurs in estuaries. To study movements of mobile fish and their relation to habitat, researchers and engineers have developed methods and technologies to overcome these environmental limitations. These methods and technologies can either be direct or indirect (Simpfendorfer and Heupel, 2004), fisheries-dependant or independent (Murphy and Jenkins, 2010) and destructive or non-destructive (Gillanders et al., 2003).

Among them, biotelemetry and biologging are technologies widely used by researchers studying fish movements (Cooke et al., 2013; Hussey et al., 2015). These methods typically provide detailed information of the spatial locations occupied by individuals repeatedly through time. Telemetry methods have been applied to numerous fish species

under a variety of environmental conditions, providing data that can usually not be obtained by other means (Murphy and Jenkins, 2010).

Biotelemetry consists of tracking or monitoring of free-ranging animals, using electronic devices that receive signals from a transmitter fitted inside or onto the animal. A wide range of equipment and types of transmitters are applied for tracking and monitoring fish, such as radio tags, satellite tags and acoustic tags, all enabling different applications depending on the species studied and the spatial scale of movements (see reviews by Murphy and Jenkins (2010) and Cooke et al. (2013)). In this chapter, I will focus on acoustic telemetry, as this method permits the study of fish movements at various spatial scales and is adapted to study coastal fish movements, whereas radiotelemetry is mostly confined to freshwater and terrestrial applications and satellite telemetry to surfacing marine species.

The principle of acoustic telemetry surveys in fish studies relies on fitting individuals with tags emitting acoustic signals with unique identification codes which can be identified by listening stations or receivers. This technology can be used in two ways: active tracking and passive monitoring, using different types of tags and equipment.

Acoustic telemetry has been widely used during the last decades to study movements of fish individuals in freshwater and marine environments. This technology has been employed successfully to study a wide range of fish movements, such as home ranges and site fidelity, diel movements, habitat use and preferences, as well as migrations (Meyer et al., 2000; Lowe et al., 2003; Egli and Babcock, 2004; Heupel et al., 2004; Hedger et al., 2009; Meyer et al., 2010; Cooke et al., 2013; Payne et al., 2013; Currey et al., 2015). Some studies monitored movements across boundaries, such as MPAs, where it was used to evaluate exportation and importation of fish from and to protected areas (Parsons et al., 2010). In the last decades acoustic telemetry has been commonly employed to study movements of a large range of aquatic animals from small invertebrates (Taylor and Ko, 2011), cephalopods (Payne et al., 2011), amphibians (Letnic et al., 2014), sea snakes (Udyawer et al., 2015), to large species such as whale sharks (Cagua et al., 2015).

Active tracking

High resolution data of movement patterns of individuals can be obtained by actively tracking the tagged fish from a vessel (powered (by petrol or electric motors) or not powered (e.g. kayak)) using a receiver coupled with a hydrophone (Holland et al., 1992). This kind of acoustic telemetry is also particularly suited for determining habitat associations by overlaying habitat maps on movement data (Simpfendorfer and Heupel, 2004). Acoustic tracking holds the advantage of avoiding potential alteration of the fish behaviour in response to the presence of the observer and, allow the collection of continuous precise data on fish movements over diel periods, including at night, without any restriction related to poor visibility, which could make diving unsafe. However this method is time and logistically demanding (personnel and equipment availability, cost, etc.) and therefore, the duration of continuous tracking sessions rarely extends beyond 48 h (Simpfendorfer and Heupel, 2004)).

Passive monitoring

Automated tracking is based on the deployment of a network of receivers at strategic locations and the use of tags, each of them differentiated with a unique code. Each time a tagged fish comes within the range of a listening station (receiver), the code emitted by its tag is transmitted and stored in the station (Heupel et al., 2006). For comparable sizes, coded tags have a longer battery life than the tags used for active tracking due to less frequent signal emission requirements (minutes instead of seconds).

Depending on the size of the tag and the emission rate, the battery can last from a few weeks to over 10 years. Therefore, this technique is versatile across spatial scales and over long periods, as long as a tagged fish comes within the detection range of a receiver. The design of the receivers' network (array) has to be developed in relation to the objectives of the study in order to provide the desired information on movement patterns at a suitable spatial scale. In their review about acoustic monitoring, Heupel et al. (2006) distinguished two types of receiver arrangements: regular or irregular grid systems, and gates or curtains. Grid networks have been employed to study movement patterns over defined home ranges, site fidelity, habitat use and movements between MPA and adjacent waters. The range detection of the receivers can overlap (Topping et

al., 2006; Chateau and Wantiez, 2008), overlap partially (Egli and Babcock, 2004) or be separated by a greater distance than the detection range to yield a larger study area (Parsons et al., 2010). The array design is a trade-off between coverage and detection potential.

Curtains and gates are adapted to detect movements across a boundary. Curtains consisting of lines of receivers can be deployed to detect the passage of a tagged fish across a zone of management interest (spawning area or MPA (Heupel et al., 2006; Murphy and Jenkins, 2010)). When set perpendicular to the shore, curtains can be used to detect movements along the coast (Lacroix et al., 2005; Luo et al., 2009; Callihan et al., 2015). However, to detect whether the individual crossed the line and get information on the swimming direction, a single curtain is not enough. This case requires the use of several curtains, or a combination of grid and curtain (Heupel et al., 2006).

Gates can be set across the entrance of a bay or at the mouth of an estuary to completely close the system and thereby detect departure and entry from and into the coastal system (Heupel et al., 2006; Kerwath et al., 2009). Linear arrays of receivers are also adapted to deployments along estuaries and rivers to study the up and downstream movements in relation to environmental parameters (Childs et al., 2008; Walsh et al., 2013; Taylor et al., 2014; Bennett et al., 2015). Single independent receivers can also be stretched along the coast line to detect movements of fish following the coast line. This design has been deployed in Hawaii, where the coastal slope is very steep, resulting in an array stretching over more than 100 km, dedicated to the study of reef fish movements (Meyer et al., 2010).

Positioning systems using acoustic receivers have been developed for fine-scale movement studies (e.g. measure of home ranges and core activity areas), concerning usually small areas (less or equal to a square kilometre (O'Dor et al., 1998; Klimley et al., 2001; Tolimieri et al., 2009)). While independent acoustic receivers record the code and the detection time of a tag when it is within their detection range (several hundred meters), these positioning systems calculate the position of the tagged fish by triangulation using several receivers. The buoys of the radio acoustic positioning telemetry system (RAPT) provide real time positions to a base via radio signals or cable

with an accuracy of up to ± 2 m (Jorgensen et al., 2006). The more recently developed VEMCO positioning system (VPS - VEMCO Ltd, Halifax, Canada) responds to the need for fine-scale resolution in position data, particularly indicated for behavioural studies (Espinoza et al., 2011a; Furey et al., 2013). The VPS positioning of tagged individuals relies on the 3-receiver time difference-of-arrival (TDOA) algorithm (O'Dor et al., 1998; Voegeli et al., 2001), and therefore, raw detection need to be post-processed by VEMCO to obtain the calculated positions (Espinoza et al., 2011b).

The limitations of passive monitoring are mainly due to the fact that fish positions (detections) can only be obtained if a tagged fish comes within the range of a receiver. Additionally, passive monitoring is limited in time due to the battery life of the transmitters (proportional to the size of the tag and the signal emission rate). Detection ranges of acoustic receivers can differ greatly depending on the environment, and fluctuate with changing surrounding conditions (Gjelland and Hedger, 2013; Kessel et al., 2014).

Acoustic tags can be fitted externally (Holland et al., 1996; Meyer and Holland, 2005) or internally in the gut cavity (Egli and Babcock, 2004; Topping et al., 2006). The decision on how to fit an acoustic tag (externally or internally) depends on the duration of the survey (external attachment is recommended only for few months) and the capacity of the species to support external tags and surgery. Although the miniaturisation of acoustic tags permits researchers to study smaller and smaller species, acoustic telemetry still has limitations in the study of very small bodied species.

Acoustic telemetry presents a very high potential towards the study of fish movements and is used worldwide. Since passive monitoring became more popular with users employing compatible systems, increasing numbers of collective networks of receivers have been appearing, such as the Atlantic Cooperative Telemetry (ACT) Network (http://www.theactnetwork.com/home), the Ocean Tracking Network (OTN, http://oceantrackingnetwork.org) or the IMOS Animal Tracking facility (https://aatams.emii.org.au/aatams/) (Callihan et al., 2015; Hussey et al., 2015). These collaborative networks and associated databases allow to decrease costs (initial purchase and maintenance of receivers) and have access to large networks of receivers, which

becomes particularly relevant for the study of large-scale movements such as migrations.

Linking animal movements to its environment and physiology - biologging

Biologging refers to the practice of logging and relaying physical and/or biological data using devices attached to animal (Hooker et al., 2007; Rutz and Hays, 2009). Biologging devices can be loggers that need to be retrieved (e.g. archival tags) or transmitters providing measured data remotely (e.g. acoustic transmitters, satellite tags) (Payne et al., 2014; Hussey et al., 2015). Biologging opened new fields of research allowing to link movements and behaviours of free-ranging animals to their surrounding environment and physiological aspects (Cooke et al., 2008; Hussey et al., 2015). Biologging also enabled the collection of environmental data such as oceanic physico-chemical information using animals roaming their environment to collect data in remote areas (Bailleul et al., 2015).

The increase in popularity of acoustic tracking technology and the miniaturisation of the components permits the development of devices equipped with pressure sensors, accelerometers measuring the activity of the animal (Murchie et al., 2011; Payne et al., 2015c) and others recording temperature or heart rate (Block, 2005; Clark et al., 2010; Payne et al., 2014). Body acceleration is considered as a good proxy for the estimation of energy expenditure during locomotion (Halsey et al., 2009). Therefore, acceleration measured by transmitters or loggers can be used to determine metabolic costs of the measured movements of individuals in their natural environment (Gleiss et al., 2011; Halsey et al., 2011). Metabolic costs associated with movement in fish can be estimated by calibrating accelerometers in systems measuring the oxygen consumption at different levels of swimming effort and applying the results to acceleration data of free-ranging fish (Lowe, 2002; Wilson et al., 2013; Wright et al., 2014).

1.5 Analysis of fish movement data

There is a large range of methods and tools available to analyse movement data. Movements of individuals can simply be expressed and analysed by path length, direction, duration and speed. The development of software dedicated to spatial analysis (e.g. Geographic Information System – GIS and associated extensions, R packages) opened up significant possibilities for the analyses of movement data (Pittman and McAlpine, 2001; Kie et al., 2010).

Home ranges can be determined on the basis of a set of spatial positions of an individual collected over a period of time. Several models, non-statistical and statistical, have been developed to calculate home ranges (see reviews by Worton (1987) and Kie et al. (2010)). The kernel density estimation (KDE) based method is commonly used to describe the utilisation of the activity space by the individual (Worton, 1989; Seaman and Powell, 1996). It gives the probability of finding an animal in a defined area within its home range with, commonly, the 95% kernel density providing an estimate of the home range (or 90% for a more conservative estimation) and 50% kernel density describing the animal core area (e.g. (Afonso et al., 2008)). Home range determinations using methods based on KDE estimates remain very popular and are widely used due to their simplicity and applicability for large datasets (Kie et al., 2010).

The advances in technologies dedicated to animal tracking and telemetry, and especially with the emergence of the global position system (GPS) technology, permit the collection of precise (m's) and numerous position data (Tomkiewicz et al., 2010). Concomitant with the popularisation of the use and access to GIS and other software such as R, the increasing needs for the analysis of large animal movement datasets has led to the development of a variety of tools dedicated to this purpose (Urbano et al., 2010). Many of these tools and packages were developed by an active community and most of them are made publicly available (e.g. Fish tracker (Laffan and Taylor, 2013); all R packages).

Modelling animal movements according to biotic and abiotic factors helps at determine which factors influence the observed movements, especially when multiple factors potentially have synergetic, antagonist, or correlated effects. Modelling is particularly recommended to determine the contribution of an environmental parameter (e.g. water

temperature, habitat) or a biotic parameter (e.g. size) to the patterns of the movements. A range of model types are commonly used such as mixed models (Borger et al., 2006; Kie et al., 2010).

1.6 Conclusions

Understanding the movement patterns of fish in relation to the factors driving and influencing them is essential to understand the ecology of a species. This information is also important to establish effective conservation programs and to develop appropriate management tools for a sustainable exploitation of these species. Indeed, a thorough knowledge of the movement patterns of a species at various spatial and temporal scales, from large (e.g. population connectivity and seasonal patterns) to finer scales (e.g. habitat preferences and diel patterns) permits to identify important ecological traits of the species in relation to biotic and abiotic factors. This knowledge provides suitable inputs for the spatial conservation (e.g. MPAs, habitat protection areas) and management of commercial and recreational fisheries (e.g. spatial and/or temporal fishing restrictions). As described earlier, a wide range of techniques and tools to study fish movements is available. The selection of the appropriate technique to answer specific scientific questions about a species' movement patterns is usually a trade-off between the spatial scale and temporal resolution needed, the potential factors to be examined, and depends as well as on the logistical and financial support available for the study.

1.7 Thesis aims

This thesis aims to understand the movement patterns of the temperate fish species luderick (*Girella tricuspidata* (Quoy & Gaimard 1824); Girellidae) at different spatial scales and in relation to environmental parameters and habitat. Luderick is a temperate teleost species found in estuaries and coastal waters of south east Australia and north New Zealand (Jones, 1988; Kailola et al., 1993; Miskiewicz and Trnski, 1998). Luderick is an abundant species in New South Wales (NSW; SE Australia) and it is present year-round in estuaries and near coastal shallow rocky reefs. Luderick recruits preferably in estuarine seagrass beds (Smith and Sinerchia, 2004) and juveniles show preferences for similar habitats (Middleton et al., 1984; Ferrell and Bell, 1991; Hannan and Williams, 1998; Smith and Sinerchia, 2004), although they are also found on shallow coastal reefs. Luderick is primarily herbivorous (Clements and Choat, 1997), feeding preferentially on green algae *Ulva* spp. and rhodophytes (Anderson, 1987; 1991; Raubenheimer et al., 2005; Ferguson et al., 2015). Although there is some evidence that some individuals may have relatively restricted movement patterns (Gray et al. 2012; Ferguson et al. 2016), adult luderick have been considered highly mobile with tagged fish detected up to 455 km from their tagging site (Thomson 1959; Gray et al. 2012).

Luderick is of commercial and recreational fishing interest, ranking second in terms of catches (in tonnage) in NSW estuarine fisheries, with a slow declining trend over the last decades (Rowling et al., 2010). Luderick is "fully fished" (NSW fisheries status; Rowling et al., 2010) and there is a need to understand luderick movement dynamics to better understand how to maintain this fishery sustainable. In addition, luderick is primarily herbivorous and most of the studies in NSW looking at movement patterns in relation to environmental parameters to date have concerned iconic carnivorous species (Payne et al., 2013; Taylor et al., 2013; Taylor et al., 2014; Payne et al., 2015c). Being primarily herbivorous, luderick may play an important ecological functional role in shallow coastal habitats, and may also display distinctive movement patterns in relation to its diet. Therefore, the findings on movement patterns of these carnivorous species might not be applicable to luderick, highlighting the need to fill this knowledge gap.

As the recruitment and habitat preferences at early stages are fairly well documented in the case of luderick (Miskiewicz and Trnski, 1998; Smith and Sinerchia, 2004), the

present research focused on adult fish, while acknowledging that movements occurring at early life stages can play an important role in dispersal of individuals and population structure (Cowen and Sponaugle, 2009; Jones et al., 2009; Planes et al., 2009). Movement patterns of free-ranging adult luderick were studied using acoustic telemetry (passive monitoring), a method which offers a large range of possible spatial and temporal resolutions (**Chapter 1**). The choice of this method was also motivated by the comprehensive network of acoustic receivers already existing in NSW (over 500 stations deployed in various systems and spread along 900 km of coastline), allowing me to address specific movement questions at different spatial scales.

Luderick is known to undertake large-scale migrations along the NSW coast, presumably linked to spawning migrations; however both the timing and synchronisation of these movements remain unclear (Gray et al., 2012). Coastal migrations, as well as the degree of connectivity between estuaries, were studied using a collaborative coastal and estuarine network of acoustic receivers (**Chapter 2**). For this research, 67 luderick were tagged and released in four major NSW estuaries spanning a 200-km stretch of the NSW coast. A suite of environmental parameters were measured to determine the factors involved in the egression from the estuarine systems. The drivers and timing of departure from the estuary of the 14 fish that egressed and migrated were identified, the extent of large-scale migrations of these luderick was characterised, and travel speeds were estimated and compared to other species (**Chapter 2**).

Luderick is of high commercial fishing interest, with ~85% of total commercial landing of luderick originating from estuaries (Gray et al., 2010). Understanding luderick estuarine movements in relation to fluctuating estuarine conditions provides valuable information for the management of this species, because changing estuarine conditions may influence the distribution and the catchability of this species. In **Chapter 3**, I examined the effects of freshwater inflow, conductivity and how these changed seasonally on the distribution of 61 acoustically tagged luderick within three estuarine systems, each equipped with a linear array of acoustic receivers. I also explored potential variations in response according to the size of the fish. How climatic variability and potential human alterations may influence estuarine conditions and luderick movements were discussed. The high number of fish tagged and the multiple

estuaries examined allowed the generalisation of my findings to SE Australia (**Chapter 2 and 3**).

The arrays of receivers spaced every 1.3 km on average along the estuary, could not address the fine-scale movements of luderick. This information is important for the understanding the ecology of this species and for its conservation. Ten luderick were monitored using an approach combining the use of accelerometer/pressure (AP) acoustic transmitters deployed within VEMCO Positioning Systems (VPS) (**Chapter 4**). This method permitted an understanding of the drivers of fine spatial and temporal scale activity and depth use patterns in luderick. This approach allowed me to gain greater insight into the behaviour of luderick, allowing the characterisation of endogenous circadian rhythms and responses to environmental drivers in a highly fluctuating environment. Luderick diel activity and depth use were paralleled to those of carnivorous fish species previously studied in SE Australian estuaries.

In addition to the generalisation of the movement patterns across the fish and the systems studied, among-individual variations in movements and responses to external factors were also discussed through this research (**Chapters 2 to 4**).

Understanding energetic expenditure in free-ranging animals is fundamental in the study of animal physiology and ecology. Metabolic rates allow us to attribute a cost to different activities and behaviours, and therefore to assess their efficiencies in terms of energy spent. The calibration of eight accelerometer transmitters in the laboratory enabled me to estimate field active metabolic rates (AMR) of four free-ranging luderick in their natural environment (**Chapter 5**). Field AMR were examined across the 24-h period of the day to reveal patterns in energy use, and discussed in relation to potential specific behaviours. In addition, the optimal speed (speed minimising the cost of transport) was estimated and compared to speeds of migrating luderick (Chapter 2) and of other species. This research on luderick contributes to the wider understanding of the field of research linking ecology and physiology, and offers new perspectives toward further research.

A synthesis and discussion of the key findings of luderick movements and factors influencing them is provided in **Chapter 6**, with a particular focus on climatic changes and the implications for spatial conservation and fisheries management of this species.

This thesis has been presented as a series of 'stand-alone' chapters formatted for publication (either submitted or in preparation). A related published manuscript which includes material from this thesis is also listed below.

Chapter 2:

Cadiou G., Booth D.J., Gray C.A., Knott N.A., and Taylor M.D. (*in revision*). Large-scale coastal migration of *Girella tricuspidata* (Pisces: Girellidae) revealed by acoustic telemetry. *Marine Freshwater research*

Chapter 3

Cadiou G., Booth D.J., Gray C.A., and Taylor M.D. (*in prep.*). Drivers of temporal and spatial estuarine movement patterns in luderick (*Girella tricuspidata*) in south-eastern Australian estuarine systems

Chapter 4

Cadiou G., Booth D.J., Gray C.A., Payne N.L., and Taylor M.D. (*in prep.*). Drivers of activity and depth use of luderick (*Girella tricuspidata*) revealed by acoustic telemetry

Chapter 5

Cadiou G., Booth D.J., Gray C.A., Payne N.L., and Taylor M.D. (*in prep.*). Active metabolic rates in luderick (*Girella tricuspidata*): from laboratory to field estimates

Other

Payne, N. L., Smith, J. A., van der Meulen, D. E., Taylor, M. D., Watanabe, Y. Y., Takahashi, A., Marzullo, T. A., Gray, C. A., **Cadiou, G**., Suthers, I. M. (2016), Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. *Functional Ecology*, 30: 903–912.

CHAPTER 2: Large-scale coastal migration of luderick (*Girella tricuspidata*; Pisces: Girellidae) revealed by acoustic telemetry

Cadiou G., Booth D.J., Gray C.A., Knott N.A., and Taylor M.D. (*submitted**). Large-scale coastal migration of luderick (*Girella tricuspidata*; Pisces: Girellidae) revealed by acoustic telemetry.

2.1 Abstract

For many marine species using estuarine systems, exchanges between estuaries and the ocean and latitudinal movements are still poorly known, with most of the information coming from unidirectional tag-recapture data. This study aimed to understand movement and spatial ecology of the teleost fish luderick (*Girella tricuspidata*, Girellidae) in south-eastern Australia. Sixty-seven adult luderick (mean FL 318 mm ± 41) were tagged with acoustic transmitters in four estuaries, and tracked on a large array of VR2W acoustic receivers (>500) deployed in estuaries and along 900 km of coastline. A suite of environmental variables was monitored concomitantly to the monitoring of luderick movements. Over three years, 14 fish (21%) left the tagging estuary (i.e. the estuary where a fish was tagged) to undertake migrations of up to 500 km, at speeds exceeding 50 km d^{-1}, predominantly in a northward direction. While luderick visited multiple estuaries, there was no evidence of return to the tagging estuary. Departures from the estuaries were generally driven by sudden changes in estuarine conditions due to large freshwater inputs, occurring outside of documented spawning periods, suggesting that egression from estuaries may not be related to reproduction only. These findings show that collaborative receiver arrays contributing data to a centrally accessible database should be widely encouraged among the scientific community using acoustic telemetry.

* in revision, *Marine and Freshwater Research*.

2.2 Introduction

Understanding broad-scale fish movement patterns represents an important element of fisheries research. Managing fisheries resources relies on a thorough knowledge of the life cycle of commercially and recreationally targeted species, and that includes their movement patterns (Zeller and Russ, 1998; Kramer and Chapman, 1999). Large-scale movement patterns are often associated with spawning migration, and occur at specific times of the year when reproductive development is the greatest (Rose, 1993; Block et al., 2005). Harvested species are particularly vulnerable during their spawning migrations, as large numbers of individuals can be removed by fisheries activities when forming large schools or aggregations for spawning (Zeller, 1998; Sala et al., 2001; Sadovy and Domeier, 2005), which may have effects on the reproductive output of the population. Consequently, predicting such migrations is important for implementing relevant spatial and temporal fishing restrictions to maintain sustainable fish resources (Palumbi, 2004; Jensen et al., 2010).

Migrations and seasonal large-scale movements are triggered by a range of endogenous and exogenous factors and often by a combination of both. A combination of internal changes such as the maturation of the gonads and exogenous signals such as seasonal fluctuations of flow can represent drivers of spawning migration (Taylor et al., 2014). These exogenous signals can be, but not limited to: seasonal changes of temperature (Ware and Tanasichuk, 1989; Sims et al., 2004), specific photoperiod (Quinn and Adams, 1996) or moon phase (Meyer et al., 2007; Starr et al., 2007) and meteorological conditions altering local environmental conditions [e.g., wind regimes altering currents (Hutchings et al., 1998)]. In estuarine systems, fish species can display movements in response to tide (and tidal currents) (Taylor et al., 2013), temperature, turbidity and salinity (Payne et al., 2013), the latter three varying both with the levels of freshwater input and the influence of tidal currents. All these factors influence the composition of fish assemblages and abundances (Whitfield, 1999; Barletta et al., 2005), and the movements and behavioural patterns of fishes in the system (Childs et al., 2008; Payne et al., 2013; Taylor et al., 2013). Regular seasonal changes in temperature and/or salinity can drive seasonal egressions from the estuaries to the ocean to avoid adverse conditions (Lazzari and Able, 1990). These drivers can be affected by broader-scale

environmental conditions (Perry et al., 2005; Harley et al., 2006; Figueira and Booth, 2010), such as an increase in coastal water temperature (Quinn and Adams, 1996), and changes in the strength, duration and penetration of marine currents (Ridgway, 2007). These broader-scale patterns are expected to have an effect on the connection between estuarine and coastal habitats (Gillanders and Kingsford, 2002), but for many marine species using estuaries, exchanges between estuarine systems and the ocean, as well as longshore movement patterns, are still poorly known.

Luderick (*Girella tricuspidata*, Girellidae) is a commercially and recreationally important species in temperate eastern Australia (West and Gordon, 1994; Gray, 2002; Gray and Kennelly, 2003; Steffe et al., 2007; Curley et al., 2013) that can live for more than 20 years (Gray et al., 2010). Luderick is found year-round in estuaries and in shallow coastal waters (Gray et al., 2012), from southern Queensland to Kangaroo Island off South Australia, and also around the North Island of New Zealand (Kailola et al., 1993; Miskiewicz and Trnski, 1998). Following the classification of Potter et al. (2015), luderick is considered a marine estuarine-opportunist species as juveniles can be found on shallow coastal reefs. Adult luderick can also periodically be abundant in shallow coastal waters (Kingsford, 2002). Luderick is a synchronous spawner, and spawns in schools in nearshore coastal waters adjacent to the mouths of estuaries or along open beaches of New South Wales (New South Wales) (Gray et al., 2012; Curley et al., 2013). The main reproductive period occurs between June and September in northern New South Wales and between October and January in the southern part of New South Wales (Gray et al., 2012). This suggests a latitudinal variation in spawning, commencing earlier for the northern latitudes, which points toward a temperature effect on gonadal maturation (Gray et al., 2012; Curley et al., 2013). Although there is some evidence that some individuals may have relatively restricted movement patterns (Gray et al. 2012; Ferguson et al. 2016), adult luderick have been considered highly mobile with adults detected migrating up to 455 km (Thomson 1959; Gray et al. 2012). These large-scale movements could represent spawning migrations (Gray et al., 2012), however, more research is required to understand both the timing and synchronisation of these movements.

This study used a large collaborative array of acoustic receivers to better understand movements and spatial ecology of luderick along the New South Wales coastline. Specifically, we sought 1) to investigate whether the species displays estuary fidelity; 2) to investigate the degree of connectivity between estuaries; 3) to investigate the timing and potential drivers of large-scale movements; and 4) to characterise the extent of large-scale migrations.

2.3 Materials and Methods

Study area

The Georges River[1] (GR; southern Sydney region, 34.008°S; 151.128°E), Shoalhaven River (SR; New South Wales south coast, 34.903°S; 150.760°E) and Clyde River (CR; New South Wales south coast, 35.704°S; 150.180°E) support major estuaries, spanning a 200-km stretch of the New South Wales coast (Fig. 2.1). These three estuaries (length = 38, 48, and 38 km, respectively) are tide-dominated estuarine systems, and are permanently open to the ocean (Roy et al., 2001). All of these estuaries are open to recreational fishing and SR (estuary only) is also open to commercial fishing. Luderick has a minimum legal size of 27 cm total length applied to both commercial and recreational fishers.

Fish tagging

Between February and October 2012, 61 fish were tagged and released (mean FL: 316 mm ± 42 S.D., sizes ranging from 261 to 418 mm), with 15 fish in the GR and CR (mean FL 294 mm ± 25 and 320 mm ± 34 respectively) and 31 in SR (mean FL 325 mm ± 47)[2]. In addition, six luderick were tagged in Jervis Bay [JB; ocean embayment estuarine type according to Roy et al. (2001)] by the Jervis Bay Marine Park researchers

[1] The term "River" in "GR", "SR" and "CR" refers the estuarine extent of these locations only. This statement is valid throughout the thesis dissertation.
[2] Further information on where the fish were tagged in the estuaries is provided in Chapter 3.

in December 2011 [mean FL 330 mm ± 16; (Ferguson et al., 2013; Ferguson et al., 2016)].

Adult luderick were captured with either hook and line or light gauge gillnets (monofilament, 98-mm mesh size, 2 m drop and 150 m long, soaking time <30 min). Fish displaying physical damage from capture were immediately released and not tagged. Following capture, fish were placed in covered 100-L tubs filled with water and a light anaesthetic (AQUI-S® 25 mg L^{-1}). Water was continuously aerated and the time between capture and surgery did not exceed two hours. Before surgery, fish were anaesthetised with AQUI-S® (60 mg L^{-1}), and an acoustic transmitter [VEMCO (Bedford, Nova Scotia, Canada) V9-2L, 145 dB, 2.5 years battery life, 180-300s transmission delay or V9-2L, 2.0 years battery life with 180 s nominal delay for fish tagged in Jervis Bay] was fitted internally as described in previous studies (Walsh et al., 2012b; Payne et al., 2013). Each individual luderick was measured to the nearest millimetre and externally tagged with a plastic T-Bar Anchor tag (Hallprint Pty Ltd, Hindmarsh Valley, South Australia) displaying a unique identification number and a telephone number. After full recovery in aerated water (indicated by normal opercular and tail movement), tagged fish was released at their point-of-capture. Tag retention and survival were tested in laboratory and showed no mortality for both tagged and control fish (incision but no tag) during the 60 days of monitoring (unpublished data).

Acoustic array and environmental variables

Each of the three estuaries were equipped with a linear array of acoustic receivers (34 to 42 VEMCO VR2W receivers) spaced every 1.3 km on average from the mouth of the estuary to the edge of the freshwater (Fig. 2.1). The average detection range was estimated at 350 m, and ranged from 280 to 420 m depending on the location for SR (Walsh et al., 2012a). In the same estuary, the chance of a fish passing past a receiver without being detected was estimated to be low (0.4%) (Walsh et al., 2012a). A comprehensive network of receivers was also deployed to gate the entrance of the main estuaries and coastal lagoons of the New South Wales coast (Fig. 2.1). These multi-receiver gates (constituted of at least two receivers) aimed at studying inter-estuarine movements, by recording fish moving in and out one estuary. Estuarine arrays and gates were in place between July 2011 and June 2014, but the Georges River estuarine array

was reduced to an estuarine gate from May 2013 and the Shoalhaven River array was incomplete between June 2012 and July 2013, following large flood events in June 2013 resulting in the loss of 50% of the receivers. A network of up to 23 receivers was deployed in Jervis Bay between December 2011 and December 2014 in a fashion that covers the south western half of the embayment (Fig. 2.1).

The study also made use of detections collected on a substantial number of receivers deployed and serviced by different research groups (Universities, national research agencies, Marine parks) around Australia, mainly in New South Wales and Queensland, through the IMOS Animal Tracking, one of the facilities of the Integrated Marine Observing System (IMOS). Researchers using acoustic telemetry can independently upload their receiver detection files through a web-based portal (https://aatams.emii.org.au/aatams/), and the detection database can be queried by other researchers and detections of their tags on other arrays downloaded. In addition, IMOS Animal Tracking facility maintains a number of coastal receiver curtains, running across the shelf perpendicular to the coast, which are designed to detect migrations at latitudinal scales. Detections from approximately 500 receivers along 900 km of the New South Wales coast (between Narooma, 36.216°S; 150.143°E and Brunswick Heads, 28.538°S; 153.559°E) were available from this database (Fig. 2.1).

Within each of the three main estuarine systems, up to 6 Odyssey temperature and conductivity data loggers (Dataflow Systems Pty. Ltd.) were deployed in mid-water from the mouth of each estuary to the limit of freshwater (Fig. 2.1). In order to reflect the larger fluctuation in estuarine water conditions in this study, water temperature and conductivity recorded by the second closest data logger to the mouth of the estuary (at a distance between 7 and 11 km from the mouth) were used. Daily river water discharge data were obtained from the New South Wales Office of Water (http://www.water.nsw.gov.au/) and lunar phase data (quarters) were obtained from Geoscience Australia (http://www.ga.gov.au).

Data processing and analysis

Estuarine and gate tag detections and associated logger data (temperature and conductivity) were downloaded every 6 months until June 2012 and then every 12

months. Tag detections and estuarine environmental parameters were stored in a Microsoft Access database. The IMOS Animal Tracking database was interrogated with the tag unique identifier (VEMCO tag ID) and the matching luderick detections were downloaded and added to the Access database. Estuarine fidelity and departure from the tagging estuary (i.e. the estuary where a fish was tagged) was determined based on the detection data and recapture by recreational fishermen. In this study we considered that a tagged fish had left the estuarine system if it had been detected or recaptured outside the tagging estuary. A fish showed fidelity to the estuarine system if it had been detected on the estuarine array of receivers. In the case of gaps in detections within the estuarine system over long periods (e.g., months) and no detection elsewhere of these fish, we could not state with certainty whether these tagged luderick had stayed in the system or had left it during the periods of non-detection. Gaps in detections can be due either to loose array issues (areas with no receiver coverage) or loss of receivers between downloads in areas where the fish were roaming or had temporarily left the system without being detected elsewhere. Single detections of a valid luderick tag ID were included in the analyses as we considered type B false detections (Simpfendorfer et al., 2015) unlikely due to the low chance of tag collision along the New South Wales coast. For each fish that had been redetected outside their tagging estuary, detection locations were visualised in the geographic information system (GIS) ArcMap v. 10.2.2, and interrogated manually for potential exchanges between estuaries.

