Seasonal and spatial variation of *Nicon aestuariensis* (Polychaeta: Nereididae) at the Manawatu Estuary, New Zealand

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Abstract

Linking population dynamics with spatial distributions is important to gain more knowledge of species ecology. In this thesis, I studied seasonal population dynamics and the spatial distribution of *Nicon aestuariensis* (Nereididae: Polychaeta), the dominant intertidal polychaete worm at the Manawatu Estuary, North Island, New Zealand. Monthly core samples taken from September 2009–September 2010 found no evidence for clear seasonal cycles in density or biomass. The average annual biomass was 6.3 g of ash-free dry mass per m^2 which is reasonably low compared to other polychaete-rich estuaries worldwide. Population size distributions showed some evidence of multiple size-cohorts, with a peak in juvenile *Nicon* during May. Heteronereids (reproductives) were present in samples from December – March, suggesting a slightly later reproductive period than documented at the Avon-Heathcote Estuary, South Island, in the 1960s. Morphological changes were evident as worms developed into heteronereids. Their width increased and length reduced. Reduced body mass of heteronereids implies high energy demands occur during these morphological changes. I also tested the role of environmental factors in determining the spatial distribution of *Nicon aestuariensis*. The proximity to the nearest channel was found to be the most important variable determining *Nicon's* distribution. Overall, 34% of the density variation of *Nicon* and 33% of *Nicon* biomass was explained by proximity to channel. When *Nicon* were separated into different size classes, no variables measured were able to explain the distribution of juveniles. Large *Nicon* were related to proximity to nearest channel and sediment organic matter. These findings are of importance to the ongoing research currently undertaken at the Manawatu Estuary.

Acknowledgements

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Thanks to Geoff Read, NIWA, for confirming the identification of *Nicon aestuariensis* at the Manawatu estuary.

Collecting monthly samples from the estuary was the main part of this research. I would like to thank Nicola Powell, Paul Boyce, Jesse Conklin, Phil Battley and Jimmy Choi for helping me with field work.

I would like to acknowledge Rachel Summers for her assistance with using GIS to create maps to show the variation throughout the estuary. This would have been even more difficult than it already was without her help and ideas throughout Chapter 3.

Finally, I would like to thank my supervisors, Phil Battley and Murray Potter for their ideas and constructive feedback throughout this research.

Preface

This thesis has been written and organised as self-contained chapters that will act as submissions to peer-reviewed scientific journals. Because of this, each chapter is written as a fully-referenced paper, which may cause some overlap of material. Both chapters present a unique aspect of polychaete biology.

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CHAPTER ONE

General Introduction

General Introduction

1.1 Estuaries

Estuaries are extremely demanding environments due to their link between freshwater and marine environments (McLay, 1976). They can have rapid environmental change due to both the regular, periodic cycles produced by the sea and also flooding events produced from the river (McLay, 1976). Extensive mixing occurs between the freshwater and marine environments. As a result, they are regions where environmental parameters are likely to be extremely variable (McLay, 1976). Estuaries are considered to be amongst the most productive ecosystems, largely due to their high levels of nutrients (De Villers, et al., 1999). As a result of these nutrient levels, estuaries can contain very high densities of invertebrates (Day, 1981). Being located between two very different environments, estuaries can be a focal point for human impacts (McLay, 1976). The communities within an estuary are crucial to the survival of the ecosystem, and in order to manage them we must understand how they function (Hutchings, 1998).

1.1.1 Intertidal systems

Estuaries are extremely productive and contain a diverse range of species. These species have evolved specialisations that have enabled them to live in such a challenging environment (van de Kam et al., 2008). Primary producers are a prominent feature comprising a range of pinnate diatoms, blue-green algae, and flagellates (Fenchel, 1978; Cahoon, 1999). Salt marshes are also a common feature, with a wide distribution in temperate zones. Studies have shown that salt marshes are among the most productive plant communities, and play important roles within an estuarine system (Knox, 2001). This is partly because they provide both a food source and refuge for inhabitants (Kneib, 1984). Zooplankton are also found in estuarine waters, however they are limited by this system. Turbidity reduces their production, thus limiting food availability to the entire system. The

currents within a shallow estuary also limit zooplankton abundance by carrying them out to sea (Knox, 2001). The intertidal environment is important to consider as this will affect the distribution of many fauna. Most estuaries face high levels of nutrient enrichment which increases the production of organic matter or algal blooms (Connell and Gillanders, 2007). This high level of organic matter results in increased decomposition, which uses oxygen. If the sediment does not obtain enough flushing with freshwater then the level of oxygen within the sediment will decrease (Connell and Gillanders, 2007). These systems contain high levels of oxygen within the surface sediments but deeper sediments are often anoxic. As a result, the top layers are where the majority of the invertebrates are found (Knox, 2001).

Intertidal fauna can be categorised as meiofauna or macrofauna. Both groups are important within an estuarine community. The meiofauna, which are smaller than macrofauna, includes representatives such as nematodes, copepods, oligochaetes, and also larval stages of benthic macroinvertebrates (Knox, 2001). Meiofauna play an important role in the breakdown of plant matter into smaller particles, and in turn the mineralisation by microorganisms (Knox, 2001). They also provide a food source for macrofauna, especially fish and crustaceans (Connell and Gillanders, 2007), which greatly increase the flow of energy through the system (Knox, 2001). Macrofauna include both the epifauna (living on sediment surface) and infauna (burrowing and tube-building species) (Jones and Marsden, 2005). The epifauna comprises motile species including snails, crabs, shrimp, and other crustaceans, but it is fish species that dominate this group in most estuarine systems (Knox, 2001). The infaunal group is dominated by polychaetes, bivalves, molluscs, and crustaceans (Little, 2000).

1.1.2 Invertebrate Importance

Deposit feeders are of importance due to their extensive reworking of sediment, microbial grazing, and increasing oxygen penetration into the sediment (Raffaelli and Hawkins, 1996; Hentschel, 1998; Knox, 2001; Botto et al., 2006). The production of mucus for stabilising burrows is common within estuarine invertebrates, and is thought to aid in the binding of

sediments and reduction of erosion (Paterson et al., 1986). Mudcrabs are an extremely important component in estuaries. Every tidal cycle their burrows are buried, so they spend a lot of their time maintaining them. This maintenance involves re-working of sediment, resulting in surface mud being buried and deeper layers being brought to the surface (Raffaelli and Hawkins, 1996). Major predators of intertidal invertebrates are migratory shorebirds which frequently visit estuaries due to the abundance of invertebrates (Connell and Gillanders, 2007). Estuarine inhabitants including shrimp, prawns, crabs, and fish are attracted to mudflats to feed on smaller invertebrates (Raffaelli and Hawkins, 1996). Deposit-feeding polychaetes are typically a dominant component of the estuarine invertebrates (Hutchings, 1998; Knox, 2001) and are an important food source for shorebirds worldwide (e.g. Kalejta, 1993; Weber and Haig, 1997; Scheiffarth, 2001; Iwamatsu et al., 2007; van de Kam et al., 2008). They are particularly important in the diet of the Bar-tailed Godwit (*Limosa lapponica*). This is prominent throughout the world at different stop-over's (see Scheiffarth, 2001, Table 4). Polychaetes made up at least 84% of godwit diet in one study (Scheiffarth, 2001). Polychaetes are a high-energy food source because they lack any indigestible body parts such as shell or skeleton (van de Kam et al., 2008).

1.2 Polychaetes

The class Polychaeta is diverse, containing over 8000 species (Ruppert et al., 2004). They burrow into the sediment for protection and in search of food (Hutchings, 1998), which in turn moves the sediments around. Many polychaetes ingest mud and particulate matter to obtain nutrients (Taghon and Greene, 1992). Processed sediment is released as faeces. This is known as bioturbation and it is likely to have major impacts on the movement of organic matter (Lopez and Levinton, 1987) and improvement of sediment ventilation within estuaries (Kristensen, 1988). The presence or distribution of polychaetes is found to be affected by changes in several variables including sediment composition, organic matter,

water moisture, salinity, and elevation (Estcourt, 1967; Geyer, 1997; Hutchings, 1998; Anderson, 2004; Thrush et al., 2005).

1.2.1 *Nicon aestuariensis*

Nicon aestuariensis is an endemic polychaete found throughout New Zealand's estuaries. It belongs to the family Nereididae, which contains roughly 500 species, grouped into 42 genera (Santos et al., 2006). There are 10 described species within the genus *Nicon,* with one of those being *Nicon aestuariensis* (Bakken, 2003). Nereididae is a well represented group in New Zealand with many species found throughout marine environments (NIWA, 2004). *Nicon aestuariensis* can reach lengths of 26 cm, but are usually no more than 15 cm (Jones and Marsden, 2005). It has a fully segmented body with parapodia on every segment. Their head region is slightly green in colouration, with two pairs of eyes and three pairs of tentacular cirri (Pettibone, 1971). Their body appears slightly pink due to the large dorsal blood vessel running the entire length of their body. *Nicon* has a retractable proboscis with jaws, but their proboscis does not contain papillae (Bakken, 2003). *Nicon* appears to have a range of feeding habits but they are thought to be primarily deposit feeders (Estcourt, 1967). They live in permanent burrows constructed within the sediment and held by mucus lining (Estcourt, 1966). Their burrows can reach depths of up to 40 cm, and are visible on the surface by small 2-3 mm depressions (Jones and Marsden, 2005).

1.2.2 Reproduction

Epitoky (having a morphologically different reproductive form) is a common characteristic in nereids (Ruppert et al., 2004). It is the change from a benthic, non-reproductive individual to a pelagic, reproductive one. This formation coincides with sexual maturity and gamete production but also involves non-reproductive changes (Ruppert et al., 2004). These involve adaptations for swimming and searching for mates, enlarged eyes, parapodia modifications, and enhanced segmental musculature (Ruppert et al., 2004). *Nicon aestuariensis* is one species that has a distinctive reproductive phase known as a heteronereid. This is of significance as estuarine species do not usually have this form of reproduction (Jones and Marsden, 2005). The reproductive form is very distinctive from the non-reproductive form

(Chapter 2; Fig 2.7). The series of individuals clearly show that *Nicon* shrinks in size during this metamorphosis. As described by Estcourt (1966) and Pettibone (1971) segments condense together and become wider with strong differences with their parapodia. Eventually all segments condense and their parapodia develop paddle-like structures. Heteronereid's eyes also enlarge, particularly the anterior pair. Estcourt (1966) concluded that *Nicon* at the Avon-Heathcote Estuary, Canterbury, had a two year life span, where they reached sexual maturity as large individuals. Breeding was found to occur mainly in spring (June - October). During this time large numbers of heteronereids could be observed swimming in the water column and spawning. Estcourt (1966) linked these mass spawning events to particular lunar and tidal phases.

1.3 Thesis aims and organisation

This project aims to describe the seasonal patterns of abundance and size of *Nicon aestuariensis* within a New Zealand estuary (Manawatu Estuary, Chapter 2), and to evaluate the impact of the estuarine environment on the large-scale distribution of *Nicon aestuariensis* (Chapter 3).

In Chapter Two, monthly sampling of 40 sites over a 12 month period (September 2009 – September 2010) is used describe the seasonal variation of *Nicon aestuariensis*. I describe the seasonal patterns in body length, body length: biomass relationships, density, and overall biomass for the estuary. The presence of heteronereids is used to describe the reproductive period, and morphological changes associated with the heteronereid stage are described. This is of importance as very little is known about reproduction in this species, despite it being a widespread endemic New Zealand species.

Chapter Three uses a geographical information system (GIS) approach to assess the effect that differing environmental variables have on the spatial distribution of *Nicon aestuariensis*. The aim was to evaluate whether spatial patterns could be explained by

physical variables including: sediment water content, particle composition and organic matter, and distance to nearest channel, river or sand dunes.

1.4 Study Site

The Manawatu Estuary is located on the west coast of the North Island, New Zealand, near the settlement of Foxton Beach at the mouth of the Manawatu River (40°28'30" S, 175°14'30" E; Fig 1.1). This estuary is the largest in the lower North Island with about 250 ha of salt marsh, mudflats and sand dunes. In July 2005 the Manawatu Estuary was declared a Wetland of International Importance under the Ramsar Convention (Ravine, 2007). The estuary is now managed by four main organisations - Department of Conservation, Horizons Regional Council, Horowhenua Regional Council and the Manawatu Estuary Trust (Ravine, 2007). The Manawatu Estuary formed about 6,000 years ago and acted as a sink for fine-grained sediment deposition from the Manawatu River (Page & Heerdegen, 1985). This estuary is classified as a bar-built estuary; these are typically quite shallow and have a characteristic bar across the river mouth (McLay, 1976).

