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Measuring productivity of Australian tropical estuaries using standing stock analysis

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Abstract

Increasingly, anthropogenic use of ecosystems is resulting in cumulative degradation of ecosystem functions and the values held by these systems. Threats from nutrient pollution, catchment scale modifications to land use and water flows are increasing. This is concerning for estuarine and coastal fisheries as estuarine producers are inextricably linked to land-derived nutrients and freshwater flows. In tropical estuarine ecosystems the complexity and variability of environmental, biological, and ecological factors culminate in a matrix of largely unknown causal relationships. Because of this, our knowledge of land use impacts on fisheries is limited. Additionally, the disjunction of current measurement scales and impact scales has reduced our ability to measure the resultant impacts on estuarine ecosystems. Therefore, to fully understand anthropogenic impacts on estuarine ecosystems, integrative measures of ecosystem health, functioning, and productive output are required. These measures must also be practical and reliable to apply at relevant scales.

In this thesis I consider how well current methods for ecological and fisheries study are suited to the meso-tidal, structurally and hydrologically complex situation common to tropical estuaries. I use a bespoke method to generate high resolution standing stock data in an estuary typical of the tropical east coast of Australia. Standing stock data were collected approximately fortnightly during the wet and dry seasons over one year. Two spatial scales were examined, reach and estuary, with three reaches included in the study. Twenty four of the 72 species recorded throughout the study contributed over 90% of total biomass. Most of these species were small bodied (<200mm length) basal-prey fish and penaeids, which were observed in large numbers frequently aggregated in schools. From the data produced, investigations of ecological spatio-temporal relationships and estimations of growth parameters of the fish and crustacean community are conducted.

The first study specifically aimed to understand how effective various data types, treatments, and measures of ecological similarity are at producing meaningful results in cases of extreme data characteristics. This study demonstrated the use of multivariate ordination techniques at multiple spatial and temporal scales to analyse standing stock data. Results from this study indicated that many of the data handling methods used in ecological studies are poorly suited to the extreme data characteristics exhibited by standing stock data in the tropical estuarine context. The study determined the use of transformations and measures of central tendency to characterise data at various spatial scales could confound ecological patterns. The extreme data characteristics and effects these had on analyses were due to the often extreme and heterogeneous spatial variability of standing stocks due to biological characteristics exhibited by many basal-prey species. These results highlighted the importance of correct usage of these methods to achieve useable and meaningful multivariate ordinations.

A second study was aimed at testing the use of industry-standard growth estimation methods for tropical estuarine basal-prey species. The basal-prey community was identified as representing the greatest portion of fish and penaeid biomass from catch data collected in the previous study. These basal-prey species represent a section of the estuarine ecosystem and productivity chain that is heavily fished in many parts of the world, and poorly understood. Results from this study revealed that many assumptions of traditional length-based methods were violated by standing stock data for species in this community. The suitability of the von Bertalanffy growth function was also tested and found to be unrepresentative of growth patterns for most species. Moreover, this study highlighted the importance of matching the spatial scales at which tropical estuarine populations function, to the scale of data collection and analysis.

The studies I have conducted demonstrate the mismatch between typical statistical assumptions and the realities of data collection in the tropical estuarine context. Many of the data characteristics exhibited by standing stock data are not easily treated without removing meaningful information. As a consequence, new approaches to the collection, handling, and analysis of data in a practical ecological context are needed. These might include conceptually different ways of measuring and communicating spatial variations in populations, e.g. quantitative measures of abundance and diversity through environmental DNA (Kelly et al. 2014, Maruyama et al. 2014, Doi et al. 2015, Thomsen et al. 2016), or spatial predictability (Mellin et al. 2007, Pittman et al. 2007). For growth estimation, a more complex shift from the paradigm of species-specific absolute growth, to measures of spatially and temporally explicit growth potential may be required, e.g. Weber et al. (2014). Additionally, the application of traditional productivity estimation techniques in the tropical estuarine context is not appropriate in many cases. It is clear that commonly used growth characterisation functions are inappropriate for many basal-prey species because the assumptions are not biologically reasonable. Overall, the assumption that current growth characterisation models accurately represent the reality of these species' existences is fundamentally flawed. This undermines the value of any management actions based on these flawed assumptions.

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Chapter 1: General Introduction

Estuarine and coastal ecosystems provide critical resources and services to coastal communities, including support of fisheries, and ecological linkages between productivity and social values (Jackson et al. 2008, Barbier et al. 2011) among many others. Our reliance on estuarine and coastal ecosystems means their health and functioning is critically important to humans. For example, fish stocks, productivity, and services such as sediment trapping, pollutant filtration, and coastal land stabilisation are some of the most important benefits provided to humans (Barbier et al. 2011). As global populations increase, often focused along rivers and coasts (Gilbert & Brodie 2001), the demand for resources and services is increasing accordingly. Growing populations are closely linked to development and changes in land use (Clark 1967, Meyer & Turner 1992, Gilbert & Brodie 2001) and these often come with associated risks and impacts to the health and functioning of surrounding ecosystems. These anthropogenic modifications are often imposed without due consideration of the associated risks and impacts (Small & Nicholls 2006). The impacts of these modifications include pollution, habitat loss, introduction of invasive species, and biomass reduction caused by extractive industries such as fishing (Gilbert & Brodie 2001, Lotze et al. 2006).

In tropical coastal, riverine and estuarine ecosystems, where human activity and resultant effects are concentrated, the risks are particularly evident. Currently along Australia's tropical east coast, the most prevalent threats are from nutrient pollution, catchment scale modifications to land use and water flows, and these threats are increasing (Brodie & Mitchell 2005, Davis & Koop 2006, Waterhouse et al. 2017). This is concerning for estuarine and coastal fisheries as estuarine producers and food webs are inextricably linked to land-derived nutrients (McClelland & Valiela 1998) and freshwater flows (Gibson et al. 2003, Hamilton & Gehrke 2005, Robins et al. 2005b, Halliday et al. 2008, Gillanders et al. 2011). In addition to these linkages, connectivity among various ecosystems and habitats within the coastal seascape, the availability and accessibility of habitats is important for the reproductive and migratory success of many aquatic organisms (Drinkwater & Frank 1994, Gillanders & Kingsford 2002, Staunton-Smith et al. 2004, Robins et al. 2005b). Fragmentation of these connected components can lead to reductions in biomass and productivity of fisheries (Valentine-Rose et al. 2007). Thus, rapidly increasing development and landscape modifications risks widespread damage to, or complete collapse of, ecosystem functions and services. Added to this, there is a deficit in many areas of fundamental knowledge, meaning that the flow-on effects of human-induced changes in estuaries are not well understood, particularly in the meso-tidal, structurally complex ecosystems such as tropical estuaries (Hamilton & Gehrke 2005).

In tropical ecosystems, how resources and services are affected by development and anthropogenic modification is still unclear (Hamilton & Gehrke 2005). By contrast, extensive research has been conducted in temperate estuaries revealing a series of predictable changes to fish communities and ecosystem functioning following various anthropogenic impacts (Lotze et al. 2006). For example, extensive monitoring in Chesapeake Bay, a temperate estuary in North America, has shown reductions in fish populations, that have been correlated with increases in the frequency and magnitude of seasonal hypoxic and anoxic zones (Officer et al. 1984, Kemp et al. 2005). These hypoxic events have been linked to anthropogenic nutrient enrichment in the Bay since the early 1800's (Rosenberg et al. 1990, Johannessen & Dahl 1996, Hagy et al. 2004). Unlike temperate estuaries, the lack of historical data and background information for tropical riverine and estuarine ecosystems and the species that inhabit them, hinders our ability to predict the impacts of human-driven ecosystem changes, like nutrient flows and other anthropogenic impacts.

In order to determine the best course of action for the restoration and conservation of tropical ecosystems, we must be able to measure the services and resources they provide, and in a way that is relevant to real world community values. Ecosystem productivity, (defined in this context as the increase in biomass of a population of fauna or flora attributed to that ecosystem), is of particular importance in this context. The ability to measure productivity allows us to predict and understand changes that underpin the success of industries such as fishing and tourism that are particularly important to tropical regions and Australian communities (Barbier et al. 2011). Productivity measures also allow us to evaluate the effectiveness of management practices and actions such as habitat restoration in a currency that is meaningful to end-user groups. Productivity estimates are also well suited to complex ecosystems because they combine many interactive components into a composite value (Valentine-Rose et al. 2007).

Effective techniques have been developed for measuring productivity in temperate estuary systems (Edgar & Shaw 1995, Minello et al. 2008), however these methods are usually inappropriate for the meso-tidal, structurally complex and physically dynamic conditions which are common in tropical estuaries. Of particular significance are limits to the effectiveness of sampling gear and techniques in areas where access is generally available only periodically due to tidal fluctuations. Even when accessible, use of large netting and trawling gears is mostly impossible due to physical structures of habitats e.g. mangrove forests. There is the lack of detailed information such as population-habitat linkages, growth and production rates, and the role of anthropogenic activities e.g. fishing pressure, all of which are needed to manage specific species in defined locations (Blaber 2002, Blaber 2008). Estimates of stocks and productivity of select targeted species in some sub-tropical and tropical estuarine ecosystems have been made with relative accuracy using traditional methods (Ault et al.

1999, Minello et al. 2008). However, an extensive, and generally impractical, amount of data are needed for full production estimates. Even more data are required to extend the calculations to whole fish and invertebrate communities and to whole ecosystems. In fact, estimating productivity requires data collected over many years, species-specific biological parameters, such as recruitment schedules, age dependent mortality, and growth rates. Estimates of the standing stock are then used with the already available data to create a productivity model for each species.

Minello et al. (2008) and Houde and Rutherford (1993) used population measures such as growth and mortality rates, which were derived from data sets spanning from 10 to 50 years, respectively. Although the methods employed by Minello et al. (2008) can be considered best practice, this methodology is rarely applied due to data and time constraints; the study utilised data collected by a fisheries organisation over 20 years, coupled with other data from an intensively studied region. More complex models for single target species that take into account various metrics such as life history characteristics, age dependant fecundity and density dependant population dynamics, are even more demanding of historical data (e.g. Levin et al. (1997). This requirement for large bodies of data is a problem for many regions in the tropics where the required data are seldom available. The paucity of the data needed for complex productivity modelling in tropical regions is a clear impediment to the valuation and management of tropical coastal ecosystems.

For management institutions there is an important trade-off between gaining meaningful and usable biological information and capital expenditure. Ideally, best practice productivity estimates such as those produced by Minello et al. (2008) and others would be the target for management departments seeking new information. However, obtaining biological information, such as productivity estimates, is usually costly and time consuming. In addition to this, much of the detailed information provided by the large and comprehensive productivity models is not essential or meaningful in the early and developmental stages in the management process. Therefore, there is a possibility to economise expenditure on new biological information. However, there is a minimum level of information required to make reliable and defensible management decisions. In any situation, determining the optimum data needs is dependent on the value of the resource/service and the pressures/impacts concerning it (Figure 1. 1). There is a further dynamic to the relationship illustrated in Figure 1. 1, that for each ecosystem being studied, there will likely be substantial differences in both the distance between levels of information, and in the relative increases in effort required to reach each level. There may also be a number of context-specific information levels which are not included in this illustration. Table 1. 1 outlines the key information requirements of each level illustrated in Figure 1. 1. Information requirements have been roughly characterised as either biological information or stock measures.

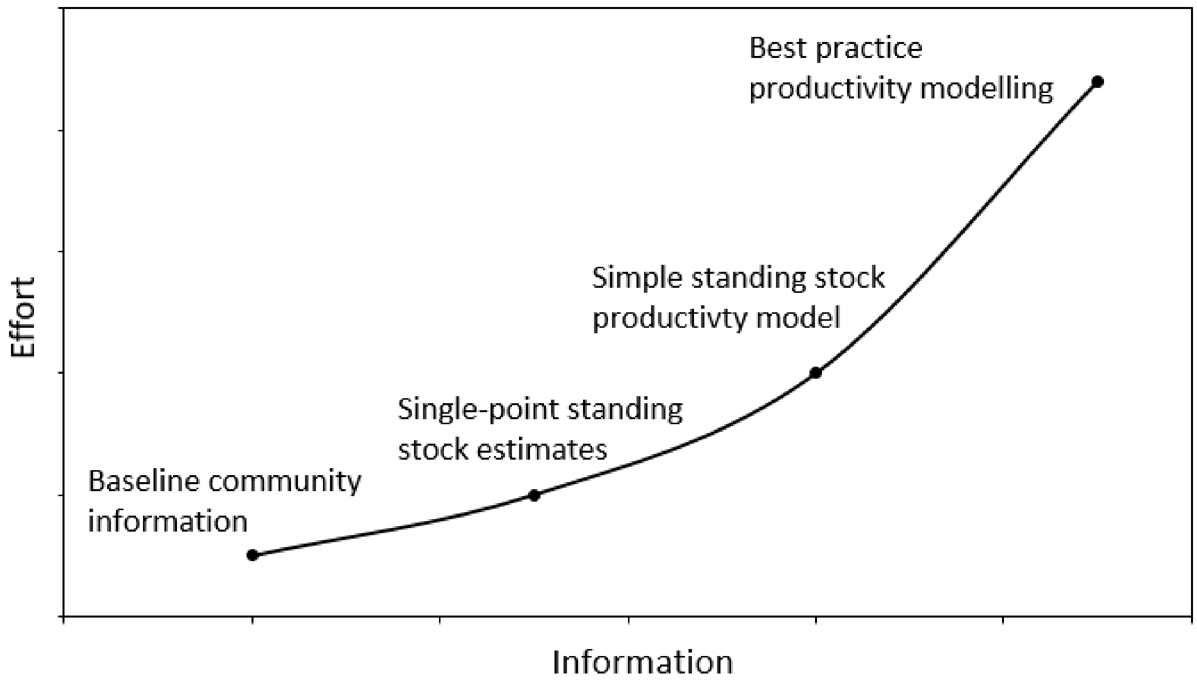

Figure 1. 1: Conceptual model of the information-effort trade-off in fisheries management with reference to productivity measurement.

Table 1. 1: Information requirements for productivity measurement levels

Measurement level	Biological information	Stock measures
Best practice productivity modelling	Mortality, growth, recruitment, fecundity, emigration, size-frequency, size-weight relationships, habitat/spatial abundance and occupancy patterns, species diversity, community composition	Biomass and abundance densities defined within multiple key habitats, seasons. Defined habitat areal extent and distribution. Community biomass distributions
Simple standing stock model	Growth, size-frequency, habitat/spatial abundance and occupancy patterns, species diversity, community composition	Biomass and abundance densities defined within key spatial units and seasons. Community biomass distributions
Single-point standing stock	Species diversity, community composition	Single-point biomass and abundance densities
Baseline community information	Species diversity, community composition	

A potentially achievable and broadly applicable way to measure productivity within estuarine and coastal ecosystems is via the development of proxy estimates based on just a few key items of information e.g. growth rates and standing stock biomass (Allen 1971, Randall & Minns 2000, Randall & Minns 2002, Meynecke et al. 2006). Estimates of standing stock biomass densities may be combined with seasonal and annual growth rates and knowledge of spatial and temporal abundance variations to develop a simple model of productivity such as that proposed by Allen (1971). There are two key components required for the simple standing stock model as defined above. These are (1) the spatial characterisation of the population in terms of both biomass and abundance, i.e. how the stock utilises and occupies various habitats and spatial units within the ecosystem, and (2) growth characterisation, i.e. species-population growth rates. These measures can be combined similar to the approaches of Johnson et al. (1994), Randall and Minns (2000), and Minns et al. (2011), to estimate per-unit-area increases in biomass. Although they may not be useful as absolute measures because they don't account for factors such as mortality, emigration, and fecundity, they can provide relative measures which enable robust comparisons to be made across space and time.

The simple standing stock model requires less data and sampling effort than full productivity estimates. When collected in an organised sampling scheme, standing stock approach can provide a number of key data components required for the simple standing stock productivity model (spatial and growth characterisation of the population). These data components include: (1) reliable replicated data estimating the abundance and biomass per unit area of each species within the system(s) over time (e.g. Robertson and Duke (1990a)); and (2) high resolution size-frequency data for each species representative of the target system(s) over time (e.g. Robertson and Duke (1990b)). The simple standing stock approach also provides additional opportunities. For instance, the potential to provide other measures required for full productivity estimates, for example: length-weight relationships, mortality, recruitment, and emigration rates for key species within the system of interest.

Where previous studies have successfully linked production estimates to relevant spatial units i.e. habitats, the useability of this information is substantially improved. This spatially-linked approach would be particularly valuable if the spatial scales at which productivity estimates are assessed can be tailored to match those of anthropogenic impacts. For example, large scale modifications to watersheds impact entire estuaries (Gibson et al. 2003), while habitat loss and modification occurs within estuaries (Gibson 1994, Jones et al. 1996, Able et al. 1999) – each requires scale-specific information. Measurement of productive capacities and attribution of fisheries value to spatial units also need to match the scales at which management decisions and actions are made (Houde & Rutherford 1993, Rönnbäck 1999, Manson et al. 2005, Meynecke et al. 2006, Dolbeth et al. 2012). However, it is not clear whether the spatial and growth characterisation components of the simple standing stock approach are able to be reliably and accurately linked to these spatial scales.

Incorporating and utilising knowledge of ecological relationships and patterns into productivity measurement requires interpretation of complex ecological gradients and interactions by analysing observational data. Decision-making frameworks such as marine spatial planning and ecosystem-based management have been developed with the specific intent of incorporating both the ecological interpretations and productivity estimates (Douvere 2008, Leslie & Kinzig 2009, Foley et al. 2010).

However, interpretations of data and analyses into ecologically meaningful information without consideration of the potential biases, inaccuracies, and uncertainties can lead to unintended and potentially deleterious outcomes from management actions. For example, the inability of scientists to quantify and recognise the uncertainty inherent in estimates of marine mammal abundance and productivity in North America led to widespread management inaction and subsequent depletion of populations (Taylor et al. 2000). Similarly, the collapse of the northern cod fishery in Canada in the early 90's was not least due to stock-size overestimation caused by the biases inherent in commercial catch per unit effort (CPUE) data when used as an index of abundance (Walters & Maguire 1996, Charles 1998, Rose & Kulka 1999). A number of recent studies have highlighted the importance of both quantifying and communicating various forms of uncertainty in ecology (Elith et al. 2002, Regan et al. 2002, Harwood & Stokes 2003, Regan et al. 2005). However, while it is important to identify and measure these uncertainties, often they are governed by the available data. In data-limited situations what is considered an acceptable level of uncertainty may therefore change. Developing a robust understanding of complex ecosystems like tropical estuaries therefore requires recognition of the uncertainties and limitations to the statistical products and methods with which ecological and biological interpretations are made.

1.1. Objectives

The overall objective of this project is to evaluate the potential for standing stock data to generate simple, practical and reliable measures that can be combined to produce useful productivity estimates. Specifically, the reliability and defensibility of current methods used to investigate spatial and temporal population dynamics, and to produce growth rates of tropical fish and penaeid species, will be examined. A series of components will contribute to the evaluation of the effectiveness and reliability of the methods, these include:

1. Design and implementation of a practicable method for the collection of standing stock data in tropical estuaries which may mitigate the practical and logistical difficulties of the tropical estuarine context. (Chapter 2).
2. Investigations of the use of standing stock data to identify spatial and temporal abundance/residence linkages for estuarine fish and penaeid populations (Chapter 3).
3. Investigations of the reliability and accuracy of methods used to estimate growth rates of fisheries stocks using examples of selected tropical estuarine species in the context of practical data limitations. (Chapter 4).

Chapter 2: Standing stock analysis: producing meaningful estimates in a data-limited context

2.1. Objectives

This chapter explores some of the theoretical issues, practical limitations, current techniques, and methodology for the collection of fish and prawn standing stock data. These methods and associated challenges are discussed specifically in relation to the logistically and practically challenging situation presented by meso-tidal, structurally complex estuaries commonly found in the tropics. I then rationalise a robust method for assessing standing stocks of fish and penaeids in these ecosystems. In this chapter I also discuss some of the challenges to implementing the spatial-characterisation and growth characterisation components of the standing stock approach to productivity measurement. For spatial-characterisation, I explore the use of multivariate ordination techniques to investigate spatial and temporal relationships of standing stocks and estuarine fish and crustacean communities. For growth-characterisation I focus on the use of length-based population-level growth estimation methods.

2.2. Ecological studies of fish communities: understanding complex systems

The persistence of knowledge gaps surrounding the fish and crustacean communities of tropical estuaries is largely due to the practical and logistical difficulties of conducting representative spatially defined sampling. The inherent variability and systemic uncertainties within the multitude of complex estuarine habitats are a considerable barrier to ecological study (Blaber et al. 1989b, Sheaves & Johnston 2010). The environmental dynamics of many estuarine habitats in tropical Australia mean that, periodically, they are either chemically or physically inaccessible to fish and crustaceans (Barletta et al. 2005, Mattone & Sheaves 2017). This necessitates movement of fish and crustaceans between multiple habitats, and even between estuaries (Blaber 2008). Adding to the complexity of providing spatially-explicit measurements, habitat compositions in tropical estuaries change between reaches, often in response to tidal and freshwater influences specific to individual estuaries (Blaber 1980, Barletta et al. 2005, Johnston & Sheaves 2007, Sheaves 2016). Therefore, a detailed understanding of fish movement and residence patterns is needed to ensure that estimates are soundly based. In addition, where measurements of abundance, occurrence and biomass are possible, there remains a challenge of attaining a useful level of accuracy. The often patchy nature of distributions of the species which make up this community can result in significant variation in data, and produce estimates which are indistinguishable across spatial and temporal factors due to the extreme error ranges (Sheaves & Johnston 2010). Despite the challenges, there are significant benefits to be gained from this type of study; measurement of biomass associations within defined habitats, or parts of a system (e.g. an estuary), may provide important information on broader habitat and within-system spatial associations for many high productivity species.

Many of the species that are common in tropical estuaries are basal-prey species, these are small and highly abundant fish and crustaceans (e.g. sardines and anchovies). The basal-prey community is important as a directly harvested resource in many regions (Ruddle 2005, Blaber 2008). It is also probable that a significant proportion of the biomass production and output from tropical estuaries, could be attributed to these species. Basal-prey species can act as conveyors of production to higher level consumers, and play important roles in structuring and stabilising food webs (Menge et al. 2002, Thayer & Sydeman 2007). The convection or transfer of productivity connects primary production (from growth of plants, algae and bacteria) with harvestable biomass both within the ecosystem of origin, and to external ecosystems (Deegan 1993, Able 2005, Jardine et al. 2012). Beyond that, the potential for them to transport biomass production within and between estuarine and other coastal systems is also an unknown. Several studies have documented abundances, seasonal variations, and diversity of the basal-prey species (Jardine et al. 2012). However, few have quantified biomass densities, movements throughout estuarine systems, habitat-biomass associations, or productivity in a meaningful way that is readily transferable to management actions.

2.2.1. *Analyses of spatial and temporal patterns using multivariate techniques*

Much of the knowledge in population ecology published in recent years has been gained through use of multivariate techniques (Field et al. 1982, James & McCulloch 1990, Clarke 1993, McCune et al. 2002, Clarke et al. 2006, Dray et al. 2012). These methods have shifted both our understanding of communities and ecosystems, and the way we approach studies of them. Examples include; multiple regression, generalised linear mixed models, classification and regression trees, analysis of similarity, and ordination techniques e.g. non-metric multidimensional scaling and principal components analysis. These multivariate techniques are advantageous as they combine data from multiple explanatory and response variables into a single analysis (Gauch & Gauch Jr 1982, Austin 2007). They are also advantageous as they are often non-parametric, and robust to many of the assumptions inherent in many traditional parametric tests, e.g. balanced replication, normality, and homogeneity of variance (Gauch & Gauch Jr 1982). Ordination methods have been particularly useful in interpreting patterns of abundance and occurrence of plants and animals as they are observed through space and time (Legendre & Gallagher 2001).