In order to determine the drivers leading to the egression from the tagging estuary, a suite of biological and environmental factors were analysed and compared to the time of departure of the fish. Gonadosomatic index (GSI) data and information about reproduction of luderick were obtained from Gray et al. (2012), and used to define periods of maximal GSI. Monthly relative GSI values were calculated (mean GSI/max GSI for the river) and ranked as category 0 (low GSI, 0-60%), category 1 (peak GSI with relative values from 60 - 80%) and category 2 (peak GSI with relative values >80%), and mapped to departure times. Several abiotic environmental parameters were investigated. For each fish and estuary departure, the time of departure was assigned and compared to the corresponding moon phase (first, second, third and fourth quarter), and daily mean temperature, conductivity and river discharge (flow) data from loggers. Chi-square tests were used to test whether proportion of all departures occurred

disproportionately at certain moon phases or under certain conditions of flow (normal *vs* "high flow" events). Flow was the only variable tested as the observed departures seemed to be related to variation of flow. High flows correspond to daily flow greater than the highest 5 % values of river flow recorded during the monitoring period, corresponding to the following thresholds: 34.4 m^3 s^{-1} for GR, 65.6 m^3 s^{-1} for SR and 20.2 m^3 s^{-1} for the CR.

The distance between the tagging site and the furthest detection was used to define the maximum extension of movement, and distances between consecutive detections were calculated with ArcMap, keeping within the 30 m depth contour, as luderick is commonly found in shallow water (Kingsford, 2002). Long distance movement rates were calculated as a Minimum Activity Index (MAI) by dividing the measured distances between detections by the time elapsed between the detections.

2.4 Results

Estuarine fidelity

A total of 270,863 detections was recorded among the 67 tagged luderick. Three fish (#26, #51 and #60) were not detected by any receiver nor were recaptured (Fig. 2.2). Explanation could be a transmitter failure or fish had died outside the detection range of a receiver. These fish were excluded from the analysis. Over half of the fish (53%) tagged in the three rivers were detected less than 20 days in the system where they were tagged. Only one fish (#27) was present for the whole duration of the study in the Shoalhaven estuarine system (Fig. 2.2). Five out of the six fish tagged in Jervis Bay Marine Park were detected over the duration of the study in that location (11 months) (Ferguson et al., 2016).

Fourteen fish (21%) were detected outside of their tagging estuary, including one of the six fish tagged in Jervis Bay Marine Park. Twelve fish were redetected by the network of receivers, and three were recaptured outside their estuary (Table 2.1). Out of the three

fish that have been caught outside and reported by recreational fishermen (and kept for consumption or bait), two had not been detected by the available network receivers. Across these 14 fish, a total of 1,276 detections were collected outside the tagging estuaries. Also, some fish remained undetected for large periods of time in the estuarine systems, or were intermittently detected. Based on the available detection and recapture data available, there is no evidence of return into the tagging estuary for any fish that undertook an alongshore migration.

Inter-estuarine connectivity

Luderick were detected traveling along the coast, by coastal receivers, gates and estuarine arrays. Most of these detections were multiple detections over a short period of time, up to six days, with fish entering estuaries or embayments and travelling up to 8 km upstream. The two fish that departed from GR were detected in Sydney Harbour area (SHA), and one of these fish was later detected in Port Stephens (Fig. 2.3). Luderick from SR were detected (or recaptured) at 10 different locations, with four out of five fish detected at multiple estuaries (Fig. 2.3). Each of the fish that egressed from CR was found again at single locations only (Fig. 2.3). Of the 14 fish that left their tagging estuary, two relocated to another estuary for periods of several months (SR to Tuggerah Lake and CR to JB, Fig. 2.3).

Drivers of estuarine egression

From the data collected for the 14 fish redetected and/or recaptured outside their tagging estuary, luderick from JB left the embayment early February 2012, whereas those from GR and SR left the estuarine system late February and early March, respectively), and four fish tagged in CR left early June, and the fifth one, in February the following year (Table 2.1). These times of departure coincide with the date of the last detection for other fish that have been neither redetected within the tagging estuary system, nor elsewhere (Fig. 2.2 and Table 2.1). One possible explanation would be that these fish also departed from their tagging estuary, without being detected again elsewhere. Fish #52 and #57 tagged in the CR may have left the estuary temporarily between April and May 2012 (Fig. 2.2), as these fish were detected travelling to the mouth of the estuary and then entering again, with movements from the mouth and upstream (data not

shown). None of the luderick departures recorded in this study appeared to match the peaks in GSI described by Gray et al (2012) (Fig. 2.4). Four fish left CR close to the GSI peak for the Clarence River (Fig. 2.4); however this estuary is located over 700 km north from CR (Fig. 2.1).

With regards to the moon phase, tagged luderick left GR and CR during the last quarter of the moon phase (Table 2), more precisely on full moon or one day on either side of the full moon. In contrast, there was no pattern in departure in relation to the phase of the moon for fish tagged in the SR, although half of the fish left during the first quarter. However, due to the small number of observations per lunar phase, no statistical test (e.g. chi-square) could have been performed; therefore it is difficult to conclude whether there is a link between estuarine egression and moon phase.

In regard to the three focal estuaries, water environmental parameters were characterised by large fluctuations of discharge and conductivity (Fig. 2.5). Sudden spikes of daily water discharges (high flows), up to 75 times higher than the daily mean discharge, were recorded over the sampling period. These peaks of daily water discharge occurred at similar times in the three estuaries, as the result of heavy rainfall events. However, the magnitudes differed in relation to the catchment sizes of the rivers (GR: 931 km^2, SR: 7,086 km^2 and CR: 1,723 km^2). The conductivity at the reference stations responded to these peaks in water discharge by sudden drops toward zero (freshwater) due to the large amount of freshwater in the river system following heavy rainfalls. Temperatures fluctuated over time following a seasonal pattern, with little short-term variation in contrast to conductivity (Fig. 2.5). For the fish redetected/recaptured outside the tagging estuary, the time of departure closely correlated to high flow events (X^2 (2, n = 13) = 6.2, $p < 0.05$) (Fig. 2.5).

Extent of large-scale migrations

Detections outside the tagging estuary were all obtained from estuarine gates or coastal receivers situated within 0.2 km from the shoreline (Fig. 2.3). No detections were recorded through the IMOS Animal Tracking curtain receivers (Figs. 2.1 and 2.3), even where it was known that a tagged fish crossed the curtain (Fish #3, #4, #32, #37, #41, #43, #45 and #56) (Table 2.1 and Fig. 2.1). Following egression from the estuary, the

vast majority (93%) of fish migrated north. The only southward migration detected was between JB and CR (Fig. 2.3). The greatest longshore migration was for fish #37, which travelled 492 km from its tagging site and was detected by several receivers before being captured by a recreational fisher (Table 2.1, Fig. 2.3). Mean distances between the tagging estuary and the furthest detection location were 168 ± 113 km overall, 118 ± 81 km for GR, 233 ± 129 km for SR and 122 ± 66 km for CR (Table 2.1). The durations that fish were detected outside of the tagging estuary ranged from 1 to 48 days.

Average MAI, as a relative measure of speed, was ~28 km d^{-1}, however the maximum speed was 57 km d^{-1} (Table 2.1 and Fig. 2.3). This same fish swam on average 47 kmd^{-1} for 6.4 days between SR and Port Stephens (Fig. 2.3). Despite fish leaving the estuary together, our data did not indicate that tagged fish travelled together, although there were some examples where fish visited similar areas at similar times. For instance, between 3/03/2012 and the 14/03/2012, seven fish were detected in the Sydney Harbour area. Also, two fish tagged in SR and GR, were detected in Port Stephens one week apart.

2.5 Discussion

Tagged luderick were capable of undertaking extensive coastal movements along eastern Australia, covering distances ~500 km, at speeds up to 57 km d^{-1}. The movements were predominantly in a northward direction, and detections were concentrated inshore, close to the coastline, with numerous estuaries visited along the way. Departures from the tagging estuary are linked to changes in estuarine environmental conditions following heavy rainfalls. These findings have several implications for our understanding of the ecology of luderick in general. In addition, the non-detection of tagged fish crossing receiver curtain has implications for the use and configuration of extensive collaborative receiver arrays.

Estuarine residency, fidelity and inter-estuarine connectivity

Luderick is considered a highly mobile species (Gray et al., 2012; Curley et al., 2013), and over 50% of the tagged fish spent only a short time in the tagging estuary. However our dataset could not confirm whether all these individuals left their tagging estuary (e.g. some of these fish could have been removed from the system (harvesting) or located in an area outside of the receiver detection range). The 14 fish that egressed from their tagging estuary and were detected outside did not display any estuarine fidelity during the course of the study as they were not detected again in this system. These luderick appeared to use estuarine systems on a temporary basis, with no particular attachment to a specific estuary. Importantly, luderick tagged in Jervis Bay were an exception to this trend, as these fish displayed a high fidelity to subtidal rocky reefs (Ferguson et al., 2013; Ferguson et al., 2016). As stated above, Jervis Bay is a coastal embayment with heavy marine influence, so these results may be more indicative of coastal behaviour. In a similar fashion, the fish that were not redetected either in the tagging estuary or elsewhere could have moved and relocated to adjacent surrounding coastal reefs, without undertaking longshore migrations (e.g. fish #50 and #61). Therefore, departure from the estuary may not necessary lead to longshore migrations consistently, suggesting variation in behaviour among individuals. Partial migrations (Chapman et al., 2011) may explain the inter-individual variability in large-scale movements of Luderick. Partial migration is a phenomenon well-documented for salmonids, with fish demonstrating a large range of migratory behaviours, from freshwater residency to full anadromy (Jonsson and Jonsson, 1993; Dodson et al., 2013). Recently, Fowler et al. (2016) described partial migration in the case of the sea mullet (*Mugil cephalus*) in NSW, with fish displaying diverse behaviours whereby most of the fish undertook irregular sea migrations and a smaller proportion of the sample remained in the estuarine system or migrating regularly for spawning. Hence, this partial migration phenomenon may be more common among “migrating” fish than previously thought (Chapman et al., 2012).

Differences in movement and in residency among individuals might be explained by variations in affinities to estuarine systems. In this study, luderick showed different degrees of residency in their tagging estuary among individuals and there was evidence of at least 21% of the tagged fish leaving the estuary to migrate along the NSW coast.

Similarly, Gray et al. (2012) reported migratory individuals among an overall population displaying a high-fidelity to the tagging estuary, with a small proportion detected elsewhere. Morrison (1990) found similar variations in movement patterns among individuals of luderick, with some fish being residents and other migrants. Therefore, different affinities to estuarine systems may exist among individuals of luderick, with more "marine" fish visiting estuaries at certain times of the year (transient), and other fish displaying more pronounced preferences to estuarine habitats (more resident). This could be associated with the energetic costs of osmoregulation (Kidder et al., 2006), resulting in intra-specific differences in behaviour according to their marine or estuarine affinities, and their pre-condition to osmoregulate in hypohaline conditions.

This study revealed that luderick can visit multiple estuaries during their broad-scale movements. These visits might be the result of specific cues rather than just the morphology of the coastline, as fish chose to enter an estuarine system and diverge from their routes. Estuarine cues are well documented for larvae of marine estuarine-dependant species ingressing into the system to settle (Kingsford et al., 2002), as is the case during spawning migrations of adults anadromous fish species such as salmonids (Quinn and Dittman, 1990). The estuarine plume plays an important role in such mechanisms for larvae (Kingsford and Suthers, 1994; Whitfield, 1994a), and could well provide the necessary stimuli to facilitate these visits. Motivations for entering a specific estuary remain unclear as luderick visited estuaries varying greatly in size (major to small systems) and type (drowned valley, barrier estuary) including over a period of several months. These motivations could be related to foraging, refuging (e.g. predation or from less favourable coastal conditions).

The main identified driver of the departure from the estuaries was a rapid and drastic change of estuarine environmental conditions resulting from freshwater inputs through heavy rainfalls. These large freshwater inputs provoked sudden increases in water discharge and decreases in conductivity, forcing a proportion of tagged luderick to leave their tagging estuary. Luderick is a marine estuarine-opportunist species that tolerates low conductivity water conditions (Chapter 3) and is commonly found in brackish water

(Kailola et al., 1993). However, fish may not possess the physiological capacity to adapt to rapid changes in conditions, such as conductivity, forcing them to migrate to a more suitable physicochemical habitat (McCormick et al., 2013). Along with the drop in conductivity, large freshwater inputs in estuaries result in an increase in the flow (river current) and water levels and a consequent increase in turbidity. Therefore, under these altered conditions luderick might also change behaviours in foraging and resting, and this needs to be further studied. It is interesting to note that at least a third of the fish stayed in the system over several high flow events and were able to cope with these adverse conditions. There was no evidence in our data to suggest that the response may vary ontogenetically, however it is important to note that only a relatively small size range were tagged. Marine estuarine-opportunist species generally display a range of behavioural and physiological adaptations that allow them to adapt to the drastic changes in water conditions that can occur within estuaries. Under heavy rainfall conditions, the yellowfin bream *Acanthopagrus australis* switches between day/night activity and depth usage patterns (Payne et al., 2013) to maximize foraging and reduce predation risk under the altered conditions. Mulloway *Argyrosomus japonicus* are forced down the estuary as a response to the press effects of freshwater flows, and pulse flows in summer are likely acting as a spawning and migration cue for mature individuals (Taylor et al., 2014). In their meta-analyses looking at the effects of river flow on fish movement and activity, Taylor and Cooke (2012) and references cited therein highlighted the large range on fish responses in relation to migratory and non-migratory (e.g. associated to spawning) movements and activity.

Although the time of departure from estuaries occurred outside the main reproductive periods described by Gray et al. (2012), the movements revealed by acoustic telemetry could still be linked to pre-spawning migrations. Luderick has an extended and variable reproductive period in eastern Australia and large numbers of fish leave the estuaries to gather at the mouth prior to commencing their pre-spawning coastal migrations. Therefore, pre-spawning migrations could be triggered by both biological and exogenous parameters, as observed in other species. Commercial fishermen reported that yellowfin bream *Acanthopagrus australis* migrate in a predominantly northward direction (Gray et al., 2000; Curley et al., 2013) and can co-occur with large schools of luderick at similar times and locations (A. Williams, commercial fishermen, NSW

central coast, pers. comm.). Also, other marine estuarine-opportunist fish species such as sea mullet *Mugil cephalus* and tailor *Pomatomus saltatrix* are known to undertake pre-spawning coastal movements along the Australian east coast in a predominantly northward direction (Thomson, 1959; Kailola et al., 1993), often one to two months before reaching spawning grounds (Kesteven, 1953). Such behaviour may reflect a similar strategy to that employed by luderick, with gonadal maturation occurring later in the migration. This is supported by the fact that all fish left the estuary well before the peak-GSI detected by Gray et al. (2012) for fish on the north coast (Tuggerah and Clarence). The pelagic larval duration for luderick is estimated at about 21 days (Miskiewicz and Trnski, pers. comm.). If related to pre-spawning migrations, these northward movements potentially represent a strategy to facilitate the dispersion of eggs and larvae by means of the Eastern Australian Current (EAC), running southward along the east Australian coast (Ward et al., 2003), as proposed by Gray et al. (2012). This strategy, along with an extended reproductive period, is also likely to contribute to the spatial and temporal variability in luderick recruitment to New South Wales estuaries (Worthington et al., 1992; Gray and Miskiewicz, 2000; Smith and Sinerchia, 2004).

Broader-scale climate-induced changes in estuarine conditions are also likely to affect the timing of egression from the estuaries (and possibly reproductive cycle and gonad maturation) and, therefore, the subsequent large-scale migrations of luderick. Elevated regional climatic variability has been shown to be responsible for changes in fish distributions and abundance in estuarine and coastal systems (e.g. Roessig et al., 2004; Perry et al., 2005). The period 2010-2012 was under a La Niña ENSO (El Niño Southern Oscillation) regime, characterised by heavier rainfalls during winter and spring on the south-eastern Australian coast. The 2010-2012 La Niña episodes was particularly strong in Australia, with 2011 being the second wettest calendar year on record (www.bom.gov.au/climate/enso/lnlist/index.shtml). The sheer volume of rainfall observed under these conditions possibly exacerbated the egression and coastal residency observed in this study. Future research should include investigating whether similar patterns are detected during a contrasting El Niño oscillation.

The movement ranges revealed by acoustic telemetry were similar to those described in the literature (Thomson, 1959; Gray et al., 2012). It did however provide information on the timing of departures of some fish from the estuaries, and swimming speeds, which conventional mark-recapture methods (i.e. dart tagging) could not have delivered. Once outside the estuary, luderick are capable of sustaining speeds of over 50 km d^{-1} over several days. Average speeds of luderick between successive coastal locations (estimated at 1.05 body lengths [BL] s^{-1}, based on average FL) are within the range of swimming speeds seen during active migration movement rates (0.4-1.5 BL s^{-1}) of salmonids and striped bass *Morone saxatilis* (Quinn, 1988; Callihan et al., 2015), while the maximum speeds recorded for luderick (2.01 BL s^{-1}) greatly exceed these rates.

The detection success of a tagged fish using a passive monitoring network of receivers depends on multiple factors inherent to the species and its behaviour, the tag specifications and the design of the array of receivers (Heupel et al., 2006), as well as the environmental conditions (Kessel et al., 2014). None of the 13 luderick that travelled northward was detected by IMOS Animal Tracking Bondi "curtain" (Fig. 2.1). This is of concern, as the curtain was constructed with the objective of detecting migrations of fish and sharks at latitudinal scales, so the configuration of the current IMOS Animal Tracking curtains may not be well adapted to track migrating teleost fish which are likely moving through the near-shore coastal migration corridor. This is not just an issue for the species in question, but also for a large suite of other estuarine species that have been tagged and can potentially migrate along the coast (e.g. yellowfin bream, dusky flathead, mulloway, sea mullet). In a recent study, rock blackfish *Girella elevata* went similarly undetected by these curtains (Stocks et al., 2015). To improve the chances of detection of such species by these "curtains", receivers could be concentrated with reduced spacing in the near-shore area where noise is greater (Stocks et al., 2014). Also, deployment of adjacent "sub-curtains" in the near-shore area (extending 2-3 km from shore), would improve detection of migrating teleost fish, and could also provide directionality of movement which would represent invaluable data for coastal migration studies. The estuarine gates performed well with multiple detections at different entries of estuaries. The IMOS Animal Tracking facility, however, provides acoustic telemetry users with the opportunity to upload tag detections for interrogation by tag owners. While the benefits of such collaboration are

obvious, the network relies greatly on the willingness of users to join and to contribute to the database. This present work is one of the first relying on a collaborative array and the IMOS Animal Tracking database to study broad-scale movements of a teleost fish in SE Australia.

2.6 Conclusions

Passive acoustic telemetry was able to provide information on the timing of estuarine departures and coastal migrations of luderick, identifying that these take place outside known peak GSI periods and appeared to be driven by large freshwater inputs resulting from heavy rainfalls. This study found similar movement ranges to previous studies (up to ~500 km) as well as for the direction of movements (predominantly in a northward). Detections were concentrated inshore, close to the coastline and estuarine connectivity was displayed with individuals visiting multiple estuaries along the way. This study also showed that luderick can travel at greater speeds (exceeding 50 km d^{-1}) than previously considered. This study provides another example of the successful use of broad collaborative acoustic arrays of receivers for large-scale movement studies as the Atlantic Cooperative Telemetry (ACT) Network (http://www.theactnetwork.com/home) and the Ocean Tracking Network (OTN, http://oceantrackingnetwork.org) (Callihan et al., 2015; Hussey et al., 2015). Collaborative acoustic arrays can provide considerably greater detection potentialities and thus improved information on the movements of tagged animals. However, receiver arrays such as curtains aiming at detecting migrating animals need to be carefully designed to minimise the possibility of tagged fish passing undetected. Collaborative receiver arrays contributing data to a centrally accessible database should be widely encouraged among the scientific community using acoustic telemetry.

2.7 Tables

Table 2.1 Summary of information for 14 acoustically tagged luderick that were subsequently detected outside their tagging estuary showing the tagging estuary (GR: Georges River, SR: Shoalhaven River, JB: Jervis Bay, CR: Clyde River), date of tagging and last detection in the estuary, fork length, number of detections outside the tagging estuary, distance travelled between the tagging estuary and place of last detection or capture (Dist.), highest MAI (minimum activity index) and direction of the travel (Dir.). *: fish recaptured and reported by recreational fishermen; **: fish redetected by the network of receivers outside the tagging estuary.

Fish	Estuary	Date tagged	FL (mm)	Last detection	Detections outside	Dist. (km)	MAI (km d^{-1})	Dir.
3	GR	02/02/12	290	08/03/12	2	198	39	N
4	GR	02/02/12	290	09/03/12	19	37	8	N
32	SR	07/02/12	311	29/02/12	3	300	57	N
36	SR	07/02/12	288	02/03/12	16	134	29	N
37**	SR	07/02/12	304	01/03/12	210	492	52	N
41	SR	07/02/12	289	27/02/12	9	169	10	N
43	SR	07/02/12	288	27/02/12	6	136	21	N
45*	SR	16/02/12	261	20/02/12	1	168	3.6	N
49	CR	03/04/12	340	05/06/12	1	134	47	N
52	CR	03/04/12	290	05/06/12	25	82	14	N
56	CR	03/04/12	313	05/06/12	13	242	23	N
57	CR	17/04/12	321	05/06/12	834	101	26	N
61*	CR	17/04/12	348	28/02/13	1	52	0.1	N
62	JB	22/12/11	333	2/02/2012	68	106	4	S

Table 2.2 Numbers of departures from the tagging estuary, in relation to moon phase (GR: Georges River, SR: Shoalhaven River, JB: Jervis Bay, CR: Clyde River).

Moon Phase	**GR**	**SR**	**JB**	**CR**
First quarter		3		
Second quarter		1		
Third quarter		1	1	
Last quarter	2	1		5

2.8 Figures

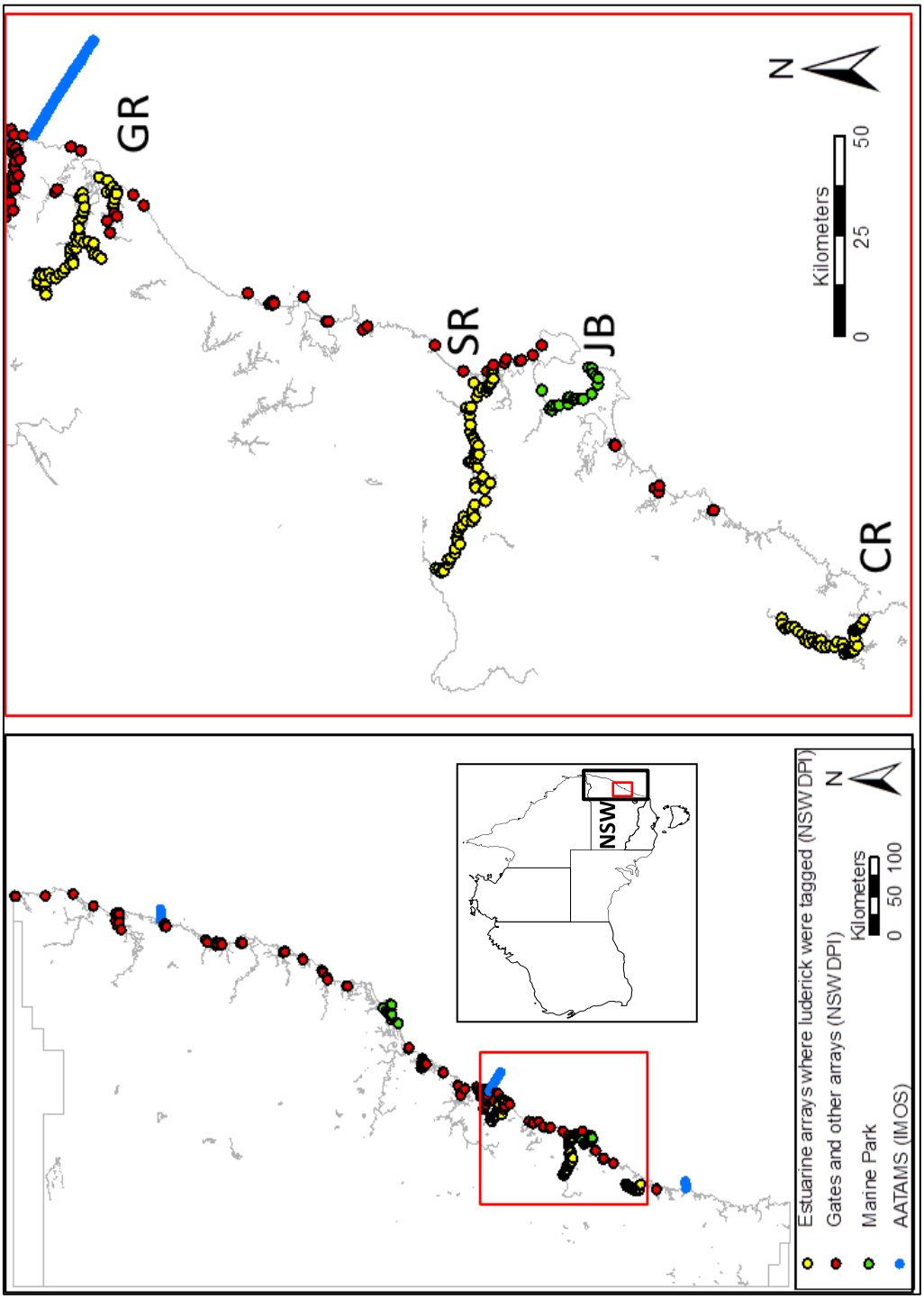

Figure 2.1 Locations of the acoustic receivers in New South Wales: New South Wales DPI estuarine arrays (GR: Georges River; SR: Shoalhaven River; CR: Clyde River), gates and other coastal arrays and other DPI receivers; Marine Parks (JB: Jervis Bay Marine Park) and IMOS Animal Tracking facility (formerly named AATAMS).

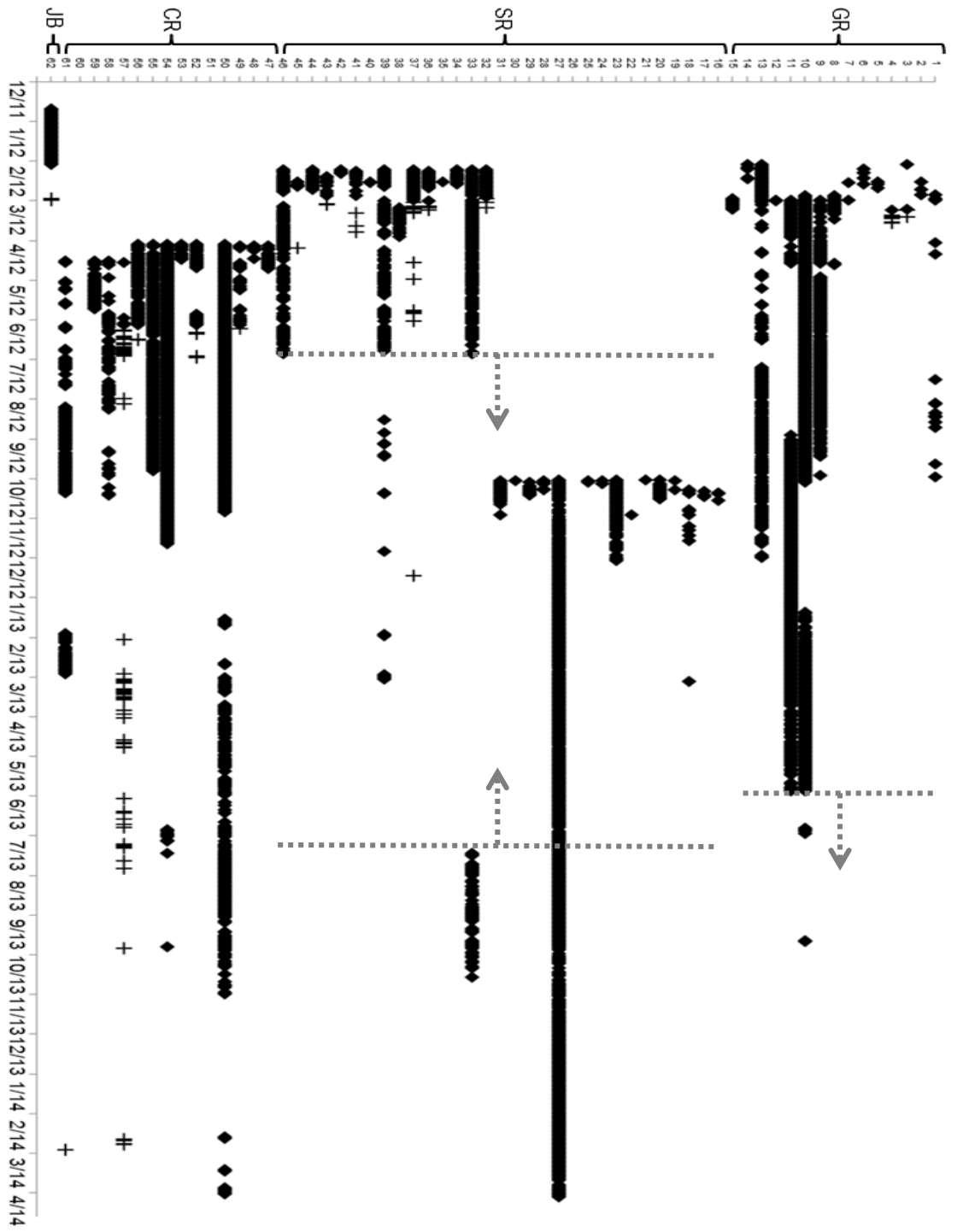

Figure 2.2 Daily receiver detections of 62 acoustically tagged luderick in three SE Australian estuaries between December 2011 and April 2014 (GR: Georges River, SR: Shoalhaven River, CR: Clyde River, JB: Jervis Bay). Daily detections for only fish #62 tagged in JB are displayed as it has been redetected outside JB. For remaining fish from JB see Ferguson *et al.* (2016). Diamonds and crosses indicate detections within and outside the tagging estuary, respectively. Dotted lines and arrows show periods when the acoustic receiver array for GR and SR were respectively reduced and incomplete.

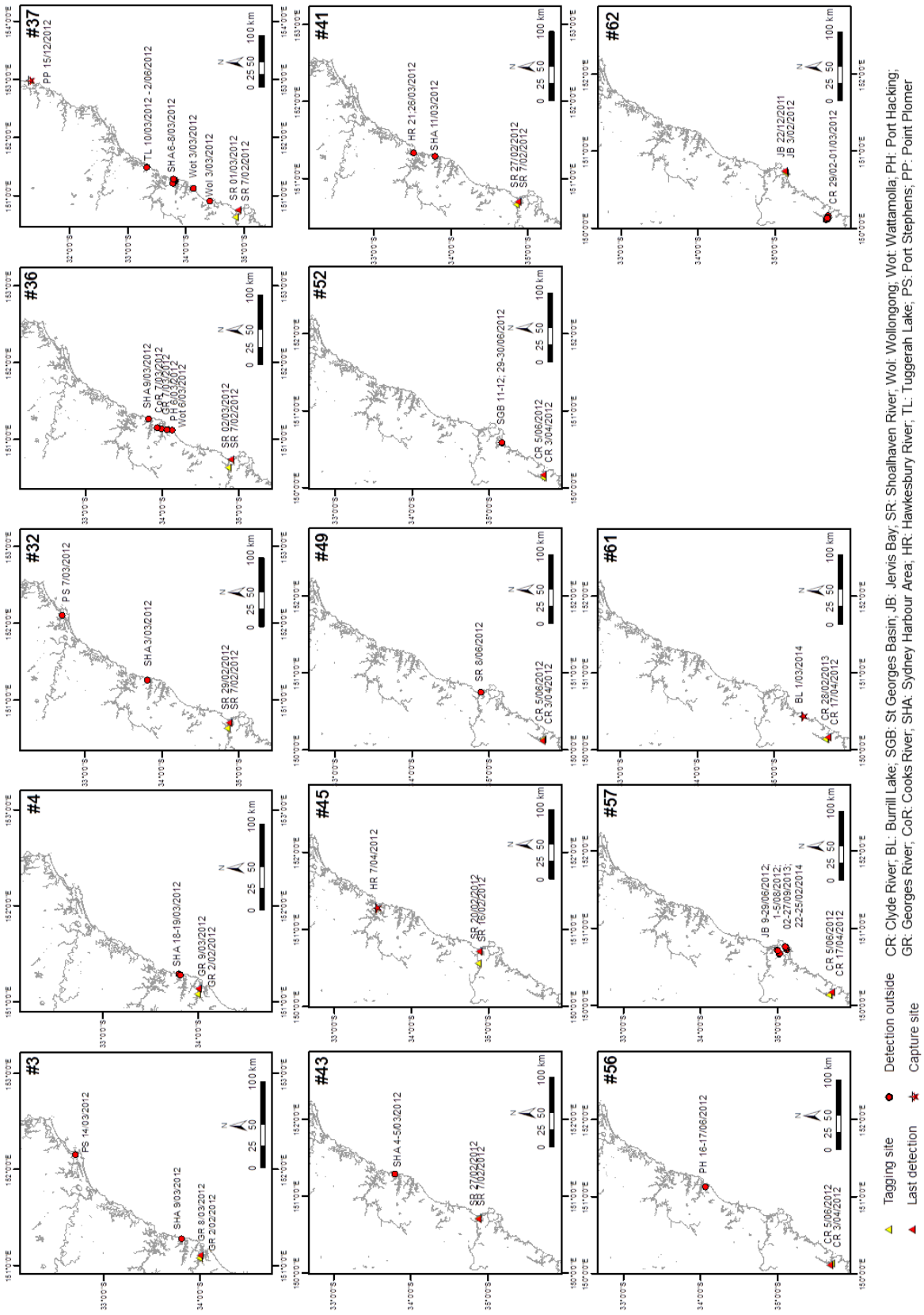

Figure 2.3 Maps of the movement trajectories of 14 tagged luderick that departed their tagging estuary, including positions and dates of tagging, last detection in the tagging estuary and detections/recaptures outside the tagging estuary.