The Manawatu Estuary has one of the most diverse ranges of bird species present throughout New Zealand. It is also a permanent home for many threatened species including birds, fish and plants (Ravine, 2007). This estuary at time holds one percent or more of the world population of Wrybills *Anarhynchus frontalis* (Ravine, 2007). It contains a salt marsh-ribbonwood community that is the largest in the district, and this provides habitat for one of the largest populations of the North Island fernbird *Bowdleria punctata vealeae* in New Zealand (Ravine, 2007). The estuary is also an important path for those native fish that migrate along the Manawatu River at some life-stage (Ravine, 2007). This estuary is an ongoing site for research, particularly involving migrant shorebirds. Studies involving the intertidal invertebrates will add to this ongoing research.

Fig. 1.1 Google Earth image showing the study area within the Manawatu Estuary and the surrounding Foxton Beach township.

1.5 *Nicon* as a component of the Manawatu Estuary benthos

A large survey was carried out on the northern mudflat at the Manawatu Estuary (Fig 1.1) in January 2010 to determine what intertidal invertebrates were present and their relative abundance. Eighty sites were sampled across a 50-m grid, with points located by GPS (Fig 1.2).

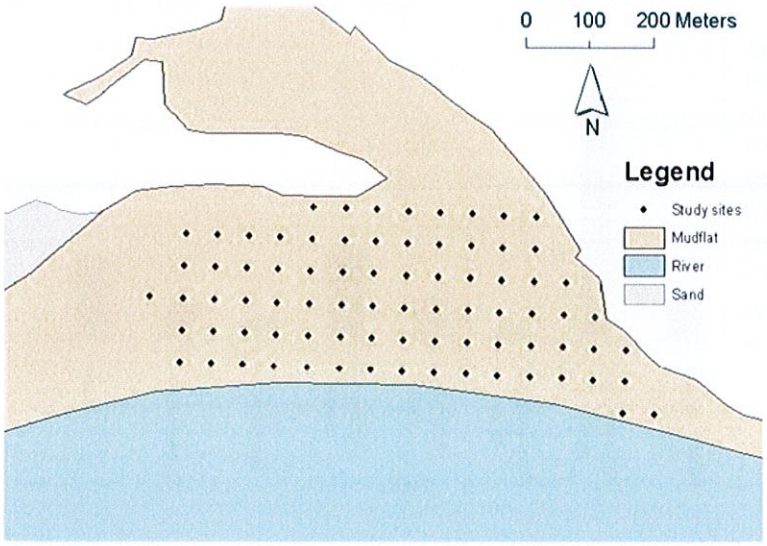

Fig. 1.2 Map of the Manawatu Estuary showing the townships side mudflat and all 80 sites sampled.

At each site a single core sample (10 cm diameter) was taken to a depth of 25 cm. The upper 3-5 cm were sieved in the field; the lower sediments were carefully broken apart by hand to locate burrowing polychaetes, as these sediments were not able to be sieved (they formed balls of mud). All invertebrates present were collected and preserved in 10% formalin. In the laboratory they were identified to species or other taxonomic groupings, and size-class (small, medium and large). Samples were then dried at 60ºC for 24 h and ashed at 600ºC for 6 h to determine the ash-free dry mass (AFDM) of each species per site and within the estuary as a whole. The density and biomass of each invertebrate species was then calculated to determine which species were dominant at the Manawatu Estuary (Fig 1.3).

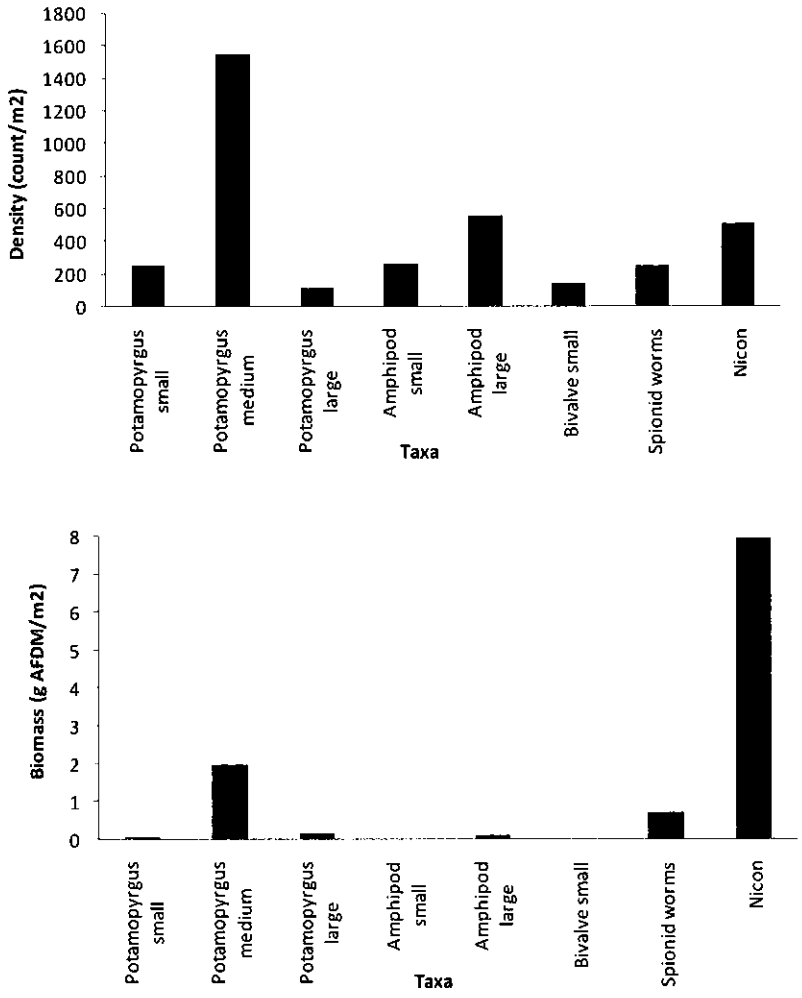

Fig. 1.3 Total density and biomass of all invertebrate species sampled at the Manawatu Estuary in January 2010.

Numerically, the commonest invertebrate by far was the small snail *Potamopyrgus estuarinus*, in particular medium sized individuals (3-5 mm). In terms of biomass, however, *Nicon aestuariensis* dominated the fauna. This shows the likely importance of this species of polychaete to other species that rely on it as a food source.

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CHAPTER TWO

Seasonal variation of *Nicon aestuariensis* (Polychaeta, Nereididae) at the Manawatu Estuary, New Zealand

Seasonal variation of *Nicon aestuariensis* (Polychaeta, Nereididae) at the Manawatu Estuary, New Zealand

Abstract

Assessing seasonal variation and changes in invertebrate biomass can give insight into the biology and ecology of a species. This was studied at the Manawatu Estuary, with the dominant invertebrate *Nicon aestuariensis* (Polychaeta) as a case study. There was no evidence of seasonal variation in density or biomass of *Nicon*. No seasonal variation in biomass between different size classes was evident. The average annual biomass was 6.3 g of ash-free dry mass (AFDM) per m^2 which is relatively low compared to other polychaete-rich estuaries worldwide. The population size distributions provide some evidence of multiple size-cohorts for some months (e.g. October, August, and September) but not in others. Heteronereids were found in samples from December – March, with a majority in February. This finding contrasts to one other study which looked at reproduction in *Nicon*. Morphological changes occur when *Nicon* become a heteronereid. Their width increased and their length reduced due to individuals "shrinking". There is also evidence of high energy demands when morphologically changing toward a heteronereid.

Keywords: seasonal variation, population dynamics, biomass, Polychaeta, Nereididae, *Nicon aestuariensis*, reproduction, heteronereid, Manawatu Estuary.

2.1 Introduction

Seasonal variation has important implications for estuarine systems. Changes in density or biomass in intertidal invertebrates will affect other species within the system. This is due to the complexity of estuaries and the energy flows through them (McLay, 1976; Raffaelli and Hawkins, 1996; Little, 2000). Seasonal changes in invertebrate abundance may have profound effects on species relying on them as a major food source, and ultimately shaping their behaviour.

The standing crop is a good indication of the health status of an estuary. It represents the energy within the system. Monitoring changes in biomass can be used to address factors including: environmental stress, management of resources, energy flows, and food web interactions (Dolbeth et al., 2005). The biomass of an individual species can also indicate productivity and health (Gonzales-Oreja and Saiz-Salinas, 1999). This is relevant to the functioning of the estuary and other species that rely on their presence.

Polychaetes are an important component of estuarine systems. Many species are deposit-feeders which aid in reworking the sediment, grazing on microbes, and increasing oxygen penetration into the sediment (Raffaelli and Hawkins, 1996; Hentschel, 1998; Knox, 2001; Botto et al., 2006). They are important prey for shorebirds globally (van de Kam et al., 2008). For example, the diet of the Bar-tailed Godwit (*Limosa lapponica*) predominantly consists of polychaetes (Scheiffarth, 2001). Analysis of godwit faecal remains in a study in Germany showed that the proportion of polychaetes in the diet never dropped below 84% (Scheiffarth, 2001).

The Manawatu Estuary is a site of ongoing research on shorebirds, particularly the Bar-tailed Godwit. In 2005 the Manawatu Estuary was declared a Wetland of International Importance under the Ramsar Convention Treaty of 1971 (Ravine, 2007). This was due to recognition of it being an important site for many endangered or threatened species which are present within the estuaries habitat. Intertidal invertebrate surveys have shown that *Nicon aestuariensis* (Polychaeta) contains the highest biomass levels (g AFDM/m^2) making it an

important food source for migratory shorebirds. Studying this polychaete will aid in the current shorebird research undertaken at the Manawatu Estuary.

Despite *Nicon* being a widespread species around the estuaries and harbours of New Zealand and being a species used in environmental monitoring (Thrush et al., 2005; Hewitt et al., 2007), the population biology of the polychaete worm *Nicon aestuariensis* is remarkably poorly documented. Just one scientific papers published has had a significant focus on *Nicon.* Estcourt (1966) studied *Nicon's* population distribution patterns throughout a year, at the Avon-Heathcote Estuary, Canterbury, including their reproductive biology and their tolerance to certain environmental factors. Read (1984) looked at the zonation patterns for intertidal invertebrates, with a brief mention on *Nicon,* at Pauatahanui Inlet, north of Wellington in the lower North Island. He also studied population distributions at different times of the year. Yet *Nicon* is likely to be an important component of estuarine food webs, as a deposit-feeder or omnivore (Thrush et al., 2003) and also as a potential prey item for fishes (Burke, 1995; Labropoulou and Eleftheriou, 1997) and birds (Mercier and McNeil, 1994; Scheiffarth, 2001).

A large-scale survey conducted in January 2010 at the Manawatu Estuary, showed that a polychaete species (*Nicon aestuariensis*) was the most abundant species based on their biomass (g AFDM/m^2) throughout the northern mudflat. Field observations have shown that this species of polychaete makes up a substantial proportion of the Bar-tailed Godwit diet during their stay at the Manawatu Estuary (J.R. Conklin, Massey University, pers. comm.). Adult godwits spend September/October to March at the estuary, and presumably increase their net energy intake from January-March when they fuel up for migration. Predation pressure on *Nicon* is therefore likely to be greatest over the southern summer. Describing the seasonal patterns in abundance and biomass of *Nicon* would therefore give a first indication of whether *Nicon* biomass or abundance change in a way that is likely to be beneficial to birds (e.g. growth or reproduction result in higher biomass during summer), and whether any declines are evident during the period of greatest predation pressure by birds.

Accordingly, I studied the population density, size structure and biomass of *Nicon aestuariensis* at monthly intervals over a 12-month period. Size-mass relationships were also assessed to evaluate seasonal changes in body condition.

2.2 Materials and Methods

The Manawatu Estuary is located on the west coast of the North Island, New Zealand, near the settlement of Foxton Beach at the mouth of the Manawatu River (40°28'30" S, 175°14'30" E; Fig 2.1). This estuary is the largest in the lower North Island with about 250 hectares of salt marsh, mudflats and sand dunes (Ravine, 2007). The main tidal flat in the estuary covers c. 35 ha along the northern side of the river, and consists mainly of comparatively firm muddy substrates bordered by sandflats and an artificial seawall. This estuary experiences a typical tidal cycle whereby every 24.5 hr there are two high and two low tides.

We sampled 40 sites evenly spaced across the northern flat each month from September 2009 – September 2010 (Fig. 2.1; in April 2010, only 18 sites could be sampled due to injury). Sites were relocated via GPS (accuracy ± 2-3 m). Sampling took 1-2 days depending on the tidal cycle and weather conditions.