Each of the common multivariate ordination methods (NMDS, PCA) are based on the use of measures of ecological distance or similarity (Williamson 1978, Beals 1984, Clarke 1993, Anderson 2001, Anderson & Walsh 2013, Anderson 2014). In principal, they work by calculating 'ecological distance' by relating replicates, sites, locations, and samples to each other using a selected similarity or distance coefficient. They are often accompanied by tests of significance on distances between data points in the ordination space e.g. ANOSIM and PERMANOVA. Multivariate ordination analyses can utilise many different data types, e.g. continuous environmental data, binary occurrence data, abundance and catch per unit effort, characteristic and descriptive data, and so there is no one-size-fits all approach. Because of this, it is difficult to determine what the limitations are when confronted with ecological data in the multitude of combinations and characteristics often present. Several authors (James & McCulloch 1990, Warton et al. 2012) have cited concerns with the use of these methods in cases of extreme uncertainty e.g. extreme variations in abundance distributions. Warton et al. (2012) found that strong mean-variance relationships can confound location and dispersion effects in ordinations, resulting in misleading interpretations of results. Application of these techniques to standing stock data can produce meaningful information on the spatial and temporal abundance linkages in estuarine ecosystems, but only where the limitations are well understood. It is necessary to understand how the analyses respond to characteristics of data produced using the standing stock method e.g. heterogeneity of variances and zero-inflation which are commonplace in catch data (James & McCulloch 1990, Warton et al. 2012). We must also understand the effects of data treatments, e.g. transformations on our interpretation of ecological information using these methods.

2.3. Practical impediments to collecting standing stock and productivity data in tropical estuaries

There are a number of practical and logistical difficulties of capturing, counting, or otherwise measuring stocks in complex meso-tidal estuaries that must be overcome in order to produce reliable data. Most commonly, biomass density data for fish and penaeids are collected using various forms of nets, traps and angling techniques. Historically, seine nets and beam trawls have been employed as the primary methods for fish and penaeid capture in coastal ecosystems, e.g. Staples and Vance (1986), Robertson and Duke (1987), Robertson and Duke (1990a), Vance and Staples (1992), Sheaves (2006). However, these are often not practical in the small, convoluted, and structurally complex creeks, drains and estuarine channels found throughout many regions, and particularly so in tropical regions. These methods are unable to capture individuals that remain close to complex physical structures such as mangrove edges, steep banks, rocky substrate, or reside within snags (fallen and submerged trees) (Vance & Staples 1992, Rozas & Minello 1997). Practial difficulties are also presented due to the nature of movement of estuarine species, often moving into structurally complex habitats when accessible (Vance & Staples 1992, Vance et al. 2002).

Most conventional capture methods are not feasible in the structurally complex habitats, and many do not provide a spatially defined sample i.e. catch per unit area, making it impossible to assess biomass density and therefore estimate production per unit area (Rozas & Minello 1997). Alternate methods such as Block and Fyke nets are highly effective at capturing both crustaceans and fish species from the small creeks and drains, as well as larger intertidal areas with defined drainage channels (Butcher et al. 2005). However, these methods require a large degree of sampling effort and processing time for the large quantities of fish and crustaceans captured (Butcher et al. 2005, Baker & Minello 2011), and their limitation to particular habitats inhibits the collection of comprehensive data in many situations. The use of traps to capture fish and crustaceans has been quite successful in tropical estuaries (e.g. Sheaves (1992), Rozas and Minello (1997)), but these are also prohibitive of quantification of the area sampled by each replicate. Traps are also subject to the selectivity of bait used to attract individuals into the trap, thus excluding or biasing estimates of many important species. Additionally, visual census techniques such as RUVS, drones, and ROV's have been used but don't provide absolute individual weight and length data. Attaining accurate and defensible estimates of biomass density and other data required to estimate growth, mortality, and productivity rates is clearly a difficult task. There are several key requirements that should be first considered when designing the sampling scheme used for collection of standing stock data:

1. Data must be spatially replicated at relevant spatial and temporal scales.
2. Sampling gear needs to effectively sample major habitats within the system utilised by the target species/community.
3. The capture method should be standardised and consistent in capture efficiency across species and habitats as much as possible.
4. The capture method must be spatially explicit, i.e. animals are captured within a defined, known and consistent area.
5. The capture method should allow sufficient replication within the study area to represent spatial and temporal variability of the standing stock.

2.4. Proposed method for collecting standing stock data

An alternative method that is both spatially explicit in its application and requires relatively little effort is the use of cast nets. This method overcomes many of the practical difficulties related to the use of more traditional techniques in tropical estuaries. In particular, it is less taxonomically selective, provides measurements within a defined and consistent area, and is logistically simpler, allowing for a greater number of replicates per unit time (Sheaves et al. 2006, Sheaves et al. 2007, Johnston & Sheaves 2008). The cast net method is also useable across many of the habitats encountered in tropical macro-tidal estuaries, although effective deployment is limited to areas where water depth does not exceed the drop of the net used (Sheaves et al. 2006, Sheaves et al. 2007, Johnston & Sheaves 2008). Though this gear is not free from disadvantages, and it is important to identify these; larger highly mobile species such as large *Mugillidae,* and small benthic nekton, are likely to be underrepresented as they are able to avoid capture (Blaber et al. 1989a, Ley 2005, Sheaves & Johnston 2009, Baker & Minello 2011). Cast nets are also unsuitable for deployment within the complex network of roots in mangrove forests and are not able to be deployed directly onto snags without damage of the net and escape of fish. Catchability is likely to be inversely linked to structural complexity for all capture methods, and therefore results in a source of non-random variation and potential bias. This bias should be considered carefully in analysis of data produced by all methods.

One of the greatest advantages of cast nets is the ease of use and ability to produce a large number of replicate samples per unit time; a typical replicate including deployment, retrieval and sorting of captured animals takes between 3-10 minutes, depending on numbers and type of animals captured. This means that as many as 100 replicates can be executed in a single tidal phase (<6 hrs), effectively allowing the entirety of a small (<20km length) meso-tidal estuary system to be adequately sampled by a single operator during a single tidal phase. Although this is a clear logistical advantage, Rozas and Minello (1997) note that gear selection not be based foremost on ease of use, rather that stability in catch efficiency across habitats and various physical conditions be the primary concern. In this respect, the cast net method provides a compromise between consistency of catch efficiency and ease/efficiency of replication. Baker and Minello (2011) discussed the importance of this trade-off, concluding that the advantage provided to statistical comparisons by increasing replication may outweigh the loss of accuracy in fish/crustacean density estimates when using the cast net method. This trade-off has been described as the ‘many-but-small’ approach by McCune and Lesica (1992) and is well suited to systems where occurrence patterns are highly variable. Rozas and Minello (1997) highlight that provided there is a suitable degree of consistency of capture efficiency across space and time, the increase in samples taken could increase the precision of the data (Moseley & Copeland 1969, Kjelson et al. 1975).

2.5. Growth estimation methods

Growth rates of species and populations are a key parameter required for estimating fisheries productivity as they quantify the foundational mechanism by which biomass is sequestered within a population or ecosystem (Chapman 1978, Downing & Rigler 1984). However, despite the need for growth estimates (Hamilton & Gehrke 2005, Barbier et al. 2011), measurement of tropical estuarine fish species has historically been restricted to a few species of high commercial interest. In tropical Australia these include just a few species, such as *Lates calcarifer*, *Polydactylus macrochir, Lutjanus johnii,* and *Lutjanus argentimaculatus*, and commercially important penaeids such as *Fenneropenaeus merguiensis* (Blaber 2008). Growth rates of many other commercially and recreationally targeted species such as *Acanthopagrus pacificus*, *Pomadasys* spp., *Mugil cephalus*, *Epinephelus coioides, Megalops cyprinoides* and *Hemirhamphus* spp. have not been estimated. This prevents productivity modelling of multi-species fisheries and restricts the breadth of information on which informed management decisions can be made. Moreover, much of the smaller basal-prey species e.g. *Thryssa* spp., *Herklotsichthys* spp. *Leiognathus* spp., *Stolephorus* spp., which form the bulk of fish biomass in tropical estuaries and coastal ecosystems, have not been studied in any substantive way (Blaber 2008).

Growth rates are most commonly measured using length-based age-based, and mark/recapture methods (Brothers 1979, Sparre & Venema 1998). Age-based methods involve the collection of calcified structures (usually otoliths), or other hard structures (e.g. scales and dorsal spines) from intact specimens where the length of the individual is correlated with the number or distance of growth increments (annuli) observed in the structure (Regier 1962, McFarlane et al. 1987, Hill et al. 1989, Casselman 1990, Campana 1992, Morales-Nin 1992, Maceina & Sammons 2006). The use of tagging and recapture requires applying a physical (or sometimes chemical) form of identification to live individuals, releasing them, and recapturing as many as possible to determine the rate of increase in body size (length increase/time between release and recapture) (Francis 1988b, a, Baker et al. 1991, Hamel et al. 2014). Each of these methods are particularly successful in their application and are often used in conjunction where possible (Francis 1988a, Hamel et al. 2014). However, both are often prohibitively labour and resource intensive. Age-based methods require substantial processing of individual otoliths, and multiple readers must be used to reduce biased estimates (Casselman 1990, Campana 1992, Morales-Nin 1992). For mark-recapture methods to be reliable, a sufficient number of individuals must be re-captured (Pine et al. 2003). Re-capture rates are dependent on both the number of individuals initially tagged, and other factors such as mortality, and movement patterns. Therefore, larger numbers of individuals will need to be tagged, and/or re-capture effort will need to be increased where mortality is high, and movements are frequent. For example, Chapman and Kramer (2000) achieved re-capture rates of between 0–100% for 35 species of reef fish, with 28 species recaptured at least once. Only 13 of the investigated species were re-captured with enough frequency to permit statistical analysis (Chapman & Kramer 2000).

In the context of tropical estuaries, a number of studies and programs have been successful in targeting key commercial and recreational species, e.g. *Lates calcarifer,* using age-based and mark-recapture methods (Reynolds & Moore 1982, Davis & Kirkwood 1984, Robins et al. 2006). Further examples of use of these methods on estuarine species include Knudsen et al. (1996), Webb and Kneib (2004), Braccini et al. (2013), though species for which the methods have been successfully applied to likely represent only a small proportion of the productive capacity of these ecosystems. Basal-prey species have seldom been the focus of growth studies, particularly in tropical estuaries. This is probably due to the relatively small and fragile nature of individuals, which have extremely high mortality rates (Whitehead et al. 1988, Robertson & Duke 1990a), thus making it difficult to implement physical marking methods. Additionally, many of these fast growing species complete their lifecycles within a number of months, rather than years (Longhurst 1971, Ingles & Pauly 1984, Whitehead et al. 1988, Milton et al. 1991, 1993), making it difficult (although not impossible) to reliably measure growth increments at the resolution required to characterise growth patterns (Brothers 1979). Caging experiments have proven particularly successful for less mobile species such as decapods (Shervette & Gelwick 2008, Baker & Minello 2010). Although these are particularly labour intensive and are potentially biased due to the restriction of natural feeding patterns and movements.

Length-based methods use length-frequency data to ‘track’ the modal length of cohort of individuals over time. These ‘length-based’ methods (Pauly & David 1980, Kirkwood 1983, Pauly & Morgan 1987), are well established and provide another way of obtaining growth estimates without requiring the massive labour demands of mark/recapture methods (Staples 1980, Haywood & Staples 1993, Watson et al. 1993). Analysis of length-frequency data to characterise growth requires a population to be sampled relatively consistently over time to produce a time-series of length frequency distributions of the population. Identification of individual cohorts within the population is then conducted and used to track the increase in modal length of each cohort through time. Additionally, other important population parameters such as mortality, can be estimated using the abundance/frequency distributions of each cohort (Jones 1981, Pauly & Morgan 1987, García & Duarte 2006). This method has a relatively small data requirement and does not require information on age structure of the population. Subsequent addition of length-at-age data can later be used to define mortality relative to the age of individuals (Baker & Minello 2010).

Length-based methods have been suggested to be well-suited to tropical species, as they are typically short-lived and fast growing and so are less susceptible to the effects of size or age-dependent mortality (Gayanilo et al. 2005). However, given much of these species are present in data-limited fisheries, it is difficult to gauge the accuracy and reliability of the method. It is important that the use of these techniques is validated in each instance, to avoid the proliferation of unreliable and potentially inaccurate basic information from which stocks are managed. Use of length-based methods requires further validation in the data-limited context common to tropical estuaries. The statistical and biological assumptions underlying application of length-based methods, particularly for the community of basal-prey species have scarcely been tested. More broadly these include whether growth characterisation functions are biologically accurate, and whether mortality and movements are size dependent. There are also a number of specific assumptions related to the analysis methods, including normality of length-frequency distributions, characteristics of recruitment and identification of cohorts and a number of others (Isaac 1990). Given the importance of this group as both a major component of standing stock biomass (Morton 1990, Robertson & Duke 1990a), and an important conveyor of productivity within estuarine ecosystems (Jardine et al. 2012), testing of both the suitability of biological and statistical assumptions of length-based methods is required.

2.6. Scales of measurement and interpretation

In addition to understanding the analytical processes of data treatment, the translation of data from the scale of observation to the scale at which ecological patterns are sought to be interpreted requires validation. The spatially-linked approach requires measurement of ecological and biological patterns and processes at scales which are practical for sampling and observation. However, these are often quite different to the scales at which both analyses and interpretations are intended to be made. For example, to understand the differences in biomass density between two estuaries, a series of replicate observations (biomass measurements) are made at small scales, i.e. the area of a net throw. The observational measurements are then combined in a representative way e.g. averaging across habitats to provide a characterisation of biomass density at the larger (estuary) scale. This process requires calculation of the central tendency (i.e. means, medians, or modes) of replicates which are likely to vary substantially through time and space. In this process of translation from one scale to another, information may be lost if individual observations are far from calculated measures of central tendency (Abrantes et al. 2019).

In the case of the standing stock approach, there is a requirement for information to be translated from observational scales, to scales of interpretation which are relevant to management actions and jurisdictions. This is required for both spatial-characterisation and growth-characterisation components of the standing stock simple productivity model. For spatial characterisation, this requires some investigation of the use of measures of central tendency in multivariate ordinations. Specifically, we must understand how patterns of abundance and occurrence are interpreted when data is translated across scales. For growth characterisation there is a need to investigate validity and appropriateness of underlying assumptions of length-based methods at various scales. This means that statistical and theoretical assumptions of common methods should be tested for standing stock data when used at relevant scales.

2.7. Key knowledge gaps

The knowledge gaps identified in this review are summarised in Table 2. 1, gaps listed here have been used to direct the research in chapters 3 and 4. Each of these is further explained and background information provided in-depth in the relevant chapters. While some of the broader knowledge gaps (1-3) are not directly investigated in chapters 3 and 4, they are discussed considering the findings from these chapters later in this thesis.

Table 2. 1: Identified knowledge gaps

1	Are productivity metrics produced using standing stock data useful and accurate, and reliable?
2	Are traditional stock metrics e.g. CPUE, biomass density, presence/absence, biologically and ecologically meaningful?
3	Can we use the standing stock method to overcome practical issues of measuring small-bodied basal-prey species?
4	How does the scale at which data are analysed using multivariate ordinations effect the interpretation of spatial and temporal abundance and occurrence patterns?
5	How do multivariate ordination techniques, and standard data treatments respond to extreme data characteristics?
6	Are the assumptions of length-based growth estimation methods biologically reasonable for the basal-prey community in tropical estuaries?
7	Can growth of basal-prey species be reliably characterised using length-based methods and standing stock data?

Chapter 3: Practical limitations of spatio-temporal standing stock studies using multivariate ordinations

3.1. Introduction

Tropical estuarine ecosystems harbour numerous exploited fish and crustacean species, and provide abundant food sources for commercially and recreationally important pelagic and reef fish species (Deegan 1993, Sheaves 2009, Sheaves et al. 2015). In many cases, activities such as commercial and recreational fishing depend on the productive capacity of estuaries, the habitats within them, and other ecosystems and habitats with which they are connected (Able 2005, Cowen et al. 2007, Meynecke et al. 2008b, Almany et al. 2009, Sheaves 2009, Jardine et al. 2012). Despite this, the contribution from tropical estuaries to other coastal and offshore fish populations has yet to be reliably measured (Nagelkerken 2009). Information required to underpin these estimates includes how the species and communities use estuarine systems, and the spatial and temporal dynamics of species' abundance and biomass. For both 'best-practice' and simple standing stock productivity models it is necessary to understand how the community of species is distributed among various habitats, reaches and other spatial units within the ecosystem of study. This understanding of spatio-temporal distributions of the community is referred to here as 'spatial-characterisation'.

Key to developing our understanding of spatial characterisation is, the use of analytical methods to distil meaningful information from community data in a way that is both practical and informative. Often, limitations of data restrict the use of well-established parametric methods (*i.e.* ANOVA), and relationships are usually non-linear and complex (Harris & Heathwaite 2012). Multivariate distance-based techniques have been favoured due to their holistic approach which matches the multivariate nature of both the ecosystems and the data (Clarke 1993). Of the many multivariate techniques, distance-based multivariate ordination techniques use measures of ecological distance or similarity to relate or distinguish samples across space and time to or from each other (Williamson 1978, Beals 1984, Clarke 1993, Anderson 2001, Anderson & Walsh 2013, Anderson 2014). Multivariate ordination methods, such as non-metric multidimensional scaling (nMDS), are non-parametric and are used precisely because they are robust to many of the traditional assumptions made by parametric analysis. The use of this type of distance-based multivariate ordination has become particularly prolific in spatial ecological applications (James & McCulloch 1990) and is the focus of this study because of this.

Despite the successes of methods such as non-Metric Multidimensional Scaling (nMDS), the application of this method in cases of extreme data variability warrant thorough assessment of the practical limitations. Use of non-parametric multivariate techniques, in-particular nMDS, relies upon generally non-specific and biologically reasonable assumptions (Faith et al. 1987, Oksanen et al. 2017), i.e. nMDS assumes only a monotonic relationship between similarities and ordination distances. However, studies such as Warton et al. (2012), Warton and Hui (2017), and McArdle and Anderson (2004) have highlighted the potential for data characteristics such as the mean-variance relationship of abundance data to confound analysis results. The standing stock approach requires the use of abundance, biomass and occurrence data to understand the spatial-characterisation of the basal-prey community. Therefore reliability and practical limitations of methods such as nMDS in this context is an important point to consider because standing stock data collected in estuaries are particularly subject to the highly variable nature of fish schooling/aggregation and distribution of these schools throughout an estuarine ecosystem (Sheaves 2006, Sheaves & Johnston 2010, Sheaves 2016).

In addition, and related to the effects of data characteristics on multivariate ordinations, the effect of scale i.e. reach vs estuary scales, on the treatment and analysis of data requires some further investigation. In chapter 2, the theoretical challenges posed by translation of data from the scale of observation to the scales of interpretation were discussed. The need to understand complex systems at scales relevant to management actions and anthropogenic impacts requires observational data, which is often collected on scales of metres, to be translated to data which represents patterns on hundreds of metres and kilometres. In the case of nMDS this is often achieved by use of measures of central tendency, where data from multiple observations across time and space are combined by way of means of abundance, biomass density and occurrence rates e.g. Sheaves et al. (2007). However, studies such as Abrantes et al. (2019), McArdle and Anderson (2004), and Warton et al. (2012) have demonstrated that characterising abundance-based data using measures of central tendency is fraught with problems. In-particular where variance is extreme, means do not represent a realistic characterisation of abundance on scales of interpretation. Because the standing stock productivity model requires a spatially-linked approach, we need to thoroughly understand the risks and consequences of use of central tendency to translate data to various scales of interpretation.

In addition to the use of central tendency and translations of scale, the standing stock measures used i.e. abundance, biomass, and occurrence, and the treatment of data can provide different information with which ecological gradients can be investigated. Data, such as catch and effort (CPUE), biomass density, and occurrence (presence/absence), provide the foundations of stock assessments and ecological studies (Costanza et al. 1997, Hamilton & Gehrke 2005, Hoggarth 2006, Barbier et al. 2011). CPUE provides a standardised measure of relative abundance (assuming equal efficiency of the gear type across space and time); biomass density is used to relate stock size between species and account for growth of individuals over time, and occurrence is used to investigate species' residence/distribution through calculation of probability of encounter (POE). Because of the issues of patchiness and extreme variability in both of these metrics in the estuarine context, data treatments and derivative metrics such as POE have been employed to distinguish meaningful patterns from natural variations (stochasticity) e.g. Rudstam et al. (1984), Bayley and Peterson (2001), Johnston and Sheaves (2007), Sheaves et al. (2010), Sheaves et al. (2012). Transformations such as square-root, logarithmic, and binary (i.e. presence/absence) are commonplace, but have been shown to be insufficient at treating the effects of heterogeneity of variances, and extreme mean-variance relationships (Legendre & Gallagher 2001, McArdle & Anderson 2004, Warton et al. 2012, Warton & Hui 2017). Because abundance information (i.e. CPUE) is difficult to treat using standard transformations, and derivative metrics such as POE use measures of central tendency, it is not clear how these approaches compare in terms of meaningfully and reliably characterising the spatial and temporal patterns of standing stocks. Nor is it clear how the numerous approaches to data treatment will affect the ecological interpretations supported by multivariate ordination analyses.

In this chapter I conduct a study of spatial and temporal trends in the standing stocks of basal-prey fish and penaeid species in a tropical estuary. I investigate the limitations of using standing stock data to discern spatial and temporal patterns of variation in fish and penaeid populations using examples of multivariate ordination techniques. I examine the effectiveness of data transformation, similarity indices, and three standing stock metrics in a common multivariate ordination analysis – non-metric multidimensional scaling. I also assess the limitations of applying the nMDS method to highly replicated standing stock data by testing the effects of measures of central tendency, and translation of data across scales of observation and interpretation. Further, I use the results of this study to discuss the importance of extreme data characteristics, and the limitations to ecological interpretation presented by them.

3.2. Methods

3.2.1. *Study site*

This study was conducted at Alligator Creek, a relatively short and narrow tidally-influenced system that drains into a dry tropics catchment. The creek has a catchment area of ~133 km^2 which includes a combination of low elevation (~1100 m) mountains at the top of the catchment, and extensive floodplains in the lower catchment area. Land use within the catchment is comprised primarily of natural vegetation grazing and nature conservation, with some small areas of residential housing and horticulture. The creek is tidally influenced for approximately 14.3 km from the mouth, with tidal influence extending to a small weir and fishway that divides the freshwater and estuarine sections of the creek for most of the year. At its widest, Alligator Creek is ~150 m, and ~6 m is its greatest depth. However, the majority of the creek is composed of relatively shallow <2 m soft sediment (mud and sand) bottom channel often with tidally exposed soft substrate banks. Vegetation is primarily mangrove forest and saltmarsh banks, with some patches of seagrass at the mouth of the estuary. Tidal regimes are meso-tidal semi-diurnal with a maximum range of ~4 m, with large areas of salt pans and saltmarsh habitat inundated on the highest tides (~>3 m).

Freshwater flows in the Alligator Creek system are regulated by the upstream weir and fishway (located above the extent of the waterway depicted in Figure 3. 1), with flows generally occurring from December to April, during the wet season. Although flow from the upstream area is regulated by the weir, a large proportion of the catchment area drains directly into the upstream estuarine reaches of Alligator Creek without any constructed impediments. A small upstream tributary, White's Creek, also drains an area of the catchment directly into Alligator Creek without regulation. White's Creek was not sampled in this study due to its inaccessibility.

Sampling was conducted within three defined reaches (Downstream, Mid-estuary, and Upstream; Figure 3.1) in the tidally influenced part of the Alligator Creek system, which extended from the estuary mouth to a weir upstream. Each reach was approximately 1.5 km in length and included all inundated areas within the main channel, small side creeks and tributaries (where accessible). The downstream reach extended from the estuary mouth to ~1.5 km upstream and included two small side-creeks that were sampled when accessible. The midstream reach was located approximately halfway between the downstream and upstream reaches and included four side-creeks. The upstream reach extended from the upper limit of boat navigation on mean low tide (~1 m), downstream towards the estuary mouth for ~1.5 km and included several small side-creeks which were not accessible by boat.