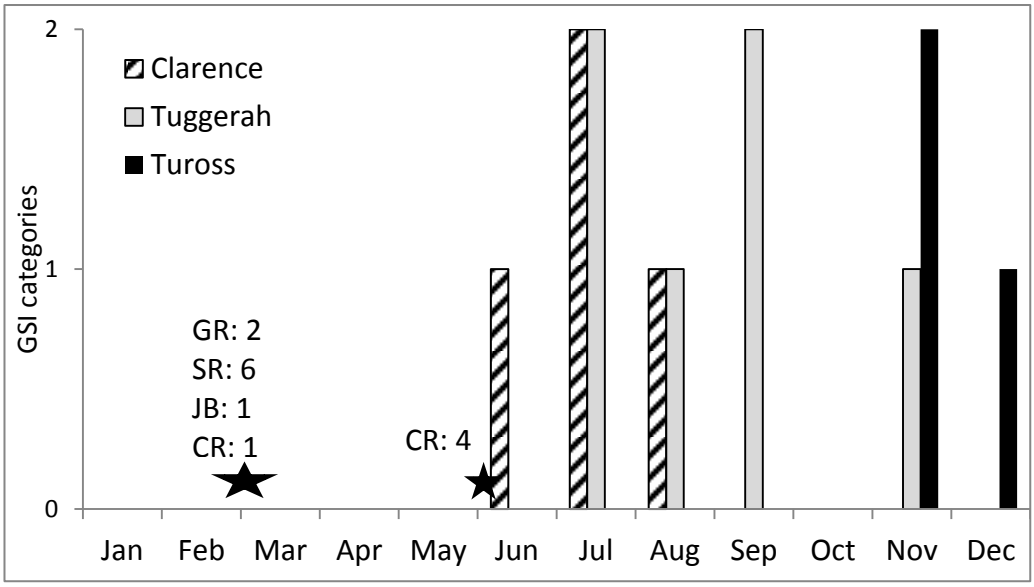

Figure 2.4 Main reproductive periods across the year 2004 for Clarence River (New South Wales North coast 29.427° S, 153.372° E), Tuggerah Lake (New South Wales Central coast 33.345° S, 151.504° E) and Tuross River (New South Wales South coast 36.067° S, 150.135° E) adapted from Gray et al. (2012) showing peak periods of GSI for these three estuaries (1 for relative GSI values comprised between 60 to 80%, and 2 for values >80% (no data were available for the month of September for the Clarence River)). The stars correspond to the dates of last detection in each tagging estuary (GR: Georges River, SR: Shoalhaven River, CR: Clyde River, JB: Jervis Bay). The numbers indicate the number of fish that departed.

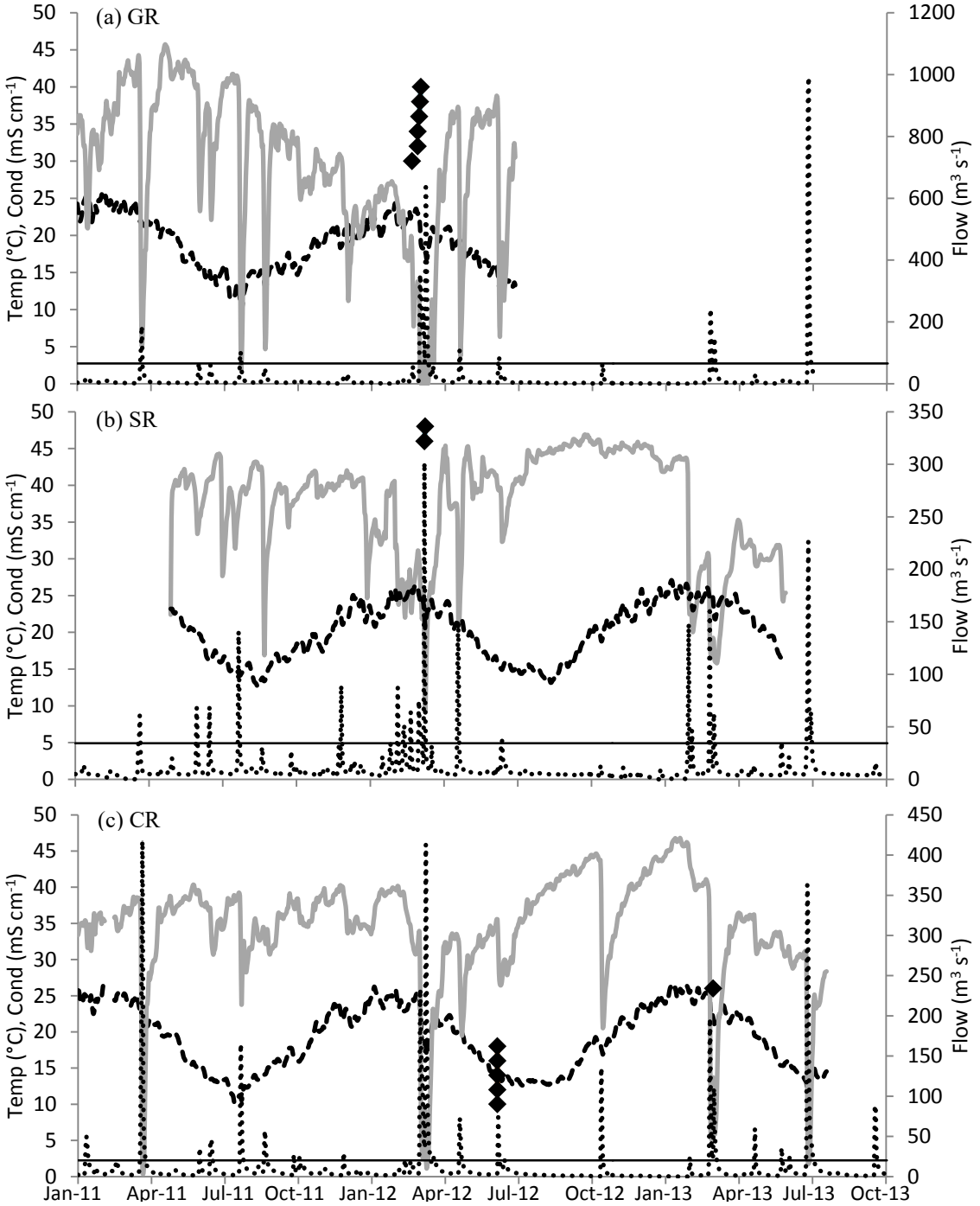

Figure 2.5 Daily mean temperature in C° (dashed line) and conductivity in mS cm^{-1} (grey line) on the left Y-axis and daily river discharge in m^3 s^{-1} (dotted line) on the right Y-axis monitored from 1/11/2010 to 30/09/2013 in three estuaries in SE Australia in which luderick were tagged. Black diamonds indicate the date of the last detection of the fish that had left each system. GR: Georges River (tagging period: 01/02 and 01/03/2012, Fig. 2.5a); SR: Shoalhaven River (tagging periods: 06/02-16/02/2012 and 02/10/2012, Fig. 2.5b); CR: Clyde River (tagging period: 03/04-17/04/2012, Fig. 2.5c). The horizontal solid line marks the high flow threshold for each estuary.

CHAPTER 3: Drivers of temporal and spatial movement patterns in luderick (*Girella tricuspidata*) in south-eastern Australian estuarine systems

Cadiou G., Booth D.J., Gray C.A., and Taylor D. (*in prep.*). Drivers of temporal and spatial estuarine movement patterns in luderick (*Girella tricuspidata*) in south-eastern Australian estuarine systems

3.1 Abstract

Rapid and long term fluctuations of physicochemical parameters within estuaries strongly structure the composition and distribution of many fish communities. In particular, variability in temperature and in freshwater inflow may greatly influence fish movements in estuarine systems. Such environmentally driven movements have ramifications for management of fisheries in these ecosystems. Luderick (*Girella tricuspidata*) commonly associates with estuaries and near-shore waters of south-eastern (SE) Australia and is heavily targeted by commercial and recreational fishers. Nevertheless, the extent, direction and timing of luderick along-estuary movements, as well as the drivers triggering these movements are largely unknown. To resolve the estuary-scale movement patterns of luderick, sixty-one individuals (mean FL: 315 ± 41 mm) were acoustically tagged in three estuaries along a 200-km stretch of the New South Wales coastline, SE Australia. In each estuary, fish movements were monitored using a fixed linear array of acoustic receivers (34 to 42 per estuary), covering the full extent of the brackish reaches of these estuaries. To investigate factors influencing luderick movements, river discharge (flow), water temperature and conductivity were measured concomitantly to acoustic telemetry. Movements of luderick appeared to covary with freshwater inputs, with fishes undergoing seaward movements during periods of low conductivity and higher flow conditions. The majority of luderick individuals appeared to respond to pulsed freshwater inputs from rainfall, with major downstream movements. However, some individuals also remained stationary or displayed moderate movements during high flow periods, suggesting variable behavioural responses among individuals under environmental stress. There were no

notable differences in movements of luderick with fish size, although larger fish tended to be underrepresented during tagging in the higher reaches of the systems, most likely reflecting ontogenetic preferences. Monitoring of luderick movements over a longer period including a larger range of sizes (e.g. juvenile fishes) are required to resolve influences of seasonal variations in movements and the potential effects of ontogeny on movement patterns. The findings of this study are discussed in a context of increasing climatic variability and anthropogenic development in the SE Australian region, and of implications for managing this exploited species.

3.2 Introduction

Estuaries are highly productive ecosystems that provide goods and services of considerable economic value (Costanza et al., 1997). Estuaries sustain fisheries worldwide (Houde and Rutherford, 1993) by providing fishes with nursery grounds, refuges, and food resources as well as representing critical adult habitat for obligate estuarine species (Paterson and Whitfield, 2000; Beck et al., 2001). As a link between terrestrial and marine environments, estuaries also deliver nutrients and organic matter to coastal ecosystems, which enhances fishery productivity by stimulating primary and secondary production (Loneragan and Bunn, 1999). A thorough knowledge of fish movements and the factors influencing them is essential to understanding the ecology of a species, and to support effective management measures to maintain sustainable fisheries (Pittman and McAlpine, 2001; Palumbi, 2004). In addition, behavioural responses to environmental factors may vary widely among species (Payne et al., 2015c), and therefore species-specific studies are required to obtain a more comprehensive understanding of the environmental factors driving fish behaviour.

Estuaries are highly dynamic environments, whereby rapid changes in physicochemical conditions strongly influence the structure and distribution of fish communities (Whitfield, 1999; Barletta et al., 2005). Salinity, temperature, turbidity, tides (and tidal currents) have been identified as important environmental variables driving the composition of estuarine fish assemblages (Cyrus and Blaber, 1992; Marshall and

Elliott, 1998; Whitfield, 1999). Fluctuations in these parameters can be rhythmic (e.g. seasonal) or arrhythmic (stochastic), and may vary over different temporal scales, from hours to years (Cloern and Nichols, 1985). Natural fluctuations of temperature, turbidity, and salinity may also influence the range and direction of fish movement in estuarine systems (Pittman and McAlpine, 2001; Childs et al., 2008; Taylor et al., 2014). The longitudinal estuarine salinity gradient and the position of the salt wedge are shaped by water flow and tidal effects, and may also depend greatly on the shape and geomorphological characteristics of the estuary (Roy et al., 2001; Potter et al., 2010). Freshwater inputs *via* heavy rainfall events can dramatically and rapidly change the salinity of the estuarine system (Wong, 1994). Estuarine freshwater inflows can be categorised as pulse or press effects (Taylor et al., 2014). A freshwater inflow pulse is characterised by a drastic and short-term increase in river discharge following heavy rainfall events, or intended/unintended releases of stored water in regulated rivers. These high flow events usually happen sporadically and lead to a sudden and steep decrease in conductivity, only lasting for a short period of time (hours to days), with conditions returning to their usual state quickly after the event. In contrast, press effects result from higher levels of freshwater discharge in estuaries, usually affecting estuarine conditions over longer periods of time (days to weeks). Press effects also tend to follow seasonal patterns, associated with annual rainfall fluctuations.

Estuarine fish species have evolved to adapt and persist in such highly dynamic environments (Whitfield, 1994b; Schulte, 2014). Fishes may have efficient physiological mechanisms to respond to the changes in environmental conditions (Whitfield, 1999). For instance, euryhaline fish species are able to tolerate drastic changes in salinity through osmoregulation (Harrison and Whitfield, 2006; Kültz, 2015), allowing these fishes to persist in locations experiencing a wide range of salinities (Childs et al., 2008). Alternatively, stenohaline fishes with reduced capacity for osmoregulation may respond to large fluctuations in salinity by modifying their behaviour, for example by relocating to avoid adverse conditions (Elliot and Hemingway, 2002). Fish responses to fluctuating estuarine environments also depend on their capacity to cope with the stress generated by new conditions (Schulte, 2014; Kültz, 2015), the presence of suitable habitats (Taylor et al., 1993; Kramer and Chapman, 1999), and their ability to balance the trade-off between minimising

predation risk and maximising foraging (Lima and Dill, 1990). Responses may also depend on the magnitude and duration of the environmental fluctuation (e.g. stress versus seasonal variation) (Schulte, 2014). Regardless of the strategy adopted, there are metabolic and energetic costs associated with responding to changing environmental conditions in estuaries (Kidder et al., 2006).

Temperate Australian rivers are characterised by highly variable flows, experiencing some of the largest fluctuations in annual discharge in the world (Peel et al., 2004). South-eastern Australian rivers are also characterised by alternating drought and flood periods driven by the El Niño Southern Oscillation (Erskine and Warner, 1998; Gillson, 2011). These regimes influence the productivity of coastal and associated estuarine fisheries, with decreased catches for estuarine gillnet fisheries observed during drought periods (Gillson et al., 2009). Rainfall and freshwater inputs, especially via episodic high flow events (Eyre, 1998), are major environmental factors affecting the productivity of estuarine fisheries in Southeast Australia. Freshwater inputs enhance fisheries production, however, they may also have detrimental effects during larger floods by triggering low-oxygen events, resulting in major fish kills (Whitfield, 1995; Dawson, 2002), and disrupting habitats (Kimmerer, 2002) as well as food web trophic structure and interactions (Leonard et al., 1998; Vinagre et al., 2011).

Luderick *Girella tricuspidata* is an abundant species found all year round in estuaries and near-shore waters of NSW (see Kailola et al., 1993 and Miskiewicz and Trnski, 1998 for full distribution). While luderick is mobile and may migrate up to ~500 km along the coast of NSW (Chapter 2), very little is known about its movement patterns in highly variable estuarine environments. Egression from the estuaries appeared to be linked with large-scale migrations and occurred following sudden and sharp changes in estuarine conditions due to large freshwater inputs (pulse effects) (Chapter 2). This species is of commercial and recreational interest (West and Gordon 1994; Gray and Kennelly, 2003; Steffe et al., 2007). In NSW, the majority of the total commercial landing (~85%) of luderick originates from estuaries (Gray et al., 2010) and therefore understanding luderick movements in relation to estuarine condition may provide valuable insights for the management of this species.

In this study, we examined the effects of freshwater flow, specifically flow pulses, conductivity and seasonality on the distribution of luderick within three estuarine systems and explored the effect of fish size on response patterns. The main hypothesis was that there is a relationship between the change of location of luderick in the estuary and the effect of conductivity and season. More specifically, we predicted that luderick would display seaward movements under high-flow and low conductivity conditions and would regain more upstream positions once discharge and conductivity returned to pre-flow event conditions. We also expected that the extent of such movements would depend on the initial fish position in the estuary, with potential differences with fish sizes. In addition, we hypothesised that luderick estuarine movement patterns may differ seasonally in relation to seasonal variations in rainfall (freshwater inputs) and water temperatures.

3.3 Materials and methods

Study area

The study was conducted in three major estuaries along a 200-km stretch of the NSW coast; the Georges River (southern Sydney region; 34.008°S, 151.128°E; GR), the Shoalhaven River (NSW South coast; 34.903°S, 150.760°E; SR) and the Clyde River (NSW South coast; 35.704°S, 150.180°E; CR) (Fig. 3.1). All three estuaries are permanently open to the ocean (Roy et al., 2001) but the geomorphological and physical characteristics, and catchment land use vary between these systems (Table 3.1). GR has a weir 38 km upstream of the estuary mouth, delimiting the uppermost tidal limit, and has a highly urbanised catchment. SR is primarily agricultural land in the lower catchment and sclerophyll woodland in the upper catchment and is dammed 75 km upstream, whilst CR is part of Batemans Marine Park, has a largely forested catchment and is unregulated. All three estuaries are open to recreational fishing, but only SR sustains commercial fishing.

Study species: luderick (Girella tricuspidata)

Luderick is a temperate species that recruits preferably in estuarine seagrass beds (Smith and Sinerchia, 2004). Juveniles show preferences for similar habitats (Middleton et al., 1984; Ferrell and Bell, 1991; Hannan and Williams, 1998; Smith and Sinerchia, 2004), although they are also found on shallow coastal reefs. Luderick is reproductively mature at around 4 years of age (Gray et al., 2012), which corresponds to a size range of 220 to 320 mm fork length in NSW (Gray et al., 2010). It is important to note the size of luderick at a given age may vary considerably (based on NSW commercial fisheries data), and fish length is therefore a poor indicator of fish age (Gray et al., 2000). This marine estuarine-opportunist species (Potter et al., 2015) is primarily herbivorous (Clements and Choat, 1997), feeding preferentially on green algae such as *Ulva* spp. and rhodophytes (Anderson, 1987; 1991; Raubenheimer et al., 2005; Ferguson et al., 2015). Luderick has a minimum legal fishing size of 27 cm total length (commercial and recreational) in NSW. The highest commercial landings and catches per unit effort (CPUE) for luderick occur during the autumn and winter months in this Australian region (Gray et al., 2000; Gillson et al., 2009).

Fish collection and tagging procedure

Between February and October 2012, 61 luderick individuals, ranging between 261 and 418 mm Fork-length (FL) and mean FL of 316 mm ± 42 S.D. were caught and acoustically tagged following similar procedures to those described in Chapter 2 (Table 3.2). An acoustic transmitter [VEMCO (Bedford, Nova Scotia, Canada) V9-2L, 145 dB, 2.5 years battery life, 180-300s transmission delay] was implanted intracoelomically following standard procedures (Walsh et al., 2012b; Payne et al., 2013) (Chapter 2). The transmitter delay was programmed between 180 and 300 s to minimise chances of transmitter collision with other fish already tagged in the studied systems. Individuals were measured to the nearest millimetre and externally tagged with a plastic T-Bar Anchor tag (Hallprint Pty Ltd, Hindmarsh Valley, South Australia) displaying a unique identification number and a telephone number. After full recovery in aerated water, tagged fish were released at their point-of-capture. Fish were caught and released at different distances from the mouth of each estuary up to 24 km upstream in order to cover a large range of estuarine conditions (Fig. 3.1). Following tagging, 31

fish were released in SR (mean FL 325 mm ± 47), whilst 15 fish were released in both the GR and CR (mean FL 294 mm ± 25 and 320 mm ± 34, respectively). Detections within the first 24 h after tagging were excluded from further analysis to avoid unusual behaviour that may have been influenced by handling and surgery.

Estuarine acoustic arrays and environmental variables

Luderick estuarine movements were studied using acoustic telemetry (passive monitoring) (Heupel et al., 2006) with linear estuarine arrays of receivers set in three major estuaries of the New South Wales coast (Chapter 2). Such arrays were successfully employed to study movements of fish in estuarine systems in relation to fluctuating environmental parameters (Childs et al., 2008; Sakabe and Lyle, 2010; Walsh et al., 2012a; Taylor et al., 2014). Unlike most of these studies, which were conducted on single estuaries, this present work looked concomitantly at fish movements in three representative south-eastern Australia estuaries, allowing a generalisation of the findings to this region.

Each estuary was equipped with an array of 34 to 42 VEMCO 69 kHz VR2W acoustic receivers, distributed every 1.3 km on average to cover the brackish extent of the estuaries (Fig. 3.1). The average detection range was estimated at 350 m, and ranged from 280 to 420 m depending on the location in the case of SR (Walsh et al., 2012a). In the same estuary, a previous study estimated the chance of a fish passing past a receiver without being detected to be low (0.4%) (Walsh et al., 2012a). Estuarine arrays were in place between July 2011 and June 2014, but the Georges River estuarine array was reduced to an estuarine gate from May 2013 and the Shoalhaven River array was incomplete between June 2012 and July 2013, following large flood events in June 2013 resulting in the loss of 50% of the receivers.

Within each of the three estuaries, five to six Odyssey data loggers (Dataflow Systems Pty Ltd, Christchurch, New Zealand) recording hourly water temperature (°C, *Temp*) and conductivity (mS cm^{-1}, *Cond*) were deployed mid-water and spaced from the mouth

to the limit of freshwater (Fig. 3.1). Hourly river discharge (flow) data were obtained from the NSW Office of Water, Department of Primary Industries (http://www.water.nsw.gov.au/).

Acoustic receivers and data loggers (temperature and conductivity) were downloaded every 6 months until June 2012, and then every 12 months using the VEMCO User environment (VUE) and Odyssey PC software, respectively.

Data processing and analysis

Transmitter detections and estuarine environmental parameters were stored in a Microsoft Access database. Luderick detections were uploaded in the IMOS (Integrated Marine Observing System) Animal Tracking database through the collaborative web-based portal https://aatams.emii.org.au/aatams/. The linear distances (km) separating the receivers to the mouth (distance-to-sea) were calculated using ArcGIS v 10.2.

A Kruskal-Wallis test followed by a Dunn's post-hoc test was used to determine differences in fish size between tagging locations, categorised by their relative distance-to-sea [close to the estuary mouth (location 1), mid-estuary (location 2) and upstream (location 3); Table 3.3.]. To investigate fish position within the estuary in relation to fish size, the kernel density estimates (KDE) distribution was calculated for each fish using the density function in R (version 3.2.2) using the Silverman's method to select the bandwidth (Silverman 1986). The modal position of each fish in the river was calculated as the modal linear distance-to-sea (*Modal_Dist*). The linear distances encompassed by the 50^{th} and the 90^{th} percentile of the kernel density were used as estimates of the core area and the total spatial utilisation (home range), respectively. Simple linear regressions were used to test the relationship between the fish length and *Modal_Dist*, as well as the core area and the home range (linear distances were log transformed), and the relationship between fish size and the average conductivity at the *Modal_Dist* of each fish.

For each fish, the daily mean distance-to-sea was calculated and corresponding daily averages of water temperature and conductivity were assigned to them based on the closest logger from the fish position. To analyse drivers of luderick movements, a single fixed logger reference station was chosen for each estuary to represent the fluctuations of these parameters at the level of the estuary (e.g. Taylor et al., 2014). This choice was made based on the distribution of the fish along the estuary (e.g. where most of the detections occurred) and on the logger providing the most continuous data set (some loggers were lost or malfunctioned during the monitoring) to ensure that water temperature and conductivity data matched the fish daily positions.

Due to equipment failure and loss of receivers in floods, corresponding environmental and fish detection data could not be obtained for the total duration of the study period. Therefore, the following time windows were retained for the analysis of the movement drivers (models): 03/02/2012 to 29/05/2013 for GR, 07/02/2012 to 27/06/2012 for SR and 04/04/2012 to 27/10/2012 for CR.

Data from the three estuaries were pooled and analysed to generalise the movements of individuals across the estuaries, and the modelling per individual estuary was used to determine potential differences in movement drivers between estuarine systems.

The daily relative position (*Dev*) was calculated for each fish based on the linear deviation to its modal position using the equation *Dev* = *Dist* - *Modal_Dist*. A positive *Dev* indicates that the fish was upstream of the modal distance-to-sea, and a negative *Dev*, the opposite. A series of linear mixed-effects models were built to identify the main drivers in luderick movements within the estuarine systems studied. The relationship between daily relative position, conductivity and season was evaluated using the following model:

$$Dev = \beta_0 + \beta_1 \cdot Cond + \beta_2 \cdot High\_Flow + \beta_3 \cdot FL + \beta_4 \cdot Season + random\ factor\ (Fish\_ID) + \varepsilon$$

The river *Flow* was not included in the model, as the response variable of freshwater inflow in the system is better described by the fluctuations of conductivity. Conductivity is commonly used as a proxy of freshwater inputs (e.g. Payne et al., 2015). The

variables *Cond* and *FL* were scaled to a value between -1 and +1. The *High flow* parameter is a dummy variable reflecting the 5% highest values of river flow recorded during the monitoring period, corresponding to the following thresholds: 34.4 m^3 s^{-1} for GR, 65.6 m^3 s^{-1} for SR and 20.2 m^3 s^{-1} for the CR. The variable *High flow* was used to examine freshwater input pulses. Temperature and conductivity are highly correlated, and therefore, both terms could not be used conjointly in the models. The variable season was used as a proxy of seasonal variations in environmental parameters over the year, including the seasonal fluctuations in temperatures. The fish ID was included as a random factor in the models (Zuur et al., 2009). Models were run using the nlme package in R. The best combinations of explanatory variables, and their contributions to explain luderick estuarine movements using stepAIC routine, procedure removing non-explanatory variables successively under the condition that the AIC obtained with the new model was lower. (Venables and Ripley, 2002) (AIC: Akaike information criterion).

3.4 Results

Fish distribution

A total of 202,514 detections was collected over the full period of monitoring (February 2012 to June 2014). Luderick were detected between the mouth of the estuary and up to 33 km for GR, 30 km for SR, and 37 km for CR upstream (Fig. 3.2). In SR and CR, fish tended to occupy lower reaches of the estuary (<17 km from the mouth), whereas most of the fish were recorded in the lower and mid-estuary of GR (16-26 km) (Fig. 3.2). Across the three estuaries, there was a negative relationship between fish length (FL) and the modal distance-to-sea (*Modal_Dist*) ($F_{1,42}$ = 4.53, p = 0.04). However, no relationship was found between FL and the linear distance of the river, the core area (50% KDE) or the home range (90% KDE), with $F_{1,42}$ = 2.05, p = 0.16, and $F_{1,42}$ = 1.61, p = 0.21, respectively (Fig. 3.3). In addition, a positive relationship was found between conductivity and FL ($F_{1,42}$ = 16.69, p < 0.001). During the tagging campaign, larger fish were rare or absent in catches in the most upstream estuary sites (e.g. at location 3). In contrast, a significantly greater number of smaller fish were tagged upstream (location 3) in GR and SR (Table 3.2; Kruskal-Wallis: H = 16.29, 2 d.f., p < 0.001). No

significant relationships between fish length and distance to estuary mouth were found in the CR for which fish were only tagged at locations 1 and 2 as no suitable fishing sites were found within the upper part of CR.

Environmental variables

The discharge and conductivity of the three estuaries was highly variable during the study period (Fig. 3.4). Conductivity at the scale of the estuary generally decreased with increasing flow rate, with rapid, temporary decreases occurring during high flow events (Fig. 3.4). Interestingly, conductivity also decreased and remained low during protracted periods of elevated flow (press effect) (Fig. 3.4). Therefore conductivity appeared to be a suitable proxy of variation in freshwater inputs for the models. Over the period of 2011-2013, which encompassed the main period of acoustic monitoring, both conductivity and water temperature exhibited seasonal patterns, with temperature displaying smoother and less short-term fluctuations (Fig. 3.4). During the same period and across the three estuaries, high flow events were more frequent in February-March (i.e. summer), and coincided with decreased conductivities (Fig. 3.4). Other major high flow events occurred in July 2011 and 2013.

Luderick were detected at a wide range of water temperatures (10 to 27 °C) (Fig. 3.5a) and conductivities [close to 0 (~freshwater) to 50 mS cm^{-1} (seawater); Fig. 3.5b]. The peak in mean daily distribution of several individuals aligned with very low values of conductivity at GR and SR (5 out of 16 fish contributed most to the 0-4 mS cm^{-1} class of conductivity).

Movements of luderick within estuaries

A total of 2,387 paired mean daily fish distance-to-sea and corresponding environmental parameters was obtained and analysed in the models (GR: 1,044, SR: 431, and CR: 912) (Table 3.3).

Conductivity, river discharge (flow) and season were the main drivers of luderick relative deviation in terms of fish position within the estuary (Table 3.4).

Responses and range of movement among individuals did not appear to differ between fish sizes. Figures 3.6a, b, and c show examples of movement patterns of luderick in association to the temperature, conductivity, and river discharge for the three estuaries. Most of the fish responded to changes in flows and conductivity, with ranges of movement appearing to be related to the magnitude of change in environmental variables (km, up to over 10 km) and the initial position of the fish in the estuary. Fish located upstream tended to move longer distances downstream compared to those occupying lower positions in the estuary (Fig. 3.6a, b and c). While most of the fish appeared closely following the fluctuations in conductivity, others only displayed noticeable movements under drastic high flow events (Fish #10, Fig. 3.6a), or showed no obvious response at all (Fish #50). From these examples, fish #37, #58, and #61 (of 14 fish) that had left their tagging estuary to undertake a coastal migration (Chapter 2). Temporary ocean excursions could explain the gaps in detections (e.g. for fish #50 and #61, Fig. 3.6c). However, during gaps in data, it is difficult to know with certainty whether a fish spent time outside the estuary or, conversely, remained in the system, out of range of the receiver arrays.

3.5 Discussion

Clarifying the interactions between environmental variability and estuarine fish movement and distribution provides essential information to establish relevant management and conservation strategies. Based on the examination of luderick movements in relation to abiotic factors in three SE Australian estuaries, it appeared that conductivity was the primary factor influencing movements of luderick. Specifically inputs of freshwater and changes in conductivity appeared to be the main factor influencing longitudinal movements of luderick, at the scale of the estuary. Across the three study estuaries, luderick, displayed prominent downstream movements in response to rapid increases in river flows during rainfall (high flow events), and moved upstream as conductivity increased on return to base-flows. Although seasonality could not be fully assessed due to lack of temporal replication in the data, luderick estuarine movements also appeared to be associated with seasonal variations of flow and conductivity, with summer and winter seasons characterised by higher levels of rainfall. Our results give increased evidence of the important roles of flow, salinity

(conductivity), and temperature (seasons) in driving fish movement behaviour in estuarine systems in NSW and other regions of the globe, with similar results also found for the spotted grunter, (*Pomadasys commersonnii*) (Childs et al., 2008), estuary perch (*Macquaria colonorum*) (Walsh et al., 2013) and mulloway (*Argyrosomus japonicus*) (Taylor et al., 2014).

Luderick are present all year round in estuaries and shallow coastal reefs (Kailola et al., 1993; Miskiewicz and Trnski, 1998). In this study, tagged luderick were found across very large ranges of conductivity and temperature and were detected throughout the estuaries, from the mouth up to the limit of the freshwater. This implies that this species is able to physiologically adjust to a wide range of environmental conditions, including the capacity to efficiently osmoregulate. All teleost fish, from marine to freshwater fish, maintain a constant osmolality of their body fluids (Kültz, 2013). Euryhaline species possess adaptive hyperosmoregulatory and hypoosmoregulatory strategies to tolerate changes in salinity when moving from freshwater to seawater and vice-versa (McCormick et al., 2013), and therefore to temporarily cope with large variations in internal osmolality (Kammerer et al., 2010).