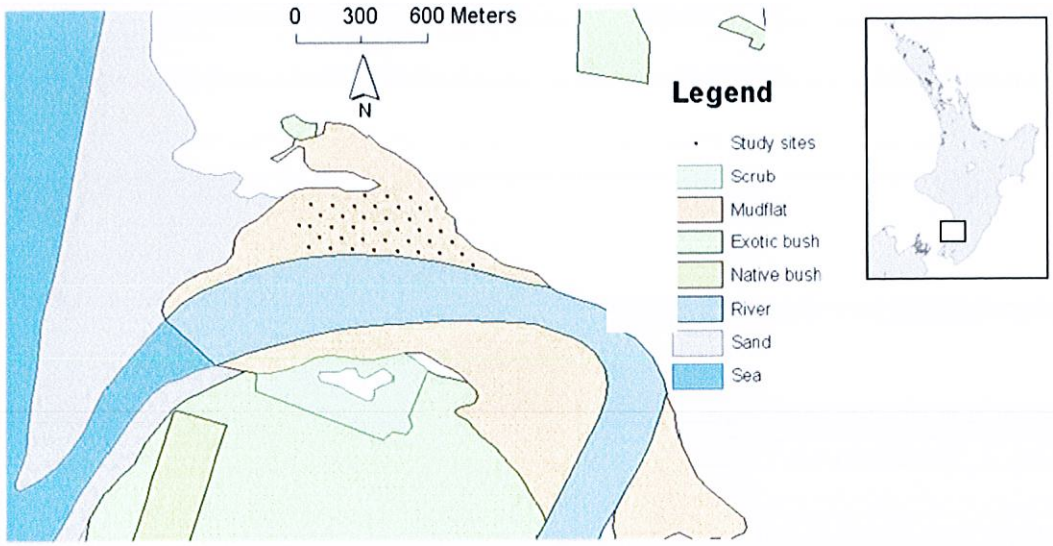

Fig. 2.1 Major habitat zones at the Manawatu Estuary and surrounding areas, including sample sites.

A single core sample (depth 30 cm, diameter 10 cm, area 0.0079 m^2) was taken at each site. Samples were collected as quickly as possible upon reaching the site to minimise

opportunities for polychaetes to react to vibrations and migrate downwards and avoid capture. The sample was then hand-sorted in the field, due to sieving causing the sediment to form balls, and any polychaetes were collected and stored in 10% formalin.

In the laboratory, each sample was sorted and all *N. aestuariensis*, including partial worms, were measured to the nearest millimetre. A binocular microscope with graticule was used to measure the width (in mm) of the 6th anterior segment, which is known to have a strong relationship with total length (Estcourt, 1966). The relationship between 6th segment width and total length was used to estimate the length of partial worms when analysing size classes. All intact worms were placed into crucibles based on their size class ranging from 0+, 1+, 2+...14+ cm long and processed as pooled samples per size class. Remaining worm pieces from each site were weighed separately.

Samples from each month were weighed wet, dried at 60°C for 24 hours, reweighed after cooling in a dessicator containing silica gel, and ashed at 600°C for 6 hours. The AFDM for each sample was calculated as the difference between the ashed mass and the dry mass.

Any *Nicon* undergoing metamorphosis towards the heteronereid stage were kept separate from the samples and not dried and ashed for length-biomass analyses (as they 'shrink' in length during this reproductive stage). Instead, they were weighed wet, and their total "pre-metamorphosis length" was estimated based on the width of the 6th anterior segment.

Statistical analyses were performed in Microsoft Excel 2007, Sigma plot, and SPSS Statistics 17.0.

2.3 Results

2.3.1 Size-length relationships

The width of the 6th anterior segment was a good predictor of total length, explaining 84–97% of the variance in each month (Table 2.1; see Fig. 2.2 for an example).

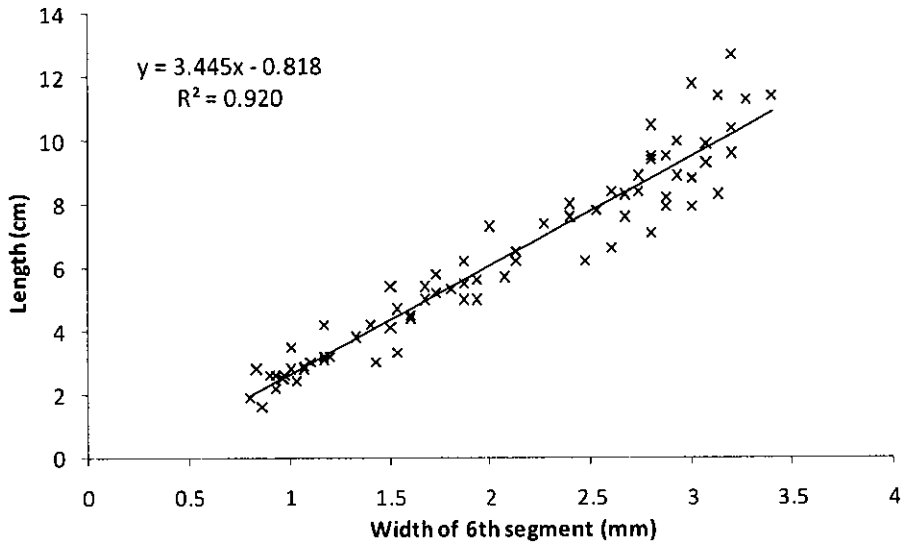

Fig. 2.2 Whole worm length versus width of the 6th anterior segment region of entire *Nicon aestuariensis* for December 2009.

Table 2.1 Relationships between width of the 6th anterior segment and total length of *Nicon aestuariensis* for each month.

Month	Slope	Intercept	R^2	N worms
Sept-2009	3.207	-0.757	0.860	103
Oct	3.510	-0.581	0.929	72
Nov	3.322	-0.861	0.918	90
Dec	3.445	-0.818	0.920	75
Jan-2010	3.617	-0.686	0.839	77
Feb	3.379	-1.112	0.900	57
Mar	3.172	-0.596	0.949	68
Apr	2.982	-0.309	0.906	28
May	3.565	-1.079	0.881	84
Jun	3.680	-1.231	0.970	75
Jul	3.401	-0.819	0.905	66
Aug	3.944	-1.403	0.914	69
Sept-2010	3.675	-0.603	0.945	59

AFDM of *Nicon* increased with body length, roughly exponentially (Table 2.2; see Fig. 2.3 for an example). There was no systematic change in exponent through the year. Consequently, AFDM of a given size class of worm showed no clear seasonal pattern (see below, Fig. 2.4)

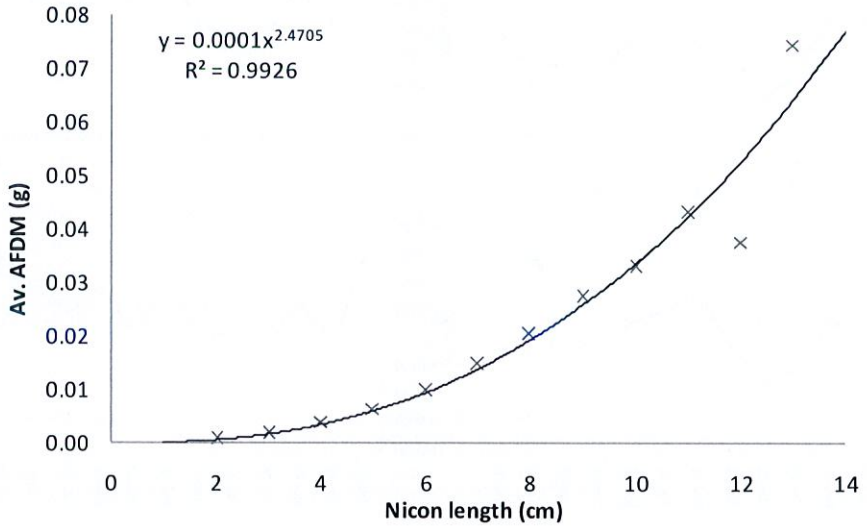

Fig. 2.3 Example of how AFDM of *Nicon aestuariensis* varies with body length. Data are pooled per 1-cm size class and are from November 2009.

Table 2.2 Exponential relationships between *Nicon aestuariensis* average AFDM and total body length for each month. Average AFDMs were determined from pooled 1-cm size-classes each month.

Month	Exponent	Intercept	R^2	N worms
Sept-2009	2.2110	0.0003	0.985	103
Oct	2.2457	0.0002	0.969	72
Nov	2.4705	0.0001	0.993	90
Dec	2.3387	0.0001	0.979	75
Jan-2010	2.2741	0.0003	0.928	77
Feb	2.3146	0.0002	0.981	57
Mar	2.1774	0.0003	0.970	68
Apr	1.8554	0.0004	0.915	28
May	2.5809	0.0001	0.996	84
Jun	2.2879	0.0001	0.989	75
Jul	2.8050	0.0001	0.985	66
Aug	2.5559	0.0001	0.994	69
Sept-2010	1.9728	0.0003	0.894	59

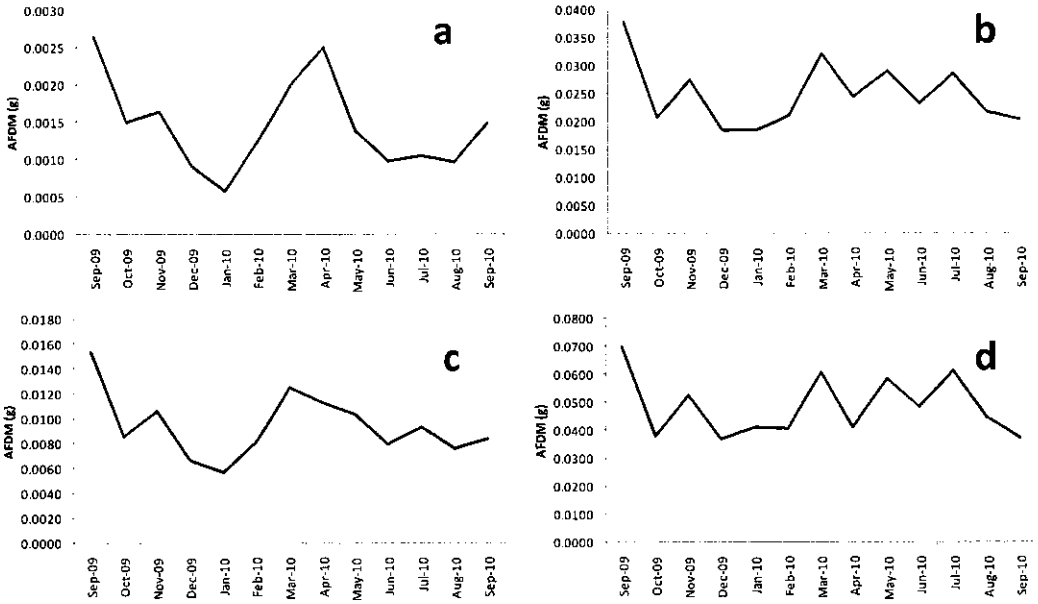

Fig. 2.4 Predicted AFDM for four lengths of *Nicon aestuariensis* through the year. a=2 cm, b=5 cm, c=8 cm, d=11 cm. Note the differing scales on the y-axes.

2.3.2 Seasonal variation

Size-frequency distributions of *Nicon* were plotted for each month (Fig 2.5 for lengths and Fig 2.6 for 6th-segment widths). There was clear evidence of multiple length-cohorts in some months (e.g. October 2009, August 2010, and September 2010) but not in others. It is possible that the 2–4 cm worms in October match the 5–7 cm worms in November, 8–9 cm worms in January and the 9 cm worms in February. Based on the width of the 6th segment, different size-cohorts were possibly evident in September, October, December, January and February.

If so, this would imply a separate cohort of worms (2–3 cm) was present from December onwards. The presence of large worms (>10 cm) varied between months, with few present

from January–May. It is likely that this was a result of metamorphosis of reproductive heteronereids (see below).