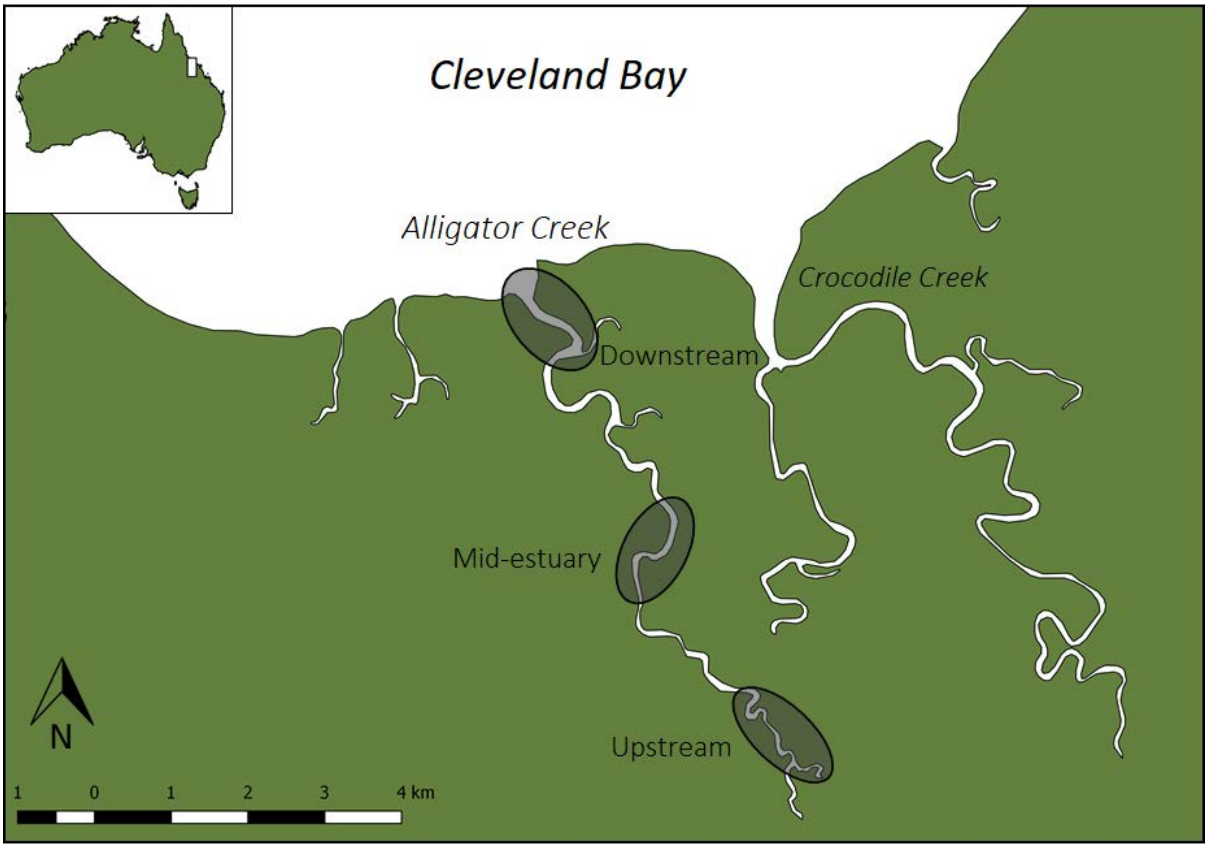

Figure 3. 1: Alligator Creek estuary, Cleveland Bay Queensland, Australia. Reaches are defined by shaded ellipses, approximating the extent of the sampling areas.

3.2.2. Biomass-abundance sampling

Fish and penaeid prawns were captured using 4.8m diameter 5mm mesh monofilament draw-string cast nets, as cast netting allows access to a broad range of relevant habitats and increased replication (Sheaves et al. 2007, Johnston & Sheaves 2008, Sheaves & Johnston 2009). Sampling was conducted approximately fortnightly, depending on tidal and weather conditions, with a total of 11 trips conducted throughout the 2015-16 wet season (Dec–April) and 7 trips conducted during the 2016 dry season (Aug–Nov). Sampling was conducted using a 4.3 m flat bottom boat with a small outboard motor. Cast nets were deployed by a skilled operator in a haphazard manner within ~5 m from banks following suggestions of Johnston and Sheaves (2007), with consecutive replicate casts deployed while moving downstream throughout each reach. Nets were deployed on both sides of the estuary to encompass as much variation in physical and biological factors which are known to be linked to variations in fish abundance (Sheaves 1992, 1996). Each replicate deployment was separated by at least 10 m along the same bank to reduce disturbance effects as described by Guillard et al. (2010) and Jacobsen et al. (2014). Although there is little information from which to determine exactly what distancing would eliminate this potential effect (Whitfield & Becker 2014), Draštík and Kubečka (2005) suggested that distances greater than 10m likely negate any effects on small-bodied fish. In the upstream reach, where navigation was difficult and creek widths were mostly less than 10 m, replicates were occasionally located on opposite banks less than 10 m apart. In the mid-estuary and downstream reaches, replicates were frequently more than 20 m apart.

Sampling was conducted when tidal levels were >1.5 m, with each replicate and reach sampled on the same tide (less than six hours duration per trip). The lower part of the tide was used as during this time animals are forced out of high intertidal habitats (e.g. mangroves and shallow saltpans) that could not otherwise be sampled effectively and into the main channel where they concentrate along banks (Krumme 2004, Johnston & Sheaves 2007, Meynecke et al. 2008a). During each trip, 15, 20, or 30 replicate nets were deployed within each reach, with the number of nets depending on low tide duration and adjusted to ensure that all reaches could be adequately sampled within the same low tide period. Where nets became entangled or caught on submerged objects, or the net was deployed with an unsatisfactory spread i.e. the spread was less than 80% (estimated by eye) of the operators maximum potential spread, or the site was unduly disturbed by boat positioning e.g. from propeller wash, the replicate was abandoned. When replicates were abandoned any animals collected were returned to the water, and the replicate was repeated in a different location.

All animals collected were immediately placed in sealed bags and submerged in an ice slurry. Collection of animals was in accordance with animal ethics permit A2184, approved by the James Cook University Animal Ethics Committee. In the laboratory, individuals were identified to species where possible and counted, measured (total length), and weighed. Some species could not be separated taxonomically due to a loss of identifying characteristics after freezing and handling. Because of difficulty in distinguishing them at all sizes, two *Sardinella* species, *Sardinella albella* and *Sardinella brachysoma,* are pooled here as *Sardinella* spp., and the two Gerres species, *Gerres filamentosus* and *Gerres subfasciatus,* are presented as *Gerres* spp.

3.2.3. Characterisation metrics

Data used should be relevant and broadly applicable to the industry-research context, i.e. applicable across areas where existing data and prior knowledge is limited. These cases provide a relevant and useful test of practical limitations, and where biological interpretations rely on robust analyses the most. Therefore, the metrics used in this study include catch per unit effort (CPUE), biomass density, and occurrence. These metrics were selected because they are commonly used in productivity, stock assessment, and habitat valuation studies (Hoggarth 2006). CPUE is defined here as the number of individuals per unit area i.e. per net or per m^2 (n/m^2) and biomass densities are similarly defined as grams per net or grams per m^2 (g/m^2), this provides a standardised index of abundance. Because capture efficiency is unknown, measures of density are treated here as relative rather than absolute. Areal calculations were based on the coverage area of the cast nets (8.5 m ±0.18), based on measurements taken from 30 successive net throws on land. Replicate throws were measured across the widest and shortest diameters to provide a mean diameter for each throw from which area was calculated. Thus, CPUE was calculated as: $\mathrm{CPUE} = n_i/8.5$ where n_i is the number of fish captured in the i^{th} net, and biomass density as: $\mathbf{biomass\ density} = w_i/8.5$ where w_i is the weight of fish captured in the i^{th} net. Occurrence was presented as Probability of Encounter (POE) calculated as: n_g/g where n_g is the number of fish captured in a defined group of nets (e.g. all Upstream nets, or Upstream nets in Trip 2), and g is the number of nets in that group (Sheaves et al. 2012).

3.2.4. Species selection

To conduct my investigations, I have selected species that form the most ubiquitous basal-prey in terms of their abundance, occurrence and biomass within the Alligator Creek estuary. The subset of species that ranked within the 90th percentile of total biomass density was further ranked by CPUE, with species contributing cumulatively to >90 % of total CPUE included for further analyses. Species that were present in <50 % of trip-reach combinations were excluded from the subset; this resulted in 24 species retained for further analyses (Table A3. 1). Multi-species ordinations can be confounded by large numbers of species vectors. To test whether there was an effect of reducing the number of species in the analyses, repeat analyses were conducted with only the ten most common species retained.

3.2.5. Data characteristics

Data collected from Alligator Creek were assessed for dispersion, error structure, mean-variance relationships, zero-inflation, and homogeneity of variance. Additionally, the schooling/aggregation patterns of species was investigated by examining relationships between CPUE and POE. These characteristics were assessed using simple exploratory graphical techniques listed in Table 3. 1. The mean variance relationship was assessed using methods described in Warton et al. (2012) using the 'mvabund' package for R (Wang et al. 2012).

Table 3. 1: Data characteristics examined in catch data from the Alligator Creek estuary.

Characteristic	Method
Error structure	Standard error of means
Mean-variance relationship	Mean-variance scatterplots
Zero-inflation	Histograms of abundance per replicate
overdispersion/heteroscedacity	Boxplots of abundance per replicate
Aggregation/schooling	Scatterplots of CPUE x POE

3.2.6. Multivariate analyses and data treatment

Analyses were conducted using non-metric multidimensional scaling (nMDS) to identify trends in the standing stock between reaches, seasons and dates, and determine whether there are clear differences in abundance, biomass density and occurrence between reaches and seasons. Input data were the arithmetic means of (replicate samples within each reach/trip) CPUE, biomass density and POE. Means calculated for each reach in each trip were used to reduce the complexity of data included in the analyses, using individual replicates led to ordinations that were difficult to interpret because of the large number of points displayed. To test the effect of averaging data, raw CPUE and biomass data from individual trips were analysed. POE data are already mean based (providing a probability value for each trip-reach combination), and so were not further averaged. To conduct the analyses the following procedure was used:

1. Data-sets for each metric were created using untransformed and transformed CPUE, biomass density and POE data. Square-root and natural logarithm transformations were used to reduce the impact of outliers (Legendre & Legendre 1998). Data-sets were also created using standardised (species-species) and unstandardised data. Species-species standardisation was selected to standardise abundances across common and rare species. Standardisation was applied to all transformation/data combinations excluding POE as values are already standardised as percentages
2. A distance matrix was created using the data-sets, with Bray-Curtis and Sorensen coefficients. The Bray-Curtis coefficient (Bray & Curtis 1957) was selected and applied to all data combinations, as it provides a relatively good representation of ecological distance, combining both diversity (number of species in common) and abundances (difference in abundance of each species) between cases (Gauch Jr 1973, Beals 1984, Clarke et al. 2006). The Sorensen coefficient (originally described by Czekanowski (1913)) was applied only to binary transformed data (presence-absence) and reduces the assumptions inherent in abundance-based metrics by removing the assumption of joint-zero similarity i.e. where sites both have no species

present they are assumed to be similar because of this shared characteristic (Magurran 2013). Binary transformations were not applied to POE data as this metric is derived from binary data.

3. A total of 35 combinations were tested, resulting in 36 unique ordinations Table 3. 2.

Table 3. 2: Factors and data treatments included in ordination tests

Metric	Transformation	Standardisation	Coefficient	Number of species
CPUE	Raw	None	Bray	24
BD	Square root	Species-species	Sorensen	10
POE	Log			
	Binary			

4. Non-metric multidimensional scaling was applied to dissimilarity matrices, with random starts and 500 iterations to reduce the likelihood of convergence at local minima (rather than the desired global minima).
5. Bi-plots of each nMDS ordination were produced and grouping factors of ‘Season’ and ‘Reach’, and species vectors were applied.
6. Model fit was assessed using ‘stress’, as described by Kruskal (1964), for each ordination. Stress represents the sum of difference between calculated dissimilarities and ordinated distances. Stress of 0 represents absolute monotonicity of the relationship between dissimilarities and distances, and stress of 1 represents no monotonicity of the relationship. Since nMDS assumes monotonicity of this relationship, the further from 0, the more likely the ordination is unreliable. Stress values of less than 0.2 were considered acceptable.
7. Shepard plots were also used to assess the preservation of dissimilarities in the final ordination of reduced dimensions.
8. The process was then repeated with the reduced species data-sets.
9. Ordinations were considered successful if stress values were less than 0.2, there was an absence of ‘stepping’ (Williamson 1978, Minchin 1987) in Shepard plots, and the resulting ordination was free from distortions and artifacts (Williamson 1978, Minchin 1987, Podani & Miklós 2002).

Following the above process, successful ordinations were fitted with centroid ellipses of group factors using 95 % confidence intervals, to compare separation and dissimilarity of CPUE and biomass density by reach and season groupings. Additionally, permutation tests (e.g. PERMANOVA) which are often performed on similarity distances calculated by nMDS ordinations are subject to the same assumptions used to produce the ordinations. They assume that that the distance scaling analyses have been performed in a reliable manner using methodology appropriate to the data conditions, i.e. appropriate choice of dissimilarity coefficients, data treatments, transformations, and ordination stress is of an acceptable level. A permutational multivariate analysis of variance (PERMANOVA) was applied to determine how significance of differences of observed group centroids were affected by the ordination process. Additionally, to test whether the PERMANOVA was affected by homogeneity of multivariate dispersions, a permutational analysis of multivariate dispersions was used. For both tests, goodness of fit was measured by sum of squares, significance was indicated by the pseudo F-ratio, 999 permutations were used for the analyses (Hollander et al. 1999, Anderson 2001). Analyses were conducted in R (v 3.5.1, R Core Team 2018) using the “Vegan”, “Ecodist”, “MASS”, and “ggplot2” packages for R Studio (Venables & Ripley 2002, Goslee & Urban 2007, Wickham 2009, Oksanen et al. 2017).

3.3. Results

3.3.1. Species composition and catch in Alligator Creek

In practical terms, the cast net standing stock method provided a workable solution to the logistical problems encountered in tropical estuaries. However, logistical difficulties with linking spatial components to abundance (CPUE) and biomass data meant that habitat specific metrics were not attainable in this study. Throughout the study, 16,490 individual fish and penaeids were identified weighed and measured. A small number of individuals that were damaged, preventing either identification or correct measurement, were discarded prior to recording. A total of 72 species within 56 genera were recorded during the study (Table A3. 1). During the wet season, 64 species were recorded, and 48 during the dry season, with the average number of species recorded per trip being 30 for the wet season and 22 for the dry season. Total number of species collected was greatest for the downstream reach, followed by mid-estuary and upstream reaches, each having 53, 44, and 36 species, respectively. Species captured ranged from pelagic species, such as *Scomberomorus commerson* (narrow-barred Spanish mackerel), surface resident species, such as half-beaks/garfish (e.g. *Zenarchopterus buffonis*) and archer fish (e.g. *Toxotes chatareus*), as well as benthic fish, such as Flathead (e.g. *Platycephalus fuscus*), whiting (e.g. *Sillago sihama*), flounder (*Pseudorhombus* spp.), and benthic crustaceans, including the highly abundant banana prawns (*Fenneropenaeus merguiensis*).

Over the duration of the study, Perciformes were the most numerous order and also accounted for the greatest proportion of biomass density measured within the Alligator Creek system. Combined, Perciformes, Clupeiformes and Decapoda accounted for ~80 % of the total measured biomass density and ~96 % of the total number of animals captured. The tropical Herring, *Herklotsichthys castelnaui,* exhibited the highest average biomass density of all species, and was followed by *Toxotes chatareus*, and *Fenneropenaeus merguiensis*. Approximately 90 % of the total biomass density sampled was attributed to 24 species. The most numerous species was *Fenneropenaeus merguiensis*, the commercially and recreationally important banana prawn, this species made up ~22 % of the total CPUE (n/m²) of all species collected. Biomass density and abundance were generally higher in the downstream reach, and lowest in the upstream reach, both metrics followed similar trends throughout the study (Figure 3. 2, Figure 3. 3). Although due to the extreme variance between replicates, there was a large degree of error surrounding means of both CPUE and biomass density. Square root transformations were applied here to reduce the effects of variance. Generally dry season samples were less variable between trips and replicates compared to the wet season. Error surrounding means was lower in the dry season and error was heterogeneous across both trips and reaches (Figure 3. 2, Figure 3. 3).

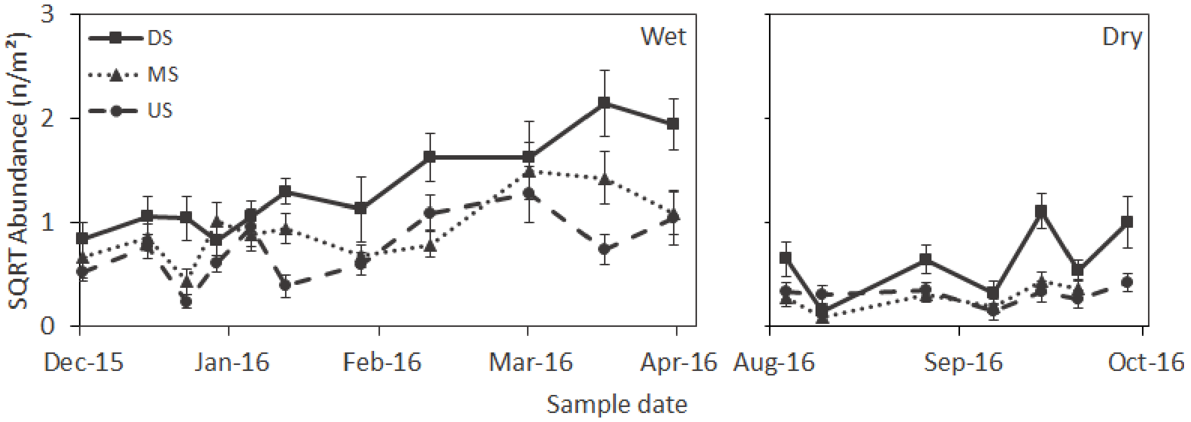

Figure 3. 2: Mean CPUE of pooled catch (all species) across reaches from wet season and dry season sampling trips in the Alligator Creek estuary (Nov-2015 to Sep-2016). Data square root transformed, error bars denote 1 standard error.

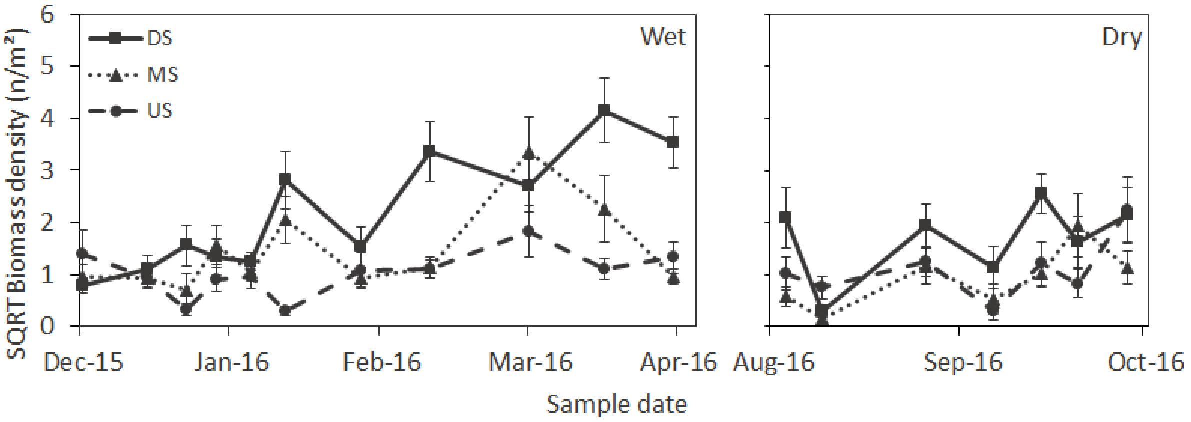

Figure 3. 3: Mean biomass density of pooled catch (all species) across reaches from wet season and dry season sampling trips in the Alligator Creek estuary (Nov-2015 to Sep-2016). Data square root transformed, error bars denote 1 standard error.

3.3.2. *Data characteristics*

Both CPUE and biomass density data were zero-inflated and over-dispersed, i.e. high frequency of replicates with zero catch and a high degree of variation between replicates. Approximately 60 % of species had a POE of < 0.01 (i.e. present in less than 1 % of nets), and ~86 % of species had a POE of < 0.05. The most frequently encountered species was *Leiognathus equulus* occurring in 36 % of nets throughout the study. Standard error of mean CPUE frequently extended to zero, indicating that the distribution of CPUE data was highly skewed. Even when the error range was not inclusive of zero, in some instances error constituted up to 97 % of mean CPUE at the reach scale. The highly skewed distribution of CPUE data was present in all trips and all reaches throughout the study (Figure 3. 4).

At the species level, zero-inflation was also pervasive, Figure 3. 5 provides an example of the distribution of CPUE values recorded between reaches and trips for one of the more common species in the estuary, *Fenneropenaeus merguiensis*. Overdispersion was also considerable at this level, differences in CPUE between reaches for many species were indistinguishable for the most part. Both data characteristics (overdispersion and zero-inflation) were particularly prevalent where schooling species were present. The overdispersion and zero-inflation characteristics are demonstrated for example in trip 9, where CPUE ranged between 0 and 185 n/net (mean 26.6 n/net) for *F. merguiensis* in the downstream reach, and similarly between 0 and 297 n/net for *H. castelnaui*. However, due to the rarity of replicates that contained any fish, calculation of arithmetic means to characterise CPUE in these instances results in extreme error ranges (1SE = ~47 % of mean CPUE). In addition to the extreme error ranges observed, there was an apparent mean-variance relationship for CPUE and biomass density data. Error ranges typically increased as mean values increased (Figure 3. 2, Figure 3. 3). This apparent mean-variance relationship was confirmed using the mean-variance plots (Figure 3. 6).

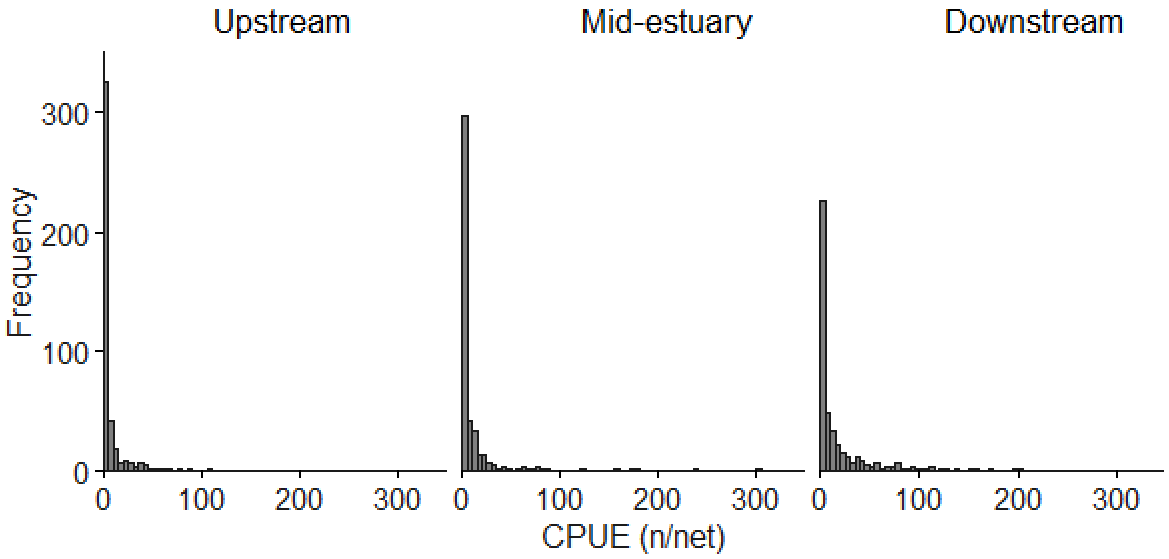

Figure 3. 4: Distribution of CPUE (all species) for replicate nets (n = 1305) from all trips conducted in three reaches of the Alligator Creek estuary between Nov-2015 to Sep-2016. CPUE bin size = 5 n/net.