A larger number of smaller fish were present in more upstream locations relative to larger fish. These differences in modal position in the estuary might reflect an ontogenetic shift towards more “marine” preferences with increase in age. Across their different life stages, individual fish change morphologically and physiologically (McCormick et al., 2013). Luderick recruit and spend time as juveniles in estuarine habitats where they find suitable conditions to develop (e.g. food, refuge from predators) (Smith and Sinerchia, 2004). This requires physiological capacities to regulate according to their local environment (e.g. osmoregulation), and therefore, these capabilities and efficiencies are expected to vary with ontogeny. Ontogenetic differences in response to variations of conductivity have also been shown for mulloway in SR. Juvenile mulloway (*Argyrosomus japonicus*), tended to reside in higher reaches of SR in comparison to adults, and shifted closer to the mouth of this estuary under the press effect of water inflows (Taylor et al., 2014). In contrast, luderick distributional responses to fluctuations of environmental variables or in home range did not appear to be related to fish length. This suggests that environmental effects on fish

behaviour are not influenced by fish size. This finding is also supported by Chapter 2, which showed there were no differences seen in fish length among the fish that departed from the tagging estuary as both small and larger fish had left or stayed in the systems over the duration of the monitoring. However, the study of movements among ontogeny was limited by the size range of luderick tagged, which was restricted to mature fish or those close to maturity.

Pronounced fluctuations in estuarine conditions, such as those driven by rainfall runoff, may represent strong signals for fish to reproduce, and hence may explain why some luderick egressed from the estuary. Pulses of freshwater inflow occurring during the austral summer months drove mature mulloway *Argyrosomus japonicus* towards the mouth of the Shoalhaven estuary, and was identified as a potential signal stimulating spawning events (Taylor et al., 2014). In the same system, increased summer freshwater inflows also triggered large-scale downstream movements of the estuarine-resident estuary perch *Macquaria colonorum* (Walsh et al., 2012a), also showing a link with reproduction. Variation in flow and seasonal differences in water temperature (seasons) are factors widely documented to trigger and time reproduction related movements of fish in rivers and estuaries (Jonsson, 1991; Svendsen et al., 2004; Taylor and Cooke, 2012). In SE Australia, luderick have a protracted spawning period which varies as a function of latitude, with the main reproductive period occurring between October and January in the southern part of NSW (Gray et al., 2012). It is commonly reported that, in NSW, luderick form large aggregations at the mouth of estuaries and coastal headlands, presumably to spawn, during the austral autumn-winter months (Gray et al., 2012). The increase in freshwater inflow occurring at this time of the year may concentrate luderick towards the mouth and may trigger a signal to reproduce. Several fish left the linear estuarine acoustic arrays in response to high river flows before coming back, weeks to months later, during documented spawning periods. It is possible that some individuals might have temporarily left the estuary to spawn nearby, without undertaking a full spawning migration, supported by the absence of detection outside the system (Chapter 2).

Such close relationship between luderick movements and freshwater inputs suggest longer term climatic variability, including ENSO (El Niño Southern Oscillation), and precipitation changes associated with climate change, may impact the future of this species. Natural variations and anthropogenic-induced perturbations play important roles in the fluctuations of estuarine environmental conditions, and consequently, fish movements. Seasonal and plurennial variations in river flow regimes have an effect on estuarine and coastal fisheries (Abrantes et al., 2015). Gillson (2011) reported higher catch per unit of effort (CPUE) in relation to seasonal increase in freshwater flow for several species of commercial interest, including luderick, which is mainly caught in NSW estuaries during autumn-winter (Gray et al., 2000; Gillson et al., 2009). Furthermore, it is expected that these movement patterns could be affected by the elevated regional climatic variability. South-eastern Australian rivers are characterised by alternating flood and drought regimes (Erskine and Warner, 1998). These plurennial fluctuations in freshwater flow influence estuarine commercial fisheries, with lower catches occurring during drought regimes (Gillson et al., 2009). Additionally, differences in estuarine movement patterns of luderick and signals triggering migration (Chapter 2) are anticipated to occur as a consequence of these contrasting river flow regimes (2011 and 2012 were particularly "wet" years falling under La Niña ENSO phase).

Flow is regulated by an upstream dam in the Shoalhaven River and management strategies in water release and maintenance of flow may influence luderick movements in this system. Human alterations of flow regimes caused by damming (flow regulation), freshwater use (irrigation, drinking water supply), and activities in the water catchment (agriculture, urbanisation) have an impact on the physico-chemical conditions of the estuary, as well as on the estuarine and coastal marine ecosystem productivity (Cloern, 2001). River flooding (natural or floodgate release) and drought (damming, water diversion and use) can have disastrous impacts on the estuarine system and fish communities. Exceptional large river floods can lead to fish mass mortality events, mainly resulting from a drastic reduction of dissolved oxygen in the water, leading to fish asphyxia (Whitfield, 1995). The risk of mass mortality can be exacerbated by human alterations of the floodplain and water catchment (e.g. agriculture, land clearing) by potentially favouring the injection of higher levels of

decomposing organic matter in the system and acidifying the water, consequently disturbing dissolved oxygen concentrations. In the past, luderick, among other species, suffered large mortalities during major flood events in NSW estuaries (Dawson, 2002; Kennelly and McVea, 2002). Moreover, substantial anthropogenic alterations of water discharges make estuarine ecosystems even more sensitive to climate change (Vorosmarty et al., 2000). Thus, these factors should be taken into account and caution should be taken when it comes to managing rivers and catchment areas.

Seasonality in luderick estuarine movement could not be well addressed, mainly due to the loss of receivers and temperature/conductivity loggers. Retrieving receivers and data loggers on a more regular basis, such as quarterly or at least every 6 months, requires more logistics and increases maintenance costs, but would significantly reduce the gaps in the data and guarantee the collection of a temporal series, essential for seasonal replication. The linear arrays were based on single receivers spread along the river, with detection ranges covering, in most cases, the width of the river. The analysis of the data revealed few cases of non-detection of fish having passed through an operational receiver station. Receiver detection ranges vary with biotic (e.g. biological noise) and abiotic factors (e.g. temperature, turbidity), both affecting the performances of the network of receivers (Kessel et al., 2014 and references therein). Detection ranges are expected to become critically reduced under certain conditions such as high flow events, potentially explaining the "skips" of detections observed during the predominant downstream movements. Luderick are capable of fast displacements (Chapter 2), which, combined with a tag programmed to emit a signal every 3 to 5 min (to assure enough battery life and limit chances of tag collisions) and a the local environment (underwater topography, presence of vegetation) that can potentially mask tag signals, could further explain these skipped detections. Such limitations are inherent to acoustic telemetry studies and the design of receiver arrays should account for them, in relation to the aims of the research, in order to increase the chances of detection.

The spatial resolution of the linear estuarine arrays did not allow for identification of movement patterns occurring at smaller scales (e.g. <1 km). Other acoustic telemetry methods such as active tracking (Gannon et al., 2015) or other recently developed systems such as the VEMCO Positioning System (VPS) (Espinoza et al., 2011a)

provide more accurate positions (m's) of the fish. Such data can be used to study movements patterns at fine spatial (e.g. habitat use) and temporal (e.g. diel) scales. Fine spatial resolution allows relating fish positions to habitat, and is especially useful within the complex mosaic of habitats present in estuaries. Swimming activity and position in the water column (Taylor et al., 2013; Payne et al., 2015c) also proved to be very useful tools to understand behavioural patterns of carnivorous fish in estuarine systems in relation to fluctuating environmental conditions, and could be applied in the future to further luderick movement behaviour studies.

3.6 Conclusions

This study contributes to the knowledge of the ecology of luderick and provides valuable information with regards to conservation and fisheries management of this species. The linear estuarine arrays of receivers provided insights on the luderick movement patterns in relation to the changing environment at the scale of the estuarine systems, across three representative estuaries of SE Australia. Overall, rainfall plays important role in the distribution of luderick within estuaries and as a cue to egress from them. Therefore catch rates may vary according to rainfall, and, in addition to influence catch rates, climatic variability may have a significant impact on the cues triggering alongshore migrations of luderick, and potential effects on spawning migrations. It would be interesting to expand this research to juvenile fish and potentially identify differences with ontogeny in movement patterns and responses to fluctuating environmental conditions. Seasonal patterns in luderick estuarine movements could not be well addressed across estuaries, due to the combination of fish leaving the systems and restrictions regarding both the environmental and detection datasets related to gear loss and faults. For future work, this latter issue could be addressed by implementing more frequent maintenance operations on the networks of receivers. The motivations for luderick to temporally visit estuaries or to stay in for extended periods remain unclear, and require further investigations (e. g. food availability, refuge from predation or from less favourable conditions in coastal areas). Advances in technology offer a panel of tools dedicated for the study of movement patterns at a smaller spatial resolution. Applied to luderick, this could provide a deeper understanding of spatial utilisation (e.g. habitat association) and finer temporal movement patterns (e.g. diel) of this species, and

to deliver complementary insights regarding the behavioural responses of luderick to fluctuating environments.

3.7 Tables

Table 3.1 Physical characteristics of the studied estuaries (source: NSW Office of Environment and Heritage and Roy *et al.* 2001 (*)).

River	Catchment area (km^2)	Estuary area (km^2)	Estuary volume (ML)	Average depth (m)	Estuary group*	Estuary type*	Evolution stage*	Length of river and (estuary) (km)
Georges River	931	27	271,394	11	Tide dominated	Drowned valley	Intermediate	96 (38)
Shoalhaven River	7,086	32	86,508	3	Wave dominated	Barrier estuary	Mature	327 (48)
Clyde River	1,723	18	50,737	3	Tide dominated	Drowned valley	Intermediate	115 (38)

Table 3.2 Tagging information for luderick (*Girella tricuspidata*) fitted with acoustic transmitters, including the estuary (GR: Georges River, SR: Shoalhaven River, CR: Clyde River (fork length – FL in mm. Tagging locations in the estuary are stated as either 1: downstream, 2: mid-stream or 3: upstream. Modal distance-to-sea (*Modal_Dist*) is calculated based on the kernel density distribution, and linear distance (km) along the estuary containing the 50th and the 90th percentile of the kernel density distribution (KDE 50% and KDE 90%, respectively).

Fish_ID	Estuary	FL (mm)	Tagging date	Tagging location	Modal_Dist (km)	KDE 50%	KDE 90%
1	GR	295	02/02/2012	1	7.8	1.3	2.5
2	GR	295	16/02/2012	2	16.9	2.1	4.1
3	GR	290	02/02/2012	1	1.3	3.0	6.0
4	GR	290	02/02/2012	1	6.5	0.0	0.0
5	GR	275	16/02/2012	2	12.1	7.0	14.2
6	GR	264	01/02/2012	1	6.5	6.5	6.5
7	GR	284	16/02/2012	2	16.0	0.0	0.0
8	GR	285	27/02/2012	2	16.2	5.0	15.3
9	GR	276	01/03/2012	3	18.2	1.1	2.0
10	GR	328	27/02/2012	2	16.9	3.0	5.2
11	GR	279	01/03/2012	3	26.0	8.0	12.8
12	GR	275	01/03/2012	3	6.6	1.1	8.2
13	GR	362	02/02/2012	1	6.5	0.5	9.1
14	GR	328	01/02/2012	1	11.7	11.7	11.7
15	GR	276	28/02/2012	3	24.7	11.9	21.4
16	SR	364	02/10/2012	1	9.3	0.3	0.9
17	SR	418	02/10/2012	1	11.5	0.6	1.5
18	SR	418	02/10/2012	1	5.5	5.1	10.0
19	SR	308	02/10/2012	1	9.3	0.0	0.0
20	SR	318	02/10/2012	1	19.2	3.5	16.2
21	SR	337	02/10/2012	1	9.9	0.1	8.6
22	SR	396	02/10/2012	1	2.5	1.1	2.4
23	SR	395	02/10/2012	1	11.6	1.9	12.1
24	SR	335	02/10/2012	1	4.5	7.4	13.0
25	SR	305	02/10/2012	1	9.3	1.1	2.0
26	SR	404	02/10/2012	1	-	-	-
27	SR	393	02/10/2012	1	1.1	2.2	4.4
28	SR	365	02/10/2012	1	28.3	0.0	0.0
29	SR	338	02/10/2012	1	19.2	1.6	7.0

Fish_ID	Estuary	FL (mm)	Tagging date	Tagging location	Modal_Dist (km)	KDE 50%	KDE 95%
30	SR	305	02/10/2012	1	9.3	1.3	12.6
31	SR	349	02/10/2012	1	18.8	0.2	1.4
32	SR	311	07/02/2012	2	15.4	1.7	7.8
33	SR	290	07/02/2012	2	15.4	3.5	6.5
34	SR	283	06/02/2012	3	21.7	5.2	9.1
35	SR	262	16/02/2012	3	20.0	20.0	20.0
36	SR	288	07/02/2012	2	15.4	4.6	9.2
37	SR	304	07/02/2012	2	15.4	5.7	13.9
38	SR	278	07/02/2012	1	9.2	0.0	0.0
39	SR	319	07/02/2012	1	8.0	9.3	16.2
40	SR	270	16/02/2012	3	12.8	1.5	12.8
41	SR	289	07/02/2012	1	6.9	0.8	2.3
42	SR	274	06/02/2012	3	19.2	0.0	0.1
43	SR	288	07/02/2012	1	8.1	8.7	17.8
44	SR	295	07/02/2012	2	15.4	5.7	13.9
45	SR	261	16/02/2012	3	11.7	6.0	16.1
46	SR	300	07/02/2012	1	8.1	0.1	0.9
47	CR	306	04/04/2012	2	9.6	0.0	0.0
48	CR	344	04/04/2012	2	13.2	1.1	4.0
49	CR	340	03/04/2012	1	8.4	0.2	0.7
50	CR	381	03/04/2012	1	6.0	0.8	4.1
51	CR	362	17/04/2012	2	-	-	-
52	CR	290	03/04/2012	1	12.2	6.9	15.8
53	CR	288	03/04/2012	1	16.6	0.0	0.1
54	CR	278	03/04/2012	2	16.8	1.4	8.5
55	CR	291	04/04/2012	2	12.8	3.9	8.7
56	CR	313	03/04/2012	1	8.5	1.7	8.5
57	CR	321	17/04/2012	2	8.6	1.9	10.3
58	CR	378	17/04/2012	2	13.0	1.0	9.7
59	CR	319	17/04/2012	2	12.1	20.8	32.7
60	CR	275	03/04/2012	2	-	-	-
61	CR	348	17/04/2012	2	33.4	20.8	32.7

Table 3.3 Sequential linear mixed-models runs and corresponding differences in AIC (Akaike information criterion) compared with the previous model. The best models are highlighted in bold.

Model	Parameters	Variable removed	Variation of AIC
Dev_all_1	***Cond* + *HighFlow* +*FL* + *Season***	**None**	**-**
Dev_GR_1	***Cond* + *HighFlow* + *Season***	***FL* (p=0.24)**	**-0.6**
Dev_SR_1	***Cond* + *HighFlow* + *Season***	***FL* (p=0.24)**	**-1.8**
Dev_CR_1	*Cond* + *FL* + *Season*	*HighFlow* (p=0.79)	-2.0
Dev_CR_2	***Cond* + *Season***	***FL* (p=0.20)**	**-0.2**

Table 3.4 Predictors of the optimised models for *Delta_Dist* (relative change of position of luderick in the estuary).

Model	Predictor	*β*	S.E.	*t*-value	*p*-value
Dev_all	Intercept	-1.13	0.49	-2.33	0.02
	Cond	2.12	0.25	8.34	<<0.001
	High Flow	-0.77	0.29	-2.61	0.009
	FL	-1.52	0.79	-1.92	0.06
	Season	0.26	0.10	2.79	0.005
Dev_GR_1	Intercept	-0.76	0.62	-1.22	0.22
	Cond	1.54	0.26	6.00	<0.001
	High Flow	-0.82	0.41	-2.00	0.045
	Season	0.25	0.11	2.15	0.03
Dev_SR_2	Intercept	0.66	0.37	1.79	0.07
	Cond	0.35	0.14	2.43	0.02
	High Flow	-0.82	0.42	-1.96	0.049
	Season	-0.63	0.18	-3.59	<0.001
Dev_CR_3	Intercept	-1.82	1.01	-1.80	0.07
	Cond	2.14	0.35	6.16	<<0.001
	Season	0.41	0.23	1.80	0.07

3.8 Figures

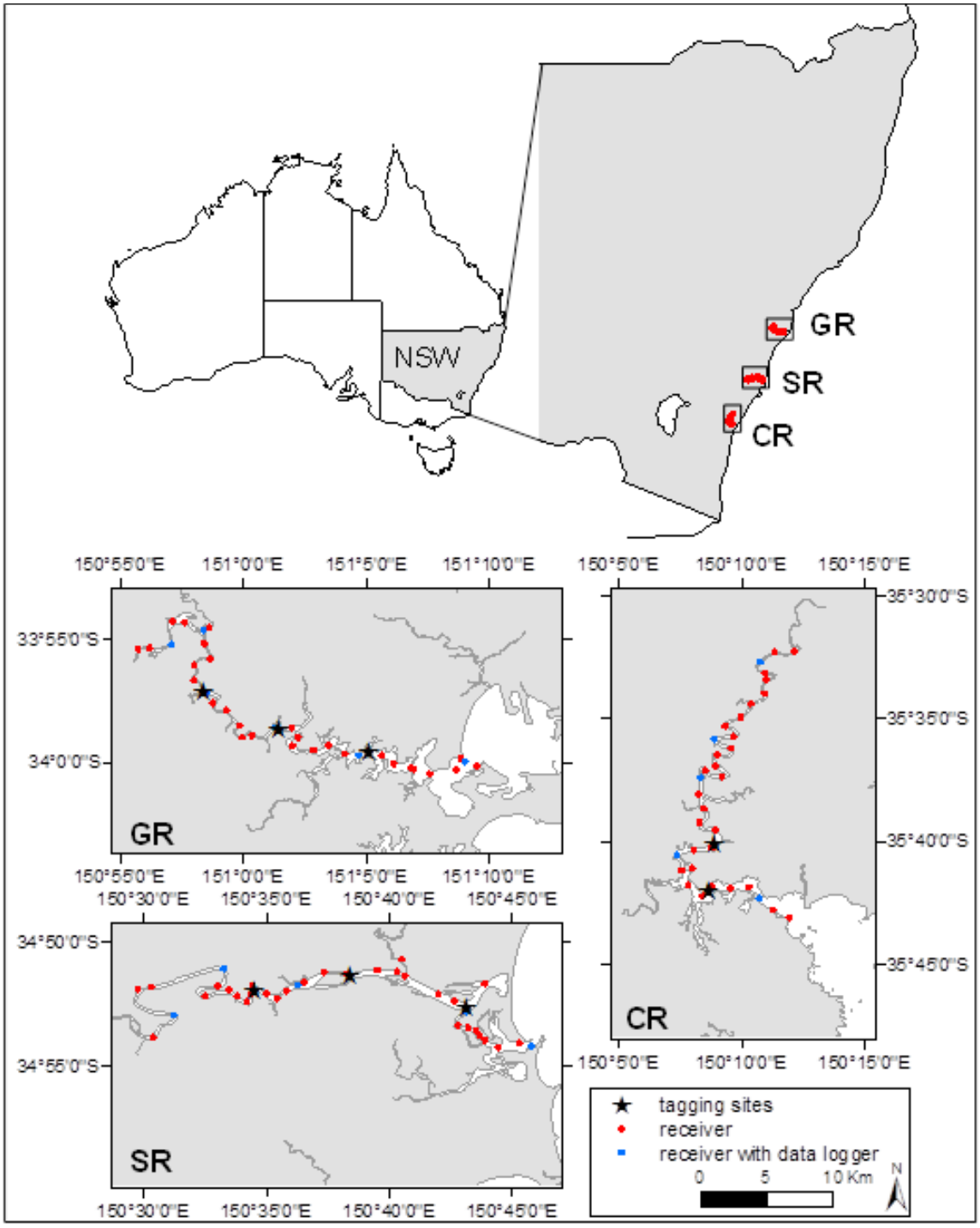

Figure 3.1 Maps of the three estuaries studied (GR: Georges River, SR: Shoalhaven River and CR: Clyde River), showing the linear arrays of receivers, the position of data loggers, and the tagging sites.

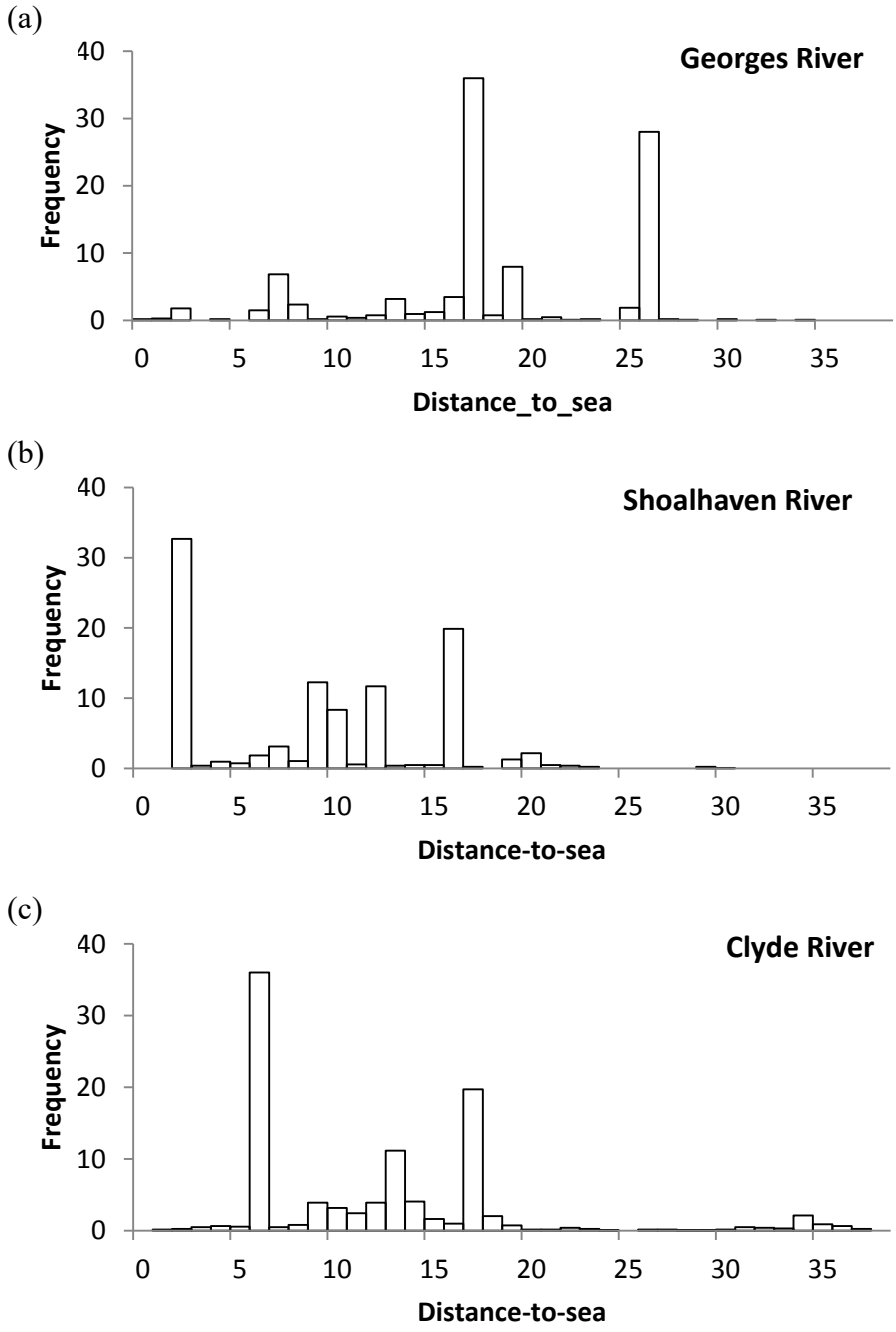

Figure 3.2 Histograms of the daily average fish distribution along the length of the three studied estuaries.

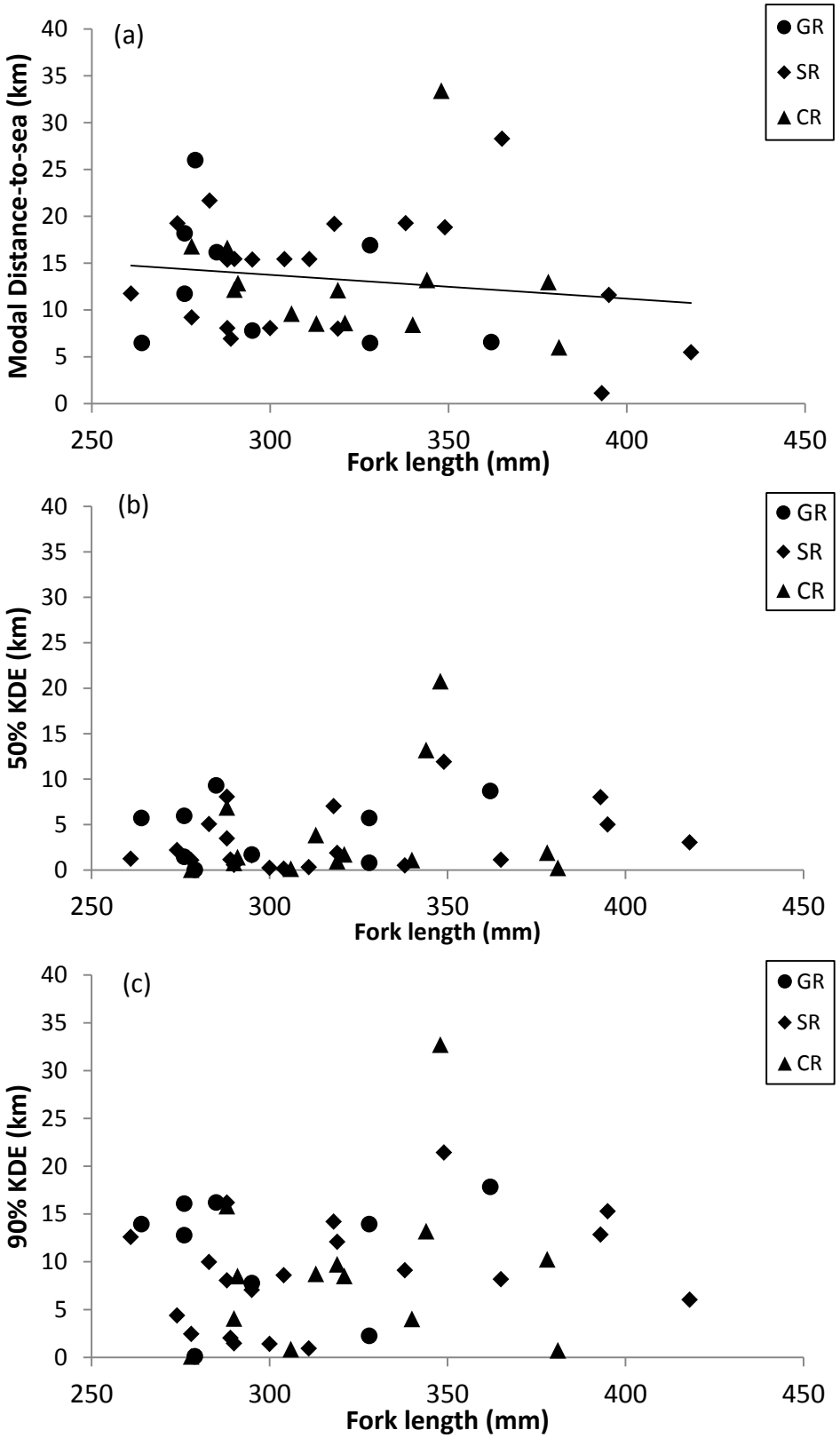

Figure 3.3 Modal distance-to-sea (*Modal_Dist*) (a) (black line: significant simple linear regression) and linear distance (km) along the estuary containing the 50th (b) and the 90th (c) percentile of the kernel density distribution (KDE 50% and KDE 90%, respectively), according to the fish length (FL, mm).

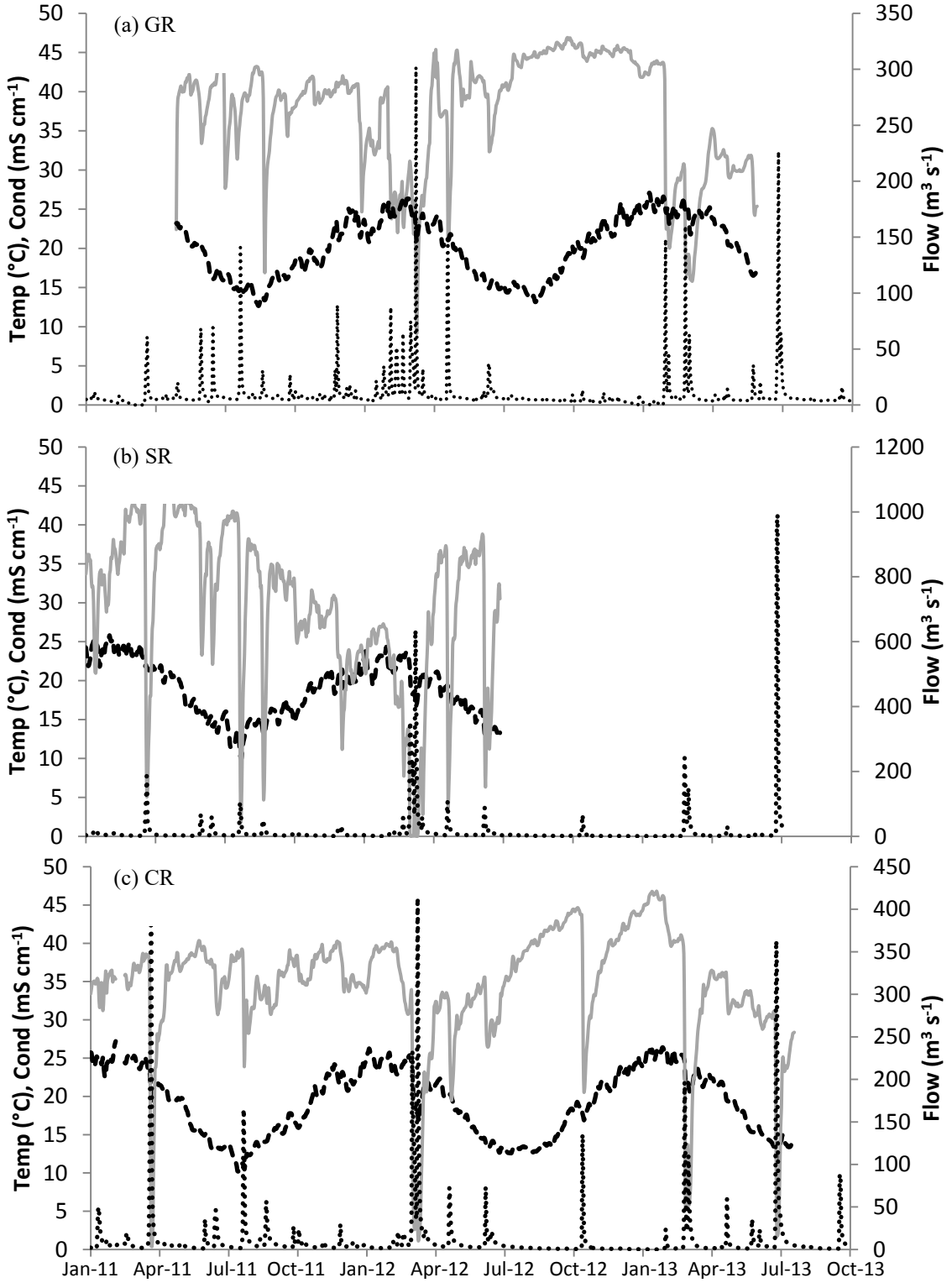

Figure 3.4 Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line) on the left Y-axis, and mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis, between January 2011 and October 2013, for each estuary (GR: Georges River (a), SR: Shoalhaven River (b) and CR: Clyde River (c)).