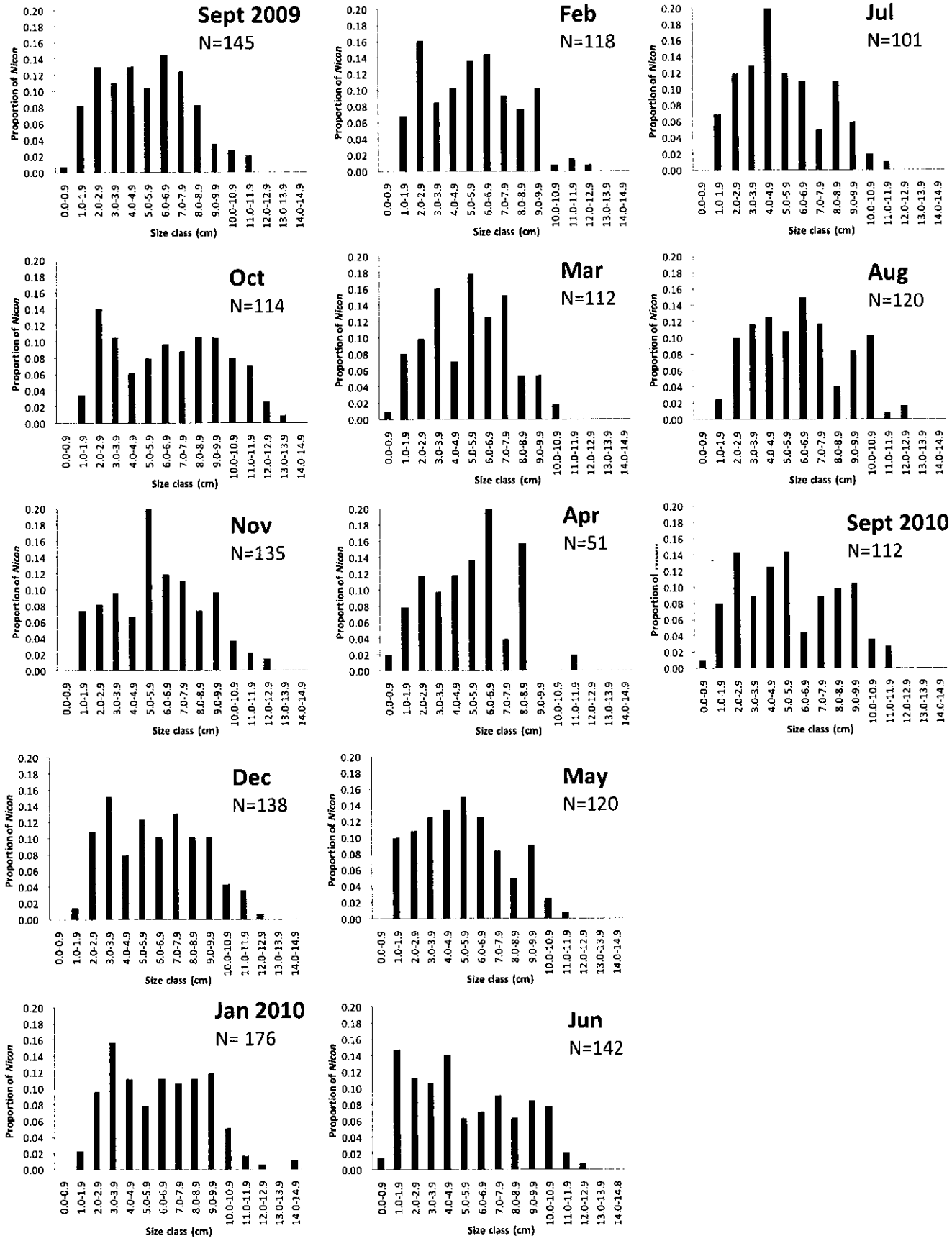

Fig. 2.5 Seasonal variation in size class distributions of *Nicon aestuariensis* for each month.

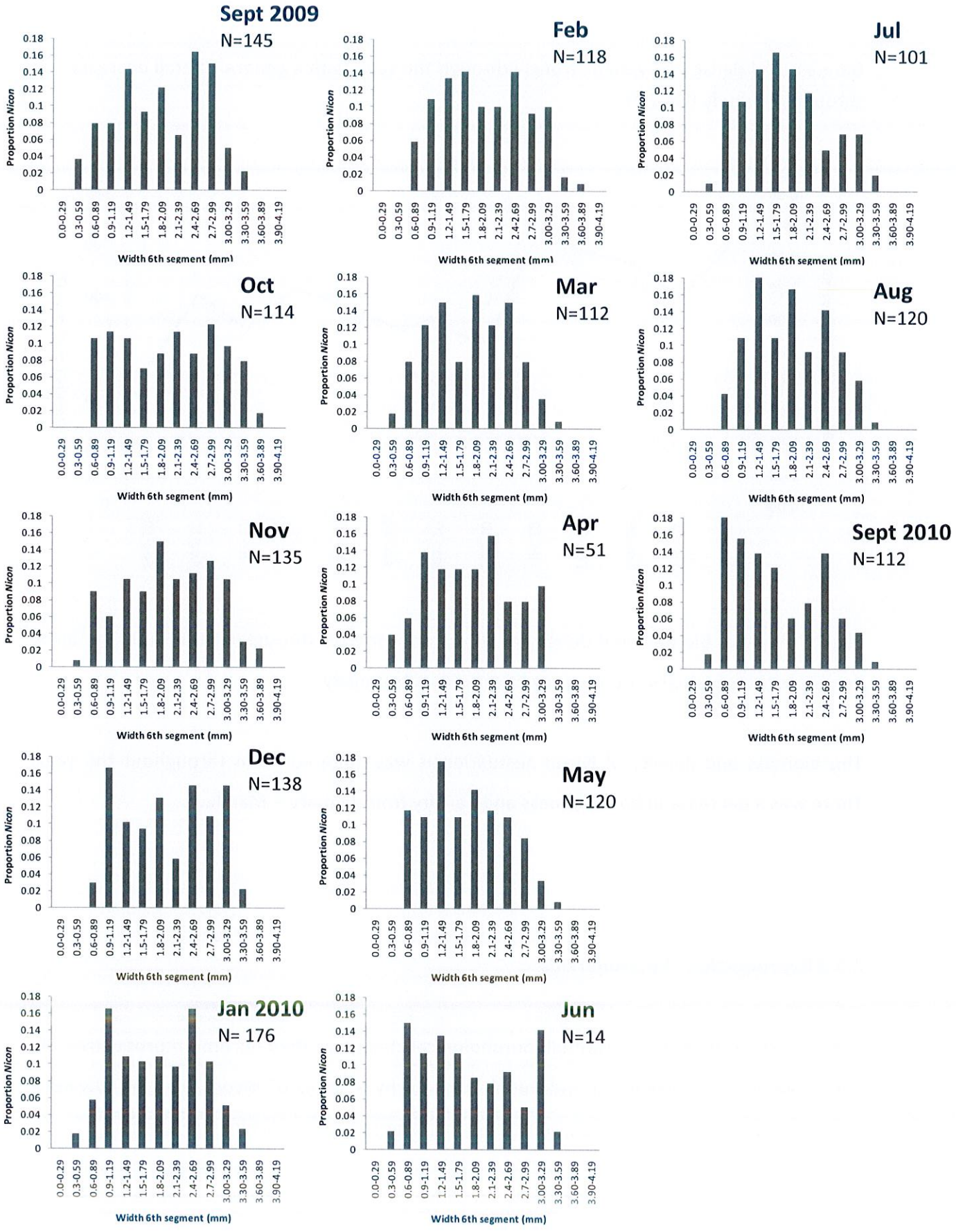

Fig 2.6 Seasonal variation in *Nicon aestuariensis*' 6th segment width for each month.

Biomass and density co-varied strongly through the year, with a general overall decrease through the study (Fig 2.7).

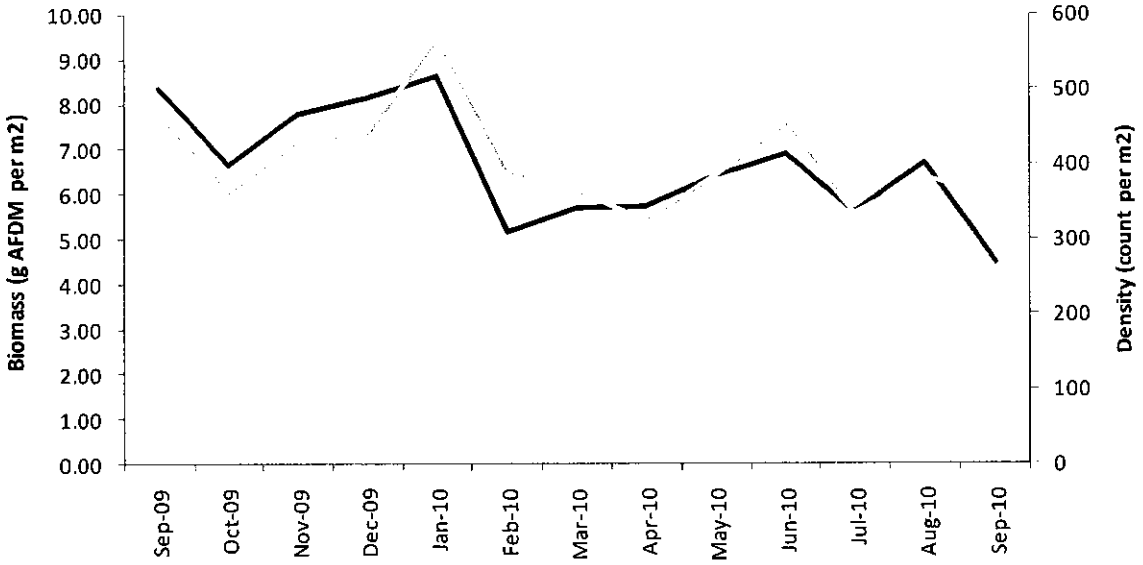

Fig. 2.7 Average biomass and density of *Nicon aestuariensis* throughout the year. The black line represents biomass and the grey line represents density.

The biomass and density of Nicon aestuariensis was quite constant throughout the year. There was a decrease in both biomass and density from January – March.

2.3.3 Reproduction - heteronereids

Heteronereids undergo substantial morphological change as they become reproductive. Fig 2.8 shows a non-reproductive individual followed by a series of *Nicon* changing toward a heteronereid. The final *Nicon* is a completely metamorphosed individual (see below).

Fig. 2.8 *Nicon aestuariensis* at different reproductive stages. (A) non-reproductive adult, (B–D) early stages of reproduction, (E) completely metamorphosed heteronereid. Photo: M.A. Potter.

From Fig 2.8 it appears as though *Nicon* condense their mid-region first with their head and tail regions remaining unchanged. They continue to condense their size, with individual segments reducing in length but becoming wider. There are also morphological differences associated with their parapodia, which appear to become enlarged in size and develop paddle-like structures.

Heteronereids were present in sediment samples from December – March. In total 17 individuals were found (Dec=1, Jan=6, Feb=7, Mar=3) at different stages of metamorphosis, with just two fully metamorphosed. Densities of heteronereids were low, peaking at 19 per m^2 in February (Fig. 2.9), suggesting that February may be the main month for reproduction of *Nicon aestuariensis* at the Manawatu Estuary.

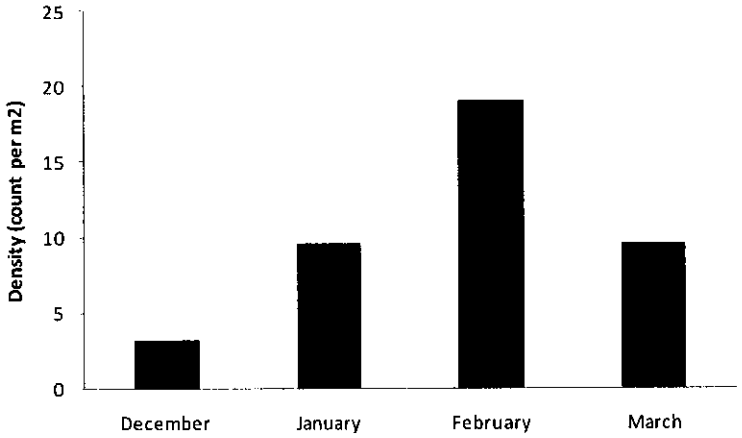

Fig. 2.9 Density of reproductive *Nicon aestuariensis* in the months they were present in samples.