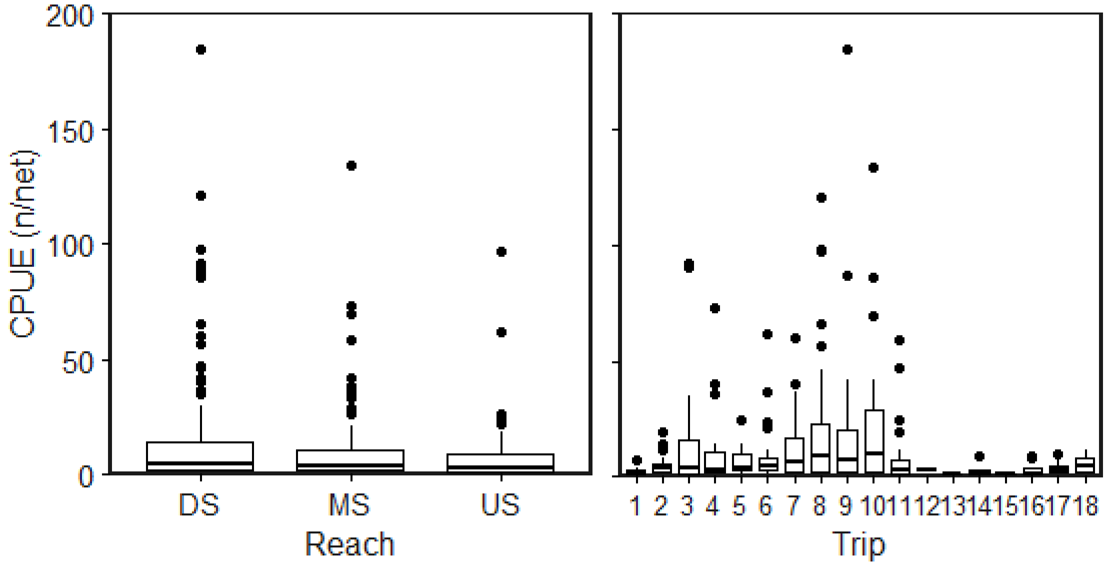

Figure 3. 5: Distribution of CPUE for *F. merguiensis* among replicates (n = 1305) between reaches (Left panel) and trips (Right panel). Zeros removed from data to show variance of presences. Reach codes: DS = Downstream, MS = Mid-estuary, US = Upstream. Whiskers = 1.5 x inter-quartile range, box bounds = 25-75th percentile, box middle line = median, points = extreme values

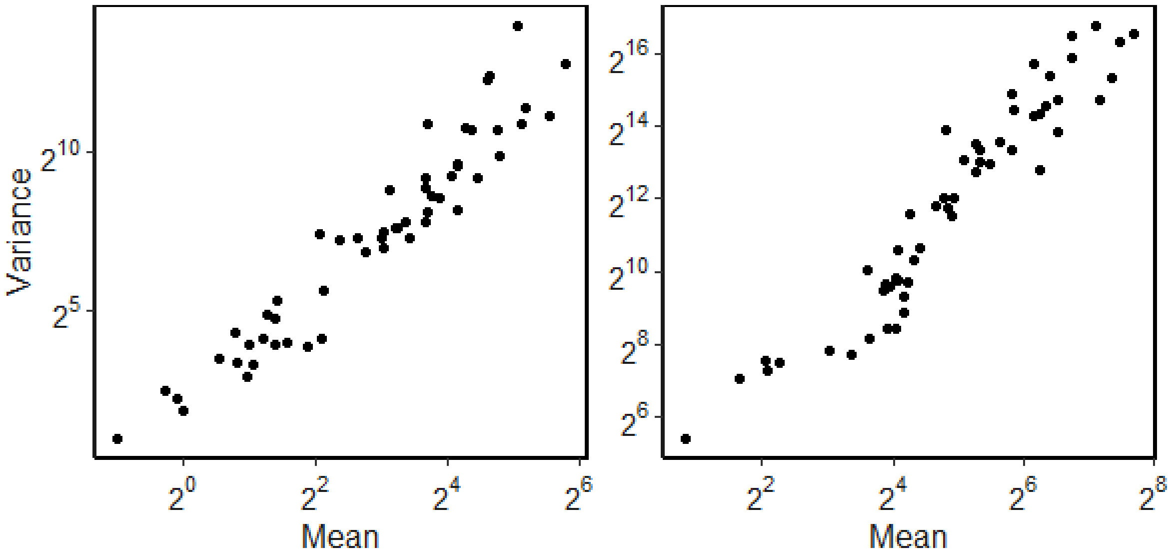

Figure 3. 6: Mean-variance relationship of CPUE (plot left) and biomass density (plot right) data collected from the Alligator Creek estuary. Data averaged within reaches for each trip.

The POE metric provided a means for quantifying (in relative terms) the spatial heterogeneity of abundance, i.e. the degree of aggregation or schooling of species. Where high CPUE combined with low POE illustrates that individuals were highly aggregated, captured in very high numbers, but infrequently captured across replicates. Some species exhibited a positive relationship between POE and CPUE, which indicated that they were relatively well dispersed and captured frequently, e.g. Figure 3. 7.

Although for a few species, e.g. *A. vachellii*, the relationship indicated that even at high mean abundances, POE was very low (see Figure 3. 7). These species were therefore highly aggregated, with heterogeneous spatial distribution. The variety and frequently differing relationships between POE and CPUE observed across species in the Alligator Creek system (Figure A.3. 1) meant that using either single metric (POE or CPUE) separately in analysis would result in a substantial loss of information.

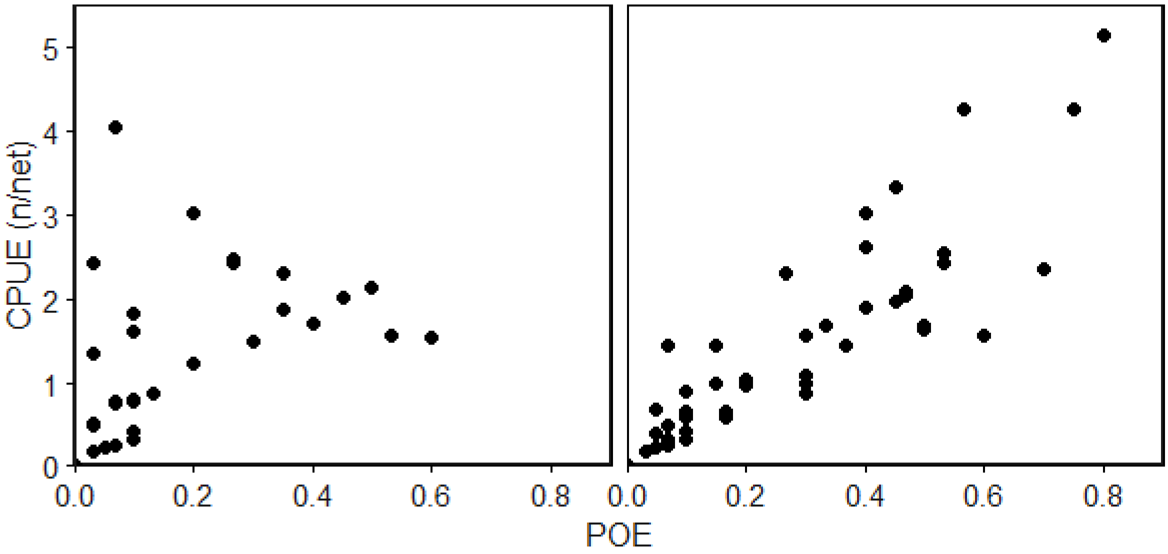

Figure 3. 7: Mean CPUE (square root transformed) vs POE of *Ambassis vachellii* (left panel), and *Fenneropenaeus merguiensis* (right panel) in the Alligator Creek Estuary during 2015-16.

3.3.3. Practical limitations and successes of multivariate ordinations

Untransformed CPUE and biomass density data resulted in ordinations with no apparent grouping or separation of points. Additionally, stress of these ordinations was often greater than 0.2, indicating a poor representation of dissimilarity distances in the two-dimensional ordination space (Table A3. 3). There was no difference in grouping, dispersion, or separation of groups in ordinations when species-species standardisation was applied to CPUE and biomass density distance matrices compared to when standardisation was not applied. Reducing the number of species included in analysis did not improve ordinations or stress in almost all cases (Table A3. 3). The POE metric did not produce meaningful results using any form of transformation, as these resulted in an arch/horseshoe effect (Figure A3. 2). This type of artifact as described in Williamson (1978) and Podani and Miklós (2002) is often the result of unimodal gradients in species richness, resulting in each point being plotted simply in successive rank order along an arch. For the POE metric, the most successful ordinations (i.e. lowest stress without arch/horseshoe effect) were produced with the full number of species (24) and without transformation or standardisation (Table A3. 3). In the case of biomass density, square root transformed data resulted in an arch. Successful ordinations, i.e. those with acceptable levels of stress and free from artifacts, are presented in Figure 3. 8, and Figure 3. 9. When the binary (presence/absence) transformation was applied to CPUE data, there was typically no reduction in stress values, and in some instances this resulted in unusable ordinations due to artifacts and distortions (Table A3. 3).

In general, the most usable ordinations (in terms of informative groupings and dispersion of points and vectors) were produced using square root transformation for CPUE and biomass density data. In general, species vectors were aggregated in one general direction, and for almost all species this aligned with the gradient along which seasonal groups were separated (Figure 3. 10). Vectors were aligned with reach groupings however, due to the lack of separation, this is unlikely to be of any consequence (Figure 3. 10).

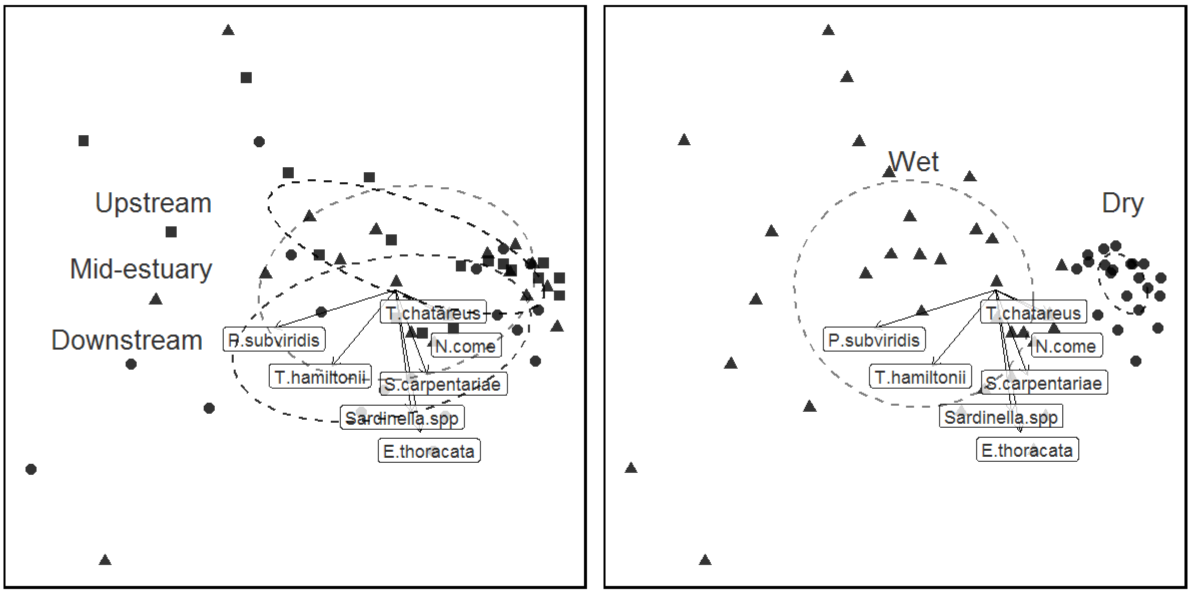

Figure 3. 8: Non-metric MDS ordination plot mean CPUE of 24 common fish and penaeid species in three reaches of the Alligator creek estuary throughout the 2015-16 wet season and 2016 dry season. Plot (Left) data groupings: Upstream (Square), Mid-estuary (triangle), and Downstream (circle). Plot (Right) data groupings: Wet season (triangle), Dry season (circle). Centroid ellipses represent 95% confidence intervals for reach and season groupings. Plot stress = 0.07, Bray-Curtis dissimilarity and square root transformation applied to data.

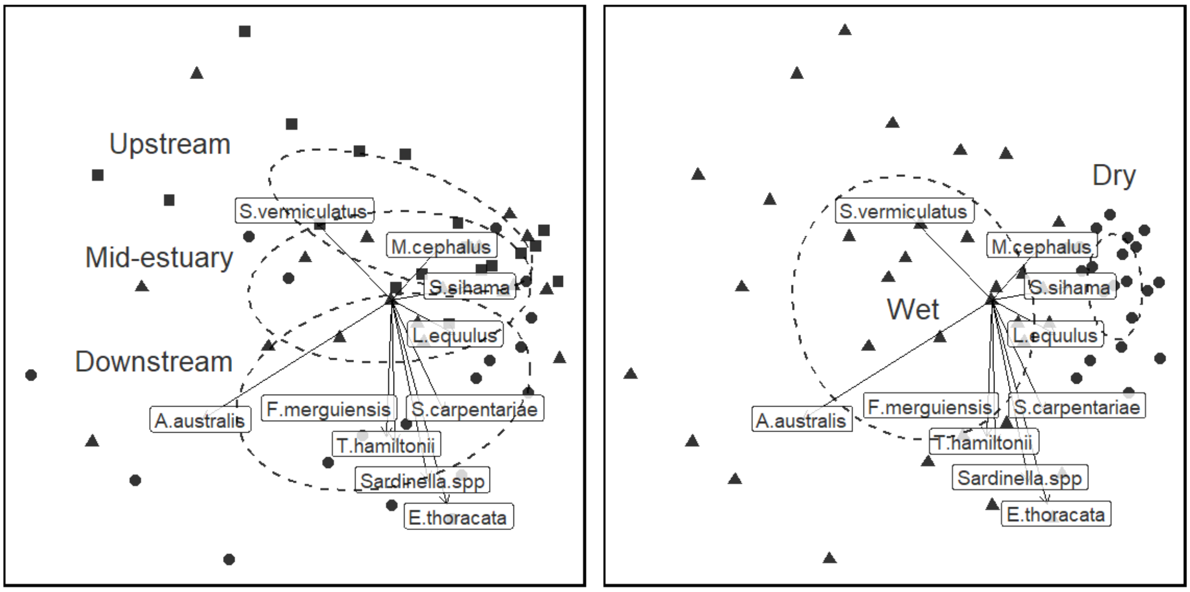

Figure 3. 9: Non-metric MDS ordination plot of mean biomass density of 24 common fish and penaeid species' density in three reaches of the Alligator creek estuary throughout the 2015-16 wet season and 2016 dry season. Plot (Left) data groupings: Upstream (Square), Mid-estuary (triangle), and Downstream (circle). Plot (Right) data groupings: Wet season (triangle), Dry season (circle). Centroid ellipses represent 95% confidence intervals for reach and season groupings. Plot stress = 0.10, Bray-Curtis dissimilarity and square root transformation applied to data.

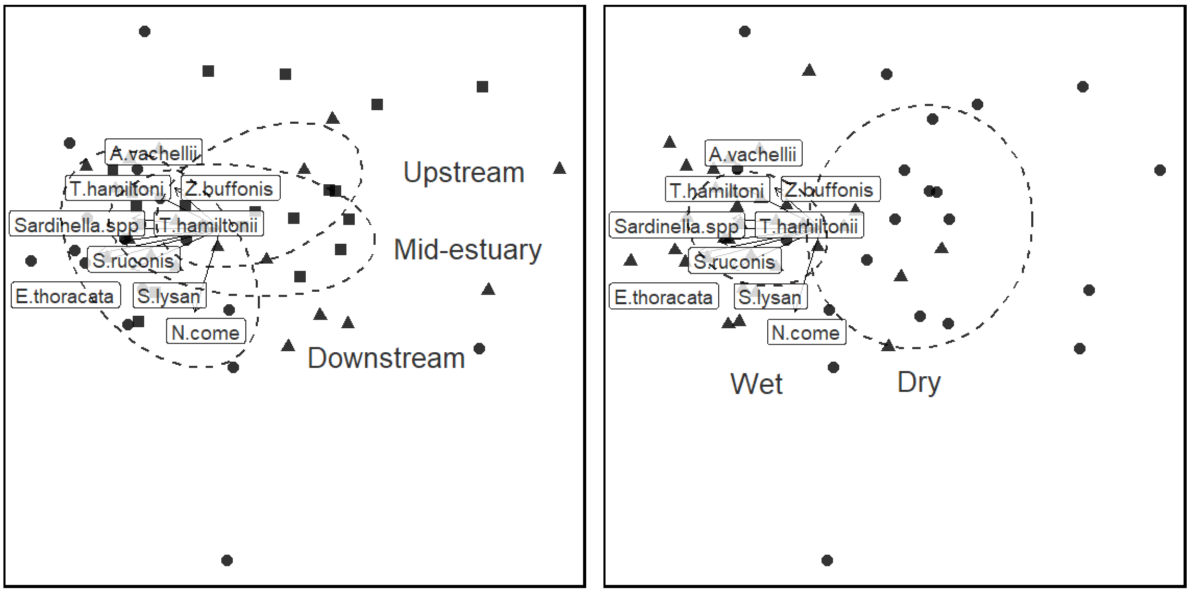

Figure 3. 10: Non-metric MDS ordination plot of probability of encounter of 24 common fish and penaeid species' density in three reaches of the Alligator creek estuary throughout the 2015-16 wet season and 2016 dry season. Plot (Left) data groupings: Upstream (Square), Mid-estuary (triangle), and Downstream (circle). Plot (Right) data groupings: Wet season (triangle), Dry season (circle). Centroid ellipses represent 95% confidence intervals for reach and season groupings. Plot stress = 0.16, Bray-Curtis dissimilarity, no transformation applied to data.

Permutational analyses of variance of the final multivariate distances showed that there were significant differences in the location (distance between groups) of season groups in all data types

(CPUE, biomass density and POE). These differences were clearly represented by both the clustering of points from wet season and dry season groups and the centroid ellipses (Figure 3. 8, Figure 3. 9, Figure 3. 10). A significant difference between reaches was also detected for POE data (Table 3. 3) despite no clear separation of groups in the ordination plot (Figure 3. 10). There were also significant differences in dispersion of points between Season and Reach x Season groups for all data (Table 3. 4). There was no significant difference in dispersion between reach groups for mean CPUE, biomass density and POE data. Dispersion was significantly different between season groups and Reach x Season groups in all instances (Table 3. 3, Table 3. 4).

Table 3. 3: Permutational multivariate analysis of variance for catch in three reaches of the Alligator Creek estuary throughout the 2015-16 wet season and 2016 dry season. CPUE/abundance and biomass density data square root transformed, transformation not applied to probability of encounter, distance matrix produced using Bray-Curtis coefficient. Permutations used = 999. (*) indicates significance

Metric	Ordination Stress	Factor	Sum of squares	F value	R Squared	Pr(f)
Mean CPUE	0.07	Reach x Season	2.64	7.77	0.45	0.001*
		Season	2.38	35.48	0.41	0.001*
		Reach	0.21	0.93	0.04	0.425
Mean biomass density	0.10	Reach x Season	2.64	6.27	0.40	0.001*
		Season	2.15	24.67	0.32	0.001*
		Reach	0.42	1.70	0.06	0.096
Probability of encounter	0.16	Reach x Season	2.96	4.62	0.33	0.001*
		Season	1.63	11.32	0.18	0.001*
		Reach	0.97	3.04	0.11	0.001*
Abundance (Trip 11)	0.08	Reach	5.17	38.89	0.52	0.001*
Abundance (Trip 16)	0.06	Reach	3.11	28.21	0.60	0.001*

Table 3. 4: Permutational analysis of multivariate dispersion for catch in three reaches of the Alligator Creek estuary throughout the 2015-16 wet season and 2016 dry season. CPUE/abundance and biomass density data square root transformed, transformation not applied to probability of encounter, distance matrix produced using Bray-Curtis coefficient. Permutations used = 999. (*) indicates significance

Metric	Ordination Stress	Factor	Sum of squares	F value	Pr(f)
Mean CPUE	0.07	Reach x Season	0.48	7.69	0.001*
		Season	0.51	47.16	0.001*
		Reach	0.01	0.15	0.861
Mean biomass density	0.10	Reach x Season	0.41	7.94	0.001*
		Season	0.42	47.81	0.001*
		Reach	0.02	0.41	0.646
Probability of encounter	0.16	Reach x Season	0.11	1.97	0.101
		Season	0.10	9.97	0.003*
		Reach	0.01	0.21	0.822
Abundance (Trip 11)	0.08	Reach	0.83	40.26	0.001*
Abundance (Trip 16)	0.06	Reach	0.28	21.83	0.001*

When CPUE data from single trips were analysed in the raw form (without averaging) some interesting differences were observed. Again, the square root transformation provided the best ordination, with reduced stress, and avoided erroneous ordinations i.e. arching/horseshoe. However, in these cases there was a clear distinction between reach groupings (Figure 3. 11). Centroid ellipses revealed clear separation of all reaches. Both mid-estuary, and downstream points were well aggregated, however upstream points were extremely dispersed. In both examples tested, there was a significant difference in both distance between, and dispersion of reach groups (Table 3. 3, Table 3. 4). Species vectors have intentionally been excluded here to highlight the differences in reach groupings, in general these were mostly directed toward mid-estuary and downstream groupings. These ordinations where data weren't averaged provided information otherwise obscured in the analyses conducted at larger temporal and spatial scales i.e. across whole seasons and reaches. Therefore, the effect of translating data from the scale of observation to the scale of interpretation resulted in a loss or confounding of information.

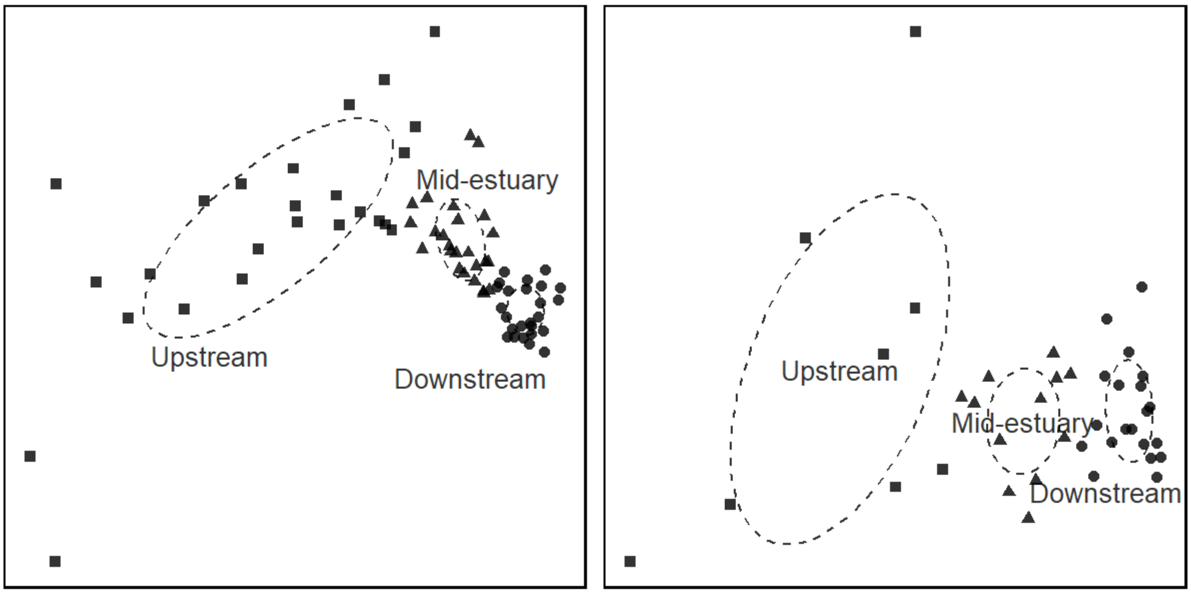

Figure 3. 11: Non-metric MDS ordination plot of square root transformed CPUE of common fish and penaeid species in three reaches of the Alligator creek estuary. Plot Left: Trip 11, 06-Apr-16 stress = 0.08. Plot Right: trip 16, 14-Sep-16 stress = 0.06 data groupings: data groupings: Upstream (Square), Mid-estuary (triangle), and Downstream (circle). Centroid ellipses represent 95% confidence intervals groupings, Bray-Curtis dissimilarity and square root transformation applied to data.