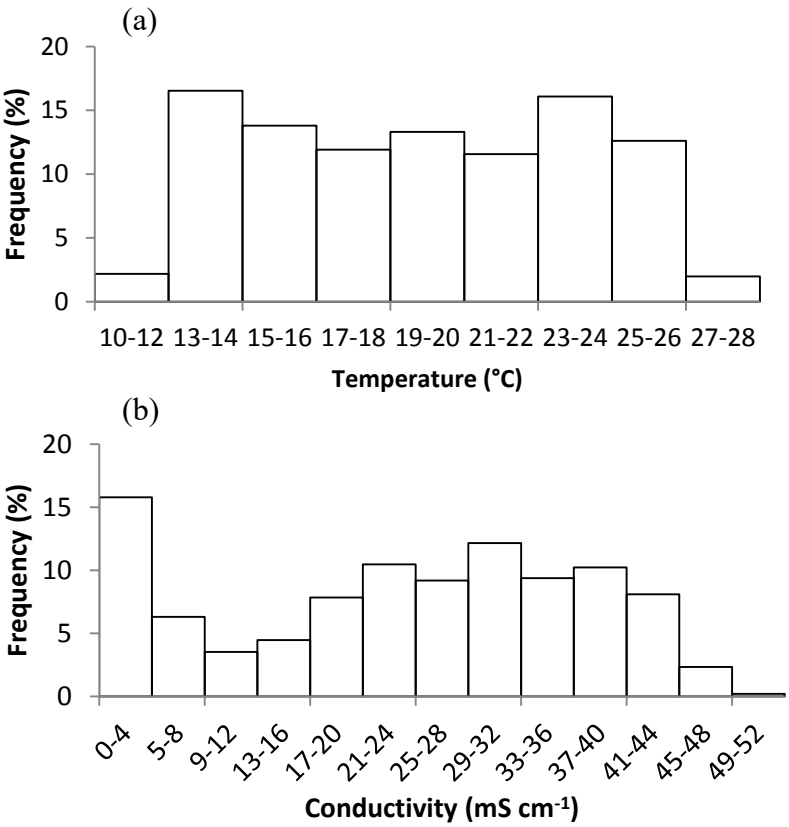

Figure 3.5 Frequencies of detection of luderick (daily averages per fish) according to the temperature (°C) (a) and conductivity (mS cm^{-1}) (b) recorded by the data loggers deployed mid-water (three estuaries combined).

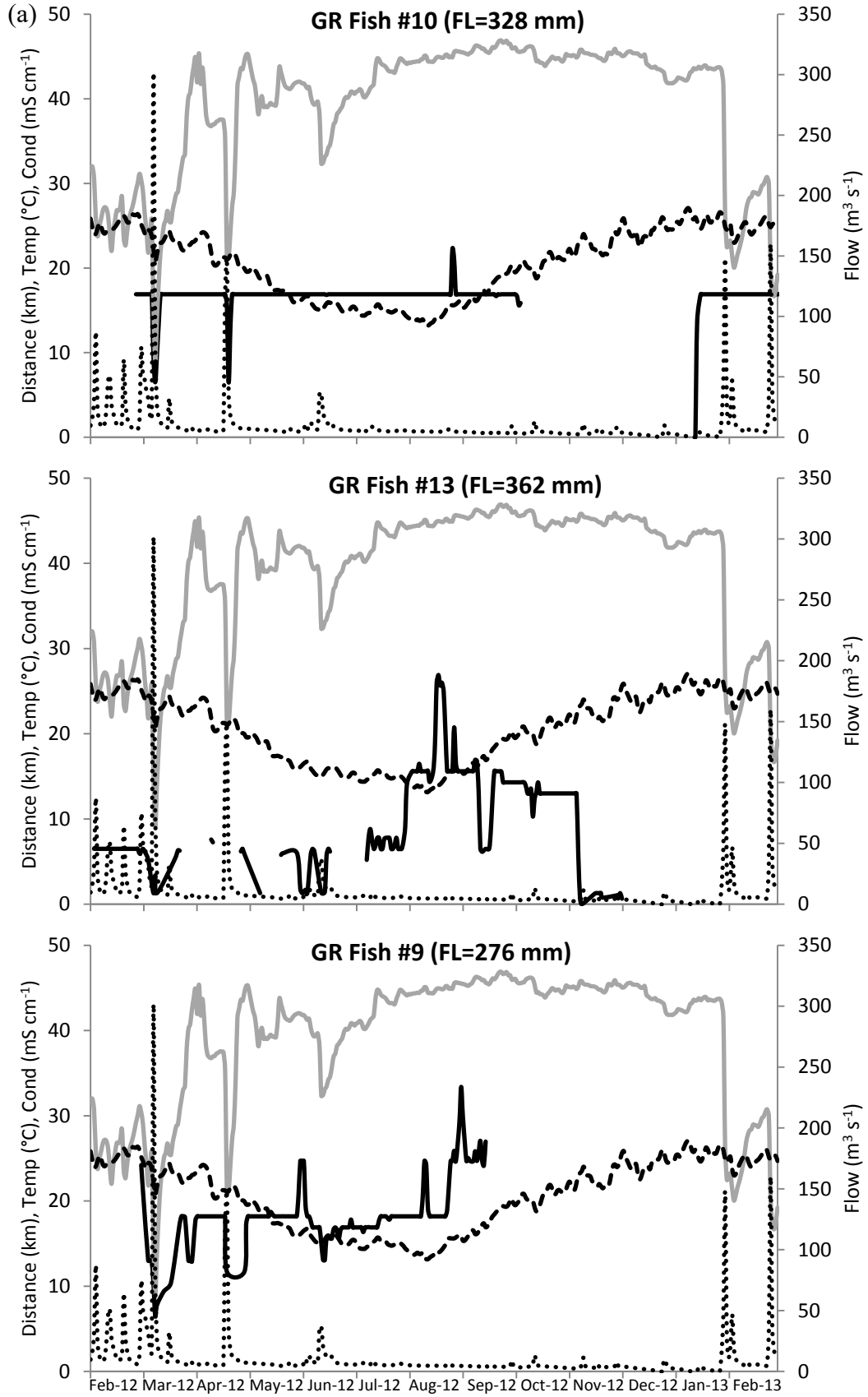

Figure 3.6a Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line), and mean daily distance-to-sea on (km) of Fish #9, #10 and #13 on the left Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Georges River.

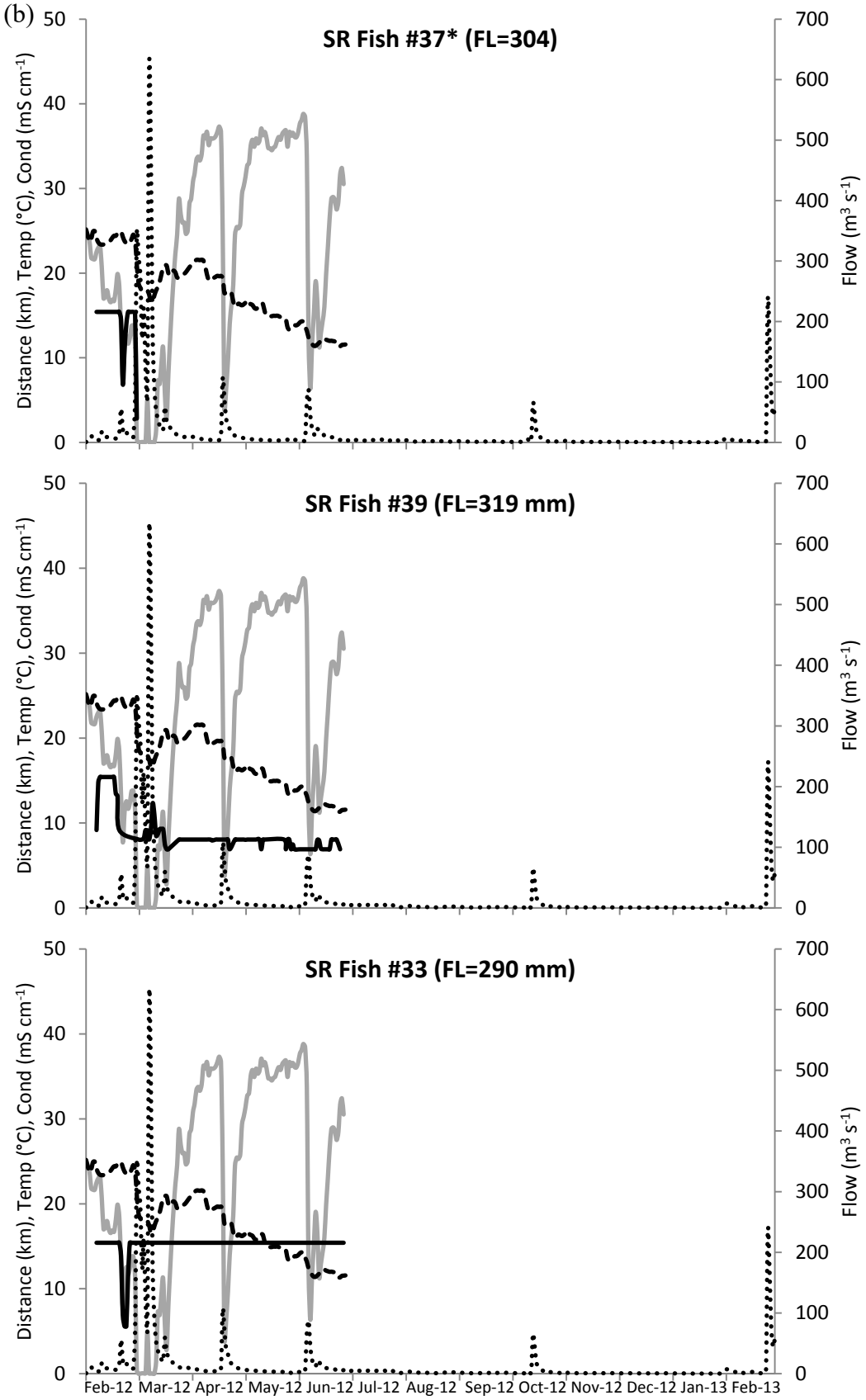

Figure 3.6b Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line), and mean daily distance-to-sea on (km) of Fish #21, #23 and #30 on the left Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Shoalhaven River. (*): fish redetected outside the tagging estuary.

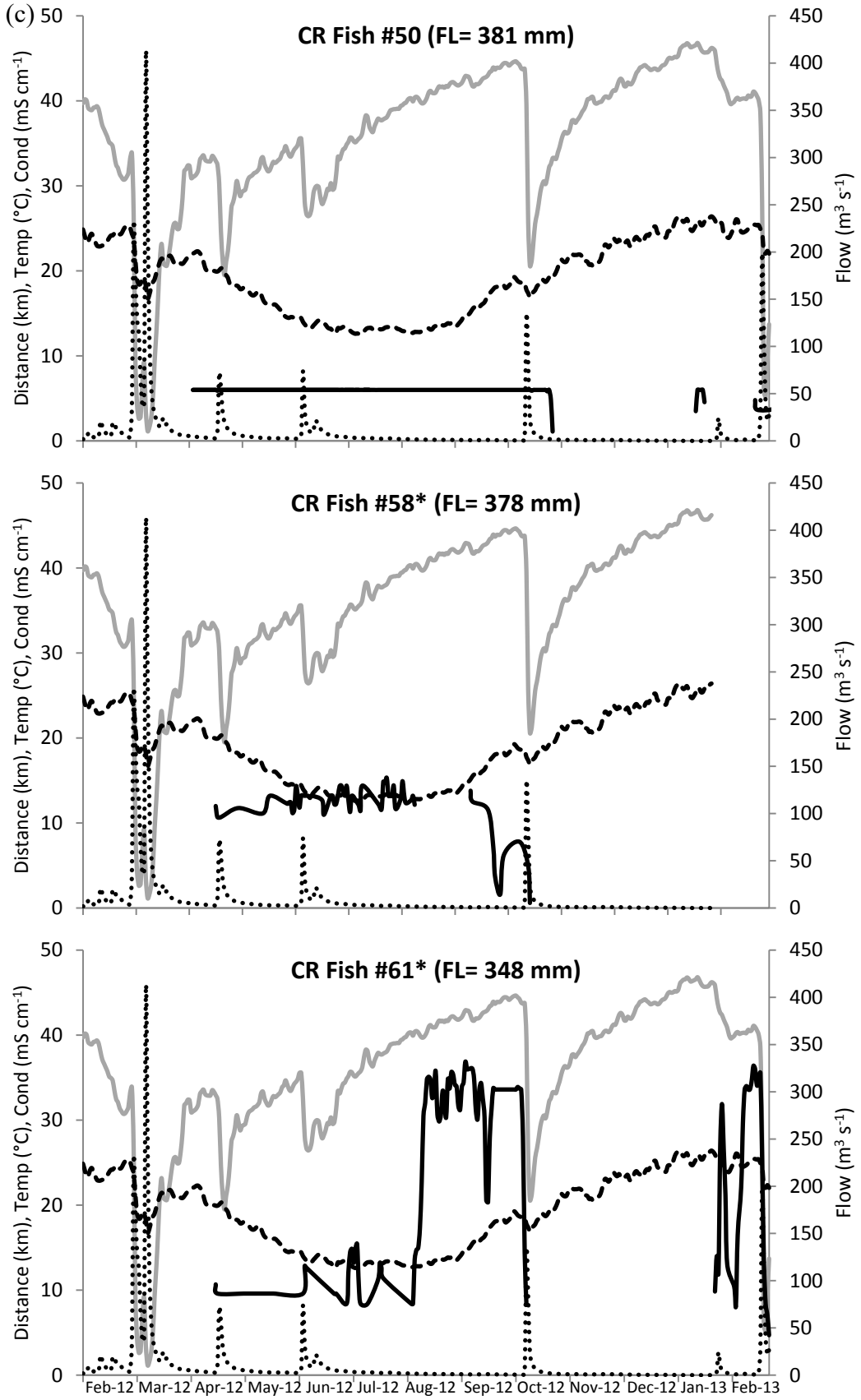

Figure 3.6c Mean daily temperature in °C (dashed line) and conductivity in mS cm^{-1} (grey line) and mean daily distance-to-sea on (km) of Fish #50, #58 and #61 on the left Y-axis. Mean daily river flow in m^3 s^{-1} (dotted line) on the right Y-axis. Estuary: Clyde River. (*): fish redetected outside the tagging estuary.

CHAPTER 4: Drivers of activity and depth use of luderick (*Girella tricuspidata*) revealed by acoustic telemetry

Cadiou G., Booth D.J., Gray C.A., Payne N.L., and Taylor D. (*in prep.*). Drivers of activity and depth use of luderick (*Girella tricuspidata*) revealed by acoustic telemetry

4.1 Abstract

Movement patterns and habitat use are critical information for understanding ecology and population structure of species. Activity patterns result from a combination of endogenous (e.g. circadian rhythm) and external (e.g. environmental variables) drivers. For many species, these drivers and their influence are still poorly known, especially in highly variable environments such as estuaries. We used acoustic telemetry to study fine-scale activity and depth use patterns of the primarily herbivorous teleost fish, *Girella tricuspidata* (Luderick, Girellidae). Ten Luderick (mean FL 305 mm ± 37 S.D.) were internally fitted with accelerometer/pressure (AP) acoustic transmitters and released within two VEMCO Positioning System (VPS) networks of receivers deployed in the Clyde River estuary (New South Wales, Australia). During the five months of monitoring, a suite of environmental variables was recorded. The positive relationship between activity and temperature could be related to the decrease in fish performances outside their optimal temperatures. Tagged luderick responded to high flow events by reducing swimming activity and shifting to deeper waters. Strong diel and sub-diel rhythm patterns were found for activity and depth, with fish being more active during the day-time and at high tidal heights. These findings could be related to diurnal foraging activity and sheltering behaviour at night-time in areas with low local current flow, consistent with luderick behavioural patterns observed in previous studies in shallow coastal rocky reefs.

4.2 Introduction

Many mobile marine organisms present rhythmic behaviours. Diel (circadian) activity patterns based on differences in activity between day and night are commonly found in aquatic organisms. Fish may present distinct diurnal or nocturnal foraging preferences, such as Haemulids which tend to forage at night-time (Nagelkerken et al., 2000b). Diel differences in foraging preferences may be related to fish diet, with for instance herbivorous fish species being commonly diurnal feeders (Helfman, 1993), and may be also a response to external pressures such predation risk and food availability (Lima, 1998b; Kadye and Booth, 2014).

Estuaries are particularly important systems for numerous species of fish and invertebrates. They are highly productive systems which enhance marine coastal productivity (Loneragan and Bunn, 1999) and provide suitable nursery grounds (Beck et al., 2001), refuges, and food for many organisms (Paterson and Whitfield, 2000). Estuaries are dynamic systems where fluctuating environmental parameters play an important role in determining spatial distribution of organisms in the system (Laprise and Dodson, 1994; Whitfield, 1999; Barletta et al., 2005). Environmental parameters vary differently either on a cyclic or an acyclic basis. The tide influences environmental conditions of estuarine and coastal systems on a sub-diel basis with an intensity varying with the lunar phase (Szedlmayer and Able, 1993; Krumme, 2009). Estuaries are also subjected to arrhythmic (pulse) events, such as large freshwater inputs from rainfall resulting in drastic and sudden changes in salinity, turbidity, dissolved oxygen and water flow (Kurup et al., 1998; Gillanders and Kingsford, 2002). Photoperiod, tide and sudden changes in environmental conditions have been shown to influence specific behaviours and movement patterns but very few studies examined linkages between the environmental conditions and behaviour at the individual level in estuarine systems (Childs et al., 2008; Payne et al., 2013; Taylor et al., 2013).

Many coastal fish species show preferences for particular habitats (Gratwicke et al., 2006), and therefore, understanding habitat distributions and their use by fish is crucial to conserve fish populations and spatially manage fisheries resources. Seagrass, mangrove, and saltmarsh are commonly found associated with estuarine systems and

play an important role for species of commercial interest and local fisheries (Jackson et al., 2001). Worldwide, anthropogenic activities and climate changes lead to the loss of these coastal shallow habitats (Gilman et al., 2008; Waycott et al., 2009; Polidoro et al., 2010), including in Australia. Understanding fine-scale habitat associations is therefore central to the conservation and fisheries management. However, fine-scale activity patterns and movements of free-ranging organisms are generally poorly known and require attention.

Acoustic telemetry is commonly employed to study movements of a large range of aquatic animals from small invertebrates (Taylor and Ko, 2011), cephalopods (Payne et al., 2011), or sea snakes (Udyawer et al., 2015), to large species such as whale sharks (Cagua et al., 2015). Acoustic telemetry overcomes the logistical difficulty of collecting movement information from mobile free-ranging animals in turbid environments such as estuarine systems (Childs et al., 2008), at night-time and in environments difficult to access by the observer (high depths, high risk conditions) (Payne et al., 2013). Acoustic telemetry allows automated and continuous data collection of the tagged individuals over time as long as they are present within the detection range of the receivers [passive monitoring (Heupel et al., 2006)] and for the duration of the transmitter's battery life. An accelerometer (A) transmitter measures the acceleration of an organism and have been successfully used to study activity rhythms of fish in estuarine systems (Payne et al., 2013; Taylor et al., 2013). Pressure (P) transmitters provide an indication of the depth where the organism is detected (Sepulveda et al., 2004). The VEMCO Positioning System (VPS) has been developed in response to the need for fine-scale resolution in position data, particularly indicated for behavioural studies (Espinoza et al., 2011a; Furey et al., 2013). The use of the combined AP transmitters deployed within a VPS is an advanced approach to study specific behavioural responses of mobile organisms in estuarine systems under regular conditions and during specific events.

Luderick *(Girella tricuspidata)* is an abundant temperate teleost species in the estuaries and coastal waters of south east Australia and north New Zealand (Jones, 1988; Kailola et al., 1993; Miskiewicz and Trnski, 1998). Luderick is present year-round in estuaries (Gray et al., 2012), and juveniles show preferences for estuarine seagrass habitats

(Middleton et al., 1984; Ferrell and Bell, 1991; Hannan and Williams, 1998; Smith and Sinerchia, 2004) even though they can also be found on shallow coastal reefs. This marine estuarine-opportunist species (Potter et al., 2015) is primarily herbivorous (Clements and Choat, 1997), feeding preferentially on green algae *Ulva* spp. and rhodophytes (Anderson, 1987; 1991; Raubenheimer et al., 2005; Ferguson et al., 2015). Many behavioural studies using acoustic telemetry in estuaries focus on carnivorous fish (Taylor et al., 2006b; Payne et al., 2013; Gannon et al., 2015), but very few studies have been conducted on herbivorous species in such systems. Luderick is considered highly mobile species capable of migrations of ~500 km (Chapter 2), but can also show a high fidelity to the estuary or near shore reefs where they were captured and released (Gray et al., 2012; Ferguson et al., 2016) (Chapter 3). Luderick is of commercial fishing interest (Gray and Kennelly, 2003), with most of the landings made in New South Wales (NSW) estuaries (Rowling et al., 2010). Luderick is also targeted by recreational fishermen with catches equivalent to the commercial landings (Henry and Lyle, 2003; Rowling et al., 2010).

We used AP tags deployed within a VPS network to better understand the activity patterns and depth use of luderick in an estuarine system. The specific aims were 1) to understand diel activity patterns in luderick; 2) to identify key environmental influences (temperature, freshwater flows pulses, tide) on luderick activity and depth use. The main hypothesis was that environmental factors would be significant predictors of luderick activity and depth, under river base flow and high flow conditions, and in relation to diel and tidal cycles.

4.3 Materials and Methods

Study site

The field study was conducted in the Clyde River (NSW South coast, 35.705°S, 150.142°E), a tidally dominated drowned river valley, 110 km long with a water catchment of 1,620 km^2. This river is unregulated (average flow 0.27 m^3 s^{-1} for 2010-2013) and the water quality is considered high, with no polluting industries present in the catchment. The estuary encompasses seagrass beds, mangroves and saltmarshes (Fig. 4.1). It extends ca. 38 km from the river mouth and is part of Batemans Marine Park. Most commercial fishing activities have been banned in the estuary since establishment of the marine park in 2006, and the Clyde River is considered as a recreational "fishing haven" where certain fishing restrictions apply, including the presence of sanctuary zones (no take areas).

Fish collection and tagging procedure

In March 2013, ten luderick (mean FL: 305 mm ± 37 S.D.) were tagged and released following similar procedures as described in Chapter 2. Adult fish were collected with either line and barbless hooks baited with sea cabbage (*Ulva* sp.) or, in areas where line fishing was not suitable, with light gauge gillnets set within, or at the edge, of seagrass beds (*Zostera capricorni*) with soaking times of less than 30 minutes. Netting was only conducted at night-time, following restrictions given by the Marine Park for the use of gillnets. After capture, the fish were placed in covered 100-L tubs filled with estuarine water containing a light sedative (AQUI-S® 25 mg/L) and fitted with aerators. Holding and handling times were minimised as much as possible, with times between capture and surgery of less than one hour. Prior to surgery, fish were anaesthetised with AQUI-S® (60 mg/L) and then placed on a V-shape padded cradle covered with plastic sheet which was wetted regularly to avoid skin damage. A bi-axial accelerometer and pressure acoustic transmitter (VEMCO V9AP-2L, 69 kHz, 46 mm length, and 3.3 g in water) were fitted internally following conventional methods (Payne et al., 2013; Walsh et al., 2013) (Chapter 2), with the transmitter X-axis aligned with the anteroposterior axis of the fish. Acceleration was calculated as an average root mean square (RMS) value for axes X and Z over the sampling time window (VEMCO "tail beat" algorithm). Acceleration and depth (pressure) were transmitted alternatively every second duty

cycle, with a random delay between 180 and 300 s to minimise transmitter collision with fish already tagged in the studied system.

Each individual Luderick was measured (fork length, FL, mm), weighed (g) and externally tagged with a plastic T-Bar Anchor tag (Hallprint Pty Ltd, Hindmarsh Valley, South Australia) displaying a unique identification code and a telephone number. After surgery, fish were placed in aerated water, and, after full recovery, indicated by normal opercular and tail movements, they were released back to their point-of-capture.

Acoustic receivers arrays (VPS) and environmental variables

A VEMCO Positioning System (VPS) consisted of two arrays of 15 and 23 VEMCO VR2W receivers (VEMCO, Bedford, Nova Scotia) deployed in the lower part of the Clyde River (Fig. 4.1). The distance between the VPS receivers was on average 219 m (acoustic receivers were spaced 200-250 m apart). The two arrays encompassed a comparable variety of habitats (Fig. 4.1) and detection data were combined and analysed together. The VPS positioning relies on the 3-receiver time difference-of-arrival (TDOA) algorithm (O'Dor et al., 1998; Voegeli et al., 2001), and therefore, raw detections have to be sent to VEMCO for processing in order to obtain the positions (calculated positions) (Espinoza et al., 2011b). The manufacturer estimated a mean horizontal positioning error of 10-12 m within the array (Payne et al., 2016). Detections were uploaded in the IMOS (Integrated Marine Observing System) Animal Tracking database through the collaborative web-based portal https://aatams.emii.org.au/aatams/.

Two Odyssey data loggers (Dataflow Systems Pty Ltd) recording hourly conductivity (mS cm^{-1}) and temperature (°C) were deployed mid-water within each VPS arrays. Hourly river discharge was obtained from the NSW Office of Water, Department of Primary Industries (http://www.water.nsw.gov.au/), tidal heights from Manly Hydraulics Laboratory (www.mhl.nsw.gov.au) and the lunar phases (0=new; 1=full) from Geoscience Australia (http://www.ga.gov.au/).

A bathymetry of the VPS areas was elaborated with ArcGIS® 10.1 based on the "Spline with barriers" interpolation method (Spatial Analyst), applied to river cross sections

depths points collected during an hydrographic survey in 2006 (NSW Office of Environment and Heritage[3]).

The Department of Primary Industries NSW provided the GIS layers of the estuarine habitats (seagrasses, saltmarsh and mangrove) (Creese et al., 2009) (Fig. 4.1). Very little information on habitat distribution was available within the VPS. In addition, the design of the networks of receivers did not encompassed important areas of seagrass (and only present at the VPS edges), limiting the study of luderick habitat association (Fig. 4.1). Available shallow habitat maps were mainly built using aerial photographs validated by video ground-truthing. The turbidity may affect the accuracy of the mapping of seagrass beds, especially for the mapping of their deeper limit.

Data processing and analysis

Pressure data were corrected for tide and standardised to the ISLW (Indian Spring Low Water) in order to provide a relative measure of the depth of the tagged fish. Raw activity and pressure data were filtered from multiple detections (where multiple receivers recorded the same acoustic transmission). Average activity and depth were calculated per 15-min time bins for each individual across the VPS monitoring period (16/03/2013 to 19/08/2013) and matched with corresponding recorded values of temperature, conductivity and river discharge. A series of linear mixed effects models were built to identify the main drivers in luderick activity and depth usage. The full models used were as follows:

$$Activity \text{ or } Depth = \beta_0 + \beta_1 \cdot Temperature + \beta_2 \cdot High\_Flow + \beta_3 \cdot Length + \beta_4 \cdot Weight + \beta_5 \cdot Moon + \beta_6 \cdot Tide + \beta_7 \cdot Diel + \beta_8 \cdot Tide * Stand\_Diel + fishID\ (random\ factor) + \varepsilon$$

The variables temperature, fork length, weight, moon phase, and tide were scaled to a value between -1 and +1. A diel index (maximum value of 5) was created based on the hours, with the highest values corresponding to the lightest hours of the day. The high flow variable is a dummy variable reflecting the high values of river flow, based on a

[3] http://www.environment.nsw.gov.au/estuaries/stats/ClydeRiver.htm

binary threshold of 20.2 m^3 s^{-1} (value = 1 if ≥ 20.2 m^3 s^{-1} otherwise the value = 0), as determined in Chapter 2. A total of 14 days with high flow events were recorded during the 166 days of the monitoring period, with a major event occurring between 24/06/2013 and 3/07/2013. Moreover, an interaction between tide and diel period (*Tide*Diel*) was included in the models to take into account the mixed effects of these variables. The fish ID was included as a random factor in each model to account for the non-independence of the data collected. Conductivity was not included in the selected models because of its high correlation with temperature and of the effects of tidal movements on this variable. High flow events (pulse effect) are characterised by a steep decrease in conductivity.

Several models were run using the nlme package in R (version 3.1.2). The best combinations of explanatory variables and their contributions to luderick activity and depth were selected using the stepAIC routine (Venables et al., 2002) (AIC: Akaike information criterion).

In order to examine rhythmicity in activity and depth use, a Fast Fourier Transform (FFT) (Hartill et al., 2003) was performed on the grand mean hourly accelerations and depths across all the fish (43 days were selected between 25/03/2013 and 18/07/2013 based on the number of hourly detection data available per 24 h). Gaps in hourly mean acceleration and depth were filled by the average value of the previous and following day for the corresponding hour (a total of 55 replacements for a total of 1,024 h).

The height of the fish from the bottom of the river was calculated by subtracting the pressure value to the matching bathymetry value available for the same position. The difference was expressed as the relative distance from the bottom (% of total depth). In terms of depth usage, expressed as the position of the fish's distance to the bottom of the estuary, four categories were used: fish on the bottom or associated to it (fish found within the first 10% of the water column with the bottom as reference), close to the bottom (10-30%), in the water column (30-90%) and close to the surface (>90%).

4.4 Results

Between March and August 2013 (166 days), 16,432 acceleration and 16,517 relative depth data were collected from the 10 luderick fitted with AP transmitters (Table 4.1). Several individuals used the VPS areas during the study. Fish #4 and #5 contributed to 70% of the detections, with the other fish being either present for a short period of time or visiting temporarily or occasionally. A total of 12,541 acceleration and 12,576 depth 15-min time bins was obtained and analysed in the models (Table 4.2). The main drivers of activity and depth usage in luderick are presented in Table 4.3 and described below.

Fish activity

Luderick activity was positively related to tide and diel period as well as to the interaction term *Tide·Diel period*, and temperature, (Table 4.3). The categorical representation of acceleration across diel and tidal periods showed differences between day and night, with accelerations rates appearing higher during day-time and a clear peak during day-time at high tides (Fig. 4.2a). Activity was negatively related to high flow (Table 4.3).

Fish depth

The relative depth (expressed as positive values, with 0 m for the surface and increasing values as the fish is further down from the surface) was negatively related to the temperature and tide heights (Table 4.3). Luderick tend to be found closer to the surface at higher tide levels (Fig. 4.2b). Conversely, luderick relative depth was positively related to the parameter diel period, describing that luderick tend to use deeper depths during the hours with greater light (Table 4.3). The categorical representation of relative depth across diel and tidal periods showed that luderick tend to be found at greater depths at low tide at both day and night-times (Fig. 4.2b). In the VPS area, tagged luderick were located at all depths of the water column, however half of the detections took place close to the bottom (categories bottom and close to bottom) (Fig. 4.3). Luderick were mostly found in the “water column” during the day-time and especially

during high tide (Fig. 4.4). Luderick relative depth was negatively related to high flow (Table 4.3).

Rhythmicity in activity and depth use

A dominant peak in spectral density occurring at approximately 23.3 h indicated a strong diel rhythmicity, as determined by the Fast Fourier Transform (FFT) performed on the grand mean of both hourly acceleration and depth data (Fig. 4.5). The second peaks observed at 7.9 h and 12.6 h for the acceleration and pressure respectively, suggested a sub-diel rhythmicity linked to diel (10.4 h of daylight on average) and tidal periodicity (ca., 12.4 h between lows and highs), with an interaction between the two cycles in the case of the activity (7.9 h sub-diel rhythmicity), as previously suggested by the models.

Habitat associations within the VPS areas

In terms of habitat association within the VPS, luderick were either detected in "unvegetated" habitat (all other habitats than seagrass, mangrove and saltmarsh) or in seagrass (Fig. 4.6). Out of the five luderick for which 36 to 1489 VPS calculated positions were obtained (Table 4.1), only one fish (#4) was frequently detected in seagrass habitat (Fig. 4.6a) within the VPS area. The other tagged individuals were mostly detected in unvegetated habitat, with fish #8 and #9 not being detected in mapped seagrass beds present within the VPS at all (Fig. 4.6). Luderick showed different spatial distributions within the VPS areas, with the exception of the area situated in VPS 1 in front of the creek flowing into the Clyde River in relation to #5, #8, #9 and #10.

4.5 Discussion

This study aimed to understand activity and depth use patterns in luderick. The hypothesis that environmental factors would be significant predictors of luderick activity and depth was supported. I acknowledge that the findings were based on a small number of fish present in the VPS, with detections mainly dominated by two individuals and, therefore, the current findings may not be representative of the overall population.

The strong diel activity patterns found for luderick in this current study were most likely related to feeding and resting behaviours. The distinct diel rhythmicity characterised by fish more active during the day-time might be related to luderick seeking foraging grounds and to feed. On shallow rocky reefs, luderick displayed a sustained diurnal feeding activity (Ferguson et al., 2015; Ferguson et al., 2016). Based on field observations, Raubenheimer et al. (2005) found that the feeding rate increases throughout daylight hours and peaks in the final quarter of the day, as do many herbivorous fish species in relation to algal dietary composition varying through the day (Zoufal and Taborsky, 1991; Zemke-White et al., 2002). It is widely understood that endogenous circadian rhythms confer an adaptive advantage allowing organisms to exploit favourable conditions (Sharma, 2003; Yerushalmi and Green, 2009).