For a given body width (the width of the 6th segment), heteronereids were substantially shorter than equivalent-width non-reproductives (most falling outside the 95% confidence

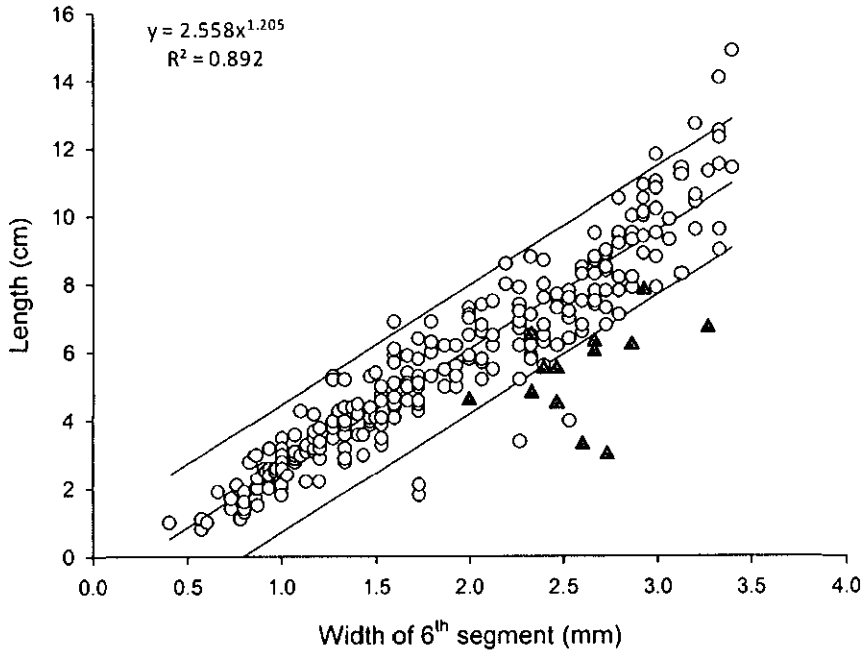

Fig. 2.10 Comparison of reproductive and non-reproductive *Nicon aestuariensis* based on their length and width of 6th anterior segment. Non-reproductives are represented by open circles, and reproductives by grey triangles. The trend line and equation is based on the non-reproductives, with 95% confidence intervals for the equation.

interval of non-reproductives: Fig 2.10). Reproductive *Nicon* are smaller in length compared to non-reproductives based on the same width. This was expected as *Nicon* "shrink" in length as they become reproductive (Fig 2.8). Reproductives are significantly smaller as shown in Fig. 2.10 by falling outside the 95% CI margins (see below).

Heteronereids are also lower in biomass for their width than non-reproductives (Fig. 2.11). This could result from heteronereids' widths increasing, or their biomass decreasing.

Fresh mass of reproductive and non-reproductive *Nicon* was then compared with their width 6th segment (Fig. 2.11 below).

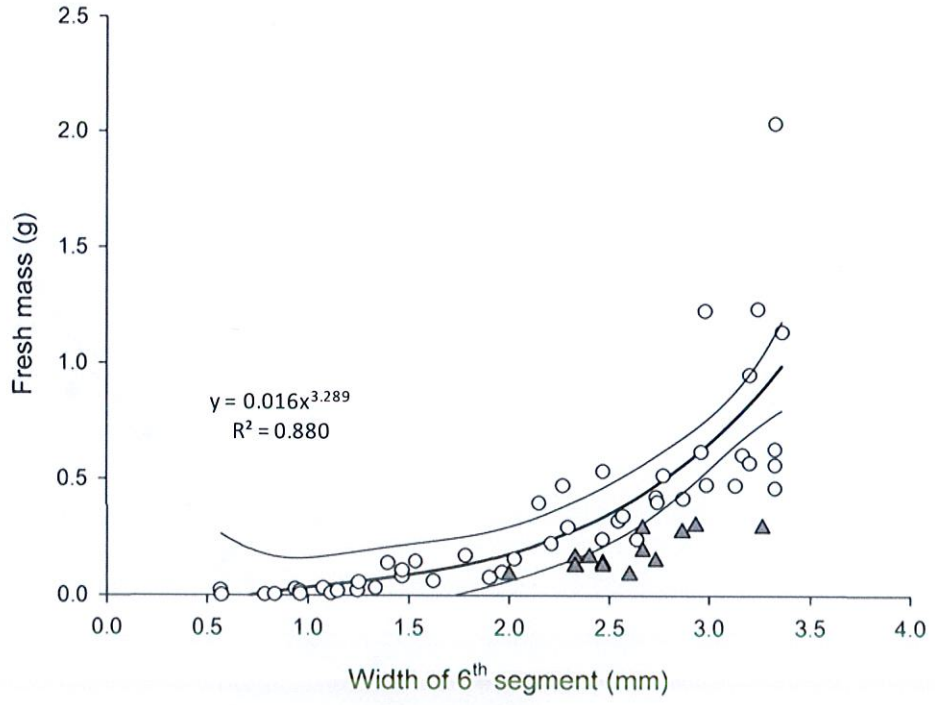

Fig. 2.11 Comparison of fresh mass of reproductive and non-reproductive *Nicon aestuariensis* in relation to the width of the 6th anterior segment. Non-reproductives are represented by open circles and reproductives by grey triangles. Trend line is shown for non-reproductives, with 95% confidence intervals.

Nicon's width of 6th anterior segment appears to change when becoming a heteronereid (Fig. 2.11). Their width was larger for a given mass than non-reproductive *Nicon*.

In order to determine whether heteronereids are likely to have changed in size alone, or both in size and mass, we estimated the total length for *Nicon* prior to changing morphologically. This was calculated based on the relationship between length and width for the months that reproductives were present in samples (Fig 2.2). This was compared with wet mass for both reproductive and non-reproductive *Nicon* (Fig. 2.12 below).

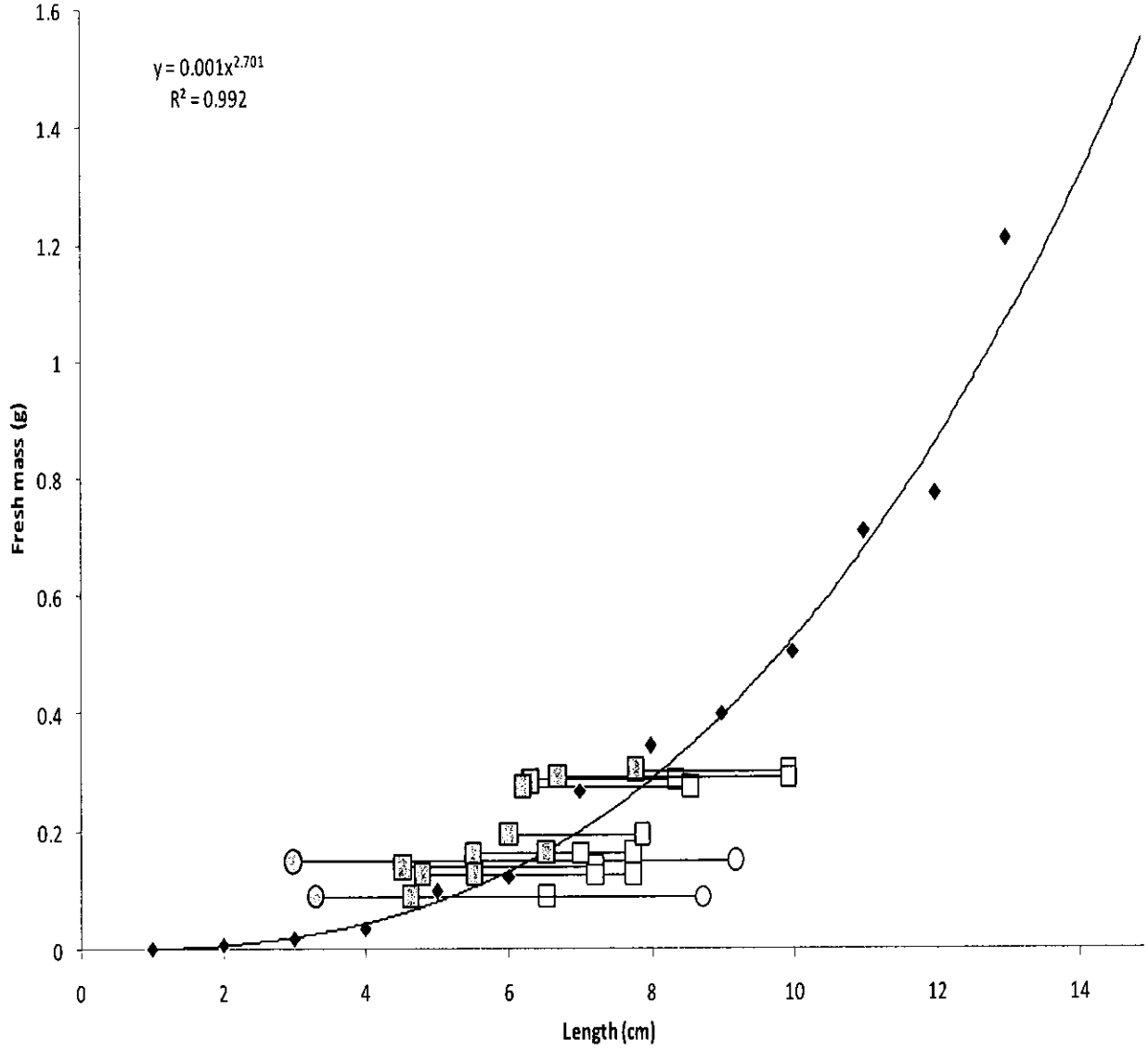

Fig. 2.12 Comparison of reproductive and non-reproductive *Nicon aestuariensis* based on their fresh mass and total length. The trend line represents the relationship between fresh

mass and non-reproductive *Nicon*. Each horizontal line on the graph represents an individual reproductive *Nicon*. Circles represent complete metamorphosis; squares represent partial metamorphosis. The point on the left (shaded grey) is each individual's measured length, and the point on the right is their expected length based on the width of their 6^{th} segment and the width–length relationship for the month they were collected in.

Heteronereids were heavier for their length than non-reproductive individuals, which is expected given that heteronereids "shrink" in length during metamorphosis. But their masses relative to their estimated pre-reproductive length were generally lower than for non-reproductive worms of that length.

2.4 Discussion

2.4.1 Population dynamics

There were differences between the growth and population dynamics data reported here for *Nicon aestuariensis* at the Manawatu Estuary and the only other detailed study on this species that was conducted by Estcourt (1966) at the Avon-Heathcote Estuary in Christchurch. Being just the second detailed study on *Nicon aestuariensis*, it is important to make comparisons between these two studies.

The overall lengths of *Nicon aestuariensis* collected at the Manawatu Estuary were much smaller than those at the Avon-Heathcote Estuary (Estcourt, 1966). The largest individual collected in this study was 14.9 cm, while Estcourt (1966) recorded lengths of 22 cm. It is likely that at least part of this difference is a result of different preservation methods. Estcourt relaxed live worms in a Magnesium Chloride (MgCl) solution before measuring them, whereas I preserved worms in 10% formalin in the field. To evaluate the possible magnitude of this effect, 12 *Nicon* were collected and relaxed in a 6% MgCl solution, measured relaxed, and then fixed in 10% formalin for at least 2 days and re-measured. All individuals did shrink through being fixed in formalin, by 0.1 cm – 2.1 cm (average 0.7 cm from a length of 7.7 cm). Worms shrank by 0.9–26.3%, but this reduction in length was not proportional across individuals of different lengths. The average increase in length required to estimate relaxed length from preserved length (1.13 x) would take the largest worm in my study from 14.9 to 16.8 cm long, still well short of those from the Avon-Heathcote Estuary. This effect of using formalin to preserve *Nicon* was unlikely to have affected their biomass values (Leuven et al., 1985).

This difference in size could be due to other factors. Studies have shown that differences in the sediment content can cause variation within a species of polychaete. Bridges et al. (1994) assessed the effect of adding sewage, algae and hydrocarbons to sediment for two polychaete species (*Streblospio benedicti* and *Capitella* sp.). *S. benedicti* showed reduced size, and age at reproduction was delayed, while for *Capitella* the opposite occurred, with

size increasing (six-fold) and reproduction occurring sooner. Different levels of enrichment could therefore cause the total length of *Nicon* to vary between different estuaries. The Avon-Heathcote Estuary was likely to be more polluted in 1966 than the current state of the Manawatu Estuary. Perhaps this is why individuals at the Manawatu Estuary are much smaller than those collected from the Avon-Heathcote Estuary.

2.4.2 Biomass levels

Nicon biomass increased clearly with body length (Fig 2.3), with biomass roughly doubling between worms of length 6 cm, 8 cm, 11 cm and 14 cm. From a predator's perspective, a large worm potentially has a much greater return than a small worm. If, however, large worms burrow deeper into the sediment than do small worms (Estcourt, 1967) then the portion accessible to predators (Zwarts and Wanink, 1993) would tend to be the lighter, smaller worms. Interestingly, biomass for a given size class did not vary systematically through the year (Table 2.2) – there was no indication of a seasonal drop in body condition.

Fig 2.3 shows a clear increase in biomass as the total length of *Nicon* increases. This was found to be similar throughout the year (Table 2.2). Although this was expected, it is still important to consider with regards to *Nicon's* predators such as the Bar-tailed Godwit. Fig 2.4 shows that it is likely to be more beneficial for a bird to search for larger individuals than smaller ones. This is likely to be important for the godwits during their time of refuelling for their continued migration towards their breeding grounds in Alaska.

The standing stock of *Nicon* varied between about 5.0 g and 9.0 g AFDM/m^2 throughout the year (Fig 2.5), with an average of 6.3 g AFDM/m^2. The average biomass of polychaetes in other studies varies between different locations. Swennen & Duiven (1982) found polychaete biomass at a South African estuary to be 0.18 g AFDM/m^2, whereas the biomasses of *Nereis virens* and *Nereis diversicolor* in Norsminde Fjord, Denmark were 50-fold higher, at 9.34 g AFDM/m^2, and 10.46 g AFDM/m^2 respectively (Kristensen, 1984). A study on invertebrate biomass in the Wadden Sea was dominated by a lugworm (*Arenicola marina*) with biomass levels as high as 24.57 g AFDM/m^2 (Reise et al., 1994). Piersma et al.