In addition to the tests of data types and treatments, testing of dissimilarity coefficients was conducted for presence absence data from trip 16 (14-Sep-16). Both Sorensen and Bray-Curtis coefficients were used to create distance matrices for the same data set (presence/absence transformed abundance data). In this test there was a clear distinction between ordinations, with the Sorensen coefficient resulting in high stress (0.22) and no discernible groupings or differences in dispersion or location (Figure 3. 12 – Right panel). The Bray-Curtis coefficient resulted in clear separation of groups, and clearly discernible location and dispersion effects i.e. upstream samples were spread further apart from each other than mid-estuary and downstream samples and reach groupings were somewhat separated (Figure 3. 12). Species vectors were not included in these plots to highlight the differences in groupings and dispersions.

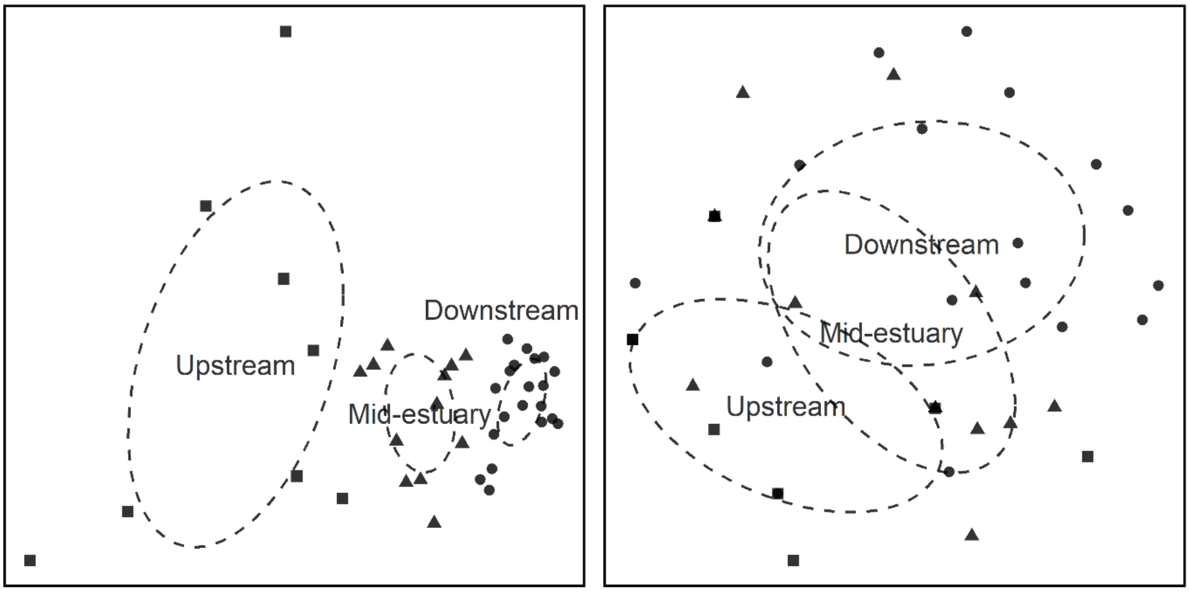

Figure 3. 12: Non-metric MDS ordination plot of presence absence data for common fish and penaeid species' density in three reaches of the Alligator creek estuary throughout the 2015-16 wet season and 2016 dry season. Plot data groupings: Upstream (Square), Mid-estuary (triangle), and Downstream (circle). Plot (Left) distance matrix calculated using Bray-Curtis coefficient, plot stress = 0.04. Plot (Right) calculated using Sorensen coefficient, plot stress = 0.22. Centroid ellipses represent 95% confidence intervals for reach groupings.

3.4. Discussion

3.4.1. Data characteristics

The characteristics of catch data from the Alligator Creek estuary present several difficulties for robust and meaningful analyses and interpretations. Characteristics observed, such as overdispersion (Figure 3. 5), zero-inflation (Figure 3. 4), high variability (Figure 3. 2, Figure 3. 3) and mean-variance relationships (Figure 3. 6) require various treatments to make meaningful patterns of abundance, biomass, and occurrence discernible. Treatment of data with characteristics as found in this study can be problematic, but well-established methods are commonplace (Legendre & Gallagher 2001). For the treatment of extreme error surrounding means, alternative measures (e.g. modes or medians) can be used. Although in this case these are also invalid, because of the zero-inflation, modes would result in near-zero CPUE for most cases, and medians for many species would be zero. The other options for treating data in this case include winsorizing and trimming, and transformations. The use of winsorizing or trimming can result in the desired reduction in error as extremes are removed (Ghosh & Vogt 2012).

However, these methods treat extreme values as ‘mistakes’, or in other words the assumption is that those values outside of the specified percentiles are not a true representation of reality. This assumption is incorrect for stocks in the Alligator Creek estuary because both extremely high and extremely low CPUE were clearly observed in the study, and there is no conceivable mechanism by which these extremes could have been observed in error. Alternatively, transformation to binary (presence/absence) data types is frequently used in cases of extreme variability in abundances (Jackson et al. 1989, Legendre & Gallagher 2001), the effects of this are discussed in section 3.4.2. All of the data characteristics observed here can be at least in-part attributed to the aggregation/schooling characteristics of much of the basal-prey community (Figure 3. 7, Figure A3. 1). The effect of schooling/aggregation is that individuals are infrequently captured, but when they are captured, CPUE and biomass densities are in the extreme. The degree of dispersion, illustrated by the CPUE-POE relationship was varied across many of the species tested (Figure A3. 1), meaning that the magnitude of zero-inflation, overdispersion and variability was also varied across species. This aggregation or schooling effect has been previously discussed by Sheaves and Johnston (2009), Downing (1991). More recently Abrantes et al. (2019), demonstrated that ‘patchiness’ of distributions could potentially lead to vastly inaccurate characterisations of biomass and abundance patterns as data is translated across spatial scales. However, the effects of patchiness and schooling on examination of ecological patterns using multivariate ordinations have seldom been investigated. The results presented in this study contribute to furthering our understanding of these effects and are discussed below.

3.4.2. Practical limits of ordination and data collection

The results of this study clearly indicated that the ecological interpretations able to be drawn from data using multivariate ordinations were dependent on how data was treated in response to the extreme data characteristics, and how the data was translated across spatial and temporal scales. Ordinations of both CPUE and biomass density data did not reveal meaningful patterns of similarity between groupings (reach and season) without transformations applied. This data required transformation to reduce the influence of extreme cases, thus variability and overdispersion were confounding spatial and temporal patterns. Additionally, these results were dependant on the type of transformation applied. When analyses of data across the whole timeframe of study were conducted using both Logarithmic and presence/absence transformations, no meaningful result (in comparison to the other treatments) was produced. This changed how spatial and temporal differences in the basal-prey community could be interpreted. Using an incorrect transformation could lead the observer to conclude that there was no dissimilarity between reaches or seasons, or that each group was different from each other, but equally variable between samples or trips.

It was evident that there was a trade-off between treating some of the 'undesirable' data characteristics to separate real patterns from extreme variations, and retaining enough information to make meaningful interpretations of the data. It seems that removing abundance information to reduce the effects of extreme variations, i.e. through presence absence transformation, meant there was not enough remaining information with which dissimilarity measures could separate samples over time and space. Similarly, the resultant arch/horseshoe ordinations obtained using the log transformation are a product of removal, or otherwise lack of information about community dissimilarity in terms of relative abundances (Podani & Miklós 2002, Morton et al. 2017). In these cases the dissimilarity coefficient (Bray-Curtis) was unable to distinguish between samples because there was not enough information on common and dissimilar features i.e. abundances or presences (Podani & Miklós 2002, Morton et al. 2017). The result of information removal was particularly evident in ordinations resulting from Bray-Curtis and Sorensen coefficients applied to presence/absence data from trip 16 (Figure 3. 12). Because the Sorensen coefficient has been specifically developed to ignore joint-absences in the distance matrix (Jackson et al. 1989). This coefficient does not assume that sites or samples are similar because they share an absence in a particular or number of species and therefore does not make use of joint-absence information (Gower 1985, Jackson et al. 1989, Clarke et al. 2006). However, if that is the only distinguishable difference between sites or samples, because observed abundances, or even presences are too variable or too uniform, then removing this information renders the ordination unable to distinguish them.

This trade-off of information and practicability in the context of ecological and statistical assumptions has previously been discussed by Clarke et al. (2006) and Field et al. (1982). They suggested that to consider samples similar because neither contained any species was a flawed assumption. Additionally, where extreme spatial clustering of organisms exists, like in the case of the Alligator Creek estuary, and indeed many tropical estuaries, low sampling volumes are likely to result in erroneous and unexplainable absences of particular species across spatial and temporal scales. In these cases, it would be flawed to assume similarity or dissimilarity between these samples based on joint-absences. However, the alternative argument to this is that, in many cases, the absence of a particular species, or indeed a reduction in abundance (or CPUE), is actually biologically meaningful. So, to remove this information, in these extreme cases, will probably reduce the ability of the observer to extract any biologically meaningful result. This trade-off was directly demonstrated here by the comparative analyses using the Bray-Curtis and Sorensen coefficients which treat joint-absences differently (Figure 3. 12). Faith et al. (1987) suggested that "a balance must be reached between assuming too little, with a loss of useful information which can constrain the solution, and assuming too much, with a loss in the method's robustness".

Another practical constraint of the method was demonstrated through use of central tendencies, which were used to operate within the limits of computational capabilities, and to produce ordinations that were meaningful and interpretable. Because of the high replication used in this study, use of raw data collected over the entire study in a single ordination or permutational analysis was not possible. Therefore, to look at temporal similarities, it was necessary to reduce these replicates by condensing the information to mean values for each trip-reach combinations, a common practice (Field et al. 1982). When raw data for individual trips were analysed, there were clear significant differences in the community of basal-prey species between reaches, which were not revealed from averaged data (Table 3. 3, Table 3. 4). Not only was the community different in terms of abundances, but the variability of abundances was also significantly different when data was analysed in its raw form. The downstream reach was clearly more variable than the mid-estuary and upstream reaches, indicated by the significant difference in dispersion between groups (Table 3. 4). Despite this pattern being obscured by ordinations using mean CPUE data, it was somewhat evident in simple plots of mean CPUE and biomass density over time (Figure 3. 2, Figure 3. 3). The disparity between interpretations drawn from ordinations using averaged data and raw data illustrate the inherent issues with using measures of central tendency in cases of extreme data variability.

These results exemplify the practical limitation of all multivariate methods, not just ordinations, but demonstrated here for this particular technique. The limitation is that when variations are extreme and heteroscedastic, true patterns are masked to the point that transformations fail to discern trends. Further, while treating extreme variation can provide some clarity, the removal of information required to do so may leave the analysis with no real meaningful information from which to interpret differences. These results also demonstrate how the multitude of approaches (data types, treatments, dissimilarity coefficients, standardisations) can determine whether ordinations result in meaningful discernment of ecological patterns, or near complete obfuscation of these patterns. Researchers should approach data treatment and analysis by first determining which data characteristics are present, and which treatments are most susceptible to bias or other conditions due to those characteristics. Secondly the trade-offs of each treatment should be clearly identified in relation to the objectives of the analysis and study. For example, if detailed information of small-scale variances in abundance and biomass distributions are needed, the information removal resulting from central tendency measures is and unsuitable trade-off.

Ultimately transformation and centralisation of estimates becomes a necessity to produce results which are both meaningful and are spatially and temporally linked to appropriate scales. The objective of this study was to characterise the spatial patterns of populations within the estuary i.e. at estuary and reach scales. Because of this, there was a need to centralise estimates across replicates within these scales, i.e. average measurements of CPUE and biomass density across reach-trip combinations. This approach is used to generalise patterns of observation to the study scales at which investigators want to understand. However, this was problematic in this case because the data in many cases were extremely patchily distributed due to the aggregation characteristics of certain species. Therefore, individual estimates (replicates) were more representative of the densities of fish/penaeids at the scale at which aggregations existed. Each school, or aggregation, exists at scales of metres, rather than at hundreds of metres to kilometres (reach and estuary scales). For some species that were relatively evenly dispersed, e.g. *F. merguiensis,* the catch data were more representative of the population at these reach and estuary larger scales which are inclusive of migratory patterns and extent. However, for many others, translation to larger scales meant abundances were no longer representative of the scales to which they were applied. The consequence of these aggregation behaviours and resultant data characteristics is that the use of any measure of central tendency, i.e. means, is inherently subject to a large degree of statistical error and uncertainty. Additionally, use of inappropriate data treatments, i.e. transformations, standardisations and dissimilarity coefficients can determine the reliability and usefulness of the results. While this is not a problem in and of itself, making generalisations using this data leads to several challenges of treatment and interpretation.

3.4.3. Conclusions

The use of ordination techniques to provide meaningful insight into measured variations along ecological gradients through time and space is constrained by both the characteristics of the data and by the analysis methods. The comparisons made here demonstrate the practical difficulties experienced by ecologists when encountering highly complex and highly variable ecosystems. Removal of information is both a mechanism and a by-product of the process of reducing the noise of natural variations. In this study, the removal of information allowed for analyses to produce somewhat usable outputs (in terms or ordination stress and artifacts), but also masked some of the potentially important ecological relationships captured by the data. Importantly, this trade-off could invalidate ecological interpretations drawn from the results if the data treatment process is flawed. Additionally, the consistent lack of correlation between species vectors, and the spatial and temporal ordination of data, indicated that the metrics used may not have been able to clearly characterise much of the patterns of variability. In other words, they were highly susceptible to the effects of schooling and aggregation behaviours, which result in patchily distributed abundances. This is important because the metrics of

CPUE and biomass density are still heavily relied upon for characterisations, and generalisations of communities, species, ecosystems, and other spatial units (e.g. habitats); and these metrics often form the basis of valuation of these natural systems (Costanza et al. 1997, Hamilton & Gehrke 2005, Hoggarth 2006, Barbier et al. 2011).

The practical limitations imposed by both computational and interpretational restrictions, and the requirement to understand complex patterns on relevant spatial and temporal scales can lead ecologists to translate data across scales, and centralise information into useable forms. This process can result in unintended and often unknown consequences, in this study these consequences were the obfuscation of patterns of similarity in the basal-prey community between reaches in the Alligator Creek estuary over time. This is particularly important in the context of tropical estuarine ecosystems, where there is a critical need for understanding the most important ecological relationships. However, the lessons from this study are broadly applicable to all marine ecosystems where data is limited. Mischaracterisation of communities of fish and penaeids can expose them to management actions that are ultimately deleterious. Therefore, caution should be used where there is a desire to fit complex and problematic data into the constraints of analyses, and requirements of interpretations. In cases similar to those presented here, where limited data is used in an attempt to understand complex ecological patterns, without having an independent point of reference from which to compare results, it would probably be prudent to reserve subsequent ecological interpretation of the results.

Chapter 4: Estimating growth rates at reach and estuary scales using standing stock data

4.1. Introduction

Length-based growth characterisation methods in fisheries have been established as a reliable alternative to age-based methods (Pauly & Morgan 1987), particularly for the short-lived, fast-growing species common in the tropics. Although, only under the provision data are free from sampling biases, and recruitment patterns are compatible with the method (Pauly & Morgan 1987, Isaac 1990, Gayanilo et al. 2005). Collection of length-based data is practical and data requirements of the length-based analytical methods are minimal (Pauly & Morgan 1987). In contrast, much of the data required by age-based methods is costly and logistically difficult to obtain for basal-prey species in tropical estuaries. In-part, this is due to the inherent difficulties of obtaining mark-recapture data, and length-at-age data using hard structures on these species, which have been discussed in chapter 2. The core requirements of data collection for length-based methods are that length-frequency data is collected at relatively consistent intervals over time, and that the capture method is free from biases (Isaac 1990). Therefore length-based methods are an appropriate choice for estimating growth of many fish and penaeid species where age-based data is not available or difficult to attain. The simple standing stock approach is well positioned to collect data that meet these requirements, and if capture of species is sufficiently unbiased, the method could produce useable growth estimates for much of the basal-prey community in tropical estuaries.

Although length-based methods may be more suited to studies of the basal-prey community in terms of data collection, the accuracy, reliability and assumptions required of this approach deserve robust scrutiny. There are a variety of methods use to fit growth curves to length-frequency data e.g. Electronic Length Frequency Analysis (ELEFAN), non-linear least squares regression (NLLS) and linear least squares regression (LLS). Each of these methods require a number of common and specific assumptions relating to data characteristics, and biological processes, a number of these are listed in Table 4. 1. Many of which have been critically investigated in temperate applications (Rosenberg et al. 1988, Isaac 1990, Drouineau et al. 2008), the lessons learned from previous works can be useful for understanding how the methods perform in other contexts. However, the assumptions required of length-based methods must be specifically validated for the basal-prey community of tropical estuaries. If any single assumption is violated, the outputs of the approach are invalid. However, in practice some assumptions are not binary in nature, and may be only partially violated, and the impact of deviation from assumed conditions is dependent on both the extent of that deviation, and the importance of the assumption. If the extent of deviation can be precisely measured, we are better able to address how the approach can be improved, and whether some use can be drawn from the outputs.

Table 4. 1: Assumptions of length-based growth estimation methods

- Data assumptions
    - Length-frequency data are normally distributed
    - Samples are independent
    - Recruitment pulses allow for identification of individual cohorts
    - Data is collected at relatively consistent time-intervals
    - Length-frequencies represent the full range of lengths at which the species exists
    - Length-frequency data is not biased by sampling design, gear efficiency or selectivity
    - Length-frequency distributions to which the growth function being fitted are representative of the same cohort throughout the study period
- Biological assumptions
    - Patterns of growth are accurately described by the growth function
    - Removal of individuals from the study population i.e. via mortality and emigration, is not size dependent
    - Increases in length-frequency modes are only due to growth of the cohort, e.g. are not due to movement patterns of individuals

A spatially-linked approach to productivity measurement requires that estimates of growth rates and other demographic metrics (e.g. mortality) are produced for populations at small spatial scales (within estuary, and between estuaries) and in relation to other explanatory variables (e.g. habitat). This approach would provide important information about relative contributions to fisheries productivity, and could improve the usefulness of outputs by linking estimates to scales which are relevant to management actions and anthropogenic activities. In order to relate growth rates of populations to particular spatial (e.g. a particular area of intertidal wetland) or other explanatory factors (e.g. habitat), catch data need to be collected on local scales. While this is possible in practical and logistical terms, it is not clear how the quality of data at these scales will affect reliability of growth estimates. This is because the biological and ecological process which operate at small spatial scales may invalidate assumptions which are typically developed at larger scales. For example; length-based methods assume that the length-frequency distributions of a species in catch data are representing the same cohort within the population as samples are collected over time, and that there is minimal or no exchange of individuals between different populations or across spatial units. This assumption is unlikely to be correct because of the movement patterns (particularly of estuarine species) and is likely to be unfounded at small spatial scales. This is because populations of fish and crustaceans, and individuals within them frequently move between habitats, reaches and estuaries (Able 2005, Johnston & Sheaves 2007, Sheaves & Johnston 2009, Jardine et al. 2012). Often these patterns of movement occur at spatial and temporal scales we have not adequately described, but have assumed. Additionally, complex variations that exist in estuarine fish communities are recognised (Sheaves & Johnston 2009, Harris & Heathwaite 2012, Sheaves 2016) but not understood (Sheaves 2016), further reducing our ability to understand possible biases and inaccuracies. In particular, variations in recruitment (Miller et al. 1984, Boehlert & Mundy 1988, Grimes & Kingsford 1996, Levin et al. 1997) and movement of post-recruitment juveniles (Vance et al. 1998, Nemerson & Able 2004). In this example, the result of such violations of assumed data characteristics and biological processes is that the growth curve may be fitted across a number of different cohorts and therefore age (time since first sample) is unknown and possibly very different from that of the original cohort.

Incorrect assumptions regarding the characterisation of growth may undermine growth estimates, and in turn assessment of productivity and productive capacities, and thus the value ascribed to many coastal ecosystems. The effects of unreasonable and flawed assumptions may be exacerbated by spatial (and other) confinement of catch data (estimates for small spatial scales, e.g. reach and habitat). However, at present, it is unclear at which scale and to what degree the effects become prohibitive for use of length-frequency methods. It is also not clear whether these methods are practicable, reasonable, and accurate for the basal-prey species that inhabit tropical estuaries. Therefore, it is important to assess the extent to which small-scale (e.g. within estuary reaches) growth estimates are affected compared to whole-of-system (e.g. estuary) estimates. Additionally, to be useful in tropical systems, the assumptions of length-based growth estimates at the estuarine and reach scale, need to be assessed using the data that are most available for these fisheries, e.g. standing stock and length-frequency data (Pauly 1983, Pauly & Morgan 1987). This study will explore the use of standing stock data collected at estuary- and reach-scales over the course of a year (wet and dry season), to produce growth estimates for common basal-prey (fish and penaeid) species. I conducted the study in Alligator Creek, a tropical mesotidal estuary, and focus on investigating the assumptions required to produce acceptably precise growth rate estimates. I determine the practicability of these methods at reach and estuary scales using robust length-based fisheries methods, and assess whether the assumptions required for current (length-based) growth fitting methods are biologically reasonable for the studied populations.

4.2. Methods

4.2.1. *Data*

Length frequency data were collected on a fortnightly basis from fish and penaeid populations in three reaches of the Alligator Creek estuary during 2015 and 2016. For more detailed methods, see previous

Chapter 3. To investigate the assumptions and effects of scale on growth rate estimation, I have implemented three commonly used methods. The selected methods are also industry-relevant.

4.2.2. *Growth rates*

Growth rates were estimated using Electronic Length Frequency Analysis (ELEFAN) (Pauly & David 1980) and regression methods. ELEFAN was considered potentially useful because results produced are readily incorporated into further population and productivity modelling (Jones 1981, Brey & Pauly 1986, Gayanilo et al. 2005). The ELEFAN method also involves less subjective assessment of cohorts (manual separation required for regressions) and exhibits less bias with highly variable data than some other length-based methods (Isaac 1990). Growth estimation for each species was first attempted using the ELEFAN method and subsequently passed to the regression methods if results were not attainable (see below for details). For species and cohorts to be included in growth rate estimation five criteria had to be met:

1. Total catch of individuals must exceed 100.
2. The species must be present in more than 75% of months included in the study.
3. Recruitment must occur in pulses and cohort distributions must be discernible.
4. The sample must include either newly recruited individuals or maximally grown individuals.
5. Cohorts did not exhibit obvious distortion or skewing of length-frequency distributions associated with size i.e. truncation.
6. Cohorts exhibited identifiable modal progression, i.e. continuous increase in modal lengths over time.

4.2.3. *ELEFAN method*

Computational estimation of growth rates was conducted using ELEFAN (Brey & Pauly 1986, Pauly & Morgan 1987) packaged in 'TropFishR' for the R statistics environment (Mildenberger et al. 2017b). Growth rates were fitted to the Von-Bertalanffy growth function (VBGF) (Von Bertalanffy 1957), with the equation as described in Pauly and David (1980), Pauly (1983). The procedure followed the multi-step process outlined below:

1. Length frequency data for each species were pooled for each month to improve data density and to improve consistency in time-between-samples (Brey & Pauly 1986, Mildenberger et al. 2017b).
2. Pooled length-frequency distributions were then plotted over time and visually assessed for progression of cohort distribution modes over time, and for consistency of distributions.

3. Initial upper and lower L_{inf} (maximum species length) parameters were estimated using either Powell-Wetherall plots with 95% confidence limits, or were determined by maximum modal length of all cohorts +/- 5mm (Brey & Pauly 1986, Wetherall et al. 1987, Mildenberger et al. 2017a).
4. Length-frequency data were restructured following procedures outlined in Mildenberger et al. (2017b), Mildenberger et al. (2017a), Taylor and Mildenberger (2017), and developed in Gayanilo and Pauly (1997), and Gayanilo et al. (2005).
5. Optimisation of parameters and outputs was conducted initially using response surface analyses to ensure local Rn (Fitment score) maxima were avoided (Mildenberger et al. 2017b, Mildenberger et al. 2017a).
6. The ELEFAN Simulated Annealing (ELEFAN_SA), and Genetic Algorithm (ELEFAN_GA) processes were used to produce final outputs with optimised input parameters for L_{inf}, K (growth parameter) range and T_0 (length at initial time) range (Mildenberger et al. 2017b, Mildenberger et al. 2017a).
7. Final growth curves were fitted to length-frequency plots to examine model fit.