Foraging and refuge-seeking behaviours and as well as associated rhythms patterns and habitat preferences may result from a trade-off between minimising predation risk and maximising foraging. For example, juvenile freshwater sawfish (*Pristis pristis*) display strong circadian behavioural patterns in a north-western Australian river. In order to maximise foraging (in relation to prey availability and predation success) and also to limit interaction with potential visual predators, freshwater sawfish display higher nocturnal swimming activity and crepuscular peaks activity whilst venturing in exposed shallow habitats of the river (Gleiss et al., 2017). Animals will seek refuge or decrease movement activity almost every time when the risk of predation becomes high (Lima and Dill, 1990; Lima, 1998b; a; Kronfeld-Schor and Dayan, 2003). Mulloway is a large carnivorous fish, which cohabits estuaries with luderick, and is a potential predator of this species. Mulloway tend to be more active at night-time for foraging (Taylor et al., 2006b). This study showed that during night-time, luderick activity halved and fish

were found closer to the bottom but at shallower depths. This suggests that luderick might find suitable resting habitats in the shallow parts of the estuary offering refuge from river flow and tidal currents, as well as from nocturnal predators such as mulloway.

High flow events forced luderick to shift depth, most likely to seek refuge from adverse conditions. High flow events deliver large pulses of freshwater inflows in the estuarine system following heavy rainfalls. Luderick that remained detected within the VPS had to cope with these new conditions [i.e. increase in river discharge and turbidity, decrease of salinity and dissolved oxygen (Kurup et al., 1998; Gillanders and Kingsford, 2002)]. Accelerometer and pressure acoustic transmitters provided new insights into the behaviour of luderick during such events. Previous studies showed that acoustically tagged luderick tend to move downstream towards the mouth of the estuary (Chapter 3), and that heavy rainfall events can even trigger large-scale migrations of adult fish along the NSW coast (Chapter 2). During these events, luderick that remained in the VPS areas were found deeper, likely seeking more saline water and protection from the water current behind structures on the bottom (e.g., holes, reefs, hard artificial structures). This behaviour has been suggested for mulloway (*Argyrosomus japonicus*) in another SE Australian estuary (Taylor et al., 2014). Luderick in the current study also displayed a lower swimming activity than under base flow conditions, probably to deal with energetic and metabolic costs of osmoregulation, and to cope with potential lower levels of dissolved oxygen, resulting in reduced normal activities such as foraging. Under stress conditions following heavy rainfall events, other species found in estuaries such as yellowfin bream (*Acanthopagrus australis*) and mulloway display behavioural changes (Payne et al., 2013; Payne et al., 2015c) and may be forced to shift habitats in order to adapt to the new conditions (Payne et al., 2015c).

Questions related to luderick habitat associations (e.g. seagrass), could not be accurately addressed due to location of the VPS network of acoustic receivers outside and the little amount of information provided by the available maps. More detailed habitat information as well as depth contours and fine-scale underwater topography would require the use of hydroacoustic technologies (Kenny et al., 2003), that were not

available for this study. During the tagging campaign, luderick were mainly caught in seagrass beds or at their vicinity at high tide. In addition, the examination of luderick stomach contents (unpublished data) caught in different estuaries including the Clyde River contained non-digested seagrass (*Zostera* sp.) fragments in the digestive tract, suggesting that luderick fed on seagrass habitats and associate with seagrass beds.

Over the five months of monitoring, the increased luderick activity as a function of temperature was most likely related to longer-term effects of seasonal temperature fluctuations on ectotherm metabolism. The change in water temperature measured in the Clyde River reflects seasonality rather than fluctuations over short periods of time. Temperature did not show drastic changes over short time frames (hours or days) in the estuarine system studied conversely to other parameters such as conductivity or river flow rates (Chapters 2 and 3). Over the monitoring period, the daily mean temperature decreased from 23.1°C to 11.0°C during the colder months (mean = 16.3°C ± 3.6 S.D.). Payne et al. (2016) defined 19.3°C (± 1.3 S.E.) as the optimal temperature (T_{opt}) for free-ranging luderick. Ectotherm performance (relative performance, growth or fitness) is thermally sensitive, increasing with temperature until reaching a maximum (T_{opt}) before declining rapidly until reaching the upper critical temperature (zero performance, upper T_{crit}), beyond which death occurs (Fry, 1947; Huey and Kingsolver, 1993). Luderick activity was temperature-dependent and this explains the positive relationship between activity and temperature over the monitoring period found in the models. Over the recent decades, ocean warming rates in coastal south-east Australia were three to four times higher than the global average (Holbrook and Bindoff, 1997; Ridgway, 2007; Matear et al., 2013), making this region a climate change "hotspot" (Booth et al., 2011). Poleward shifts in distribution ranges in response to increase in sea surface temperature have been documented for luderick and other Australian coastal species (Stuart-Smith et al., 2010; Last et al., 2011). Changes in range and increase in abundance of herbivores such as luderick in southern estuaries and coastal areas may have an impact on local algal communities and therefore on ecosystem functions (Taylor and Schiel, 2010; Vergés et al., 2014; Ferguson et al., 2016).

4.6 Conclusions

Luderick activity is characterised by strong endogenous circadian rhythms, with a distinct diel rhythmicity characterised by fish more active during the day-time probably related to foraging and resting behaviour. Luderick activity responds also to estuarine environmental drivers, under base flow conditions, with higher activity at high tide during the day and under specific events such a high flows, characterised by a lower activity and a shift to higher depths. Luderick activity was temperature-dependent, with a positive relationship between activity and temperature, characteristic of a typical ectotherm performance curve.

The combined use of accelerometer/pressure acoustic transmitters deployed within VEMCO Positioning Systems (VPS) is a relevant approach resolving fine-scale resolution of behavioural activity patterns of free-ranging fish. The AP transmitters combined to the VPS allowed the collection of activity and depth data of several individuals simultaneously, and continuously, over long periods of time (over months, as long as tagged animal stayed within the acoustic arrays). This study illustrates the application of emergent technologies to study free-ranging organisms. Acceleration and pressure (depth) are two parameters widespread in biologging research (Payne et al., 2014). The miniaturisation and the use of various sensors (e.g. heart rate, body temperature) bring additional tools, allowing ecology to be directly linked to physiology (Block, 2005; Hussey et al., 2015) and enabling further exploration and understanding of fish behaviours.

4.7 Tables

Table 4.1 Information from tagging luderick (*Girella tricuspidata*) by fitting AP transmitters, including the size (fork length – FL in mm) and the weight of the fish (g), the site and day of release, the number of days with detections for each fish in the VPS, the number of unique detections (filtered detections: detections excluded the same detections of a specific fish by multiple receivers), VEMCO calculated positions based on the VPS and algorithm developed by the manufacturer), dates of first and last detection. (Det. = detection).

Fish ID	FL	Weight	Site	Tagging date	Det. (days)	Filtered det.	VEMCO calculated positions	first det.	Last det.
1	262	369	VPS2	16/03/13	134	2224	1	16/03/13	27/08/13
2	248	307	VPS2	16/03/13	37	956	3	16/03/13	17/05/13
3	309	538	VPS2	24/03/13	3	17	0	24/03/13	8/04/13
4	393	1015	VPS1	24/03/13	157	11920	1489	24/03/13	29/08/13
5	300	487	VPS1	24/03/13	135	11631	1477	24/03/13	26/08/13
6	322	598	VPS1	24/03/13	32	2683	27	24/03/13	25/05/13
7	308	544	VPS2	24/03/13	4	165	23	24/03/13	6/04/13
8	288	479	VPS1	24/03/13	4	656	312	25/06/13	29/06/13
9	314	579	VPS2	16/03/13	81	2298	326	16/03/13	16/08/13
10	303	499	VPS1	24/03/13	3	399	36	24/03/13	27/03/13

Table 4.2 Sequential linear mixed-models runs and corresponding differences in AIC with the previous model. The best models according to AIC are highlighted in bold.

Model	**Parameters**	**Term removed**	**Variation of AIC**
Activity_1	Temp+HighFlow+Length+Weight+Tide+Diel+Tide·Diel	Moon (p=0.57)	-9.11
Activity_2	Temp+HighFlow+Length+Tide+Diel+Tide·Diel	Weight (p=0.19)	-7.58
Activity_3	**Temp+HighFlow+Tide+Diel+Tide·Diel**	**Length (p=0.16)**	**-8.96**
Depth_1	Temp+HighFlow+Length+Moon+Tide+Diel+Tide·Diel	Weight (p=0.98)	-9.44
Depth_2	Temp+HighFlow+Moon+Tide+Diel+Tide·Diel	Length (p=0.93)	-9.05
Depth_3	Temp+HighFlow+Moon+Tide+Diel	Tide·Diel (p=0.25)	-8.13
Depth_4	**Temp+HighFlow+Tide+Diel**	**Moon (p=0.06)**	**-5.62**

Table 4.3 Predictors of the optimised activity and depth models. Negative β values (slopes) describe a negative relationship.

Model	**Predictor**	***β***	**S.E.**	***t*-value**	***p*-value**
Activity	*Temperature*	0.17	0.01	12.75	<0.001
	High Flow	-0.13	0.02	-5.31	<0.001
	Tide	0.21	0.01	15.17	<0.001
	Diel period	0.49	0.01	60.06	<0.001
	Tide · Diel period	0.42	0.02	22.07	<0.001
Depth	*Temperature*	-0.74	0.03	-24.35	<0.001
	High Flow	0.36	0.05	6.66	<0.001
	Tide	-1.71	0.03	-54.82	<0.001
	Diel period	0.53	0.02	30.75	<0.001

4.8 Figures

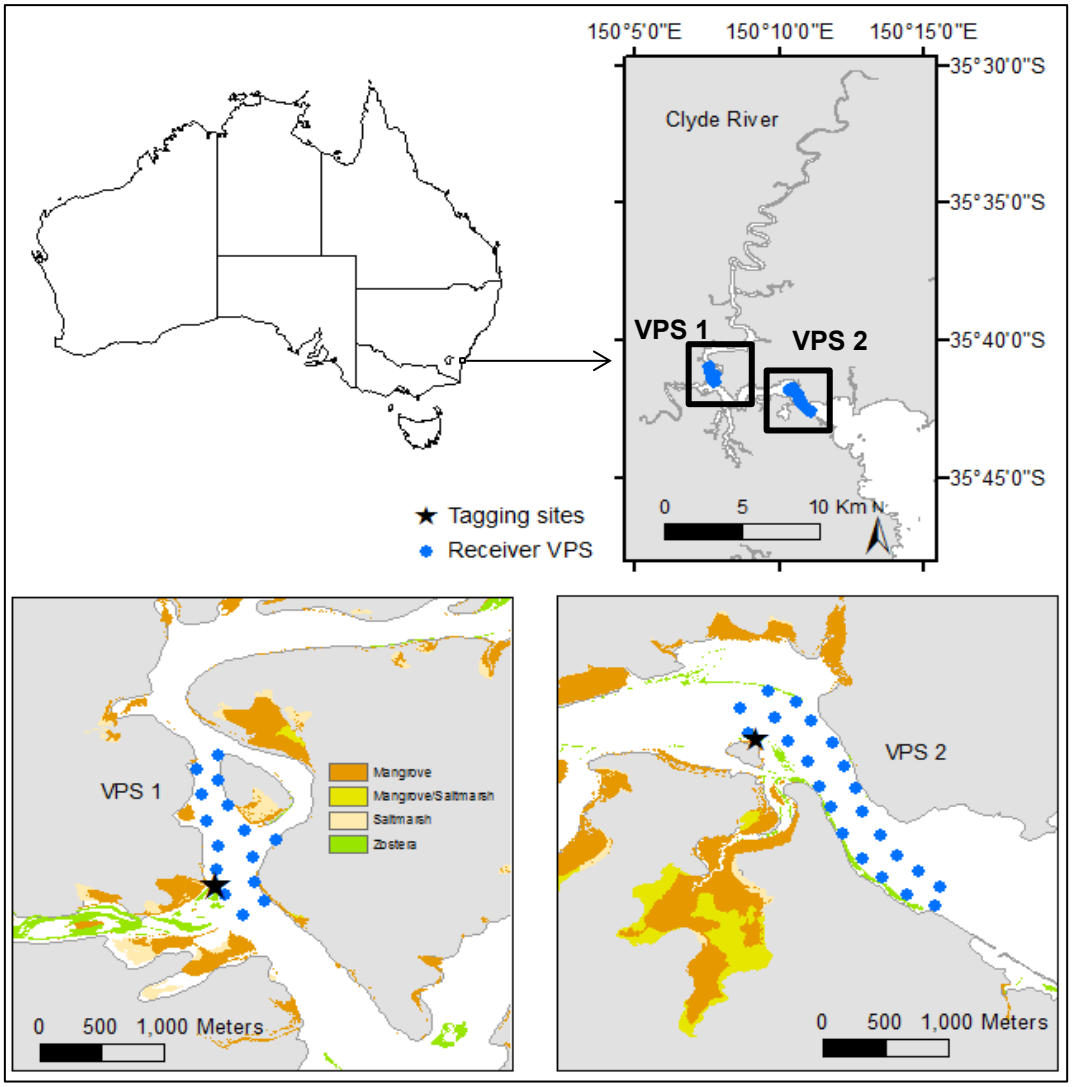

Figure 4.1 Map of the study area showing the two VPS networks, the estuarine array, tagging sites and the distribution of the main habitats (seagrass, saltmarshes and mangroves).

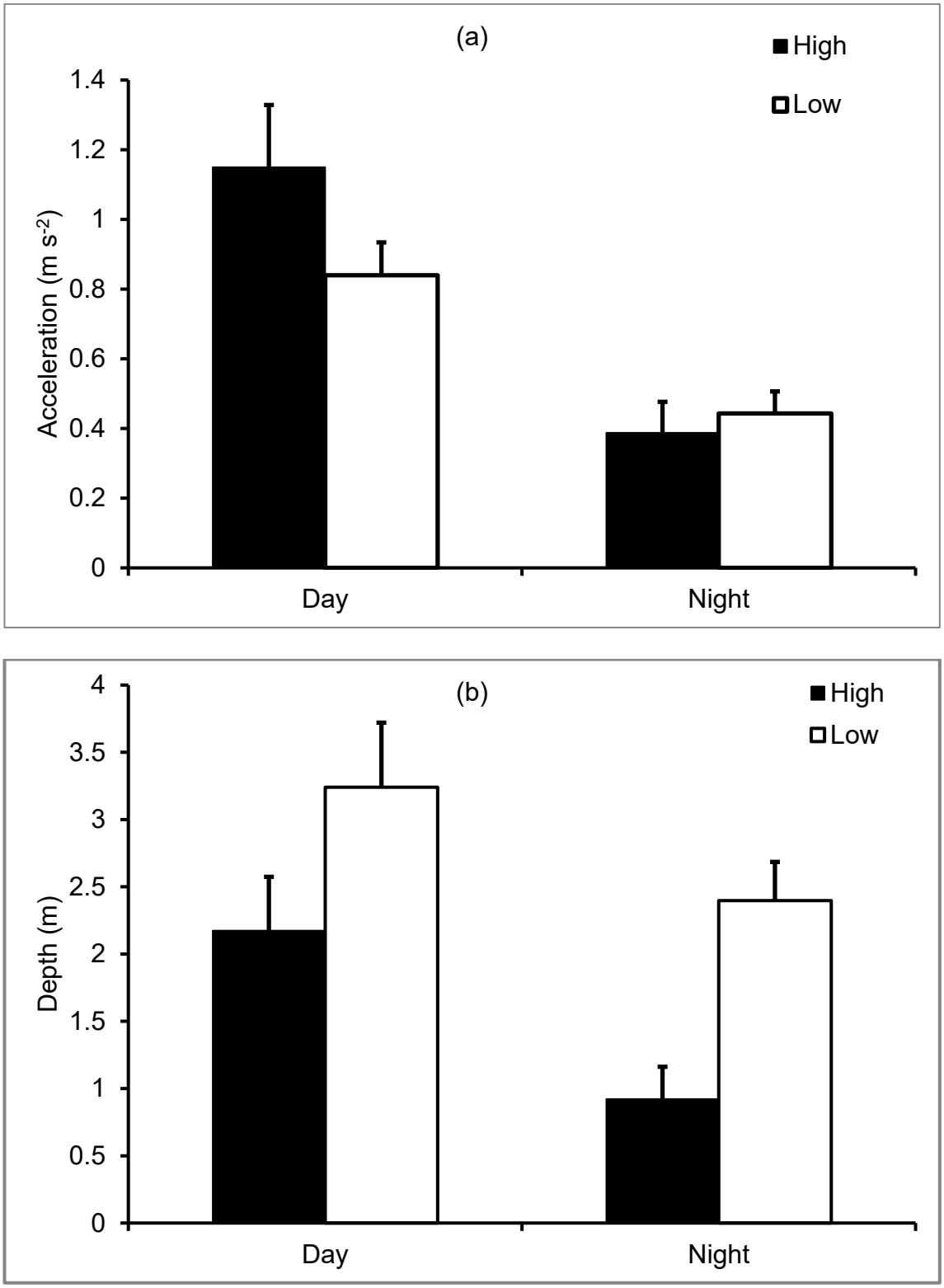

Figure 4.2 Acceleration (a, top) and depth (b, bottom) across diel period (day and night) and tidal phase (error bars correspond to the S.E.).

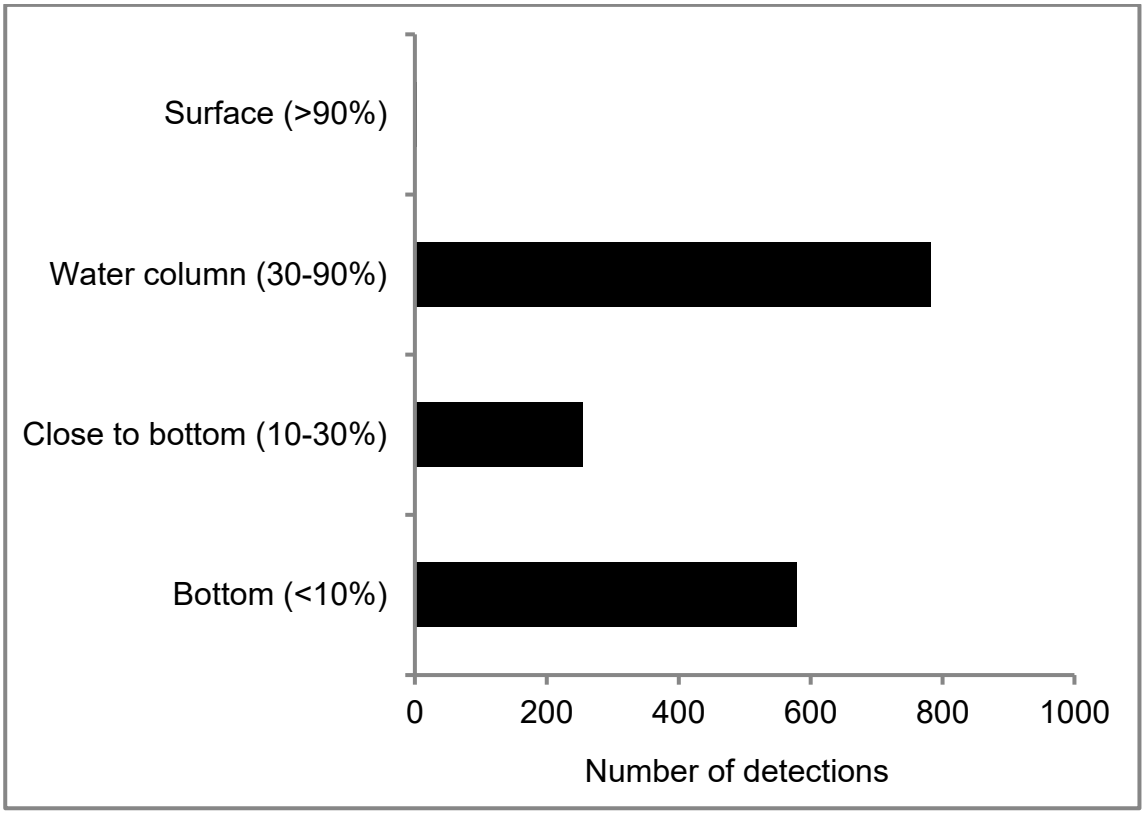

Figure 4.3 Number of detections per depth categories. The fish were detected in reference to the bottom (percentage of the difference between depth obtained by the AP tags and the river bathymetry divided by the river bathymetry at the point of detection).

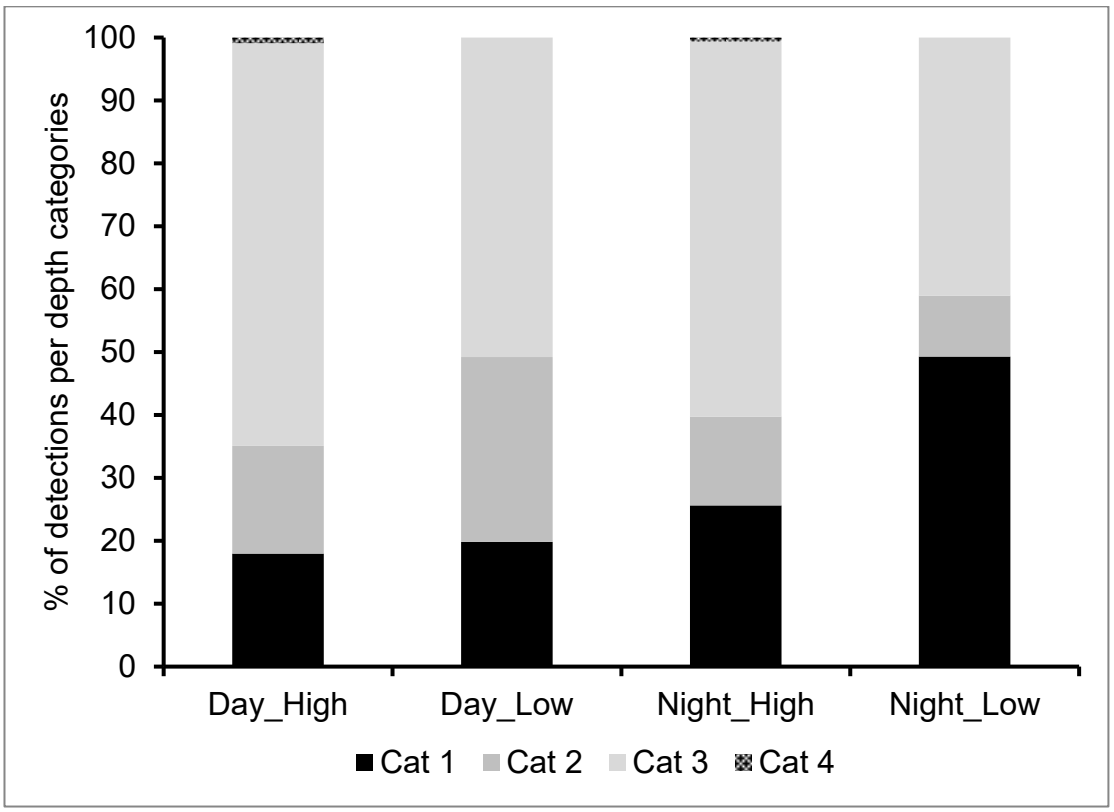

Figure 4.4 Fish depths expressed in percentages and divided into 4 categories (Cat 1=bottom (<10%), Cat 2=10-30%, Cat 3=30-90% and Cat 4=surface (>90%), % relative depths) across diel (day and night) and tidal (high and low) periods.

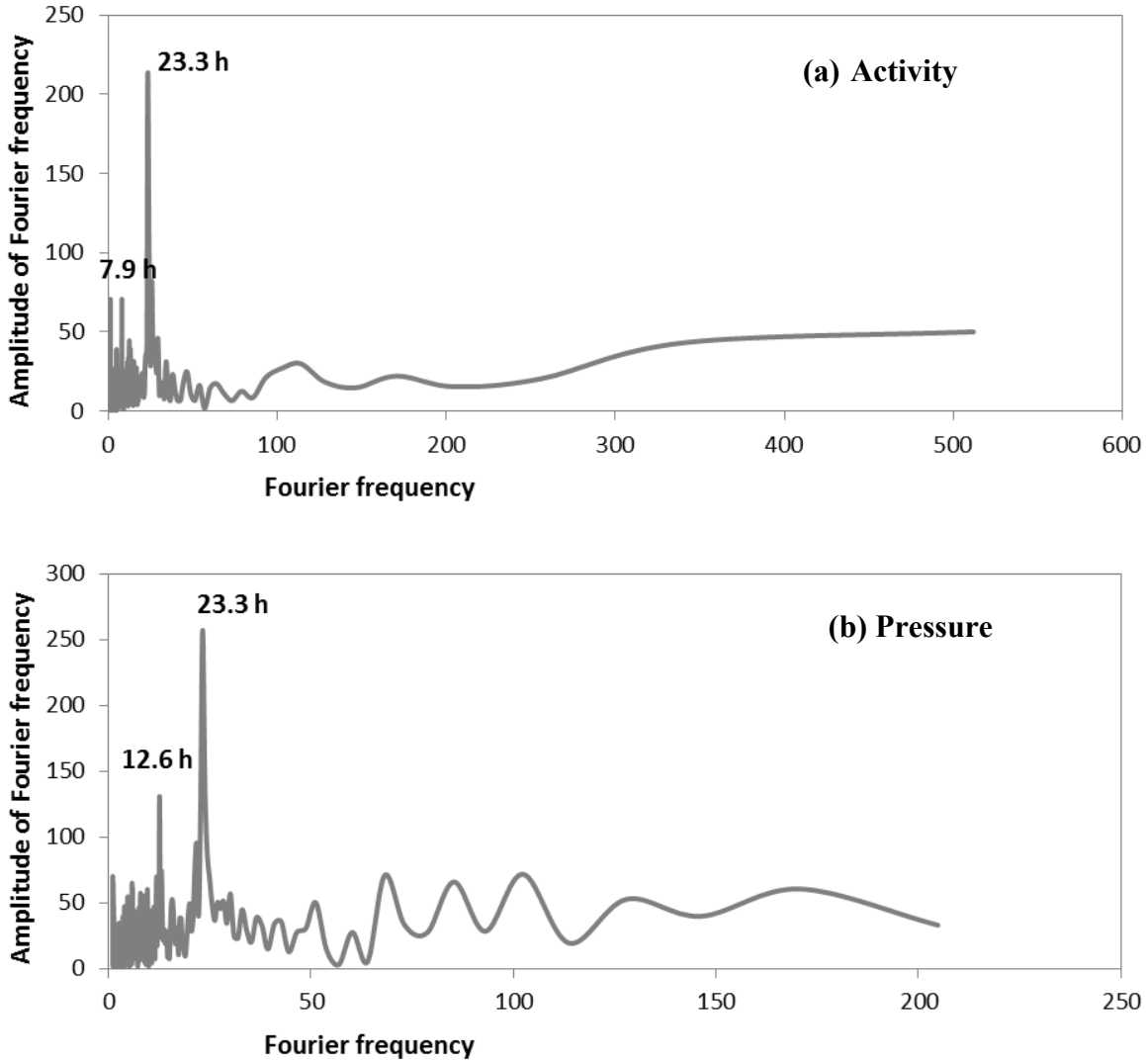

Figure 4.5 Fourier analysis of detection periodicity for activity (a) and pressure (b). (FFT based on 1024 frequencies but truncated at 205 and 512 for activity and pressure, respectively, for visualisation purposes).

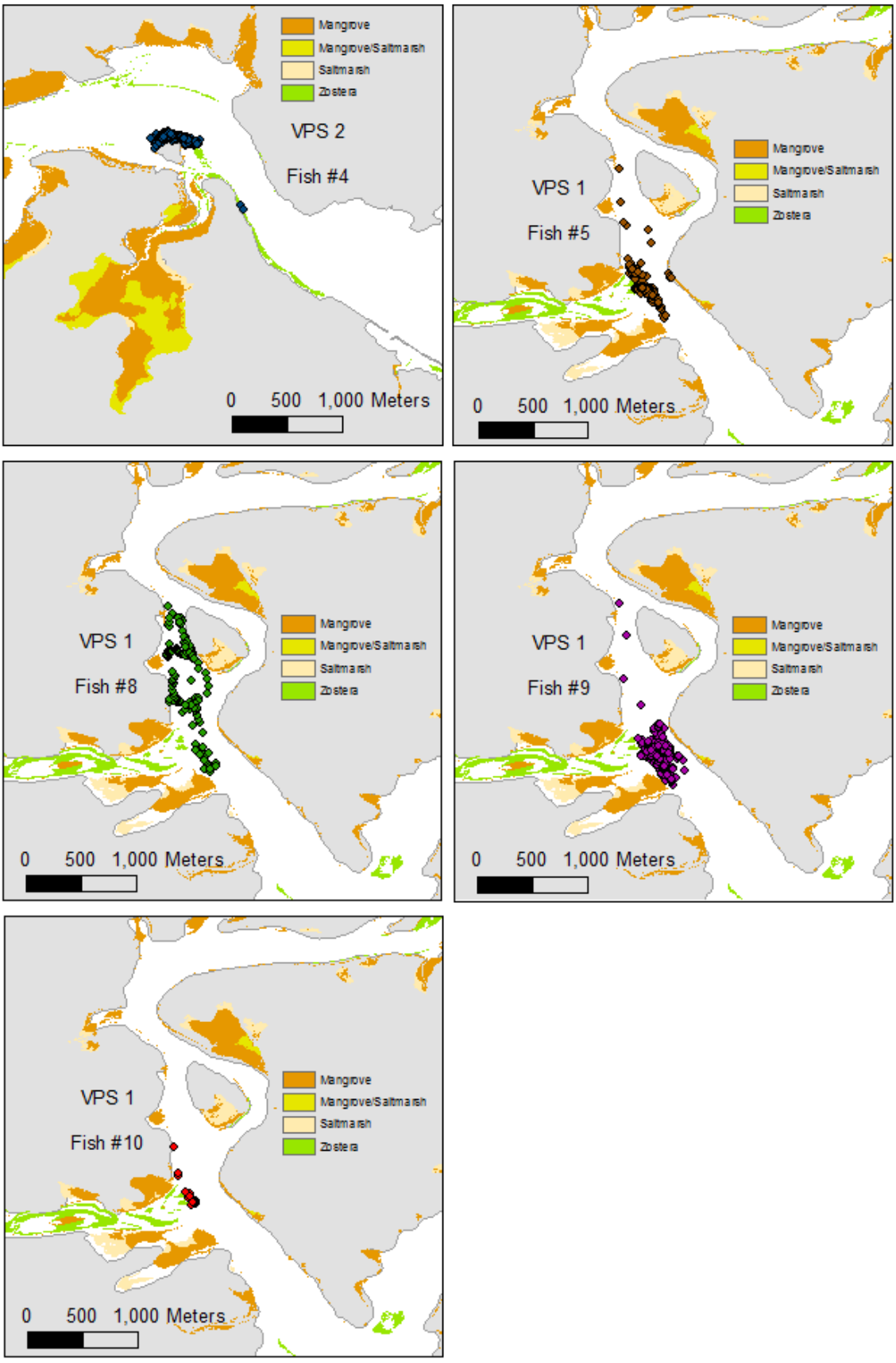

Figure 4.6 Spatial distribution of the VEMCO calculated positions for fish #4, #5, #8, #9 and #10 (fishes with 36 to 1489 positions available) within the VPS areas.

CHAPTER 5: Active metabolic rates in luderick (*Girella tricuspidata*): from laboratory to field estimates

Cadiou G., Booth D.J., Gray C.A., Payne N.L., and Taylor D. (*in prep.*). Active metabolic rates in luderick (*Girella tricuspidata*): from laboratory to field estimates

5.1 Abstract

Measuring the active metabolic rate of wild animals is important for understanding the ecology and the biology of a species. Active metabolic rate is the metabolic output associated with animals undertaking different behavioural activities, and can be determined by measuring the relationship between body activity and oxygen consumption. The aim of the study, for the coastal marine and estuarine fish luderick (*Girella tricuspidata*), was: (*i*) to experimentally calibrate body activity with oxygen consumption rates to determine active metabolic rates – AMR; and (*ii*) to estimate the AMR of free-ranging fish. Eight luderick (FL = 300 mm ± 30 S.D.) were fitted with acoustic accelerometer transmitters to measure body activity, and were swum in a swim-tunnel respirometer at different speeds to determine the relationship between body activity and oxygen consumption. Ten accelerometer transmitters were deployed in wild luderick (FL = 305 mm ± 37 S.D.) within a VEMCO Positioning System (VPS). Estimated field AMR were 1.5 times lower at night-time compared to day-time, possibly related to luderick diel variations in behaviour. AMR of wild fish increased with temperature until reaching 19°C to then stabilise (up to 22°C), indicating a possible optimal performance temperature for luderick. The optimal swimming speed, velocity minimising the cost of transport, was estimated at 57 cm s^{-1} (1.9 BL s^{-1}) for luderick, a value comparable to those of a range of other fish species. Acoustic telemetry using accelerometer transmitters was a valuable tool for estimating the AMR of free-ranging animals in aquatic environments, and to better understand the link between physiology and animal behaviour.