(1993) collated biomass data from 19 sites worldwide. Polychaete biomass ranged from 0 – 16.57 g AFDM/m^2 (refer Table 1, Piersma et al., 1993). The highest biomass was recorded in Deep Bay, Hong Kong, with no polychaetes present in Merja Zerga, Morocco and Swartskop Estuary, South Africa. Based on these figures, the biomass of *Nicon* at the Manawatu Estuary was towards the lower end of the range.

2.4.3 Seasonal Patterns

The biomass and density of *Nicon* showed substantial differences, but no clear cyclical change throughout the year (Fig 2.6). However, there was a drop in both density and biomass from January - February. Without data from multiple years it is difficult to deduce what the likely reasons are for this reduction, or if the reduction is of any significance at all. It is possible that the decline in biomass in February is due to the effect of predation by godwits fuelling for migration. The godwits need to increase their body fat stores for their northward migration in March. The months prior to migration are spent intensely foraging on invertebrates. However, the biomass and density did recover after this period (Fig 2.7). These results suggest that even though shorebirds are feeding on *Nicon*, they are not having a major impact on the numbers of *Nicon*. There is obviously an abundance of this food source and Fig 2.6 shows that there is very little change throughout the season. There is a difference in biomass between both Septembers, however differences in invertebrate biomass over many years is not uncommon. Beukema et al. (1993) conducted biomass studies on macroinvertebrates in the Wadden Sea over a 20 year period. Biomass was found to vary each year with no consistency between years for two polychaete species (*Nephtys hombergii* and *Lanice conchilega*) and a tellinid bivalve (*Macoma balthica*). This shows the importance of not concluding that *Nicon* decreased through the year, given that the following season is likely to be quite different.

There did not appear to be any seasonal pattern in biomass when comparing different size classes of *Nicon* (Fig 2.3). Each of the four different size classes had a similar pattern throughout the year. This suggests that this species of polychaete is not affected by factors such as a reduction in their prey items during winter months. Each size group did, however,

have a drop in biomass from September – January. This corresponds with the presence of the godwits, and the reproductive period of *Nicon*. Perhaps the predation threat from godwits has some effect on the foraging behaviour of *Nicon* during this time. This could result in a decrease in *Nicon* numbers during these summer months. It has been found that larger individuals show greater variation in body condition throughout the season compared to smaller individuals (Chambers & Milne, 1979). This is related to reproduction of these larger and older individuals (Chambers & Milne, 1979). Individuals may gain body condition leading up to reproduction due to the production of gametes or sperm. This pattern was not observed in larger *Nicon.*

Estcourt (1966) found metamorphosing heteronereids from April to October, with spawning occurring mainly in September and October. He suggested that juvenile *Nicon* grew at around 1 cm per month from December to June, and individuals that were not large enough to metamorphose during the main period continued to grow and became a larger size-cohort in summer (December and January). He concluded that the life-cycle is probably two years and proposed that "worms hatched in spring reach three to four cm in late spring of the following year, grow rapidly through the summer and autumn, [at around 1 cm per month; p. 181] then metamorphose during winter and spawn in the spring" (p. 193). His size-frequency plots showed evidence of bimodality from November–January, with the smaller peak (6–8 cm worms) presumed to be the previous year's offspring, and the larger peak (16–18 cm) being pre-reproductive adults. He also suggested that some worms might spawn throughout the year, as small worms were present in all months.

These interpretations are broadly consistent with the findings from the Manawatu Estuary. Two size-class peaks were evident at some times of the year, including in spring-summer, and a wide range of sizes was present in all months. But it is difficult to unequivocally ascribe cohort status to different size classes, suggesting that reproduction may occur over a longer span that heteronereids were detected in (December–March), or growth rates may differ substantially between individuals so that worms change size-classes at different times. It should be noted that Estcourt's size-frequency plots were convincingly bimodal arguably

just in December and January, and the length of the commonest size in the smaller cohort did not change from December to March or even June.

Read (1984), working at Pauatahanui Inlet north of Wellington, found that the *Nicon* population there had a left-skewed distribution in May due to an increase in juvenile recruits, which became more evenly distributed by August. This agrees with the suggested timing of reproduction at the Manawatu Estuary. These findings do not suggest that Estcourt (1966) was incorrect, as polychaete populations can vary in their behaviour and reproduction due to differences in geographical location and sediment quality (Bridges et al., 1994; Omena and Amaral, 2000).

Heteronereid reproduction in *Nicon* is unique as estuarine polychaetes do not usually have this form of reproduction (Jones and Marsden, 2005). Fig 2.9 showed that reproductive *Nicon* are shorter than a non-reproductive of the same width. This is not surprising as *Nicon* "shrink" in length as they become reproductive (Fig 2.7). Completely metamorphosed individuals were about 3 cm in length. Fig 2.10 suggests that reproductive individuals also increased in width compared to non-reproductive individuals. This is expected as heteronereids change morphologically as they develop. Changes due to heteronereid development include: enlargement of their eyes, development of paddle-like structures in their parapodia, and an increase in segmental musculature (Ruppert et al., 2004). Fig 2.11 shows the overall effect that reproduction has on *Nicon*. Their estimated length was calculated based on the length and width relationship of non-reproductives. Based on Fig 2.10 is it likely that the estimated length is an over-estimate as their width was shown to increase as reproductives. Despite this, there is still a substantial difference between the mass of a non-reproductive and that of a calculated reproductive prior to changing. This difference suggests that there are high energy demands associated with reproduction. Individuals will also be actively producing gametes or sperm in preparation for mass spawning events. The two completely metamorphosed individuals (circles in Fig 2.11) are near the bottom of the graph and are among the individuals furthest from the curve. This implies that there are substantial costs in changing into a heteronereid.

2.4.4 Additional notes

Nicon aestuariensis is a very delicate and soft-bodied species of invertebrate. As a result of this there was a large proportion of worms that were partial when removed from the sediment or cut by the corer. Fig 2.1 shows that there is a strong relationship between the width of their 6^{th} segment and overall length. Because of this, the equations in Table 2.1 can be used to calculate what an individual's worm length was likely to have been prior to being broken. This then allows all individuals to be used in size-class analyses.

It appears as though this species of polychaete is well adapted to estuarine conditions. When collecting the monthly samples, the August 2010 sample had to be delayed by a week due to large amounts of rainfall around the Manawatu and Horowhenua region. Because the river covers such a long distance it is susceptible to flooding events. Flooding causes the estuary to be completely submerged under water for about 4 days. During this time there was no cyclic pattern of high and low tides. If *Nicon* was particularly sensitive to factors such as water content and exposure times then you would expect a large decrease in the total biomass or density in September as a result of death. While there is a decrease between August – September it is not large. Because this is not the case it would appear that *Nicon aestuariensis* is an invertebrate which has become accustomed to natural events such as flooding.

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CHAPTER THREE

Assessing spatial variation of *Nicon aestuariensis* (Polychaeta: Nereididae) at the Manawatu Estuary, New Zealand.

Assessing spatial variation of *Nicon aestuariensis* (Polychaeta: Nereididae) at the Manawatu Estuary, New Zealand.

Abstract

The spatial variation of a species is driven by environmental and ecological factors. Estuaries are challenging environments and fauna living within these systems have to locally adapt to these variations. Understanding what factors drive the distribution of a species gives insight into some of the complex interactions occurring within estuarine systems. In this study, we assessed what factors determined the spatial variation of the polychaete *Nicon aestuariensis* across a tidal flat in a small estuary in the southern North Island, New Zealand. The use of a geographical information system (GIS) enabled us to visually assess variations throughout the mudflat. We tested whether sediment water content and organic matter, sediment particle sizes, distance to nearest channel, distance to river, and distance to sand dunes explained variations in density and biomass of *Nicon*. Multiple regression analyses found that distance to channel and distance to river significantly affected *Nicon* density, and those two factors plus organic matter significantly affected *Nicon* biomass. Overall, the variables tested explained 34% of *Nicon*'s density and 33% of biomass. Relationships varied between size-classes, however. Small worms (0-3.9 cm) showed no association with any variable, the distribution of medium-sized worms (4–7.9 cm) was related to distances to channel and nearest body of water, whereas large worms (8 cm+) were affected by organic matter and distance to channel. These results give insight into *Nicon*'s habitat preferences and have important implications for shorebirds at the Manawatu Estuary.

Keywords: spatial variation, environmental variables, sediment composition, channels, *Nicon aestuariensis*, Polychaeta, Nereididae, Manawatu Estuary, GIS

3.1 Introduction

Estuaries are extremely variable systems. They are located where two very contrasting environments meet: freshwater and marine (McLay, 1976). This results in rapid environmental changes due to periodic tidal inundation and flooding events (McLay, 1976). Strong environmental gradients can occur between high and low tidal elevations, as variations in exposure time can cause fluctuations in temperature, light, heat and desiccation (Raffaelli and Hawkins, 1996). Osmotic challenges can also occur due to tidal mixing of saline and fresh water (Raffaelli and Hawkins, 1996). Strong winds will affect salinity levels of shallow estuaries by completely mixing the water (Geyer, 1997). All of these factors may have profound effects on the invertebrate communities that reside within estuaries.

Estuaries are some of the most productive ecosystems worldwide. This is largely due to the high biomass and abundance of fauna found within tidal flats. Although there are examples of low abundance (e.g. Wolff et al., 1993), productivity is often still high enough to support vast numbers of seasonal migrant shorebirds. Given that these environments are unpredictable and extreme in nature, estuarine species may have evolved and adapted to these conditions (e.g. Dunson and Travis, 1994; Jones and Marsden, 2005; van de Kam et al., 2008), enabling them to thrive. Extremes include being submerged by water at high tide and then exposed during low tide. Exposure and warm temperatures can lead to desiccation, particularly for soft-bodied species. They may also have to contend with predation pressure from high numbers of shorebirds foraging on the mudflats, as well as fishes foraging at high tide.

The biomass of intertidal species can determine the overall productivity of an estuary (Gonzales-Oreja and Saiz-Salinas, 1999). Collecting information on species density and biomass enables us to identify biologically important areas within an estuarine system. This could be used to drive conservation efforts when preserving these areas. Habitat choice for a species can be affected by heterogeneity in environmental and biological factors (Engels and Jensen, 2010). Determining what environmental factors may be driving the distribution

of intertidal species, is therefore of great importance to an understanding of the associated ecological processes (Thrush et al., 1989).

Here we study the spatial variation in a common polychaete worm, *Nicon aestuariensis*, at the Manawatu Estuary, New Zealand. Globally, polychaetes are an important food source for many shorebirds (e.g Kalejta, 1993; Weber and Haig, 1997; Scheiffarth, 2001; Iwamatsu et al., 2007; van de Kam et al., 2008). In New Zealand, species such as Bar-tailed Godwit (*Limosa lapponica)*, Wrybill (*Anarhynchus frontalis)* and Pied Oystercatcher (*Haematopus finschi)* may feed extensively on polychaetes (Battley et al, 2005; Anderson, 2003). Previous studies have found that polychaetes are influenced by factors including salinity, sediment water content, sediment particle sizes and organic matter, dissolved oxygen, temperature, and exposure time (Estcourt, 1967; Geyer, 1997; Hutchings, 1998; Anderson, 2004; Thrush et al., 2005).

A geographical information system (GIS) is a tool to visually display spatial distribution patterns. It allows data to be investigated, interrogated, interpreted, and visualised in a variety of ways to reveal relationships and patterns in the form of maps (ESRI, 2011). We use GIS to map (1) major environmental variables across the major tidal flat at the Manawatu Estuary (water content, organic matter and sediment composition), and (2) the density and biomass of *Nicon*. We then use multiple regression to analyse the relationships between *Nicon* density and biomass and environmental variables.

3.2 Materials and Methods

The Manawatu Estuary is located on the west coast of the North Island, New Zealand, near the settlement of Foxton Beach at the mouth of the Manawatu River (Latitude - 40°28'30" S, Longitude - 175°14'30" E). This estuary is the largest in the lower North Island with about 250 hectares of salt marsh, mudflats and sand dunes (Ravine, 2007). The main tidal flat in the estuary covers c. 35 ha along the northern side of the river, and consists mainly of comparatively firm muddy substrates bordered by sandflats and an artificial seawall. This estuary experiences a typical tidal cycle whereby every 24.5 hr there are two high and two low tides.