Where poor or incorrect fitting was observed, the process was repeated with confined input parameters until the model fit was improved. This was determined using the Rn Max score (Brey & Pauly 1986, Mildenberger et al. 2017b). Final model successful estimates were then plotted with observed data to compare the fit. Where curve fitting did not match cohort progressions, models were considered invalid. For cases that could not be modelled with a resulting Rn Max score of >0.3, or did not fit the observed cohort progressions, data were passed to regression methods. Seasonal oscillation was determined by improvement in Rn Max Score; where no improvement to Rn Max score was achieved, seasonal oscillation was not used not used (Brey & Pauly 1986, Gayanilo et al. 2005, Mildenberger et al. 2017b). The process was then repeated for catches confined to each of the three reaches sampled. For species where cohort modes were consistently identifiable in multiple reaches, the ELEFAN method was applied to data separated by reach. The ELEFAN method is considered to be sensitive to biases of L_{inf} (Isaac 1990), and so L_{inf} input parameters from either the pooled estuary standing stock data, or from published records were used for the modelling of reach scale catch data.

4.2.4. Non-linear regression methods

For species where ELEFAN was not appropriate (i.e. poor fit – determined as described in previous section – 4.2.3), a combination of the Peterson method (described in Pauly and Morgan (1987)) and Modal Progression Analysis was used (Pauly 1983). Individual fish were assigned age classes based on time from first observation of their respective cohort, i.e. individuals in the first instance of recruitment were assigned t_0, and individuals of the same cohort captured in the next month were assigned t_1. This provided age estimates for suitable length frequency data for use in subsequent regression analyses. This process does not assume t_0 is the start point of biologically defined growth (i.e. birth/hatching/recruitment), it is only used to provide a start point for the model. Length frequencies were then plotted by assigned age class for regression fitting.

Growth rates for species that exhibited non-linear growth were fitted using non-linear least squares regression (NLLS) (Sparre & Venema 1998). This method is considered the most robust for non-linear growth data (Allen 1966, Kimura 1990). NLLS regressions were fit to the Von-Bertalanffy growth function (VBGF) (Von Bertalanffy 1957), with the equation as described in (Pauly & David 1980, Pauly 1983). Regressions were fitted using the TropFishR package for R (Mildenberger et al. 2017b) with confidence intervals of 95% estimated. Initial estimates of L_{inf} were used to assist in fitting of the regression model, these estimates were set in the same manner as for the ELEFAN method. Species that exhibited linear growth were fitted with a linear regression using R base package (R Core Team 2018), which did not require input parameter ranges. Regression analyses were applied to catch data from individual reaches for species where cohort modes were consistently identifiable in multiple reaches. Growth rates were then compared between reaches and spatial scales. Fit of NLLS models was assessed visually, comparing distribution modes to the model and using residual standard error (discussed in section 4.2.5). Fit of the linear regression models was assessed using R-squared values and F-tests of residuals (discussed in section 4.2.5).

4.2.5. Assumptions

Assumptions of each of the growth estimation methods employed were determined from relevant published literature. Assumptions tested in this study are listed in Table 4. 2. A number of assumptions could not be assessed with the available catch data, these included size-independence of mortality, whether catch data were representative of the actual population, and whether catch data were biased by gear selectivity or other methodological biases (e.g. over-representation of particular habitats). Assumptions that were dependent on sampling methods (e.g. independence of replicates) were not included here as these can be modified by the researcher during design of sampling methodology. Additionally, cohorts and species that were excluded from growth estimation due to invalid criteria results were excluded from testing of accuracy of growth characterisation. However, these were assessed for violation of the remaining assumptions.

Table 4. 2: Assumptions of length-based growth estimation and methods for testing conformity

	Assumption	Confirmation method
1	Growth is adequately characterised by the VBGF	Relative accuracy of biological characteristics and model fit
2	Full range of lengths represented	Length ranges in catch data match previously observed and published records
3	Recruitment is in defined pulses	Length-frequency distributions of recruiting cohorts and visual assessment of cohort progressions
4	Normality of length-frequency distributions	Q-Q plot of residuals, Shapiro-Wilk test. Percentage of distributions conforming to normality

1. Characterisation of growth using the VBGF

As the true values of the growth model parameters are not known for each species, it is not possible to make a completely empirical assessment of growth characterisation by the VBGF using the selected methods, as used in studies such as Pardo et al. (2013). However, it is possible to make an objective assessment by making comparisons to known biological and statistical references, i.e. using measures of goodness-of-fit and comparing predicted and known biological characteristics. Following similar testing of growth characterisation used by Helidoniotis et al. (2011), I have made these assessments using a known biological characteristic and a measure of model fit relative to the catch data. Assuming both accuracy of the predicted biological metric and model fit are equally important, the final score is given as an average of the two metrics. This process provides an index of the characterisation accuracy of both the VBGF and the fitting methods in relative terms (percentage). I do not proceed further to assign an arbitrary cut-off beyond which the characterisation was deemed unacceptable as this would make the assessment no more useful. Hence the degree to which growth was successfully characterised by the VBGF is presented as simply a percentage.

The biological characteristic used is the median length of adults (Lmax), derived from either catch data or published records. Using catch data, Lmax was estimated as the median length of individuals within each cohort at maximum observed length (in catch data). Because maximum lengths varied between cohorts, only the largest median length for each species was used. Published records were used where catch data did not represent the full range of lengths known for each species. The relative fit of predicted vs actual biological characteristics was calculated as the percent difference. The model fit parameter used for growth models produced using ELEFAN is the Rn score, calculated as the ratio of “estimated sum of peaks” (ESP) to “available sum of peaks” (ASP).

The calculation of Rn is specified as:

$$Rn = 10^{\frac{ESP}{ASP}}/10$$

Where ASP represents the number of positively scored length classes in the restructured data, and ESP the number of positively scored length classes that are crossed by the fitted growth curve. The final score is expressed as a percentage where 100% illustrates a ‘perfect’ fit (Pauly 1985, Gayanilo & Pauly 1997, Mildenberger et al. 2017b, Taylor & Mildenberger 2017).

As fitting of a growth model to catch data will always include some level of data variability, and fit will never be ‘perfect’, fitment to catch data should be evaluated relative to the best practical fit, rather than the best ‘possible’ fit. To evaluate model fit in relation to the best practical fit, I compared results from the Alligator Creek catch data to a reference data-set. The reference data-set was derived from a synthetically generated population catch data-set and length-frequency data was used to estimate growth under the same conditions and methods as the catch data from Alligator Creek. I generated the synthetic population data using the fishdynr package in R (Taylor & Mildenberger 2019), with growth specified according to the VBGF using parameters in Table A4. 1. The synthetic population was constructed to be similar in biology to many of the species collected in this study. Namely, that the species was fast growing and short lived, and with minimal seasonal oscillation in growth. This provided a theoretical ‘optimum’ characterisation of growth by the VBGF within practical limits, using the ELEFAN and NLLS methods, from which to compare the populations in Alligator Creek. Using this reference model also allows for the measure of fit to account for differences in fitting methods. This also accounted for the inherent capabilities of each method to correctly model growth using length-frequency data. Figure 4. 1 shows the ‘practical’ optimum fit of a growth curve to the synthetic population, and the actual growth to which the population was created.

For the NLLS method, the Residual Standard Error (RSE) was used to assess model fit (Gelman & Hill 2006). RSE values of catch data from Alligator Creek were then expressed as percent difference from the RSE of the synthetic population. This provided a measure of fit of the VBGF to each cohort/population, where the ‘relative fit’ provided a measure of the degree to which catch data were accurately characterised by the VBGF using each method. Linear Least-Squares growth estimates were assessed using the R^2 value alone as linear growth is not biologically relevant to growth of species and individuals over the entirety of their life. However, this measure is useful for estimating growth over short timeframes for the purposes of comparative analyses, e.g. Haywood and Staples (1993).

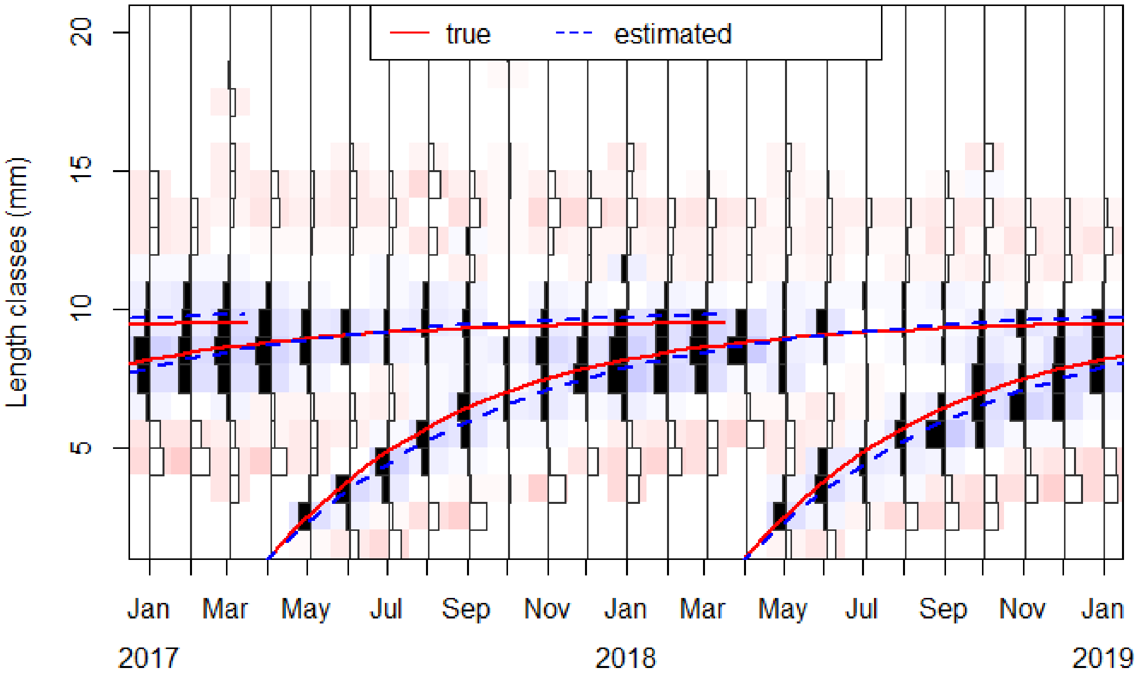

Figure 4. 1: Growth curve fitted on restructured synthetic length frequency data using ELEFAN, with true and estimated growth curves. Shading/fill: blue shading/black fill indicates positively scored classes; red shading/white fill indicates negatively scored classes.

2. Full range of lengths represented

Length ranges in catch records for individual cohorts/reaches of each species were compared with both pooled whole-of-estuary catch data and with previously observed and published records, where available. The assumption that catch data were representative of the full-length range of each species was considered to be met if observed median lengths of maximally-grown cohorts were within 10% of comparative published records. Minimum/recruit lengths were assessed as fairly represented in catch data if initial recruitment pulses were identified during the study.

3. Recruitment is in defined pulses

This is assessed by applying the length-frequency restructure process developed by Gayanilo and Pauly (1997) to distributions. This function restructures the length-frequency data by assigning a count score for each length class according to deviations from the moving average across a specified number of bins/length classes. The process, simply put, calculates the difference between the mean length of each length-class and the mean length of each class around it. The number of classes included in the comparison are selected based on the observed cohort size. The restructuring process scores each length-class according to these calculations, which emphasises cohorts and modes. Further details of the process are found in Gayanilo and Pauly (1997). Where there were no visible cohorts using the restructuring process, recruitment was determined to be without defined pulses.

4. Normality of distributions

Testing for normality of distributions required testing of the multiple distributions used in each individual analysis. Normality was tested using a combination of inferential visual tests (Q-Q plots) (Figure A4. 2) and statistical significance tests (Shapiro-Wilk), where each test was considered equally valid (Buja et al. 2009). Thus, the normality was determined as the percentage of distributions used in each analysis that were normal. Results from each method were subsequently averaged to produce a final score. Each monthly pooled distribution was separated into individual cohorts were applicable and tested for normality. Distributions of less than 20 individuals were excluded from both tests of normality and from the calculation of percentage of normality for each cohort/species. No threshold value was used to determine a binary violation of the assumption, rather the degree of conformance/violation is presented as a percentage.

4.3. Results

4.3.1. *Growth estimates*

A number of species for which clear recruitment pulses were absent resulted in erroneous growth rates and poor model fitting (Rn max score <0.3; results not included in this thesis). However, satisfactory fit of growth rates was possible for several species using all three methods (Table 4. 3, Table 4. 4, Table 4. 5, Figure 4. 2). Growth rates were produced using the ELEFAN method for four species at the estuary scale and three species at the reach scale (Table 4. 3; Figure 4. 2). Non-linear and linear regression methods produced growth rates for an additional three and five species, respectively (Table 4. 4, Table 4. 5). Regression methods required separate analysis of cohorts for each species and resulted in multiple estimates for some species (Table 4. 4). Growth estimates (k) produced using the VBGF (ELEFAN and NLLS methods) ranged from 1.21 to 3.38. Linear growth rates ranged from 10.01 to 40.53 mm/month. The non-linear least squares method was useful for species where a poor model fit resulted using ELEFAN, but clear cohort progressions were still observed, e.g. *Planiliza subviridis* (Figure 4. 2). No valid estimates were possible at the reach scale using the regression methods; this was because either too few observations over the study period were available, or because the cohort progressions became unclear. Reach level estimates were not possible for the majority of species analysed due to inconsistent and insufficient catch data at this scale. Additionally, the length-frequency distributions at this scale were greatly affected by the variability in spatial distributions of stocks within the estuary.

Truncated distributions (compared to estuary scale data) were also present at the reach scale. Catch data for species that had high representation across their entire length range appeared more robust to the reduction in spatial scale, e.g. *H. castelnaui* and *A. vachellii*.

Table 4. 3: Von-Bertalanffy growth of common species of fish in the Alligator Creek estuary in three reaches.

Species	Scale/reach	Rn Max	L_{inf}	K	T_0	Phi_L
Herklotsichthys castelnaui	*Estuary*	0.61	9.8	2.4	0.8	2.4
	Upstream	0.56	9.2	2.4	0.8	2.3
	Mid-estuary	0.82	10.4	1.8	0.7	2.3
	Downstream	0.45	9.9	2.4	0.7	2.4
Ambassis vachellii	*Estuary*	0.82	5.3	3.0	3.7	1.9
	Downstream	0.67	5.3	3.0	0.5	1.9
Leiognathus equulus	*Estuary*	0.57	7.7	1.2	0.8	1.9
	Upstream	0.39	7.2	1.5	0.8	1.9
	Mid-estuary	0.39	5.0	3.0	0.8	1.9
	Downstream	0.87	7.9	1.9	0.8	2.1
Sardinella spp.	*Estuary*	0.79	10.9	3.4	0.9	2.6

Table 4. 4: Linear growth rates estimated for species in the Alligator Creek estuary during 2015-16 using length frequency data. Where m = growth rate in mm increase per month.

Species	Cohort	R^2	m (mm/month)	L(intercept)	Residual SE	df
Nematalosa come	C1	0.75	22.7	29.2	8.6	37
	C2	0.89	17.7	37.2	5.5	24
Gerres spp.	C1	0.55	10.0	24.8	8.2	165
	C2	0.31	12.6	10.9	11.7	127
Acanthopagrus pacificus	C1	0.38	13.2	37.4	18.8	70
Fenneropenaeus merguiensis	C2	0.37	16.9	59.2	10.4	411
	C3	0.74	29.9	5.1	11.8	1261
	C4	0.82	40.5	-18.1	8.9	307
	C5	0.45	22.4	14.8	12.8	1337

Table 4. 5: Non-linear growth rates estimated for fish species in the Alligator Creek estuary during 2015-16 using length frequency data.

Species	Cohort	L_{inf}	K	T_0	Residual SE	df
Planiliza subviridis	*C2*	140.2	2.8	-06.6	10.6	223
Stolephorus carpentariae	*C1*	66.0	3.7	-10.4	8.7	1014

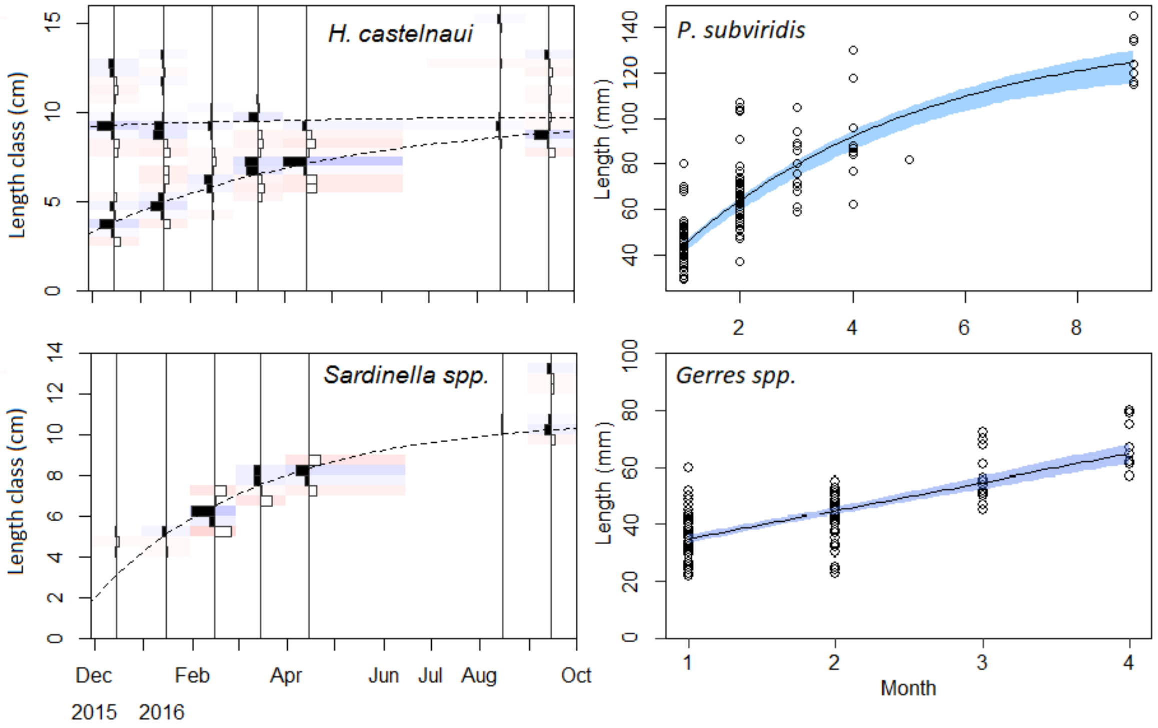

Figure 4. 2: Growth of four species of fish in the Alligator Creek estuary captured in 2015-16 estimated using ELEFAN (*H. castelnaui*, *Sardinella spp.*), NLLS (*P. subviridis*), and LLS (*Gerres* spp.). Shading on ELEFAN plots indicates scores for length classes determined by the restructuring procedure (High scored = blue shading/black bars, negative scored = red shading/unshaded bars). Shading on regression methods indicates 95% confidence limits.

4.3.2. *Testing of assumptions*

Testing of assumptions revealed that, for most species, the appropriateness of the growth function and the complete representation of species lengths in catch data were violated (Table 4. 6). The only assumption that was met for most species was that of distinct and identifiable recruitment pulses (Table 4. 6). It was also determined in analyses of normality, that most species exhibited non-normal distributions at some stage in their cohort progressions. The combined tests reveal that no species investigated in this study conformed to all of the assumptions tested (Table 4. 6). The differences between reach and estuary scale catch data were evident in *Ambassis vachellii* catch, where cohort progressions at the reach scale did not follow the VBGF and length ranges were both restricted and patchy. This was not the case at the estuary scale for this species, indicating a scale effect on catch data. Although for *L. equulus*, definition of recruitment pulses was improved at the reach scale, making clear distinction of cohorts possible in most instances, and thus a better characterisation of growth using the VBGF was achieved (Table 4. 6). In total, only three species scored higher than 80% in terms of accuracy of growth characterisation by the VBGF at the estuary scale. As normality of distributions is not assumed or required by the ELEFAN method, two species, *Herklotsichthys castelnaui* and *Ambassis vachellii*, met all tested assumptions required for growth estimation.

Table 4. 6: Degrees of violation of assumptions required for growth rate estimation by length-based methods for common species sampled in the Alligator Creek estuary. (X) indicates assumption was met, ( ) indicates assumption was violated, numerals denote degree of conformity (%).

Estuary scale	Growth adequately characterised by VBGF	Full range of lengths represented	Recruitment is in defined pulses	Normality of distributions
Herklotsichthys castelnaui	82	X	X	30
Fenneropenaeus merguiensis	60		X	42
Acanthopagrus pacificus	39			75
Planiliza subviridis	23		X	65
Nematalosa come	82		X	75
Leiognathus equulus	52			29
Ambassis vachellii	89	X	X	35
Sardinella spp.	91		X	34
Escualosa thoracata	--		X	67
Stolephorus carpentariae	48			14
Gerres spp.	44		X	29
Thryssa hamiltonii	--		X	100
Reach scale				
Herklotsichthys castelnaui	81	X	X	39
Ambassis vachellii	49		X	51
Leiognathus equulus	81		X	38

4.4. Discussion

4.4.1. *To what degree were assumptions met?*

Catch data for all species exhibited some degree of non-conformity to the assumptions tested here; namely, representation of the full range of species lengths in catch data, conformity of growth to the VBGF, and normality of length-frequency distributions. In general, the testing of assumptions revealed that growth estimates produced from the standing stock data probably included a high degree of uncertainty due to the unknown effects of these violations. It is likely estimates were somewhat biased, but the extent remains unquantified. Other assumptions were not assessed here due to their complexity and limited data available; these included size-independence of mortality, size-independence of migrations, and whether length distributions in catch data are representative of the stock (Isaac 1990). For estimates to be robust and defensible, certainty that undue biases have not been introduced are paramount. The effects of violation of assumptions are described in a number of studies (Pauly & David 1980, Brey & Pauly 1986, Pauly & Morgan 1987, Rosenberg & Beddington 1987, Wetherall et al. 1987, Francis 1988a, Rosenberg et al. 1988, Isaac 1990, Punt 2003, Drouineau et al. 2008), those relevant to this study are summarised in Table 4. 7.

Table 4. 7: Effects of violated assumptions on growth estimation by ELEFAN and regression methods used in this study.

	Assumption	Effect
1	Growth does NOT conform to VBGF	Mischaracterisation of growth, biologically unrepresentative. Reduced reliability and repeatability
2	Catch data represents restricted range of lengths	Underestimation of maximum length and overestimation of growth factor
3	Recruitment is NOT in defined pulses	Inaccurate separation of cohorts, incorrect assignment of cohorts, invalid/inconsistent cohort progression and invalid model
4	Length-frequency distributions are NOT normal	Regression methods result in biased estimates

Assumptions investigated in this study can be defined as those related to data collection and those related to biological factors. Data collection includes how the sampling design and capture method was designed and implemented to minimise biases and maximise accuracy of data representation of the population. Biological factors refer to processes, characteristics, and phenomena that have impacts on the data and analyses. For example; the range of lengths in catch data for each species is dependent on the gear type used and the sampling design, e.g. mesh size, or locations sampled. Representation of length ranges is continuous in nature, rather than categorical, and so this assumption requires additional processes to ensure its effects are known. This can be done for example by placing minimum requirements on the degree to which length ranges are represented in catch data, e.g. if a species' known length range is between 5mm (recruit size) and 300mm (median adult size), >80% of this range must be represented in the catch data prior to conducting any analyses. Although this is an arbitrary simplification, the principal enables a consistent approach to be applied and maintains known levels of uncertainty. This is important, and in the case of length ranges, inconsistent representation of length ranges can result in unreliable estimates of L_{inf} and K parameters (Berumen 2005). Conversely, the size-dependent mortality of individuals (due to natural predation effects, e.g. as described in banana prawns by Wang and Haywood (1999), or induced by harvest selectivity) does not impact on the way the population is measured (via sampling design or capture method), but it does impact the way the data are analysed. The consequences of size-dependent mortality (and emigration) are that the number of remaining fish within each length-class is heterogeneously effected over time, and therefore do not represent the growth of the cohort, rather they represent the length distribution of survivors, or those remaining in the study site. Because of this, any size or density dependence must be accounted for (Aanes et al. 2007, Brodziak et al. 2011).