5.2 Introduction

Understanding energetic expenditure in free-ranging animals is fundamental in the study of animal physiology and ecology (Cooke et al., 2004a). The partitioning of energy between different activities has a great influence on the animal's fitness and, therefore, on its success and survival, from the individual to the population levels (Sims, 1999; Brown et al., 2004). Thus, knowing where energy is allocated is important in providing a better understanding of behavioural and physiological ecologies of a species. Animals require energy for growth, metabolism, reproduction, and waste (Olson and Boggs, 1986). Metabolism includes the energy required for basal processes, and the energy required for activity, with active metabolic costs capable of representing a large and variable proportion of an animal's energy budget (Boisclair and Sirois, 1993; Briggs and Post, 1997; Halsey et al., 2015).

Measuring active metabolic rates of free-ranging aquatic animals is challenging, with methods commonly used for terrestrial animals such as doubly-labelled water and heart rate measurements (Butler et al., 2004) having limitations and suffering from inaccuracies when applied to aquatic animals (Nagy and Costa, 1980; Thorarensen et al., 1996; Speakman, 1998; Iversen et al., 2010). Electromyogram (EGM) telemetry has been successively employed to estimate metabolic rates in fish (Cooke et al., 2004a), although the applicability of this method is limited due to the advanced surgery skills required to implant the electrodes correctly (Cooke et al., 2004b; Gleiss et al., 2010). The metabolic activity generated through the movements of the body during locomotion is governed by muscle contractions. Therefore, body acceleration can be used as a proxy of energy expenditure during activity (Halsey et al., 2009) and therefore to determine active metabolic rate (Halsey et al., 2011). Body acceleration measured by loggers or transmitters, in conjunction with metabolic rate experiments, has been successfully employed to determine active metabolic rates of a wide range of animals (Wilson et al., 2006; Halsey and White, 2010; Payne et al., 2011), including fish (Clark et al., 2010; Gleiss et al., 2011; Wright et al., 2014).

Body acceleration can be measured along 2, or 3 dimensions using bi- or tri–axial accelerometers. Tri-axial accelerometers provide detailed information about body

movement; however, external forces such as the local hydrodynamics (e.g. swell, currents) may influence body acceleration without relation to muscular contraction (Payne et al., 2011). Bi-axial accelerometers may more closely reflect mechanical swimming movements by measuring the movement of the caudal fin (e.g. tail beat frequency). Accelerometers fitted in fish are either loggers that need to be retrieved or transmitters sending measured data remotely (Payne et al., 2014; Hussey et al., 2015). Accelerometer transmitters are capable of calculating the root mean square of acceleration across the axes, and transmitting a single value which indicates the relative body activity of monitored animals. The key advantage of transmitters over loggers is that they do not need to be retrieved to gather the data. However, the collection of transmitted information from mobile species in the wild can be challenging and in this regard attention is needed when designing networks of receivers (Heupel et al., 2006).

Networks like the VEMCO Positioning System (VPS) have been developed to study fish movements at a fine-scale resolution, making them particularly useful for behavioural studies (Espinoza et al., 2011a; Furey et al., 2013). Therefore, systems like the VPS may maximise chances to record transmitted acceleration data of tagged individuals and to provide valuable data to estimate metabolic rates. Accelerometer transmitters have been successfully used to study activity patterns and fish behaviours in natural environments (Payne et al., 2013; Taylor et al., 2013; Payne et al., 2015b; Payne et al., 2015c) and to evaluate energetic costs associated with the observed activity (Murchie et al., 2011; Brodie et al., 2016).

The primary aims of the study were to: (*i*) calibrate accelerometer transmitters (body acceleration) with oxygen consumption during fish swimming activity in the laboratory (active metabolic rate, AMR), and (*ii*) apply this calibration to free-ranging fish in order to determine field AMR. Luderick (*Girella tricuspidata*) was chosen as a model species. Luderick is a primarily herbivorous fish and is abundant in shallow coastal waters and estuaries of south-eastern Australia. From observations made in previous studies, it is known that *G. tricuspidata* displays a large range of movements, including strong diel movement patterns (Ferguson et al., 2013; Chapter 4). In addition, Raubenheimer et al. (2005) found that luderick feeding rate increases throughout daylight hours, reaching a

peak in the final quarter of the day; therefore, variations in activity through the 24-h period of the day are expected for this species. There is limited information on the physiology and swimming performance of luderick, so estimating the active metabolic rates of free-ranging luderick will contribute to understanding of behavioural and physiological ecology of this species.

5.3 Materials and methods

Laboratory calibration of Active Metabolic Rate

The luderick used for the laboratory experiments were caught using barbless hooks baited with sea cabbage (*Ulva* sp.) in the Port Hacking estuarine system next to the Cronulla Fisheries Research Centre (CFRC) (Sydney, NSW, 34.073°S, 151.147°E). Just after capture, fish were transferred to a 4000-L flow-through tank housed in a covered open-side outdoor area receiving natural light. Prior to surgery, fish were anaesthetised with AQUI-S (60 mg/L) in a 100-L tub and then placed on a V-shape padded cradle. A bi-axial accelerometer (and pressure) acoustic transmitter (VEMCO V9AP-2L, 69 kHz, 46 mm length, and 3.3 g in water – VEMCO, Bedford, Nova Scotia, Canada) was implanted following the procedures described in Chapter 4. Transmitters were inserted in the peritoneal cavity via a small incision (20 mm long) in the ventral side of the fish in a fashion that allowed the transmitter X-axis to be aligned with the anteroposterior axis of the fish. The V9AP transmitters used a VEMCO algorithm to estimate fish tail beats by sampling acceleration at 10 Hz for 22 s sampling window. Transmitted acceleration values were the root mean square (RMS) value for axes X and Z over the sampling time window.

Luderick recovered from surgery for at least 21 days before being introduced to the swim-tunnel respirometer. Fish were fasted 48 hours before the swim trials to avoid influence of digestion on oxygen consumption rates. Fasted fish were placed in the observation chamber of a 91-L Brett-type swim-tunnel respirometer (Brett, 1964) and acclimated for at least 4 hours at a low flow rate (~3 cm s^{-1}) ensuring water circulation, with the fish remaining stationary without swimming. The swim tunnel was

continuously flushed with fresh seawater except during the swim trials, when the system was fully sealed. The observation chamber consisted of a transparent PVC pipe (150 mm internal diameter, 550 mm length) fitted with honeycomb shaped plastic grids at each ends to keep the fish within the chamber and ensure an even and laminar flow. In order to avoid direct outside stimuli that may affect fish behaviour, during the experiments, the observation chamber was taped with black lining, leaving an 80 mm-stripe free area at the top of the chamber. A mirror positioned at a 45° angle above the observation chamber allowed observing the fish without direct interaction. A high definition camera recorder (Sony HDR, 25 frames per seconds) was set up on a tripod facing the mirror to record vertical views of the fish swimming. A 12 V impellor encased within the swim tunnel generated water flow. Eight fish fitted with an AP tag (FL=300 mm ± 30 S.D.) were swum at five incremental speeds (6, 18, 30, 42, 54 cm s^{-1}) each applied for 15 min (speeds were calibrated prior to trials).

The oxygen consumption (VO_2) was determined by measuring the decline of dissolved oxygen (DO) during the 15 min swim trials. DO measurements were taken every 5 s during the trials using a WTW multi 3430 model interfaced with a notebook computer and fitted with a calibrated optical FDO® 925 probe (salinity and temperature corrected). All equipment was calibrated following the manufacturer's specifications and the DO probe accuracy checked every day before the trials. The concentration of oxygen was maintained over 80% saturation at all times. Runs without fish were made at the start of the day and at the end of each session to measure any background oxygen depletion due to microbial oxygen uptake in the respirometer and its value was subtracted from the VO_2 slopes if needed. Fish were lightly sedated (AQUI-S 25 mg/L) when transferred between the holding tank and the swim-tunnel respirometer, and before taking the lengths and weight measurements after swimming sessions. Swim trials were all conducted during day-time, to avoid any potential diel variations in metabolism (Page et al., 2011).

The acceleration data were recorded using a VEMCO VR100 unit connected to a VH165 omnidirectional hydrophone taped outside the swim chamber. Raw acceleration data were averaged for each swim speeds. An additional five fish with no tags (FL=274 mm ± 6 S.D.), caught and reared in the same conditions to the tagged luderick, were swum similarly to tagged fish to assess the potential effects of the tag on metabolic rate during swimming activity. AMR of tagged fish and untagged fish were compared by

unpaired t-test for the following swimming speeds: 6, 12, 18, 42, and 54 cm s^{-1}. After all the swim trials finished, the fish were euthanized humanly following the approved ethics protocol and the acoustic tag was retrieved.

Trials were run at a temperature of 20.1°C (± 1.0) and a salinity of 33.7‰ (± 0.7). The trial temperatures fell into the range of the optimal temperature of free-ranging luderick, estimated by (Payne et al., 2016) (19.3 - 20.5°C). All fish occupied more than 10% of the cross section area of the swim chamber, which can influence the flow rate of the swim-tunnel. Blocking correction factors were applied to the fish swimming speeds to take the effect of fish size into account (Bell and Terhune, 1970; Korsmeyer et al., 2002). VO_2 measurements were converted to mass-specific active metabolic rate (AMR; active metabolic rate; mgO_2 kg^{-1} h^{-1}) using a scaling exponent of 0.79 (Clarke and Johnston, 1999).

The relationships between AMR and swimming speed, and between AMR and acceleration were estimated using linear mixed-effects models in R (v3.3.0; R Core Development Team 2016), with fish ID as a random factor. Based on the literature, the relationship between AMR and swimming speed was fitted with an exponential curve (Brett, 1964; Wright et al., 2014). The relationship between AMR and acceleration is commonly described as a linear relationship (Halsey et al., 2011; Wilson et al., 2013; Mori et al., 2015). Standard metabolic rate (SMR) of luderick was estimated by extrapolating the relationship between AMR and body acceleration at zero swimming speed, corresponding to the intercept of the fitted AMR versus acceleration (Mori et al., 2015). The cost of transport (COT) was calculated by dividing AMR by the swimming speed at which AMR was measured (Lee et al., 2003; Clark and Seymour, 2006). The optimal swimming speed of luderick was estimated from the COT curve and corresponds to the velocity with the lowest COT (COT_{min}) (Schmidt-Nielson, 1972).

Field Active Metabolic Rates estimates

The field study was conducted in the Clyde River (NSW South coast, 35.705°S, 150.142°E), a tidally-dominated drowned river valley estuary of 110 km long with a water catchment of 1,620 km^2. This river is unregulated and the water quality is

considered very high with no polluting industries present in the catchment. The estuary extends 30 km from the river mouth and is part of Batemans Marine Park. Two VEMCO Positioning System (VPS) arrays were deployed in the mid-lower reaches of the estuary (Chapter 4). Ten luderick (FL=305 mm ± 37 S.D.) were caught, tagged with V9AP transmitters, and released within the two VPS arrays (procedures described in Chapter 4). The monitoring period extended from 16/03/2013 to 19/08/2013. Two Odyssey data loggers (Dataflow Systems Pty Ltd) recording hourly conductivity (mS cm^{-1}) and temperature (°C), were deployed mid-water within each VPS. Conductivities were converted in salinities using corresponding field temperature values (Fofonoff and Millard, 1983).

Different fish were used in laboratory calibrations and field measurements to avoid translocating fish between estuaries, because luderick might be associated with certain habitats or areas of the estuary, and translocation may have affected fish behaviour. Tagging fish in their current environment with minimum manipulation was the best option to obtain realistic acceleration data. Detections that occurred during the first 24 h were ignored to take into account potential abnormal post-surgery behaviour.

Hourly field AMR (mgO_2 kg^{-1} h^{-1}) were estimated from the average hourly activity values from free-ranging luderick, and converted to metabolic rates using the laboratory-derived relationship between AMR and acceleration. The range of speeds generated by the swim tunnel did not result in a maximum activity value being sampled. Therefore, hourly averaged activity values were used to prevent extrapolation beyond the laboratory calibration.

During the field monitoring period, the temperature ranged from 10.4 to 22.9 °C and salinity from 2‰ ≤ to ~36‰[4]. Temperature has significant effects on the metabolism of fish (Johnston and Dunn, 1987; Claireaux and Lagardere, 1999). Therefore, the field AMR estimates (calibration at 20.1°C) were corrected by the temperature recorded in the field. This was done using a Q_{10} principle (Q_{10} of 1.83 (Clarke and Johnston, 1999)),

[4] High salinities values over 35‰ are most likely due to conductivity logger inaccuracies (3% accuracy given by the manufacturer)

which describes the rate of change in metabolism over a 10 °C range (Guppy and Withers, 1999; Gillooly et al., 2001). The metabolic costs of fish may vary with salinity (Swanson, 1998; Claireaux and Lagardere, 1999). However, correcting field AMR for salinity was not possible, as no generalised formula for fish is available and measuring the overall metabolic cost associated with osmoregulation is challenging and outside the scope of this study (McCormick et al. 1989). In addition, for euryhaline species (e.g. luderick), the effect may only be noticeable for large magnitudes of salinities (e.g. between 20‰ and 5‰; (Claireaux and Lagardere, 1999)). Therefore, in order to avoid biased field AMR estimates due to the large range of salinities recorded during the monitoring period, salinities with less than 5‰ variations from the calibration conditions were retained (28.7 to ~36‰).

5.4 Results

Laboratory calibration of Active Metabolic Rate

Luderick exhibited two main forms of swimming locomotion in the swim-tunnel respirometer. At the lowest speed (6 cm s^{-1}), fish maintained their position by either arching sideways in the chamber, or by pectoral locomotion. At speeds higher than 12 cm s^{-1}, luderick were observed to use body and caudal locomotion to achieve steady swimming in the respirometer. The AMR of luderick increased exponentially with increasing swimming speeds (Fig. 5.1), and linearly with increasing body acceleration (Fig. 5.2). The standard metabolic rate (SMR) was estimated at 49.1 mgO_2 kg^{-1} h^{-1} from the intercept of the linear relationship between AMR and body acceleration (Fig. 5.2). No significant differences in AMR were detected between tagged and non-tagged luderick for the swimming speeds tested (6, 12, 18, 42, 54 cm s^{-1}; unpaired t-tests, with $p > 0.05$ for all comparisons; Table 5.1). The size range between the two treatments (tagged: FL=300 mm ± 30 S.D.); non-tagged: 274 mm ± 6 S.D.) was not significantly different (unpaired t-test: $t(11) = 1.7$, $p = 0.1$).

There was a typical U-shaped relationship between the COT and swimming speed, with the COT decreasing as speed increased until reaching a minimum speed (57 cm s^{-1}), before increasing again (Fig. 5.3). The COT at the lowest speed (~ 6cm s^{-1}) had a high

level of variance associated with the pectoral swimming behaviour at this speed (Fig. 5.3). The optimal swim speed (U_{opt}) of 57 cm s^{-1} corresponds to 1.9 BL s^{-1}, based on the average fork length of the fish used for the calibration (300 mm FL).

Field Active Metabolic Rates estimates

The size range for the fish used for the calibration (FL=300 mm ± 30 S.D.) and tagged in the field (FL=305 mm ± 37 S.D.) did not differ significantly (unpaired t-test: t(16) = 0.3, p = 0.8). A total of 1,902 hourly averaged acceleration transmissions from four fish was sampled within the salinity range within the 5% range to the laboratory experiment ((28.7 to ~36‰). The four fish were detected in the VPS between 23 to 149 days (average: 76.5 days). The hourly averaged acceleration values (range: 0.04 – 3.2 m s^{-2}; Fig. 5.4) were mainly within the range of laboratory acceleration, which permitted field metabolic rates to be estimated. At night-time, the average field AMR was low (87.3 mgO_2 kg^{-1} h^{-1} ± 34.6 S.D.), but was higher than the SMR extrapolated from the laboratory experiment (49.1 mgO_2 kg^{-1} h^{-1}). Day-time field AMR was on average 1.5 times higher and more variable than night-time rates (132.9 mgO_2 kg^{-1} h^{-1} ± 57.6 S.D.). The examination of average hourly field AMR showed a strong diel pattern across the 24-h of the day (Fig. 5.5). From dawn, the metabolic rates rose steadily until 173.8 mgO_2 kg^{-1} h^{-1} (± 44.5 S.D.), then slowly increase throughout the day to reach a peak in the late afternoon, before falling back to night-time low levels (Fig. 5.5). Luderick field AMR was estimated across a 9°C range, with field AMR lowest at 12°C and increasing steadily to 16°C, and starting to asymptote near 19°C (Fig. 5.6).

5.5 Discussion

Estimating active metabolic rates of free-ranging animals contribute to a better understanding of behavioural and physiological ecology of the species. This study provided the first estimates of field metabolic rates of free-ranging luderick and valuable information on swimming performances of this species.

Luderick displayed diel differences in field AMR which were higher during day-time than at night. These diel variations of field AMR could be reflect foraging and resting behaviours. In shallow coastal reefs (Ferguson et al., 2013) and in estuaries (Chapter 4), acoustically tagged luderick were moving up to five times more during the day than at night-time. Based on field observations, Raubenheimer et al. (2005) found that the luderick feeding rate increased throughout daylight hours to reach a maximum in the final quarter of the day. Therefore, foraging might explain the higher diurnal activity and field AMR rates, as well as their large variations during the day, as luderick may be actively searching for suitable grounds where they can stop and feed. The lower field AMR at night may indicate sheltering behaviour. It has been suggested that luderick are more likely to rest during the night in specific locations that can offer shelter from high currents, mostly in shallow areas (Ferguson et al., 2013; Chapter 4). The night-time field AMR estimates were higher than the SMRs extrapolated from the laboratory experiments, indicating that luderick still exhibited activity above that of standard metabolic rate. Providing that luderick may adopt a resting behaviour at night, fish still have to maintain their position in the water column and to adjust to the local hydrodynamic environment such as river and tidal flows. It is interesting to note that, based on the COT curve, these low acceleration values were not the most energy efficient swimming speed. This may reflect luderick behavioural responses balancing the trade-off between maximising foraging and minimising predation risk (Lima and Dill, 1990).

Across the temperatures recorded in the field (12 to 21°C), the field AMR were the highest around 19°C, close to the optimal temperature for free-ranging luderick (Payne et al., 2016). Ectotherm performance, in relation to relative performance, growth or fitness, is thermally sensitive and is often described by a thermal performance curve, where performance increases with temperature until reaching a maximum (T_{opt}) and then declines rapidly (Fry, 1947; Huey and Kingsolver, 1993). Although field AMR could not be obtained for higher temperatures, field AMR appeared similar to luderick thermal performance curve (Payne et al., 2016).

U_{opt} is the swimming speed most likely adopted to minimise the energetic cost of movement, a behaviour that is important during large-scale movements such as migrations (e.g. for spawning or foraging). This energy-efficient speed enables the fish to sustain long range distances relying on internally stored energy reserves, since often, no food is ingested during migratory movements (Weihs, 1973). The estimated optimal swimming speed of luderick (1.9 FL s^{-1}) may be adopted when they migrate along the coast of NSW. Based on coastal detections, the average ground swimming speed was measured at 1.05 FL s^{-1}, with a maximum swim speed of 2.01 FL s^{-1} (Chapter 2). Both of these migratory speeds are very close to optimal swim speed estimated from the swim-tunnel experiments. No detections from accelerometer transmitters were recorded during luderick coastal migrations to provide data on free-ranging fish. Nonetheless, based on laboratory and field estimates, luderick appear to swim at optimal speed during large-scale movements. Luderick's optimal speed falls into the higher range of other teleost fish species measured using lateral undulation of their body and caudal fin for swimming [0.4–2.8 BL s^{-1} (Quinn, 1988; Videler, 1993; Callihan et al., 2015; Mori et al., 2015)]. To cover long distances at the optimal speed, luderick may not stop to rest or forage. Migrating species such as eels (*Anguilla* spp.) or several salmonids species are known to stop eating during their spawning migrations and only relying on their reserves of energy they previously stored (Kadri et al., 1995; Tudorache et al., 2015). There is no evidence that luderick stop eating; however, luderick may fatten on highly energetic foods (e.g. animal matter) before undertaking large-scale migrations. Luderick can be caught with animal-sourced baits or lures when fishing for carnivorous fish is estuaries (pers. obs.). Luderick diet can vary during the year with the animal component representing 16% of its the diet (Clements and Choat, 1997) and even up to 65% during winter (Raubenheimer et al., 2005). Estuaries can potentially represent sources of animal food for luderick at certain times of the year; however, the gut content analyses done during this study (unpublished data) and the information gathered from the literature are sparse and further research is needed.

Active metabolic rate (AMR) can represent a large portion of the total energetic budget of animals (Boisclair and Sirois, 1993; Halsey et al., 2015), and large-scale migrations require a significant amount of energy. It was previously suggested (Chapter 3) that partial migration (Chapman et al., 2012) may explain differences in luderick migrating

behaviour along the NSW coast, with fish residing in estuaries over a 2-year period and others undertaking movements over 100'km (Chapter 2 and 3). The factors and cues influencing migrating behaviours and distances covered are numerous and interactive (Alerstam et al., 2003; Chapman et al., 2011); however, from a metabolic point of view, the costs associated with large-scale movements may play a role in determining migrating behaviours. Furthermore, in the case of spawning migrations, a greater proportion of energy expenditure is dedicated to gonad maturation, varying greatly between sexes [e.g. six times higher for females than for males Atlantic salmon (*Salmo salar*) (Fleming, 1996)]. Animals may alter their migrating behaviours in response to a reduction of their overall energy expenditure. Migrating behaviour may reflect the trade-off between ensuring the reproduction and foraging success at the population level, while limiting energetic expenses (individual fitness). Variations in migrating behaviours in relation to this trade-off have been well documented in migrating birds (Alves et al., 2013; Flack et al., 2016), and may be extended to fishes.

Accelerometry-based methods offer great possibilities and advantages in energetics studies, with a large range of accelerometers now available. The choice of the type of accelerometer (e.g. logger vs transmitter; bi vs tri-axial) depends on the aims of the study, the species, the capacity to retrieve loggers, the trade-off with battery life, and the pre-existing infrastructures (e.g. networks of receivers). All of them require calibration for their use in field energetics studies. However, respirometers can be source of limitations. Most swim-tunnel respirometers are designed for relatively small individuals (e.g. < 10 kg) due to logistical issues regarding the dimensions of the swim chamber, the volumes of water, and current speeds required, limiting the range of sizes and species and therefore restricting the scope of application of accelerometers in energetics studies for large fishes (Payne et al., 2015a). The swim-tunnel used for the laboratory experiments provided a suitable calibration of the accelerometer transmitters to estimate field metabolic rates from data collected from free-ranging luderick. Despite the known relationship between temperature and fish metabolism (Rice et al., 1983; Claireaux and Lagardere, 1999; Clarke, 2006), the laboratory calibrations were conducted at one temperature (20.1°C ± 1.0). The laboratory set-up and available logistics for this study did not allow acclimating and swimming luderick at various temperatures or salinities, and specific scaling for metabolic rates could therefore not be

obtained. There is scope to extent the laboratory work to evaluate the metabolic costs and associated swimming activities under a range of temperatures and salinities [effect of salinity may be temperature-dependant (Wuenschel et al., 2004; Wuenschel et al., 2005)], and also, under simulated drops of salinity, similar to the conditions luderick are exposed to during high flow events. Under such scenarios, the active metabolic rates are expected to increase due to both the increase in costs related to osmoregulation (physiological) and the behavioural response to the stress (e.g. increase in AMR due to higher opercular ventilation). Such further research can improve our understanding of field metabolic rates of free-ranging fish.

5.6 Conclusions

This study provided the first estimates of the cost of movements associated with swimming activity for luderick. Luderick exhibits higher estimated field active metabolic rates (field AMR) during day-time, 1.5 times higher compared to night-time rates. This is possibly related to luderick diel variations in behaviour, especially in relation to foraging and resting, with fish being more active during day-time (foraging) and probably resting during night-time as found in Chapter 4. AMR of wild fish followed a typical ectotherm performance curve and increased with temperature and starting to asymptote near 19°C, temperature close to the optimum temperature found for luderick in a previous study (Payne et al., 2016). The optimal swimming speed, velocity minimising the cost of transport, was estimated at 57 cm s^{-1} (1.9 BL s^{-1}) for luderick, a value comparable to the maximum swim speeds of luderick during coastal migrations (Chapter 2), suggesting that luderick travel at the most efficient velocities during coastal migrations. Further research using accelerometers deployed in wild fish within large-scale networks of receivers and based on experimental studies with fluctuating environment conditions may strengthen these findings. Nevertheless, the active metabolic costs provided here represent a major input towards the construction of realistic bioenergetics models (Brodie et al., 2016) which are of great interest to better understand the partitioning of energetic costs in animals.

5.7 Tables

Table 5.1 Results of the unpaired t-tests comparing the active metabolic rates (AMR) of tagged versus non-tagged luderick for the 5 swim tunnel speeds used in the laboratory calibration (SD = standard deviation; d.f. = degree of freedom).

Speed (cm s^{-1})	Mean AMR tagged (± SD)	Mean AMR non-tagged (± SD)	t	d.f.	p-value
6	64.4 (14.4)	48.4 (23.0)	1.5	11	0.15
18	87.3 (13.7)	78.2 (26.7)	0.8	11	0.4
30	116.4 (8.9)	110.5 (20.4)	0.7	11	0.5
42	139.8 (13.6)	159.0 (28.7)	-1.7	11	0.1
54	160.4 (14.3)	171.7 (17.3)	-1.3	11	0.2

5.8 Figures

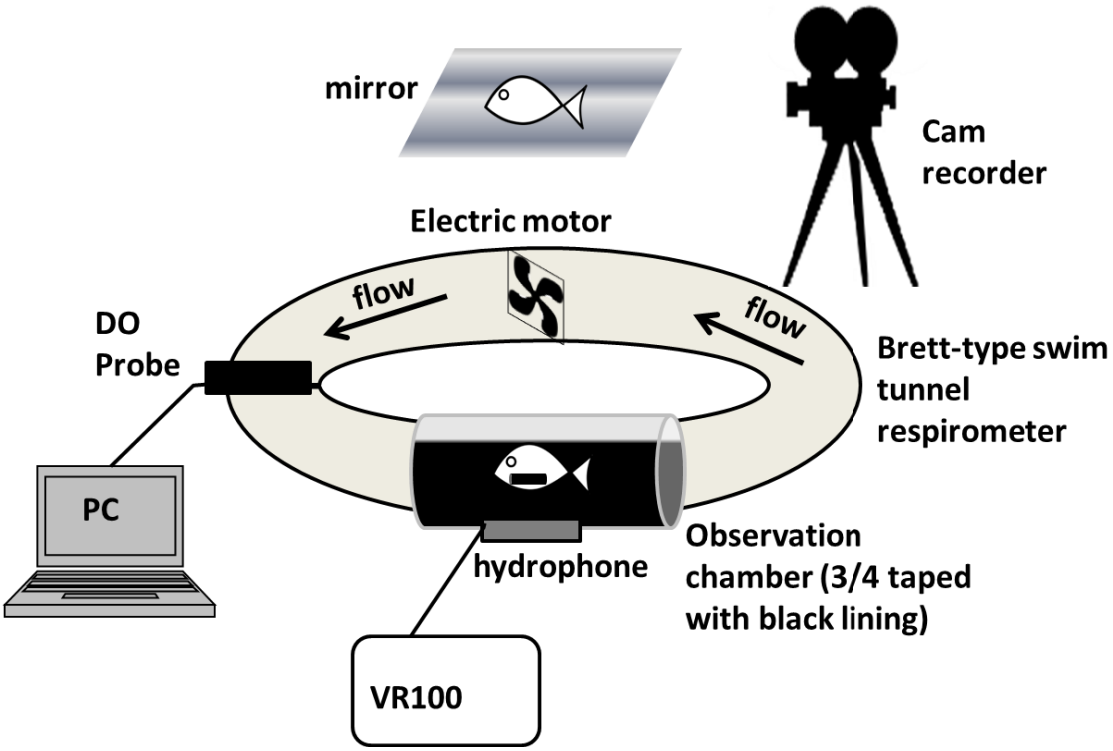

Figure 5.1 Schematic representation of the laboratory setup used to experimentally calibrate active metabolic rate in luderick.

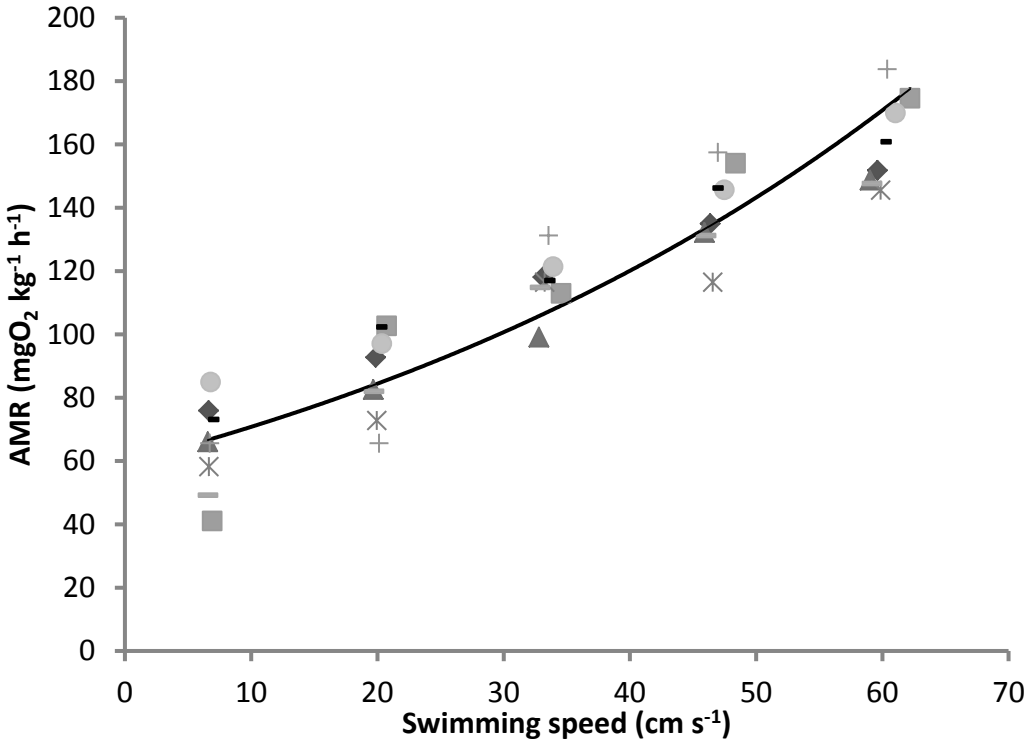

Figure 5.2 Relationship between active metabolic rate (AMR) and swimming speed for luderick (n = 8, symbols represent individual fish). The solid line represents the exponential relationship derived from the linear mixed-effect models (AMR = $59.36*e^{(0.0176*speed)}$).

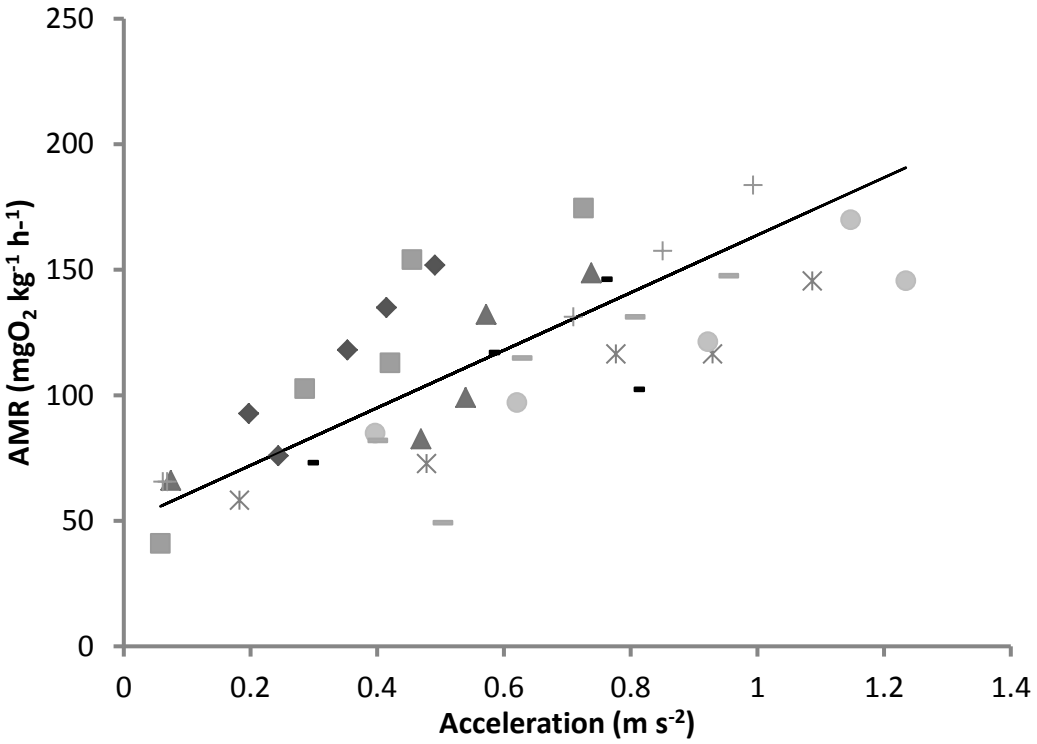

Figure 5.3 Relationship between active metabolic rate (AMR) and acceleration (body activity) for luderick (n = 8, symbols represent individual fish). The solid line represents the linear relationship derived from the linear mixed-effect models (AMR = 49.16 + 114.61*acceleration).