We sampled 40 sites evenly spaced across the northern flat each in September 2010 (Fig. 3.1). Sampling took 1-2 days depending on the tidal cycle and weather conditions.

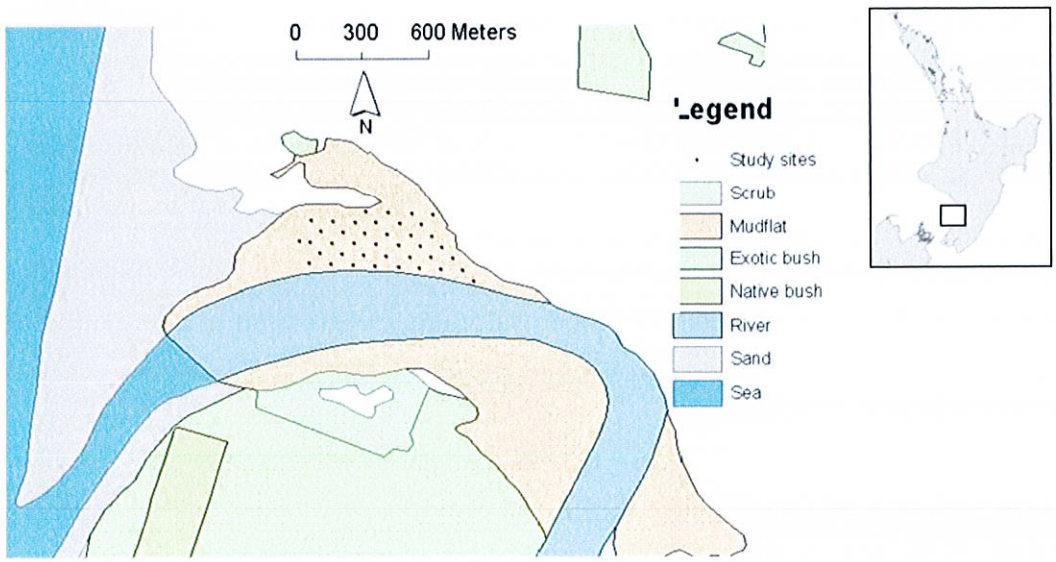

Fig. 3.1 Major habitat zones at the Manawatu Estuary and surrounding areas, including sample sites.

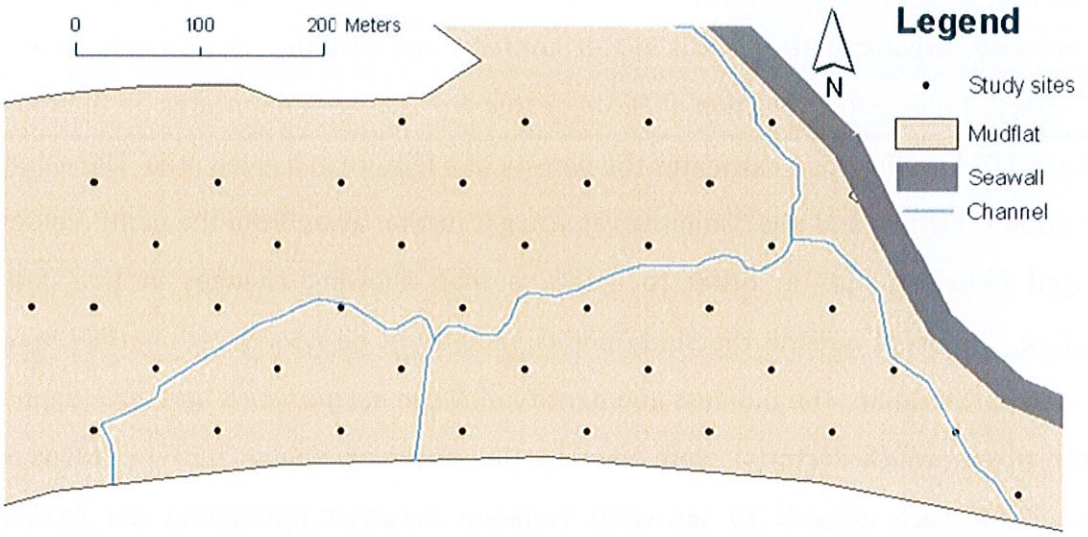

Fig. 3.2 Close-up of the mudflat showing the 40 sites, main channels, and seawall.

A small sediment sample from each site (20cm depth, 5 cm diameter, area 0.0020 m^2) was collected and frozen for later analysis. Twenty grams of the sediment was placed in a crucible, weighed wet, oven-dried at 60°C for 48 hours, and reweighed to determine the wet and dry weights (and by subtraction, water content). Samples were ashed at 600°C for 6 hours and organic matter calculated as dry mass minus ash mass. Samples were then placed in a stacked sieve system containing a series of different mesh sizes (1 mm, 0.5 mm, 0.125 mm, 0.063 mm, and catchment) and sieved to determine the percentages of sediment particle sizes. The percentage of sand or silt/clay could then be determined.

A topographical map of the Manawatu region was downloaded as a shape file from the LINZ website (http://www.linz.govt.nz/topography/topo-maps/index.aspx). This was used to create a base map of the area surrounding the Manawatu Estuary. The 40 sites used for this study were mapped from their grid positions to show their placement across the northern mudflat. The projection between the base map data and the sites added was not the same so a transformation was needed in order for these to line up correctly. The projection used for the maps was NZGD 2000 UTM Zone 60S. This transformed the base map data so it was the same as the GPS co-ordinates. The main channels were mapped using a Garmin GPS and then added to the map. The distance measure within ArcGIS was used to measure distance from each site to the nearest channel, sand dune, and river.

The Spatial Analysis Kernel Density function was used to assess how the different variables (percent clay, organic matter (OM), water content, and distance to channel, dunes and river) affected the spatial variation of *Nicon aestuariensis* between the sites on the mudflat. The Kernel Density function calculates the density of a feature in a given area. The value at a given point is highest and this diminishes as you get further away from the point. Values are averaged between sites in order to create a map showing changes in that feature. Therefore, the areas outside the study points should not be considered as they may not reflect actual variation. The biomass and density of *Nicon aestuariensis* was also mapped to visually assess which factor(s) were causing the observed spatial pattern. Maps were produced for each variable to see what variation occurred throughout the Manawatu Estuary.

Density maps were also produced for *Nicon aestuariensis* of different size-classes (0.0-3.9 cm, 4.0-7.9 cm, and >8.0 cm) to assess whether their responses to the environmental variables were similar.

Statistical analyses were carried out in SPSS. Multiple regression analyses were used to determine the correlation between the variables and distributions of *Nicon*. This was used to see which variables were having the greatest affect on *Nicon's* distribution throughout the mudflat.

3.3 Results

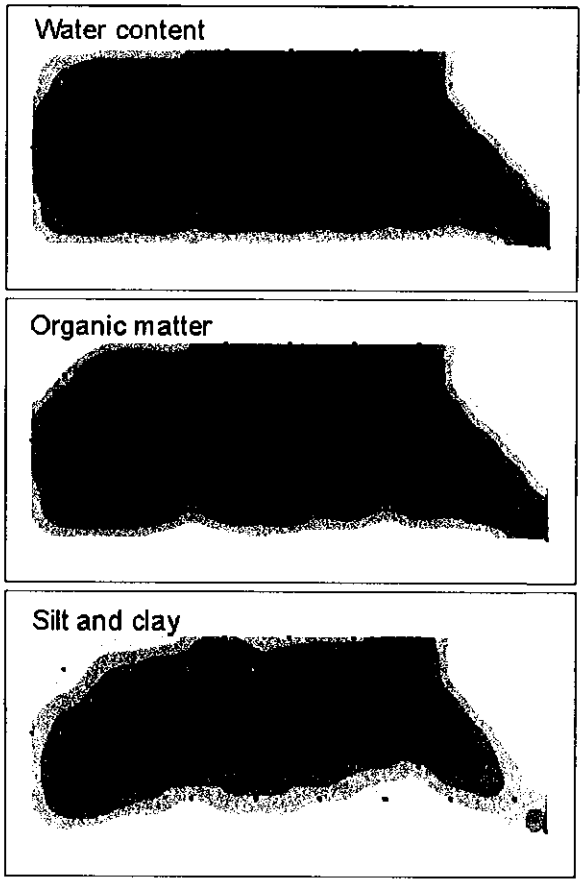

Fig. 3.3 Series of maps showing Kernel Density variation of each environmental variable throughout the mudflat.

Each of the variables in Fig 3.3 had higher levels toward the centre of the estuary. Water content, OM, and percentage silt and clay had higher levels at either end of the estuary. This is the opposite for percentage sand as sites with highest levels of sand had lowest levels of silt and clay. All variables were found to be strongly correlated to one another (Table 3.1)

Table 3.1. Correlations for all of the environmental variables. Pearson correlation coefficients and significance values are denoted by asterisks (***=<0.001).

Variable	Organic matter	Silt/clay	Distance to channel	Distance to river	Distance to sand dunes
Water content	0.882***	0.855***	-0.600***	-0.019	0.115
Organic matter		0.828***	-0.670	-0.034	0.133
Silt/clay	0.828***		-0.655***	0.092	-0.016
Distance to channel	-0.670***	-0.665***		0.399***	-0.486***
Distance to river	-0.034	0.092	0.399***		-0.719***
Distance to sand dunes	0.133	-0.016	-0.486***	-0.719***	

The spatial distribution of *Nicon aestuariensis* was then mapped to look for any systematic variation or pattern (Fig 3.4).

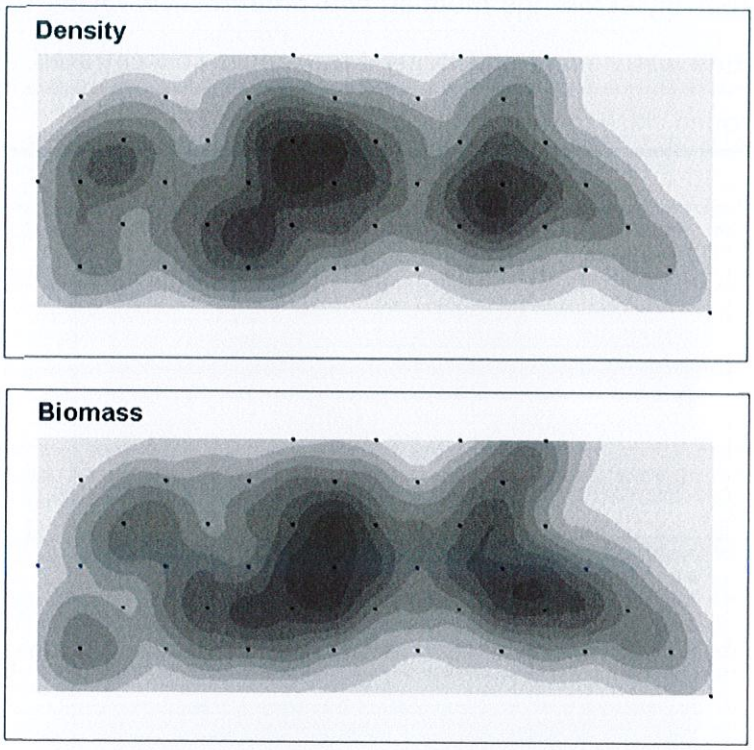

Fig 3.4 Kernel Density maps showing variation in density and biomass of *Nicon aestuariensis* in September 2010 at study sites.

Kernel density maps indicated that *Nicon* was densest, and with the highest biomass, at mid-flat level, particularly near the centre of the mudflat (Fig. 3.4). Density and biomass were strongly correlated ($r = 0.749$, $P = 0.000$). Multiple regression was then used to evaluate the influence of the environmental variables on *Nicon* biomass and density.

Sediment organic matter ($r = 0.313$, $P = 0.049$) and distance to channel ($r = 0.475$, $P = 0.002$) significantly affected *Nicon*'s biomass. In combination, the variables measured in this study explained 33% of the biomass variation ($F_{7,32} = 2.297$, $P = 0.05$, $R^2 = 0.33$). Density variation was driven primarily by distance to channel ($r = 0.412$, $P = 0.008$). Overall 34% of this variation was explained by all variables combined ($F_{7,32} = 2.351$, $P = 0.047$, $R^2 = 0.34$).

The size classes of *Nicon aestuariensis* may play a part in the species' distribution within the mudflat. Smaller individuals may have different preferences for the factors tested in this study than larger individuals. Figure 3.5 shows that the density of small, medium and large

Nicon varied substantially across the mudflat, with smaller *Nicon* being more concentrated towards the high tide water mark and larger *Nicon* more concentrated towards the river. Adult *Nicon* were found close to the channels.