In this study it was clear both biological factors and data collection methods impacted on the conformity of assumptions. Recruitment pulses of each species were important for separation of cohorts, where clearly defined pulses usually enabled separation of cohorts of the stock through time. This was an important factor for all estimation methods; ELEFAN relying on the restructuring process to accurately score cohort modes and regression methods relying on the investigator's subjective separation of cohorts. Some species- such as *L. equulus,* which exhibited a constant influx of recruits during the wet season- proved prohibitively difficult to reliably separate cohorts in much of the catch data. This issue has been recognised previously in many tropical species, and some methods have been developed to assist in separation on cohorts (e.g. Bhattacharya, mixed distribution analysis by maximum likelihood). However, even if separated using one of the less-subjective methods, identification of each cohort through time is problematic for these species, where multiple cohorts exhibiting similar distributions and abundances are present. In the case of *L. equulus,* it is possible that growth of cohorts is actually significantly faster than identified by either ELEFAN or regression. Without age-based data to validate model outputs, the likelihood of incorrect cohort tracking–and hence incorrect growth estimates–is significant. Similarly, the restriction of sampling to within estuary, and within reach scales highlighted the need to match scales of data collection to species movements and distributions. Reach scale data was highly patchy and cohort progressions were inconsistent, resulting in growth estimates being successfully generated in very few instances at this scale.

A number of assumptions could not be assessed with the available catch data, these included size-independence of mortality, whether catch data were representative of the actual population, and whether catch data were biased by gear selectivity or other methodological biases (e.g. over-representation of particular habitats). Size-independence of mortality or migration are particularly important for length-based methods. This is because these methods are actually characterising growth of the study population, rather than growth of individuals within the population. Hence, while we may assume the data represent size classes fairly over time, i.e. without preference for any particular size group, the data are also inclusive of biases introduced by individuals leaving (or being removed from) the studied area. This may occur either through mortality, or migration, and where there is an association between size and these two factors, length-frequency distributions become biased. Thus, any characterisation of growth of that population will be biased. Additionally, the targeting of sampling to within the wet and dry seasons resulted in a gap in length-frequency data in this study. This could have resulted in misidentification of cohorts during this time. Future studies should therefore avoid seasonal stratification of sampling, rather sampling should be consistently conducted for the study duration, inclusive of all seasons.

4.4.2. *Impact of spatial scale on growth rate estimation*

In most cases, the reduction in consistent catch data meant it was not possible to make comparisons of scale. Interestingly, many of the reach scale cohort progressions that were attempted exhibited apparently linear increases in modal lengths of each cohort, compared to the non-linear cohort progression observed at the estuary scale. The reduction in scale also reduced consistency of representation of length classes in data. This is highly problematic as this type of inconsistency can bias growth estimates (Berumen 2005). Despite the difficulties with reduced catch data, reach scale analysis improved cohort separation for one species, *L. equulus.* This is a potential indication that for this species, the scale at which data was collected, was better matched to the scale at which the species functions within the ecosystem. *L. equulus* probably resides and moves between habitats localised within reaches more often than movements between reaches and estuaries. Conversely, species such as *Sardinella* spp. and *Escualosa thoracata* exhibited inconsistencies and patchiness of data at the estuary scale, indicating their movements might be broader i.e. between the Alligator Creek estuary and other nearshore areas. Length frequency distributions for *Herklotsichthys castelnaui* were consistent at the estuary scale indicating this species probably frequently resides and moves between reaches but less frequently between estuaries. The impact of these variations in movement and residence patterns is that growth estimates must use data at scales that match each species, rather than applying one particular scale of investigation to all species. While this may mean estimates for some species are less easily used in management frameworks, estimates will be more reliable and accurate.

Considering the assumptions discussed here, a trade-off is evident between the benefit of linking growth rates to small spatial scales or explanatory variables, and the uncertainties of how reliable those estimates are. To assess this, we may consider the value of those estimates and the likelihood of bias and uncertainty, and hence defensibility. There is a clear need for understanding linkages between productivity and anthropogenic activities in marine ecosystems as this knowledge will support relative valuation of ecosystem services at scales relevant to management actions. It is likely that differences in growth rates between local scales such as reaches and habitats, and over time are an innate characteristic of tropical estuaries. Our ability to measure and monitor these differences is critical to the sustainable management of estuarine ecosystems and the habitats within them. Therefore, the value of conducting analyses at finer scales (reach/habitat) is supported. Linking productivity and productive capacities to explanatory factors such as habitats, flow regimes, and anthropogenic activities will require reliable and defensible estimates of growth at these small scales. However, given the issues of flawed assumptions that exist at both the whole-of-estuary, and reach scales, a large degree of uncertainty is assured at smaller scales i.e. habitats. This could result in incorrect assessment of growth rates, and in turn inaccurate valuation arising from productive capacity estimates. Not only is there a possibility for overestimation and underestimation of productive capacities, but a lack of confidence/certainty in studies where conflicting interests (e.g. from development, industry, and environmental values) are present can lead to ill-advised management actions (Poff et al. 2003) and unintended environmental outcomes (Harris & Heathwaite 2012).

4.4.3. *Are current growth rate estimation methods biologically reasonable considering the assumptions required to produce them?*

The results of this study highlight some of the issues of length-based growth estimation, particularly for stocks that have little or no prior data to validate and supplement analyses. It was evident that few of the species investigated here were adequately characterised by the VBGF using standard methods. This is problematic and indicates that either the length-frequency distributions of the cohorts in this study were not representative of the true growth of individuals within the population, or that the VBGF is not a suitable descriptor of growth for the stocks studied here. Both possibilities are just as likely, and there is no argument to say each is exclusive of the other. Most likely both are correct, leaving us with a considerable impediment to further analysis. It is possible to account for these violations in analyses, however, there are differences in the extent to which we can correct these flawed assumptions. For example, the issue of growth mischaracterisation due to inadequate descriptors, i.e. the VBGF, can be ameliorated by development and use of more appropriate functions, e.g. Gompertz, inverse-logistic (Schnute 1981, Tsoularis & Wallace 2002). However, improving the representation of true growth patterns by length-frequency data requires in-depth knowledge associations between mortality and individual size, migration and individual size, gear selectivity and efficiency and variability of growth of individuals within cohorts.

The use and appropriateness of the VBGF has been discussed in-depth by several authors (Ratkowsky 1986, Essington et al. 2001, Helser & Lai 2004, Hernandez-Llamas & Ratkowsky 2004, García & Duarte 2006, Cope & Punt 2007) and a number of alternate growth descriptors have been used to mitigate this problem (Pauly et al. 1992, Hernandez-Llamas & Ratkowsky 2004, Kimura 2008, Helidoniotis et al. 2011). Although many of these alternate growth functions have been proven more suitable for particular species and stocks e.g. Helidoniotis et al. (2011), the VBGF remains the most prevalent in current growth assessments (Katsanevakis & Maravelias 2008) despite widespread criticisms from the scientific community (Roff 1980, Sainsbury 1980, Day & Taylor 1997, Essington et al. 2001, Hernandez-Llamas & Ratkowsky 2004, Katsanevakis & Maravelias 2008). One of the advantages of using the VBGF is the ability to compare growth–using the two standardised parameters K and L_{inf} –by calculation of the growth performance index (=Log10 K + Log10 L_{inf}) (Moreau et al. 1986). This is particularly useful, and any new method would need to offer a similar metric for comparability. In practice, the prolific use and comparability of the VBGF has led to the creation of a large database from which comparisons can be made (see 'Fishbase', a global biological database on fish (Froese & Pauly 2010)). The VBGF is the only growth function present in Fishbase, and this has further encouraged its use over alternatives.

The issue that modal progressions of length-frequency distributions are not representative of actual cohort growth is also considerably difficult to deal with. Sampling is almost invariably confined to representing a spatially restricted subset of the population. Thus, for many species that move within, out of, or between habitats and estuaries, catch data can only represent a snap-shot of their lives. Movements within estuarine ecosystems are particularly problematic; for example, movement of resident and transient species within tropical estuarine ecosystems occurs on seasonal, daily, and even semi-diurnal timeframes (Garcia et al. 2003, Sheaves & Johnston 2010, Jardine et al. 2012). Additionally, the length-frequency distribution of each cohort that is represented by catch data, is shaped by a plethora of factors such as mortality, migrations and movements, gear selectivity, avoidance behaviours, recruitment, and, importantly, variations in growth of individuals. Some of these factors can be addressed by modifications to sampling design, e.g. use of multiple gear types or variations i.e. mesh sizes, to reduce selectivity. However, the effects of size-dependant mortality cannot be corrected by improving data collection, they must be thoroughly understood in order to apply corrections to data and outputs. Similarly, variation in growth between individuals is an intrinsic characteristic of populations (Rosenberg & Beddington 1987, Jobling & Koskela 1996, Mangel & Stamps 2001, Bacon et al. 2005), and so requires characterisation of growth patterns on an individual level to understand how population level estimates might be impacted. Because much of this information is not available for the basal-prey community of tropical estuaries, extreme caution should be used in describing growth patterns for these species. In these cases, the expense of age-based methods to attain reliable growth information may be justified.

4.4.4. *Conclusions*

The interplay of biological and ecological patterns expressed within estuarine fish populations have important implications for length-based growth estimation. Patterns such as aggregation behaviours, movement between and within ecosystems, and migrations due to ontogeny and environmental cues occur on multiple spatial and temporal scales. Therefore, matching of spatial scales at which populations are studied, to scales at which the patterns occur, has significant bearing on analyses of growth patterns. This study has indicated that the assumptions of two common growth estimation methods (Regression and ELEFAN) are not reasonable for many basal-prey species in a typical tropical estuarine ecosystem. Additionally, the effects of unexplained movement and migration were magnified at smaller scales of assessment. Calculation of growth rates using length-frequency methods for many of these species may remain possible only at larger spatial scales to limit assumptions within reasonable bounds. Further, the effect of scale on data quality was clearly demonstrated here, where the accuracy of tracking cohorts through time was diminished for most species at reach scales. This is important as data quality will remain a key constraint on analyses. The scale of study must therefore be appropriately tailored to the scales at which populations exist and function, including patterns of migration, movement, and residence.

The effects of various assumption violations are likely to be proportionate to the degree to which they are violated, as many are continuous in nature. This is important because, in most cases, some degree of violation will be present, but some use may be made of estimates where this can be quantified and understood. The point at which uncertainty and biases become unacceptable needs to be established to provide a more consistent approach to growth estimation methods across all species and ecosystems. Additionally, the cumulative and interactive effects of multiple assumptions require investigation to further improve defensibility and reliability of estimates. My results exemplify the broader issues of the use of standardised growth characterisations (e.g. VBGF) for under-studied fisheries. This study also highlights the need to develop more biologically reasonable descriptions of growth patterns, which can be applied to less well-studied species such as those in the basal-prey community.

Despite the impediments discussed here, the uncertainties and biases of length-based estimates should not entirely prevent growth estimation of estuarine populations. Rather, the uncertainties, biases, and assumptions should be recognised to make estimates meaningful and defensible. This recognition has largely been absent in previous works, and it is likely that many of the foundational estimates used in fishery management are unreliable and probably inaccurate. There is clear need for recognition of the limitations, accuracies, and uncertainties in this area to ensure management decisions are robust and defensible. Quantification of the biases and effects introduced by the non-conformity to assumptions, and the effectiveness of various mitigation strategies should be a constant focus of fishery research. Further, my research has highlighted a need to understand and match the scales at which measurement of population parameters are most accurate and useful to the scales at which species function within and between ecosystems.

Chapter 5: General discussion and conclusions

5.1. Suitability of assumptions to population studies in tropical estuaries

The emerging interest in habitat-specific productivity assessment and valuation relies on some of the broader assumptions investigated in this thesis. Principally, that biological traits and relationships can actually be characterised reliably and accurately at small defined spatial units i.e. reaches and habitats. This has previously been possible in other situations e.g. in temperate regions and other aquatic ecosystems (Hubert & Rahel 1989, Johnson et al. 1994, Garcia et al. 2003, Harvey et al. 2005). However, in the case of the meso-tidal, structurally and hydrologically complex systems that topical estuaries often are, my studies suggest there is a large body of work still required to achieve this. Moreover, because of the data-limited nature of these ecosystems, a practicable, efficient approach is needed. The studies of spatial-characterisation and growth-characterisation demonstrated that while standard methods of data collection an analysis can be employed in an efficient manner, the assumptions and limitations of current methods were not suited to the tropical estuarine context.

The specific assumptions of most concern were related to the use of measures of central tendency in multivariate analyses, representative characterisation of growth by the VBGF, and the translation of standing stock data from scales of observation to scales of interpretation. Results from chapter 3 demonstrated that measures of central tendency did not characterise trends in data without obscuring real differences in patterns of abundance and biomass. Therefore, the assumption that central tendency provides a representative means of characterising abundance patterns for multivariate analyses was invalid. The assumption that the VBGF is an accurate mathematical representation the patterns of growth of basal-prey fish and crustacean species in tropical estuaries was also invalid. Chapter 4 revealed that growth patterns exhibited by most species and populations in the Alligator Creek estuary did not follow the patterns of growth described by the VBGF. Importantly, the assumption that both spatial and growth patterns of standing stocks could be investigated and characterised at small spatial scales with a consistent level of accuracy was incorrect. Analyses of growth rates and spatio-temporal abundance patterns revealed that analyses must be conducted at the scales within which populations function, and within which movement patterns typically occur.

Although there is a tendency to think of assumption validity as binary i.e. valid or invalid, in reality many are somewhat valid, or somewhat violated. To further explain this, some assumptions are made in relation to characteristics described in categorical, or binary terms i.e. whether a statement is true or false, e.g. 'are the replicate samples independent?' Other assumptions however are better described by a continuum of values, i.e. Fuzzy Logic (Zadeh 1965, Zadeh 1975), or in other words 'degrees of truth' e.g. 'how accurate was the growth function for this species?'. The assessments of both normality and growth characterisation used in my study, which were expressed as a percentage, are by nature fuzzy. This is important because the degree to which data are non-conforming will affect the degree of potential bias, and uncertainty created in the analyses. To make some use of estimates in the absence of meaningful quantification of these impacts, we can speculate that in cases where critical assumptions have been substantially violated, outputs should be determined as completely invalid. For example, in the case of growth estimates for a number species made in Chapter 4, the VBGF was not a suitable characterisation of growth of the populations. Therefore, any growth estimates are completely invalid. However, for the species *Herklotsichthys castelnaui*, for which the only violation was the normality of length-frequency distributions, the estimate may actually be considered useable and somewhat accurate. This is because the assumption of normality is not critical to the operation of ELEFAN (Pauly & David 1980, Isaac 1990, Gayanilo & Pauly 1997, Gayanilo et al. 2005).

5.2. Practical limitations to analysis and treatment of standing stock data for productivity measurement

Tropical estuaries present a particularly challenging combination of practical, biological, and ecological settings for collection and analysis of data. The practical and logistical difficulties of sampling in a standardised approach across the diverse range of habitats and structural settings have resulted in the current data-limited situation managers and scientists are facing. This is pervasive throughout tropical regions, with little data often available to support management strategies and settings (Roberts & Polunin 1991, Johannes 1998). The standing stock data collected in my study of the Alligator Creek estuary represents a practicable approach to this problem by using a dynamic and efficient capture method. However, the characteristics of the data produced were often extreme in nature and difficult to treat. Despite the high replication used, variability in occurrence and abundance of many species between trips and reaches resulted in highly confounded ecological interpretations, and characterisation of biological traits of questionable reliability. The inconsistency of traditional stock metrics (CPUE, biomass density, POE) to reliably characterise spatial and temporal patterns of the basal-prey community may also indicate that these metrics, are not well suited to measure or translate ecological patterns in these circumstances. Without metrics specifically tailored to understanding underlying and complex ecological relationships in cases of extreme variability, the standing stock approach may not result in useable and meaningful characterisations of the basal-prey community in complex meso-tidal estuaries.

5.3. Can we reliably characterise fish and penaeid populations at small spatial scales using traditional metrics?

The importance of scale in understanding and measuring responses to ecosystem and habitat alterations is a key feature when designing and implementing ecological and fisheries studies (Costanza & Maxwell 1994, Minns et al. 1996). Estimates of productivity should be made at meaningful and relevant spatial scales to provide the most benefit to management and impact assessment. This may mean that some studies are tailored to seascape and estuary scales, and others are tailored to within-estuary scales. There is however a trade-off between translating ecological and biological patterns across spatial scales, and making ecological interpretations and estimating biological parameters with adequate levels of reliability. This trade-off was clearly demonstrated by my attempts to estimate growth rates at both reach and estuary scales. For most species, examination of data at the reach scale resulted in unusable estimates. While reach scale or even habitat scale growth estimates would be extremely useful for managers, these estimates are completely unreliable. However, at the estuary scale, for some species, reliability may be adequate. This trade-off occurred because underlying patterns of movement and residence of individuals within the population were occurring at larger scales, and thus reach scale data was unable to represent the whole population of each species most of the time. Similarly, many of the basal-prey species studied here exhibited highly aggregated, patchy distributions. Therefore, when attempts were made to characterise abundance patterns at reach and estuary scales using measures of central tendency, error and variance were extreme, and differences between spatial and temporal units were indistinguishable.

The difficulties in studying occupancy, and abundance patterns of fish and penaeid populations in the tropical estuarine context is linked to the complexity of these ecosystems. There are pervasive interactions of numerous factors which affect the way communities utilise spatial units, and these operate on multiple spatial scales. Fish and penaeid populations are often highly mobile and selective of the diverse range of habitats within the estuarine system (Robertson & Duke 1990a, Vance et al. 1998, Barletta et al. 2003, Sheaves & Johnston 2009). Not only do organisms preferentially select habitats based on physical and biological characteristics e.g. food availability (Shervette & Gelwick 2008) and refuge availability (Vance et al. 2002), their occupancy is also dependent on the context of each habitat e.g. position with the system in relation to freshwater inputs or coastal connectivity (Vance et al. 1998, Vance et al. 2002, Roth et al. 2008, Bradley et al. 2019). Occupancy and abundance of fish and prawns is similarly influenced by environmental factors such as turbidity, temperature, salinity, hydrogeology and hydrology, and habitat availability (Newton 1996, Barletta et al. 2005, Robins et al. 2005a, Blanck et al. 2007). The culmination of various factors into a combined causal mechanism which determines the presence, absence or abundance of particular species within spatial and temporal dimensions has been termed a 'causal thicket' (Harris & Heathwaite 2012). These are largely unknown to the observer and are prohibitively difficult to analyse and quantify due to their complexity. Mostly, the effects of causal thickets are recognised as stochasticity, or natural variation. This means that at smaller spatial scales we may not be able to account for factors which function at larger scales.

The studies I have conducted here show that, although standing stocks can be examined at small spatial scales, some processes operate at larger scales (i.e. growth and development of stocks), and that these scales may be incongruous with the scales at which anthropogenic impacts occur. Spatially defined factors (i.e. habitats) are likely to be important determinants of productivity. However, there are also several other factors that influence productive capacities that are spatially variable in nature, but are not correlated or causally linked to any of these spatial factors. To further complicate this issue, even if we could for instance accurately characterise patterns of abundance and occupancy between habitats, it would be difficult to infer why these differences occur, and thus apply the knowledge to other areas, systems or scales. This predicament has been exemplified for artificial reefs in temperate regions by Bohnsack (1989). Their investigation showed that observed increases in abundance of fish associated with artificial reef habitats did not result in perceived production benefits, but were a result of context dependant behavioural preferences (Bohnsack 1989). In the tropical estuarine context, we are still not able to accurately characterise differences in occupancy between reaches for the bulk of standing stock biomass.

Future attempts to estimate spatially-linked productivity will require biological parameters such as growth to be estimated at the scales at which populations exist and function. For many species in the basal-prey community of tropical estuaries, this will be at estuary or coastal seascape scales in order to encompass movement and migration patterns. For characterisation of abundance and spatial usage patterns, a completely different approach may be needed. This should incorporate information of both the patchiness of distributions, and abundance. This could be achieved for example by combining probability of encounter with catch per unit effort to create an index of relative usage patterns across spatial and temporal units. These two approaches may be combined, retaining the scales at which measurements are most reliable, i.e. applying a single growth rate for a species across multiple reaches or estuaries. Combining this information with whole of system biomass and relative usage patterns could then enable estimates of relative productivity value for the estuary of interest. Rather than applying any new metric to defined scales of interpretation, a more flexible approach to spatial characterisation might be required. For example, heat maps of indices could be applied to an area of interest to first examine what spatial scales are most appropriate for further analysis.

5.4. Conclusions

Investigating fish and penaeid populations typical of tropical estuaries through a lens of restricted spatial scale demonstrated some of the practical difficulties of small-scale productivity assessment. The studies I conducted highlighted the limitations of current statistical approaches to population ecology, when faced with challenging practical scenarios. The issues presented by extreme data variability were not easily treated, and traditional methods resulted in confounded interpretations and loss of information. Therefore, there is a clear need to question the reliability of population characterisations in marine ecosystems. Smaller spatial scales exacerbated the difficult-to-treat effects of variability beyond bounds of reliability. It should also be considered whether we should be changing our management approaches to fit the scales at which we can make reliable judgements, rather than changing the scales of inquisition to fit those of management.

Current methods used to characterise growth and spatial patterns of fish populations depend on high quality data and rely on specific assumptions about the species biology and the data itself. In the tropical estuarine context, catch data for the basal-prey community is difficult to reconcile with either of these requirements. My research has shown that there is a mismatch of assumptions and data requirements to the populations in this context. The implications of this research are pertinent to number of areas of research and management applications. For example, studies such as Scott et al. (2000), Jackson et al. (2015), Taylor et al. (2018), make use of stock spatio-temporal usage patterns to equate economic values to habitat-fishery linkages. While this may be reliable in temperate situations, the practical limitations to data collection and analysis in the topical estuarine context mean that significant uncertainties would inevitably be attached to any conclusions. Similarly, recent attempts to explain growth variability in whole communities i.e. multiple species and populations e.g. (Morais & Bellwood 2018), have used growth estimates from an array of studies. The underlying assumptions of this research is that the growth estimates used are actually valid, and that the growth functions used are accurate descriptors of growth of species and populations. In many cases these assumptions are probably not valid, particularly for tropical estuarine and coastal ecosystems, and so caution should be used in these instances.

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Appendices

Chapter 3 appendix

Table A3. 1: Fish and penaeid species collected during 2015 – 2016 standing stock biomass sampling, including measured species metrics for the total collected population. * indicates species selected for multivariate analyses.