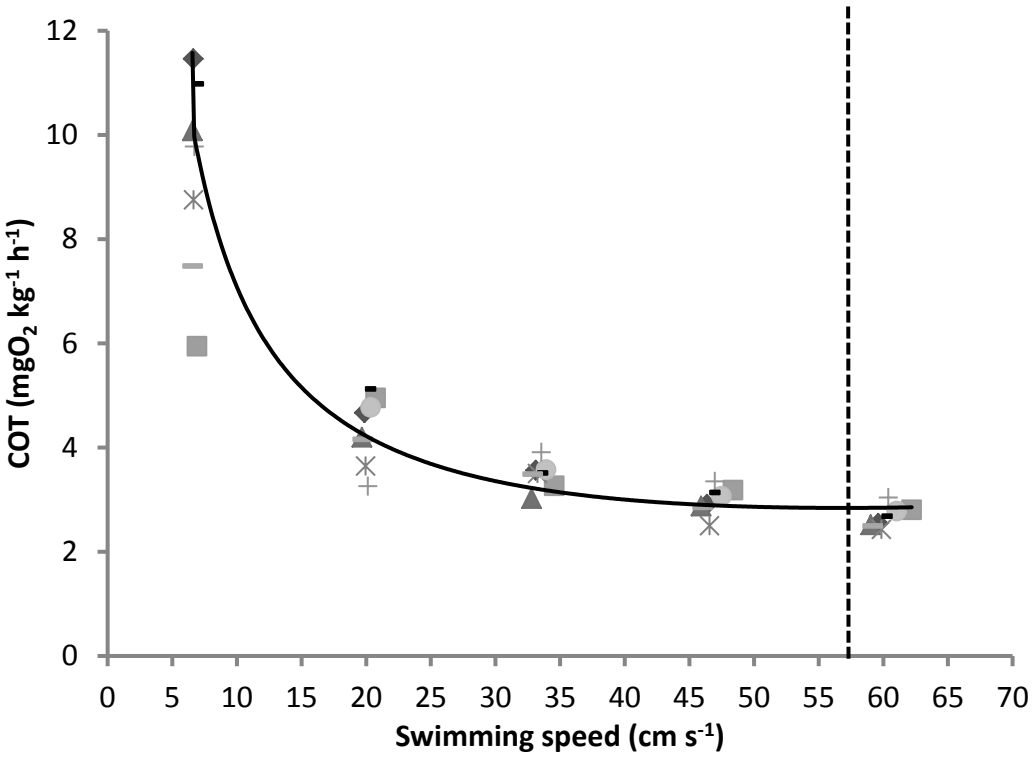

Figure 5.4 The relationship between the cost of transport (COT) and the swimming speeds for luderick (n = 8, symbols represent individual fish). The COT is at a minimum (COT_{min}) when the swimming speed was 57 cm s^{-1} (dashed line).

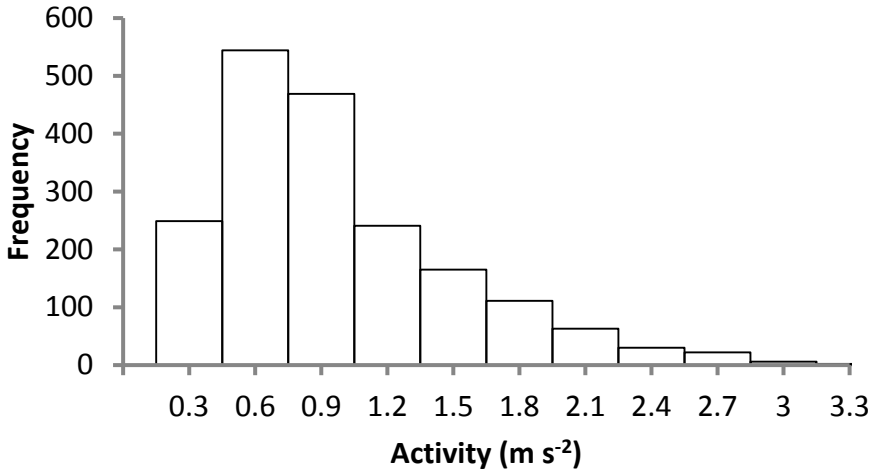

Figure 5.5 Frequency distribution of field activity values for wild luderick (n = 4) for the selected period used to estimate field AMR.

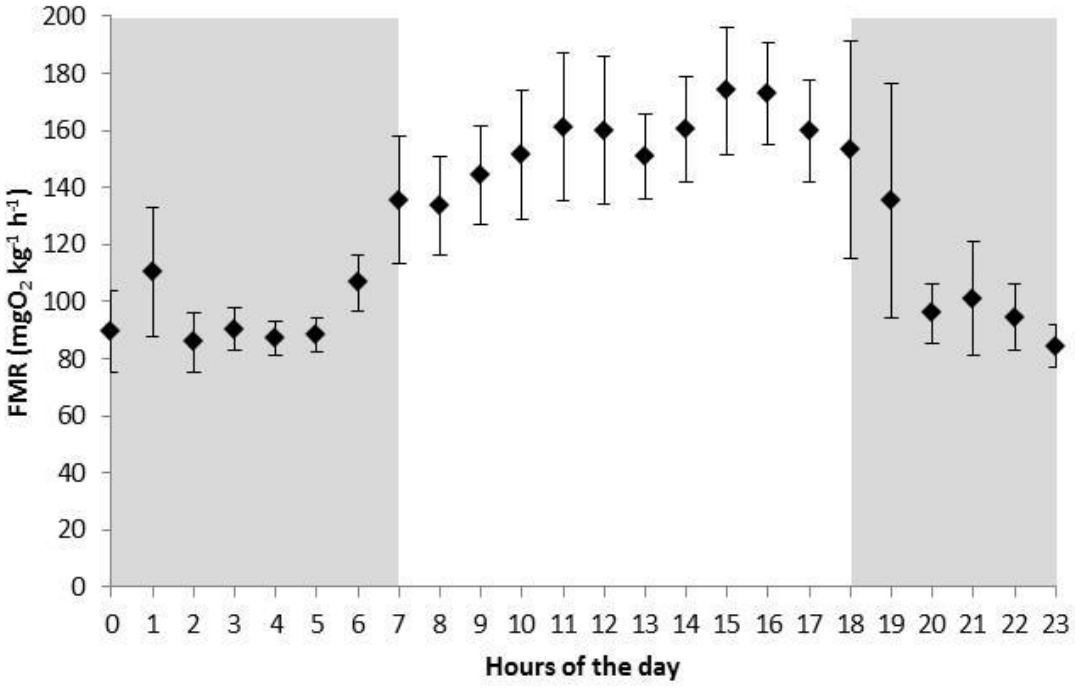

Figure 5.6 Diel patterns in estimated field AMR estimates across the 24 h of the day (overall mean across fish, n = 4). Error bars indicate the standard error and the shading represent night-time (includes dawn and dusk).

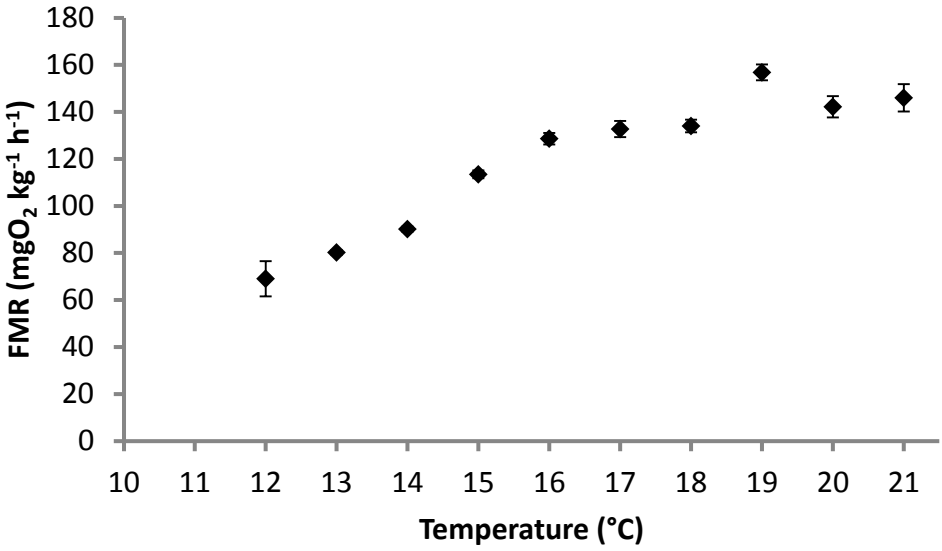

Figure 5.7 Field AMR estimates across the range of field temperatures (averaged per 1 °C bins). Error bars indicate the standard error. N = 4.

CHAPTER 6: General discussion

Animal movement plays an important role in ecological processes and this knowledge is essential for a better understanding of population dynamics (Nathan et al., 2008), especially in the context of climatic changes and anthropogenic activities (Chapman et al., 2011; Seebacher and Post, 2015). Movement is an important behaviour for an animal, allowing it to maximise growth, survival and reproduction by effectively responding to changing environmental conditions (Gillanders et al., 2015). However, animal movement is driven by many factors (internal and external) (Holyoak et al., 2008) that occur over a range of spatial and temporal scales (Fryxell et al., 2008; van Moorter et al., 2013), making its study complex and challenging.

A thorough knowledge of fish movements and the factors influencing them is essential to understanding the ecology of a species, and underpins effective management actions and conservation outcomes (Driscoll et al., 2014). Indeed, identifying the environmental drivers of fish movement patterns at a range of spatial and temporal scales reveals important ecological traits of species, and supports the management of commercial and recreational fisheries (e.g. spatial and/or temporal fishing restrictions) and the spatial conservation (e.g. Marine Protected Areas (MPAs), habitat protection zones) (Zeller and Russ, 1998; Pittman and McAlpine, 2001; Palumbi, 2004; Gaines et al., 2010). It is important to note that the scales, patterns and responses of fish movement may vary widely among species and individuals (Pittman and McAlpine, 2001; Babcock et al., 2012), and therefore, require specific studies dedicated to the species of interest with suitable replication at the individual level.

The movements of the temperate teleost fish luderick (*Girella tricuspidata*) were studied at different spatial scales and under fluctuating environmental conditions. This researched aimed to (i) fill gaps in the ecology of luderick and (ii) provide a better understanding of the movements of this species, highly valued for both commercial and recreational fishing. This was achieved using a series of field monitoring studies in major estuaries in south-east Australia, complemented by laboratory-based experiments. Luderick inhabits shallow coastal habitats and estuaries of south-east Australia and is an

abundant species in NSW. However commercial catches fluctuate temporally and showed a declining trend in recent decades (Rowling et al., 2010). Although the biology, reproduction survival and mortality (e.g. natural and fishing) of luderick in NSW are already documented (Gray et al., 2010; Gray et al., 2012), there are still traits of luderick ecology that remained poorly understood, in particular their movements and associated drivers. The primarily herbivorous diet of luderick is also of interest in regard to estuarine fish movements. Most of the research in NSW examining movement patterns in relation to environmental parameters targets iconic carnivorous fish species. Being primarily herbivorous, luderick may play an important ecological functional role in shallow coastal habitats, and may also display distinctive movement patterns in relation to its diet compared to these carnivores.

6.1 Movements of *Girella tricuspidata*: patterns, drivers and spatial scales – key findings

A thorough understanding of the movement patterns, especially larger scale migrations, along with the drivers triggering temporary relocation of a large number of fish, is important in the spatial management of fisheries and resolving patterns at the population level. Luderick are known to undertake alongshore, migrations related to spawning (Gray et al., 2012); however the current study is the first to address the timing and cues of egression from the estuary. Using a collaborative network of receivers spread along the NSW coast and selected estuaries, I identified the main drivers triggering the observed coastal migrations for 21% of the acoustically-tagged luderick. Egressions from the estuary followed by alongshore migrations were related to pulses of freshwater inflows in the study estuaries, reducing drastically the conductivity. From the fish detected or recaptured outside their tagging estuary, there was no clear directional relationship with reproduction patterns based on the timing of egression and periods of spawning described in the literature (Chapter 2). This research supports the results from previous studies based on mark-recapture, in terms of ranges (up to ~500 km) and directions (predominantly northward) (Thomson, 1959; Gray et al., 2012) (Chapter 2). In SE Australia, luderick have a protracted spawning period which varies as a function of latitude (Gray et al., 2012). Other marine estuarine-opportunist fish species undertake pre-spawning coastal movements along the Australian east coast in a predominantly

northward direction (Thomson, 1959; Kailola et al., 1993), often one to two months before reaching spawning grounds (Kesteven, 1953). Luderick may follow a similar pattern, with maturation of the gonads occurring during the migration. As proposed by Gray et al. (2012), the northward migrations of mature fish may represent a strategy to facilitate the dispersion of eggs and larvae by means of the Eastern Australian Current (EAC), running southward along the east Australian coast (Ward et al., 2003). This strategy, along with an extended reproductive period, is also likely to contribute to the spatial and temporal variability in luderick recruitment to New South Wales estuaries (Worthington et al., 1992; Gray and Miskiewicz, 2000; Smith and Sinerchia, 2004).

Pronounced fluctuations in estuarine conditions, such as those driven by rainfall runoff, may represent strong signals for fish to reproduce (Walsh et al., 2012a; Taylor et al., 2014). Pulses of freshwater inflow drive fish towards the mouth of the estuary and may stimulate spawning events. Luderick can form large aggregations at the mouth of estuaries and coastal headlands, during the austral autumn-winter months, presumably to spawn (Gray et al., 2012). Several fish left the linear estuarine acoustic arrays in response to high river flows before coming back, weeks to months later, occurring at documented peak times of gonad maturation (Gray et al., 2012) (Chapter 3). It is possible that some individuals might have temporarily left the estuary to spawn nearby, without undertaking a full spawning migration. These findings and previous mark-recapture studies suggest that luderick populations may partially migrate, as do other euryhaline species in NSW (Fowler et al., 2016). Partial migration might be a more common phenomenon than previously thought (Chapman et al., 2011; Chapman et al., 2012), and may explain the inter-individual variability in residency and large-scale movements of luderick (Chapters 2 and 3). Partial migration may provide some resilience of luderick populations to harvesting, as has been suggested for other species (Childs et al., 2015; Fowler et al., 2016).

I also showed that migrating luderick were travelling close to the shore and could enter multiple estuaries. In addition, I showed that fish originating from different estuaries converged at similar areas. These findings provide further understanding of the connectivity of populations along the NSW coast, which was poorly documented by mark-recapture studies due to the low recapture rates. Movements and estuarine

connectivity found in this study tend to support the contention that luderick populations may form a single stock in SE Australia (Gray et al., 2000), which is also suggested by genetic studies (Curley and Gillings, 2006; Curley, 2007).

I found that luderick can travel at greater speeds than previously known, exceeding 50 km d^{-1} over several days. This swimming velocity corresponds to the optimal speed estimated in my laboratory experiments for this species (Chapters 2 and 5). Field and experimental data both suggest that luderick travel at the most efficient velocities during large-scale coastal migrations. Migrations are driven by internal and external factors (Alerstam et al., 2003); however the choice of migrating or not, and the distances covered, may be also be dictated by the cost and benefits of such movements (Alves et al., 2013; Flack et al., 2016). This is even more noteworthy in the case of spawning migration, when a large part of the overall energy budget is allocated to gonad maturation (Fleming, 1996). In this study, the tagged luderick were likely adult fish, but were not sexed; therefore potential differences in movements between males and females were not examined.

The along-estuary movements of luderick were related to fluctuations in conductivity, driven by freshwater inflows (Chapter 2). While the estuarine conductivity gradient influenced the distribution of the fish based on size, with smaller fish tending to occupy higher reaches of the estuary, there were not obvious differences in movement responses to conductivity with body size. It is important to note that this study focused on a narrow size range of adult fish and that the differences between juveniles and adults were not assessed. Ontogenetic variation should be investigated. Although conclusions about seasonal variations in estuarine movements were limited (lack of replication over time; Chapter 3), temperature had an influence on luderick activity over five months of fine-scale monitoring (Chapter 4). The positive relationship between swimming activity and temperature was related to the decrease in fish performances outside their optimal temperatures (Payne et al., 2016). As discussed in Chapter 5, metabolic rates decreased with temperature in ectotherms. Therefore, even if seasonality could not be fully addressed in this study, I expect that estuarine movement patterns of luderick may show differences with the seasonality, driven by seasonal fluctuations in rainfall and temperatures.

This study revealed strong diel and sub-diel rhythms in activity and depth use. Luderick tagged with an accelerometer transmitter data showed that they were more active during the day and periods of high tidal heights (Chapter 4). Across the 24-h period, luderick dedicated increasing energy to body activity from dawn and throughout the day, until the field metabolic rates declined after dusk to reach the low levels seen in night-time hours (Chapter 5). These findings can be related to diurnal foraging activity, increasing throughout the day, and a sheltering behaviour during night-time in areas with low local current flow, as suggested by Ferguson et al. (2013) for luderick inhabiting shallow costal reefs habitats. Interestingly, the fine-scale study in the mid-lower reaches of the estuary found that luderick reduced swimming activity and shifted to deeper waters in response to high flow events (Chapter 4). This reinforces the findings that luderick respond to variation in environmental parameters by adopting a range of behavioural responses (Chapters 2 to 4) as found for other species in estuarine systems (Payne et al., 2013; Taylor et al., 2013; Payne et al., 2015c).

6.2 Luderick movements in a context of climatic changes and anthropogenic pressures

The increase in regional climatic variability is responsible for changes in fish distributions and abundances in estuarine and coastal systems (Roessig et al., 2004; Perry et al., 2005). It is expected that luderick movement patterns would be influenced by the elevated regional climatic variability and anthropogenic alterations. SE Australian rivers are characterised by alternating flood and drought regimes (Erskine and Warner, 1998) which have great effects on estuarine commercial fisheries (Gillson, 2011). In addition, flow regimes may be altered by human activities resulting from damming, freshwater use, and developments occurring in the water catchment (Poff and Zimmerman, 2010). Therefore it is anticipated that these natural fluctuations and alterations in freshwater flow would alter the estuarine movement patterns of luderick and the signals triggering their coastal migrations.

Over the recent decades, ocean warming rates in coastal south-east Australia were three to four times higher than the global average (Holbrook and Bindoff, 1997; Ridgway,

2007; Matear et al., 2013), making this region a climate change "hotspot" (Booth et al., 2011). Multiple terrestrial and marine species have shown geographical range shifts in response to changes in environmental conditions associated with climate change (Perry et al., 2005; Harley et al., 2006; Figueira and Booth, 2010). Latitudinal shifts in distribution ranges in response to increase in sea surface temperature (STT) have been documented for many Australian coastal species, including luderick (Last et al., 2011). Stuart-Smith et al. (2010) recorded that the southern limit of luderick distribution (Tasmania) shifted approximately 250 km between 1994 and 2006, and Last et al. (2011) observed an increase in luderick abundance in the same region. This was most likely caused by the strengthening and southward extension of the EAC warming this region at a rate of 2.3°C/100y (Ridgway, 2007). With the increase in STT in eastern Australia, the luderick northern distributional range edge currently in south Queensland, is also expected to shift southwards, most likely leading to the decrease of luderick catches in this area, and eventually to end this fishery in Queensland. Increase in sea surface temperature and shifts in distribution ranges of marine species are likely to have cascading effects on marine ecosystems (Johnson et al., 2011). Changes in range and increases in abundance of herbivores such as luderick may have an impact on local algal communities and therefore on ecosystem functions (Taylor and Schiel, 2010; Vergés et al., 2014; Ferguson et al., 2016).

Another consequence of climate warming is the change in global oceanic circulation patterns, which have altered the strength, duration and extent of marine currents (Ridgway, 2007), as well as mesoscale structures (e.g. eddies) which play an important role in coastal productivity and population connectivity (Bruce et al., 2001; Suthers et al., 2011). These modifications to currents may affect large-scale movements of adult luderick by potentially altering migration routes and ranges of movements, with important consequences on the transport and dispersal of egg and larvae and therefore on the population connectivity (Harley et al., 2006; Brierley and Kingsford, 2009). Furthermore, climate change and human activities are responsible worldwide for the degradation and loss of coastal habitats (Gilman et al., 2008; Waycott et al., 2009; Polidoro et al., 2010). Shallow coastal habitats such as seagrass, mangrove, and saltmarsh play an important role for species of commercial interest and local fisheries (Jackson et al., 2001), by providing suitable nursery grounds (Beck et al., 2001),

refuges, and food for many organisms (Paterson and Whitfield, 2000). In NSW estuaries, seagrasses support the recruitment and sustain early life stages (e.g. juveniles) of many species of commercial interest, including luderick (Hannan and Williams, 1998; Rotherham and West, 2002; Smith and Sinerchia, 2004). Therefore, alterations of such key habitats can have important consequences as they play a major role in supporting luderick populations, from recruitment to adult stages.

6.3 Acoustic telemetry, performances, improvements and recommendations

This present research was based on acoustic telemetry. This method offered great advantages to determine movement patterns of luderick at different spatial scales. The large-scale movement study of luderick benefited from the collaborative network of receivers present in the eastern Australian coast and the related database (Chapter 2). Acoustic telemetry-based research is expected to become more widely used in Australia, and globally. Therefore, the maintenance of such infrastructure is essential to sustain research targeting multiple species having various movement ranges.

As stated in Chapter 2, the network of receivers available during this study could be improved, especially in the case of the coastal "curtains" designed to detected tagged animals migrating latitudinally. To improve the chances of detection of teleost fish moving through the near-shore coastal migration corridor by these "curtains", a recommendation would be to concentrate receivers with smaller spacing in the near-shore area where noise is greater (Stocks et al., 2014). In addition, deployment of an adjacent receiver line inshore (e.g. a few kilometres from the coast, parallel to the curtain), could increase chances of detections and also provide an indication of the directionality of movement, information particularly important in migration studies. In this research, the estuarine gates detected tagged luderick multiple times at different mouths of estuaries, however gates performance is difficult to assess. Such set-ups are highly recommended for the study of species which are likely to enter in estuarine systems, but attention should be given to (i) where to place the "gate" receivers, and (ii) using a suitable number of stations set in strategic positions in order to decrease gaps and increase chances of detections. The IMOS Animal Tracking facility database proved to be a valuable tool to access to luderick detections that originated from other

users' receiver arrays. Collective arrays and associated databases offer obvious benefits to acoustic telemetry research communities. However such networks rely greatly on the willingness of users to join and contribute to the database. This present work is one of the first relying on the collaborative array and the IMOS Animal Tracking database to study broad-scale movements of a teleost fish in SE Australia. The beneficial outcomes in this present research could be used as an example to promote such collaboration and the participation of the community.

The estuarine linear arrays of receivers and the VEMCO Positioning System (VPS) were relevant and complementary tools to respectively study movements at the level of the estuary and to study fine-scale movement patterns, such as diel and tidal activity patterns. Allocating luderick to habitats present within the VPS of receiver arrays deployed in the Clyde River was limited by the quality of the habitat maps available and the localisation of the networks (e.g. outside main seagrass beds). Further mapping using hydroacoustic technologies (Kenny et al., 2003) could greatly improve habitat association for luderick and other species of interest. Detailed habitat maps, as well as depth contours and fine-scale underwater topography information, influence significantly the quality of acoustic telemetry outputs. Such detailed information allows precise tracking of fish movements, activity patterns and specific behaviours relative to physical features.

While estuarine arrays could be improved in terms of receiver spacing and coverage, it is important to maintain regular and frequent receiver downloads to limit chances of gear loss and therefore gaps in data (Chapters 2 and 3). A common limitation in acoustic telemetry and more generally in animal tracking studies is the limited number of replicates that can compromise population-level inference (Hebblewhite and Haydon, 2010). The small sample size results from the trade-off between cost and number of telemetry units and also the possibilities of detections. Tracking methods are valuable tools to better understand the ecology and behaviours of free-ranging animals; however caution should be taken to obtain suitable level of replication to fulfil the aims of the study. A major strength of this thesis was tracking of multiple fish simultaneously across three estuaries.

6.4 Further research

This study was conducted under a strong La Niña ENSO (El Niño Southern Oscillation) regime, characterised by heavier rainfalls during winter and spring on the south-eastern Australian coast. The 2010-2012 La Niña episode was particularly strong in Australia, with 2011 being the second wettest calendar year on record. The large volumes of rainfall received during this period possibly intensified the egression and coastal residency observed in this study. Investigating whether similar patterns are detected during a contrasting El Niño oscillation requires further research.

Studies based on ecogeochemical methods using elemental and isotopic ratios in biological tissues as markers to back-track animal movements (McMahon et al., 2013), could provide complementary information to acoustic telemetry studies. Otolith microchemistry has been successful in determining in which environment the fish have been living and to spatially discriminate fish populations by the relative abundance of microchemicals (chemical signature) integrated in otolith calcium carbonate growth rings (Elsdon and Gillanders, 2003; McCulloch et al., 2005). Therefore these methods can be applied to study fish movements *a posteriori* (Thorrold et al., 1998; Gillanders and Kingsford, 2000). In the case of luderick, elements such as strontium and barium, which are present in distinct levels in seawater and freshwater, could be used as relevant markers to detect up and downstream estuarine movements, and also between marine and estuarine environments, similarly to the study of migrations of diadromous and catadromous species (Secor and Rooker, 2000; Zimmerman and Reeves, 2000; Tsukamoto and Arai, 2001; Chang et al., 2004; McCulloch et al., 2005). In addition, partial migration behaviour of sea mullet (*Mugil cephalus*) and black bream (*Acanthopagrus butcheri*) has been recently confirmed using otolith chemistry (Gillanders et al., 2015; Fowler et al., 2016) and that method could further clarify migration and estuarine residency behaviours in luderick.

The motivations for luderick to visit (or not) estuaries, temporarily or for long periods of time, remain unclear (Chapter 3). Further research could be done to determine potential reasons, such as variable food availability, specific environmental conditions in estuaries and adjacent coastal areas, and predation risks. Natural predators of luderick

in coastal waters and the lower reaches of estuaries include dolphins and seals (N. Hardy, University of Sydney, comm. pers.) and waterbirds like the great cormorant (*Phalacrocorax carbo*) feeding on smaller size classes of fish (Coutin and Reside, 2007). The large estuarine teleost fish mulloway (*Argyrosomus japonicus*) could be another predator of luderick in estuaries, although, presence of luderick in mulloway's diet is not verified (Taylor et al., 2006a). Seasonal variation in predation rates and in the presence of these predators in estuaries could influence the luderick distribution in these systems.

The physiological component of this research (Chapter 5) could be improved by additional replication in field metabolic rates, especially during coastal migrations. Field metabolic rates of migrating luderick could provide valuable information on the energy expenditure associated to these large-scale movements. While the effects on temperature on fish metabolism and performances are well documented, the influences of salinity are less well known and could be studied by complementary laboratory experiments.

Salinity was found to have great effects on growth (Boeuf and Payan, 2001). The metabolic costs of euryhaline species may vary with salinity (Swanson, 1998; Claireaux and Lagardere, 1999), although, the effect may only be noticeable for large variations in salinities (Nordlie and Leffler, 1975; Claireaux and Lagardere, 1999). The energetic cost associated with osmoregulation represents approximately 10-15% of the standard metabolic rate in seawater (Kirschner, 1993), therefore osmoregulation is likely to remain a small cost compared to movement, digestion, and growth. However, the overall osmoregulation metabolic cost in changing conditions remains difficult to quantify due to interactive effects of salinity on physiology and behaviour, adding costs beyond the basic osmotic and ionic regulations (Swanson, 1998; Claireaux and Lagardere, 1999; Boeuf and Payan, 2001). The study of metabolic rates under conditions mimicking changes in environmental conditions (e.g. decrease of salinity occurring during high flow events) could provide valuable information on the costs associated with these drastic changes. Such experiments could be also coupled with the evaluation luderick stress levels by looking at specific hormones (Barton, 2002).

6.5 Implications for management and conservation of *Girella tricuspidata*

A thorough knowledge of the movement patterns of a species at various spatial and temporal scales, from large (e.g. population connectivity and seasonal patterns) to finer scales (e.g. habitat preferences and diel activity patterns) is essential to identify important ecological traits of the species. This information, coupled with responses to biotic and abiotic factors, may provide suitable inputs for spatial conservation (e.g. MPAs, habitat protection areas) and fisheries management (e.g. spatial and/or temporal fishing restrictions).

In this study, a small proportion of the tagged luderick showed estuarine residency over the monitoring period (ca. 2 years). A strong residency and fidelity of luderick to their release sites within small no-take areas ($\leq$ 2 km^2) of MPAs was also described by Ferguson et al. (2016) and suggested by Curley (2007) for fish tagged in shallow coastal reefs in NSW. The results of a mark-recapture study also suggested that luderick may reside for long periods of time in the tagging estuary or coastal lake (up to 2 years) (Thomson, 1959; Gray et al., 2012). In addition, it has been suggested that luderick could positively respond to a "reserve effect" with larger and more abundant fish found in protected zones compared to adjacent non-protected areas (Curley, 2007; Ferguson et al., 2016). All this evidence suggests that luderick could benefit from small MPAs (no-take areas) in NSW. Temperate fish species exhibiting high mobility and resident behaviours in the same population are known to respond positively to protection within relatively small MPAs (Willis et al., 2001; Egli and Babcock, 2004; Curley, 2007; Parsons et al., 2010). In addition, movement patterns and presence of suitable habitats for the species of focus are important parameters to consider in the design of marine reserves, and influence greatly their success (Kramer and Chapman, 1999).

In 2002, 30 estuaries in NSW were completely or partially closed to commercial fishing activities (Gray et al., 2010). Since luderick is mainly commercially harvested by estuarine fisheries, this measure may partially relieve pressure on luderick stocks. In addition, the minimum legal size of luderick has been raised from 250 mm to 270 mm (total length) in 2005, providing greater protection to immature fish from both, commercial and recreational fishing (Gray et al., 2010; Gray et al., 2012). Future assessments of the status of luderick populations will provide information on whether

these measures supported a sustainable exploitation of this currently fully-fished species.

Harvested species are particularly vulnerable during their spawning migrations, as large numbers of individuals that form large schools or aggregations for spawning can be removed by fisheries activities (Zeller, 1998; Sala et al., 2001; Sadovy and Domeier, 2005), which may have effects on the reproductive output of the population. Consequently, predicting such migration is important for implementing relevant spatial and temporal fishing restrictions to maintain sustainable fish resources (Palumbi, 2004; Jensen et al., 2010). Large aggregations of luderick forming in late austral autumn and winter travel along open surf beaches of central and northern NSW and are targeted and captured in large quantities by the coastal beach-seine fishery (Gray et al. 2000). Migrating luderick (presumably undertaking spawning migrations) may be vulnerable to such activities and needs to be closely monitored and assessed. Due to the large distances covered by migrating luderick and the wide spatial scale of this fishery activity, temporal fishing restrictions and a quota would be best over spatial closures. Luderick beach hauling activities occur during a relatively short period of time of the year. In addition, partial migration behaviour, with a proportion of the population "skipping" coastal migrations, most likely makes luderick resilient to such fisheries practices, if kept at sustainable levels.

Estuarine systems support many fisheries worldwide including in NSW (Rowling et al., 2010). This research showed that adult luderick could utilize multiple estuaries. As stated previously, estuaries provide nursery grounds and juvenile habitats to luderick. Maintaining key estuarine habitats (seagrasses, mangroves and saltmarshes) and functions is an essential consideration in the management of luderick and many other fisheries.

6.6 Conclusions

Integrating scientific evidence in decision and policy making is important and encouraged (Pullin et al., 2004; Barton et al., 2015). It is well recognised that animal

movements play an important role in the distribution and the persistence of biodiversity (Trakhtenbrot et al., 2005; Jeltsch et al., 2013). Therefore, a thorough knowledge of animal movement must be an essential component in decisions concerning biodiversity conservation (Driscoll et al., 2014). This study provides a better understanding of luderick (*Girella tricuspidata*) movements at spatial scales of m's to 100's km, in relation to fluctuating environmental conditions. My findings can be used to improve the management and conservation of luderick, as well as of other fish species, by using similar tools and methods, making this research beneficial for fisheries managers and the scientific community.

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