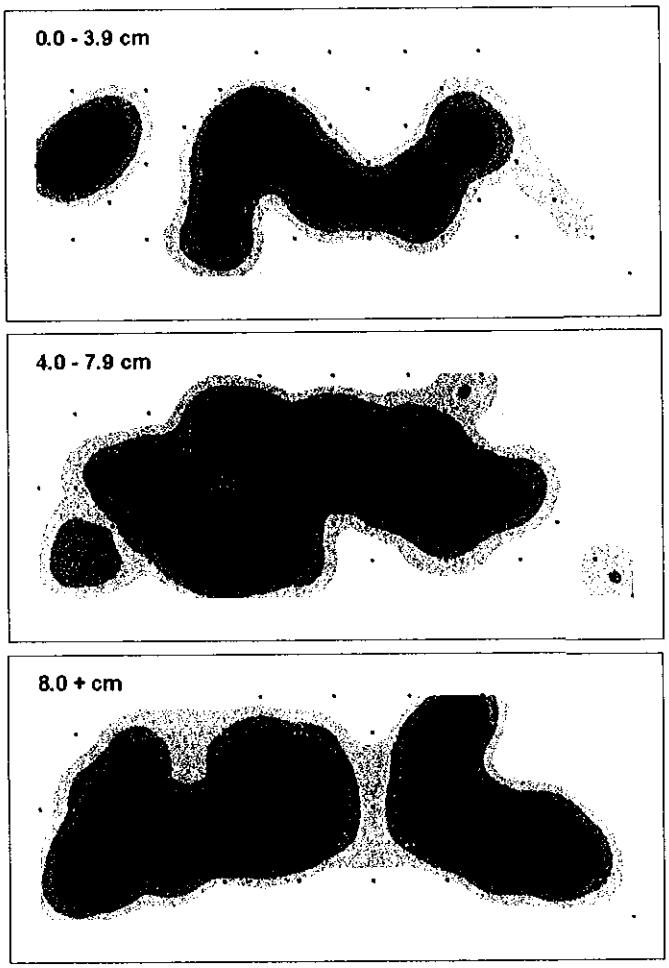

Fig. 3.5 Kernel density maps of *Nicon aestuariensis* of three different size classes in September 2010.

Multiple regression failed to detect any significant environmental impacts on the density of small (0 – 3.9 cm) worms. Distance to channel ($r = -0.314$, $P = 0.016$) was related to the density of medium (3.9 – 7.9 cm) *Nicon.* Adult *Nicon* (8.0 + cm) were found to be distributed in relation to sediment organic matter ($r = 0.365$, $P = 0.010$) and distance to channel ($r = -0.426$, $P = 0.003$).

3.4 Discussion

3.4.1 Environmental variables

Each of the variables measured varied across the northern mudflat (Fig 3.2). The highest levels of organic matter (OM), water content, and clay/silt were found towards either end of the mudflat, and areas near the channels. The organic content within mudflat sediments is high and increases with the fineness of sediment (Knox, 2001). This is apparent in Fig 3.2 where the highest levels of organic matter coincide with areas of highest silt and clay. Regression analysis between these variables showed that water content, organic matter and sediment particle size were all strongly auto-correlated.

The water content within the sediment is likely to be affected by both the tidal inundation period and the composition of the sediment. Silt and clay particles are extremely fine (>0.063 mm) and are able to retain higher levels of water within them, compared to larger grained sediments such as sand. A site with higher levels of silt or clay will contain lower levels of sand and, as a result, higher levels of water. The water velocity within channels is much greater than on the mudflat itself (Little, 2000). Very fine silts that travel up the channels from the river are usually deposited near channels when the water flows on to the mudflat (Little, 2000). This may explain the pattern observed in the silt/clay map (Fig 3.2). The greatest level of silt and clay is found near the beginning of the first channel and near the corner of the channel by the sea wall. It is likely that water flowing over the channel wall deposits a lot of fine sediment.

3.4.2. Drivers of population structure

The density and biomass maps show that *Nicon* varies spatially across the mudflat (Fig 3.3). In general, more *Nicon* were found towards the centre of the mudflat. It appears as though they prefer areas from the mid-water to low-water mark. The high water mark (at the top of Fig 3.1) contained the lowest abundance of *Nicon*. Regression analysis showed that *Nicon* density across all sizes was driven by distance to channel and that biomass was driven by

distance to channel and sediment organic matter content. All variables measured had a significant influence on the distribution of *Nicon*, explaining 33% of the variation in biomass and 34% of the variation in density. This level of explained variation is comparable to other studies. For example, Ysebaert and Herman (2002) found that environmental variables tested explained 27 – 56% of the variation in benthic macrofauna species. Estuaries contain extremely complex interactions and as a result not all of the variation was explained. Butcher (1976) looked at the ecology of intertidal invertebrates at scattered sites in the Manawatu Estuary. He found the distribution of *Nicon aestuariensis* was correlated negatively with mudflat exposure time, and positively with organic content, and sediment silt content.

The spatial distribution of *Nicon* of different ages also differed across the mudflat (Fig 3.4). Small *Nicon* appear to be denser towards the high water mark. Medium sized worms occupy the largest area of the mudflat, while adult *Nicon* are congregated around the channels. These sites would have the shortest exposure times and longest inundation times.

No correlation was found between the variables tested and the distribution of juvenile *Nicon* (Table 3.1). This suggests that something else is driving their spatial distribution. Intraspecific predation or competition with larger *Nicon* could be possible factors. Juveniles were found towards the high water mark whereas large *Nicon* were congregated towards the channels in the mid-to-low water mark (Fig 3.4). Juveniles may be avoiding areas densely populated by adult *Nicon* to avoid predation. The sediment in the upper mudflat contains higher levels of sand, and as a result juveniles would be more susceptible to desiccation. This could also make it easier for juveniles to burrow into sediment containing larger particles due to more interstitial spaces between them (Wieser, 1959). This spatial distribution could also result if juvenile *Nicon* had a different diet to adults (e.g. Hentschel 1998) and that food resource was distributed higher on the shore.

The distribution of medium and large *Nicon* was associated with distance to channels. This could be due to a reduction in exposure time at low tide. There are several reason why this variable was the most important for *Nicon*. Firstly, these areas would be exposed the least,

reducing the chance of desiccation. It is thought that *Nicon* is predominately a deposit-feeder (Estcourt, 1967) and likely feeds when the burrow is inundated to avoid predation. Reduced exposure time would also reduce temperature fluctuations, resulting in a more constant temperature near the surface where *Nicon* are found. No *Nicon* were observed foraging on the sediments surface during this study. Organic matter was found to be important for the distribution of adult *Nicon*. As shown in Fig 2.12, becoming a heteronereid is energy demanding. Adult *Nicon* may be found in areas containing high organic matter as these areas would have the greatest levels of food. Deposit-feeders need to process large amounts of sediment to obtain enough nutrition. Perhaps adult *Nicon* are associated with higher levels of organic matter as they need to obtain more nutrition prior to reproduction.

3.4.3. Additional Notes

It is possible that some of the variation not explained in this study is due to predation pressure by foraging shorebirds. Shorebirds forage with the moving tide, and areas exposed for the least amount of time in a day could potentially be subject to lower predation pressure. Perhaps the pattern observed in Fig 3.4 is somewhat explained by bird predation on this species of polychaete. The Bar-tailed Godwit is one of the main predators of *Nicon* at this estuary. Godwits forage for polychaetes by probing into the sediment (Evans, 1976). Smaller *Nicon* are potentially less likely to be detected by a randomly-probing godwit compared to larger individuals; conversely, larger worms may bury more deeply and therefore be less detectible or accessible by birds. Studying the foraging patterns of godwits and adding this factor to this study could increase the amount of variation explained. However, godwits are unlikely to be the main driving force as they will forage in shallow waters and tidal inundation between sites at the Manawatu Estuary is quite small (<1 hr to cover mud flat once the incoming tide reaches the top of the channels).

If sediment samples were collected throughout the season it would have been interesting to also include temporal variation. The level of suspended particulate matter is determined by tidal mixing on the estuary and differences in tidal cycles. Both factors will vary the

sediment composition geographically and temporally (Hardisty, 2007). Taking temporal variation into account may have explained even more of *Nicon's* spatial distribution.

Based on field observations it seems likely that the ease of building and maintaining burrows is of some importance to *Nicon*. The sites present within the south-east corner of the mudflat contained large amounts of decaying plant matter. This possibly explains the low level of *Nicon* found there, despite intermediate levels of each of the four variables tested (Fig 3.1 and Fig 3.2). Houte-Howes et al. (2004) found similar patterns in three New Zealand estuaries, where burrowing polychaetes and molluscs were absent in areas containing seagrass due to dense root-rhizome mats restricting their burrowing behaviour. This demonstrates the complexity of estuarine systems and the difficulty in trying to tease out what variables are driving invertebrate distribution.

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CHAPTER FOUR

General Summary

General Summary

Linking population dynamics with spatial distributional patterns is important to gain a better understanding of species ecology. The spatial arrangement of a species in any given area is affected by both the biology of that species and the patchy nature of the environment in which it lives (Thrush et al. 1989). Because of this, it is important to study both aspects of a species as they correspond with one another. The distribution of *Nicon aestuariensis* may reflect both their general biology and behaviour and also environmental variables that differ throughout the estuary. This thesis looked at both the behaviour and distribution of *Nicon aestuariensis* to gain more knowledge of this polychaete species.

Nicon aestuariensis is the dominant invertebrate species at the Manawatu Estuary. Their biomass levels were comparable with those of polychaetes at other sites throughout the world. This level of biomass remained reasonably stable throughout the year from September 2009 – September 2010. There was a decrease in both biomass and density levels during February 2010 which coincides with the main period of reproduction (Chapter 2; Fig 2.6) and the fuelling of the Bar-tailed Godwits (*Limosa lapponica*) before migration. As shown in Fig 2.6, larger worms have a much greater body mass than smaller individuals and therefore it is probably beneficial for birds to actively search for larger individuals. Because the length-mass relationship is not linear, an individual bird would need to feed on many small *Nicon* to obtain the same nutrition provided by a single large *Nicon*.

Prior to this research there was only one other specific paper published on *Nicon aestuariensis* (Estcourt, 1966). There were some differences between my study and Estcourt's. The breeding season at the Manawatu Estuary (December – March) is later in the season than it was at the Avon-Heathcote Estuary 1966 (August – November). Many polychaete species have an ability to adapt to local conditions. This can have effects on their population dynamics, including their lifespan and reproduction. Within a single year, spawning of *Nereis diversicolor* has occurred once, twice, or monthly depending to their geographical location (Omena & Amaral, 2000). The level of pollution has also been shown

to effect different species of polychaete. Bridges et al. (1994) assessed the effect of adding sewage, algae and hydrocarbons to sediment for two polychaete species (*Streblospio benedicti* and *Capitella* sp.). *S. benedicti* showed reduced size, and age at reproduction was delayed, while it was the opposite effect for *Capitella* with size increasing (six-fold) and reproduction occurring sooner. Based on these findings it is possible that environmental differences between the Manawatu Estuary and the Avon-Heathcote Estuary result in the behaviour of *Nicon aestuariensis* varying between these two locations. Read (1984) studied zonation patterns of intertidal polychaetes at Pauatahanui Inlet, Wellington. His population size distributions showed a large proportion of juvenile recruits in May (Read, 1984). This is consistent with the late summer reproductive period found in my study.

Nicon aestuariensis is an estuarine specialist well adapted to the environment (Jones and Marsden, 2005). The most important variable determining their distribution at the Manawatu Estuary was the proximity to the nearest channel. This variable would affect the exposure and inundation periods. *Nicon aestuariensis* is predominantly a deposit-feeder, and it is likely that this is why distance to channels was of greatest importance. Sites closest to the channels would have been inundated by water for the longest periods during a tidal cycle. This would allow *Nicon* to maximise their feeding time. They are unlikely to forage on the surface when their burrow is exposed as this increases their chances of being eaten by shorebirds. Overall 34% of *Nicon*'s density variation was explained and 33% for biomass variations. None of the variables measured were able to explain the spatial distribution of juvenile *Nicon* (Chapter 3; Fig 3.5). This could possibly be due to intraspecific predation by larger *Nicon*, or because small worms use a different food source; neither topic was addressed in this study. Large *Nicon* were found to be related to the distance to channel and sediment organic matter. They may congregate in these areas in order to increase their food intake levels prior to morphological changes in becoming a heteronereid.

Nicon aestuariensis is believed to be a principle food source of shorebirds such as the Bar-tailed Godwit and, as such, knowledge of their population dynamics and distribution is a crucial first step towards understanding the ecological interactions in the intertidal communities. This study has provided insight into the population biology of *Nicon*

aestuariensis and the complex interactions which occur within estuarine systems. The Manawatu Estuary is an ongoing site of research, particularly involving migrant shorebirds. The findings of my research will add substance to these long-term studies.

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