Family	Species	Count	Mean length (mm)	Length range (mm)	Mean weight (g)	Weight range (g)
Ambassidae						
	*Ambassis vachellii**	2178	43	12 - 108	1.2	0.02 - 113
Belonidae						
	*Strongylura strongylura**	26	243	74 - 402	22.6	0.5 - 85.5
Butinae						
	Butis melanostigma	8	49	30 - 65	1.3	0.26 - 2.77
Carangidae						
	Caranx sexfasciatus	12	116	75 - 210	31.0	7.11 - 137
	*Scomberoides lysan**	42	65	28 - 111	3.3	0.26 - 13.15
Clupeidae						
	*Escualosa thoracata**	517	63	39 - 92	2.8	0.48 - 132.5
	*Herklotsichthys castelnaui**	2290	72	25 - 150	4.9	0.21 - 37.32
	Herklotsichthys lippa	8	121	95 - 140	24.0	9.98 - 35.91
	*Nematalosa come**	145	98	40 - 161	15.6	0.69 - 56.41
	Sardinella albella	1	60	60 - 60	1.8	1.8
	*Sardinella spp.**	307	72	41 - 134	7.1	0.71 - 365.8
Drepaneidae						
	Drepane punctata	1	195	195	234.5	234.5
Engraulidae						
	Thryssa aestuaria	83	73	32 - 179	4.4	0.36 - 43.13
	*Thryssa hamiltonii**	312	73	34 - 123	2.9	0.22 - 12.84
	Thryssa setirostris	12	62	52 - 103	1.8	0.73 - 8.14
	Thryssa sp.	4	54	52 - 56	0.9	0.75 - 0.95
	*Stolephorus carpentariae**	1159	49	15 - 165	1.2	0.04 - 55.90
Ephippidae						
	Platax batavianus	1	175	175	172.8	172.8
Gerridae						
	*Gerres spp.**	359	48	14 - 147	2.8	0.03 - 49.16
Gobiidae						
	Acentrogobius sp.	10	49	30 - 82	1.8	0.29 - 5.99
Haemulidae						
	Pomadasys argenteus	14	139	57 - 257	67.5	1.99 - 352.4
	*Pomadasys kaakan**	90	64	35 - 127	5.6	0.62 - 30.22
Hemirhamphidae						
	Arrhamphus sclerolepis	26	127	97 - 160	10.7	4.25 - 21.50
	*Zenarchopterus buffonis**	226	158	20 - 231	9.9	0.10 - 28.28
Latidae						
	Lates calcarifer	1	460	460	1312.2	1312.2
Leiognathidae						
	Equulites elongatus	3	48	46 - 50	1.5	1.36 - 1.58
	Eubleekeria splendens	37	40	19 - 58	1.2	0.11 - 3.27
	Gazza minuta	57	56	23 - 91	3.6	0.23 - 11.92
	*Leiognathus equulus**	2720	29	10 - 106	0.9	0.02 - 22.43
	*Nuchequula gerreoides**	576	29	12-85	0.6	0.02 - 10.90
	*Secutor ruconius**	209	31	16 - 54	0.7	0.07 - 2.96
Lethrinidae						

Lethrinus genivittatus	2	63	57 - 69	3.6	2.55 - 4.60
Lethrinus laticaudis	1	68	68	4.5	4.46
Lutjanidae					
Lutjanus argentimaculatus	1	168	168	70.2	70.24
Lutjanus carponotatus	2	51	48 - 53	2.0	1.53 - 2.50
Lutjanus ehrenbergii	1	28	28	0.4	0.38
Lutjanus johnii	1	35	35	0.7	0.68
Lutjanus russellii	10	76	42 - 130	9.1	1.09 - 34.22
Lutjanus sp.	6	60	44 - 75	3.4	1.08 - 6.65
Megalopidae					
Megalops cyprinoides	7	326	235 - 374	304.3	106 - 479.9
Monacanthidae					
Paramonacanthus otisensis	1	68	68	5.6	5.64
Mugilidae					
*Planiliza subviridis**	269	72	29 - 250	10.4	0.2 - 314.3
Ellochelon vaigiensis	1	271	271	303.7	303.7
Moolgarda cunnesius	9	141	79 - 208	46.6	6.65 - 118.4
*Mugil cephalus**	62	97	11 - 245	27.4	0.02 - 180
Valamugil buchanani	8	200	106 - 340	172.4	14.52 - 484
Mullidae					
Upeneus vittatus	3	63	57 - 67	3.1	2.31 - 4.13
Paralichthydae					
Pseudorhombus arsius	9	96	32 - 209	25.8	0.33 - 102.5
Penaeidae					
*Fenneropenaeus merguiensis**	3689	70	20 - 131	2.2	0.02 - 12.83
Penaeus esculentus	1	80	80	3.4	3.44
Penaeus monodon	15	53	16 - 98	1.3	0.05 - 5.59
Platycephalidae					
Platycephalus fuscus	1	34	34	0.2	0.21
Platycephalus indicus	2	58	55 - 61	180.0	1.17 - 358.9
Polynemidae					
Polydactylus macrochir	21	26	21 - 32	0.1	0.07 - 0.27
Pseudomugilidae					
Pseudomugil signifer	23	33	23 - 43	0.4	0.14 - 0.84
Scatophagidae					
Scatophagus argus	2	117	34 - 200	175.5	1.57 - 349.4
Selenotoca multifasciata	16	59	13 - 265	64.3	0.1 - 492.6
Sciaenidae					
Johnius borneensis	1	59	59	3.0	3.02
Scombridae					
Scomberomorus commerson	2	65	50 - 80	2.0	0.74 - 3.22
Seregestidae					
*Acetes australis**	500	28	13 - 39	1.2	0.02 - 97.14
Serranidae					
Epinephelus coioides	1	286	286	315.4	315.4
Siganidae					
*Siganus vermiculatus**	36	57	24 - 214	13.0	0.19 - 304.7
Sillaginidae					
Sillago maculata	8	71	65 - 84	3.2	2.26 - 5.47
*Sillago sihama**	68	102	25 - 187	11.7	0.87 - 51.34
Sparidae					
Acanthopagrus australis	1	163	163	75.8	75.75
*Acanthopagrus pacificus**	101	89	30 - 262	28.6	0.13 - 379.9
Sphyraenidae					
Sphyraena barracuda	2	105	104 - 106	4.8	4.62 - 5.02
Tetradontidae					
Arothron manilensis	1	36	36	1.7	1.66
Tetraodontidae					
Dichotomyctere erythrotaenia	1	51	51	3.9	3.89

*Tetractenos hamiltoni**	57	39	14 - 162	6.9	0.08 - 121.9
Tetrarogidae					
Paracentropogon vespa	3	39	34 - 44	1.1	0.64 - 1.56
Toxotidae					
*Toxotes chatareus**	78	154	19 - 261	108.8	0.13 - 370.1

Table A3. 2: Average biomass and numeric density of the most abundant fish and penaeid species in Alligator Creek 2015 – 2016, measured using standing stock cast net method, includes relative percent contribution to total biomass density, () = standard error, (--) indicates standard error < 0.001.

Species	Biomass density (g/m²)	Percent of biomass density	CPUE (n/m²)	Percent of CPUE
Other sp	1.10 (0.30)	17.7	0.039 (0.003)	2.7
Herklotsichthys castelnaui	1.05 (0.42)	16.9	0.204 (0.026)	13.8
Toxotes chatareus	0.79 (0.28)	12.7	0.007 (0.001)	0.5
Fenneropenaeus merguiensis	0.74 (0.23)	11.9	0.350 (0.046)	23.7
Acanthopagrus pacificus	0.27 (0.07)	4.3	0.009 (0.001)	0.6
Planiliza subviridis	0.27 (0.05)	4.3	0.024 (0.003)	1.6
Nematalosa come	0.23 (0.08)	3.8	0.014 (0.002)	1.0
Leiognathus equulus	0.23 (0.07)	3.7	0.241 (0.025)	16.3
Zenarchopteris buffonis	0.21 (0.05)	3.4	0.021 (0.002)	1.4
Ambassis vachellii	0.20 (0.06)	3.2	0.185 (0.024)	12.5
Sardinella spp.	0.19 (0.09)	3.0	0.027 (0.005)	1.8
Mugil cephalus	0.15 (0.06)	2.4	0.006 (0.001)	0.4
Escualosa thoracata	0.14 (0.12)	2.3	0.050 (0.016)	3.4
Stolephorus carpentariae	0.13 (0.04)	2.1	0.109 (0.015)	7.4
Gerres spp.	0.10 (0.02)	1.6	0.033 (0.003)	2.2
Silago sihama	0.08 (0.02)	1.3	0.007 (0.001)	0.5
Thryssa hamiltonii	0.07 (0.03)	1.1	0.024 (0.004)	1.6
Pomadasys kaakan	0.05 (0.02)	0.8	0.008 (0.001)	0.6
Strongylura strongylura	0.05 (0.02)	0.8	0.002 (--)	0.2
Acetes australis	0.04 (0.02)	0.7	0.040 (0.007)	2.7
Siganus vermiculatus	0.04 (0.02)	0.6	0.003 (--)	0.2
Tetractenos hamiltoni	0.04 (0.02)	0.6	0.005 (0.001)	0.4
Nuchequula gerreoides	0.03 (0.008)	0.5	0.048 (0.008)	3.2
Scomberoides lysan	0.01 (0.004)	0.2	0.004 (--)	0.2
Secutor ruconius	0.01 (0.005)	0.2	0.017 (0.003)	1.2
Total	**11.72**	**100**	**2.78**	**100**

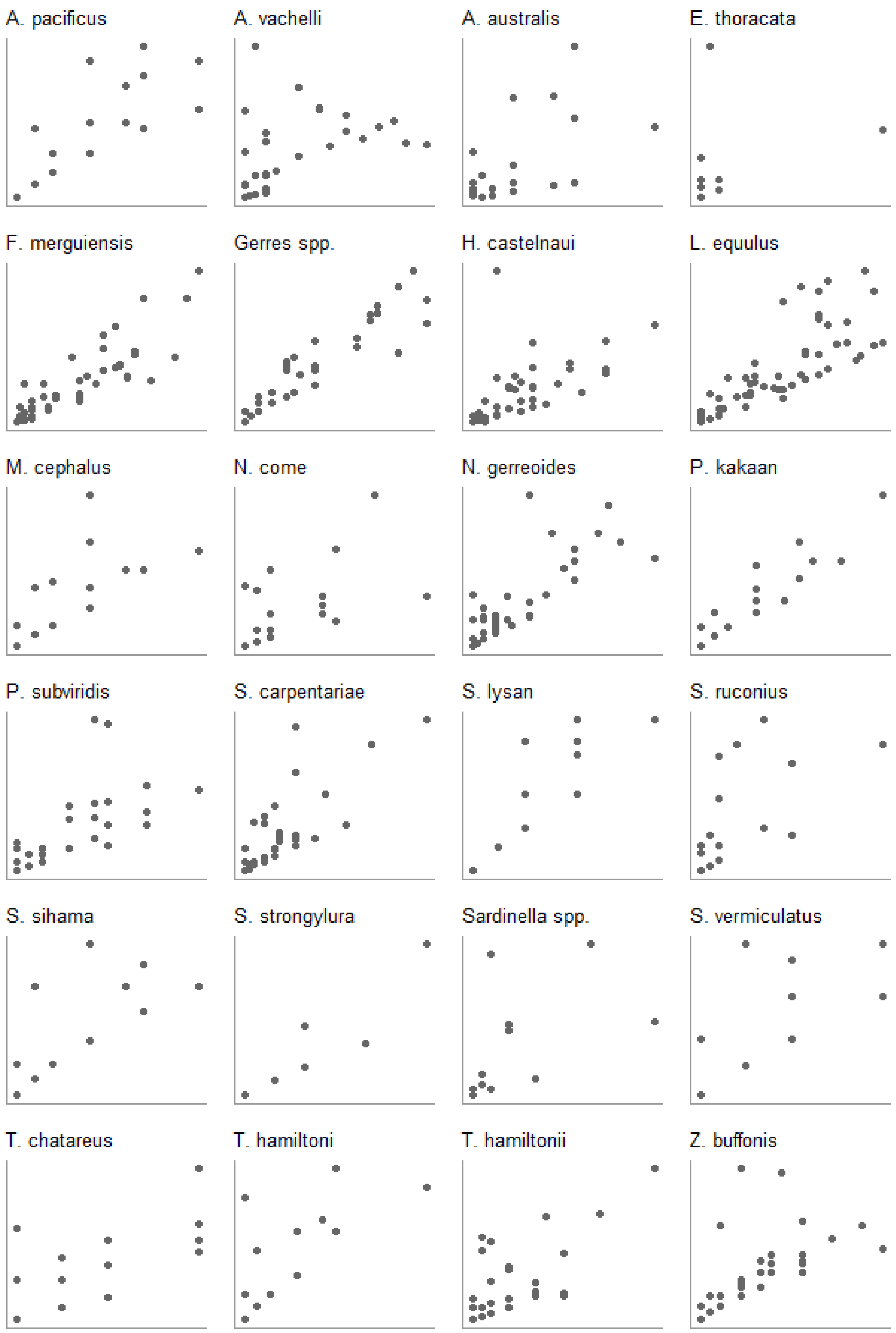

Figure A3. 1: Scatterplots of probability of encounter (POE) vs mean catch per unit effort (CPUE) for 24 selected species from the Alligator Creek estuary. Relationships used to demonstrate aggregation/schooling characteristics of species exhibited in standing stock data.

Table A3. 3: non-Metric Multidimensional Scaling of catch data metrics with resultant stress values. Coefficients used include Bray-Curtis, and Sorensen, 500 random starts applied to all analyses, standardisation applied to vectors (Row-standardisation).

Species	Metric	Transformation	Standardisation	coefficient	Stress
24	CPUE	NO	NO	Bray	0.15
24	CPUE	NO	Yes	Bray	0.21
24	CPUE	SQRT	NO	Bray	0.07
24	CPUE	SQRT	Yes	Bray	0.07
24	CPUE	Log	NO	Bray	0.031
24	CPUE	Log	Yes	Bray	0.036
24	CPUE	PA	NO	Sorensen	0.2
24	CPUE	PA	YES	Sorensen	0.2
24	CPUE	PA	YES	Bray	0.085
24	BD	NO	NO	Bray	0.22
24	BD	NO	Yes	Bray	0.25
24	BD	SQRT	NO	Bray	0.10
24	BD	SQRT	Yes	Bray	0.12
24	BD	Log	NO	Bray	0.052
24	BD	Log	Yes	Bray	0.069
24	POE	NO	NO	Bray	0.16
24	POE	SQRT	NO	Bray	0.036
24	POE	Log	NO	Bray	0.009
10	CPUE	NO	NO	Bray	0.15
10	CPUE	NO	Yes	Bray	0.21
10	CPUE	SQRT	NO	Bray	0.064
10	CPUE	SQRT	Yes	Bray	0.057
10	CPUE	Log	NO	Bray	0.03
10	CPUE	Log	Yes	Bray	<0.001
10	CPUE	PA	NO	Sorensen	0.17
10	CPUE	PA	YES	Sorensen	<0.001
10	BD	NO	NO	Bray	0.2
10	BD	NO	Yes	Bray	0.22
10	BD	SQRT	NO	Bray	0.05
10	BD	SQRT	Yes	Bray	0.06
10	BD	Log	NO	Bray	0.02
10	BD	Log	Yes	Bray	0.05
10	POE	NO	NO	Bray	0.16
10	POE	SQRT	NO	Bray	0.025
10	POE	Log	NO	Bray	0.006
Trip 11 (Raw)					
24	Abundance	SQRT	NO	Bray	0.08
Trip 16 (Raw)					
24	Abundance	SQRT	NO	Bray	0.06
24	Abundance	PA	NO	Bray	0.04
24	Abundance	PA	NO	Sorensen	0.22

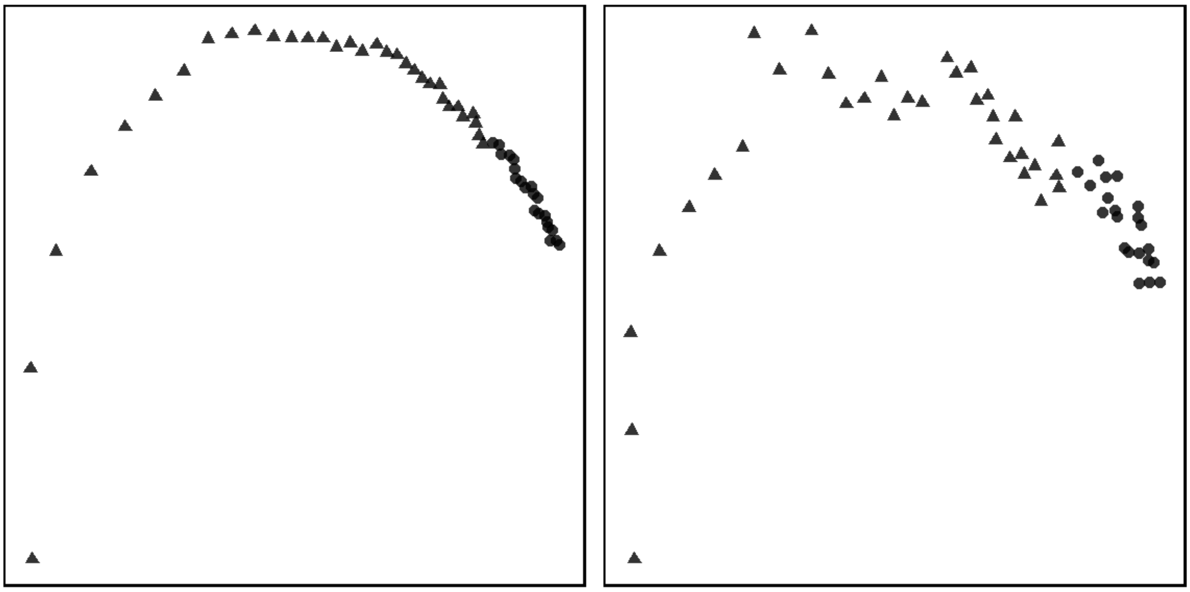

Figure A3. 2: Non-metric MDS ordination plot of POE of common fish and penaeid species in the Alligator creek estuary throughout the 2015-16 wet season and 2016 dry season. Plot (Left): POE is Log transformed, stress = 0.007. Plot (Right): POE data is square root transformed, stress = 0.027, Bray-Curtis dissimilarity applied to data in both cases. Markers: triangles = wet season samples, circles = dry season samples.

Chapter 4 appendix

Table A4. 1: Population parameters for synthetically generated length-frequency catch data. Parameters set according to VBGF. K = growth, CV = coefficient of variation, Linf = maximum median length, C = seasonal oscillation.

K	K (CV)	Linf	Linf (CV)	C
2.4	0.3	9.6	0.18	0

Table A4. 2: Evaluation parameters for VBGF characterisation assumption. Lmax difference = difference between modelled and actual maximum median length of species/population, relative fit = difference in model fit between Alligator Creek estuary catch data and synthetic population catch data. Lmax difference not calculated for linear growth models.

Method	Species	Reach	Cohort	Lmax difference (%)	Relative fit (%)	Final score
ELEFAN	*A. vachellii*	*E*	All	10	89	89
ELEFAN	*A. vachellii*	*DS*	All	10	73	81
ELEFAN	*H. castelnaui*	*E*	All	2	66	82
ELEFAN	*H. castelnaui*	*US*	All	4	61	78
ELEFAN	*H. castelnaui*	*MS*	All	8	89	91
ELEFAN	*H. castelnaui*	*DS*	All	3	49	73
ELEFAN	*L. equulus*	*E*	All	57	62	52
ELEFAN	*L. equulus*	*US*	All	60	42	41
ELEFAN	*L. equulus*	*MS*	All	72	42	35
ELEFAN	*L. equulus*	*DS*	All	56	95	69
ELEFAN	*Sardinella spp.*	*E*	All	3	86	91
NLLS	*E. thoracata*	*E*	2	17	29	56
NLLS	*S. carpentariae*	*E*	1	9	4	48
NLLS	*P. subviridis*	*E*	2	62	8	23
LLS	*A. pacificus*	*E*	1	--	39	39
LLS	*F. merguiensis*	*E*	2	--	37	37
LLS	*F. merguiensis*	*E*	3	--	74	74
LLS	*F. merguiensis*	*E*	4	--	82	82
LLS	*F. merguiensis*	*E*	5	--	45	45
LLS	*Gerres spp.*	*E*	1	--	55	55
LLS	*Gerres spp.*	*E*	2	--	32	32
LLS	*N. come*	*E*	1	--	74	74
LLS	*N. come*	*E*	2	--	89	89

Table A4. 3: Source of Lmax parameter estimates for assumption testing.

Species	Source for Lmax estimate
Ambassis vachellii	Catch data
Herklotsichthys castelnaui	Catch data
Leiognathus equulus	Sousa and Gjøsaeter (1987)
Sardinella spp.	Catch data
Escualosa thoracata	Abdussamad et al. (2018)
Stolephorus carpentariae	Catch data
Planiliza subviridis	Ingles and Pauly (1984)

Acanthopagrus pacificus	Iwatsuki et al. (2010)
Fenneropenaeus merguiensis	Holthuis (1980)
Gerres spp.	El-Nasr (2017)
Nematalosa come	Catch data

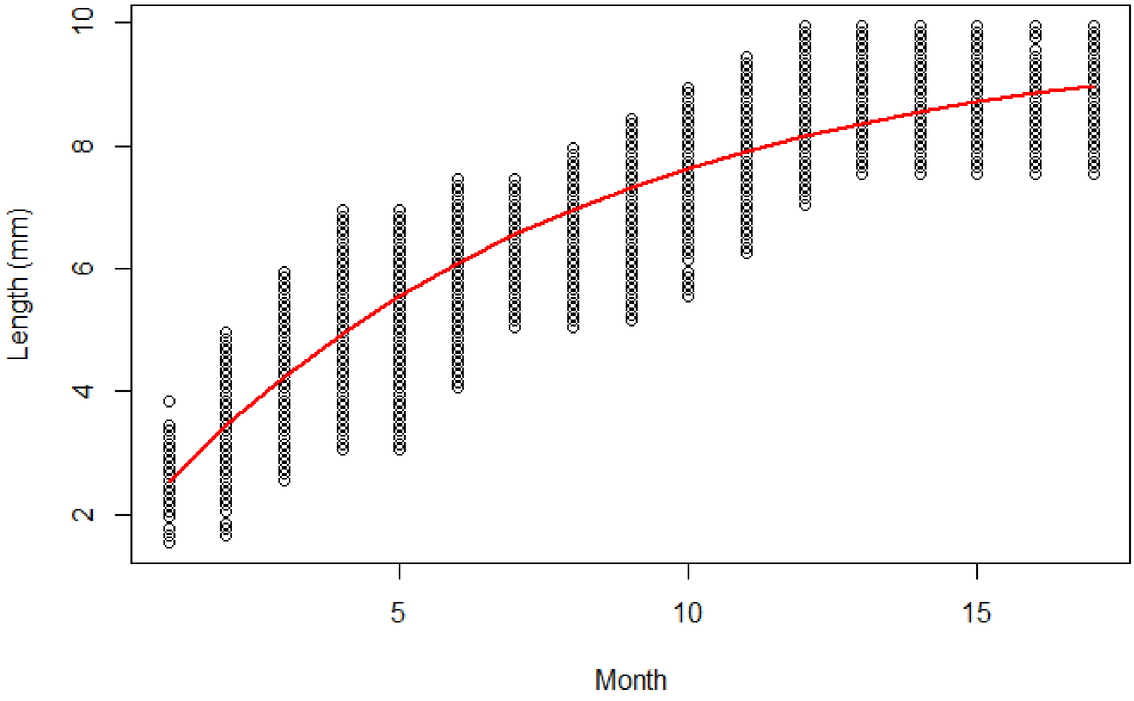

Figure A4. 1: Growth model for synthetic length-frequency catch data using Non-Linear Least Squares method.

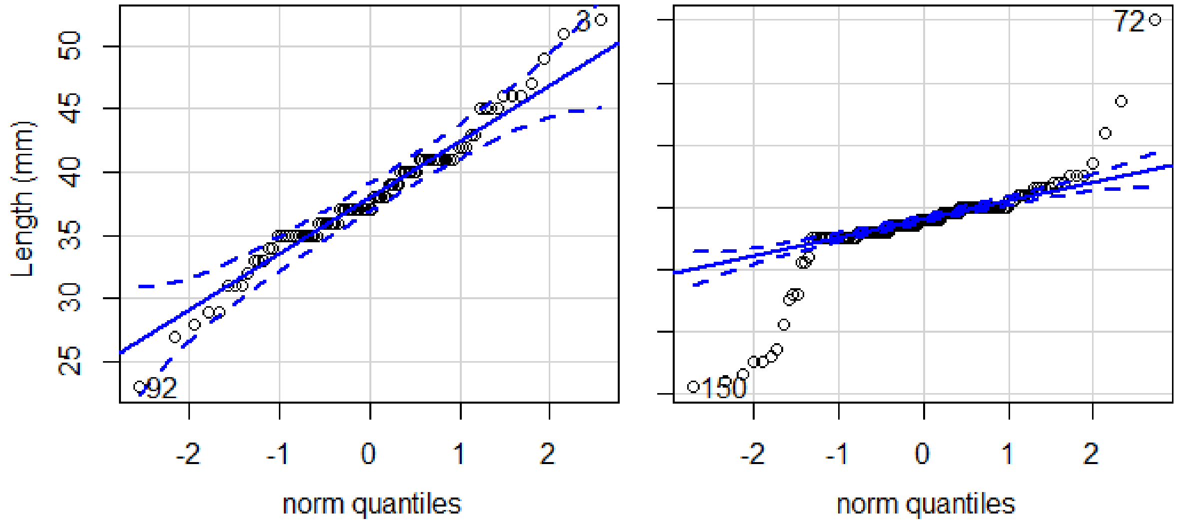

Figure A4. 2: Example Q-Q plots for tests of normality of length-frequency distributions used in growth estimation. Left panel = Normal, right panel = non-normal. Left panel = Ambassis vachellii Cohort 1, downstream, Dec-2015. Right panel = Ambassis vachellii Cohort 1, downstream, Mar-2016.