Ecosystem modelling of the data-limited, oligotrophic KwaZulu-Natal Bight, South Africa

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As the candidate's supervisor I have/have not approved this thesis for submission.

Signature:…………………… **Name:**…………………………… **Date:**………………………

ABSTRACT

Ecosystem modelling allows for an understanding of the structure and functioning of ecosystems. During this study, the oligotrophic KwaZulu-Natal (KZN) Bight, a data-limited system on the east coast of South Africa, was modelled. A framework for modelling data-poor systems, incorporating the construction of multiple models, sensitivity analyses and comparative analyses was applied to the Bight using literature data. Models converged on general trends of ecosystem functioning showing 99% of flows originated from detritus, primarily imported from rivers. The largest source of riverine detritus is the Thukela River which flows into the central Bight. This area supports a shallow-water prawn trawl fishery which targets penaeid prawns. Fisheries time series' were incorporated into the model framework to study the effects of prawn trawling and the decrease in prawn recruitment, caused by estuarine nursery loss, on the central Bight ecosystem. Dynamic simulations suggest the biomass of biotic groups were more affected by prawn recruitment level than trawling effort level. To understand the importance of nutrients in more detail, nutrient content, biomass and stoichiometric ratios were documented for various pelagic and demersal functional groups, and compared between areas in this oligotrophic system. Results showed the central Bight had the highest carbon, nitrogen and phosphorus biomasses, due to riverine nutrient sources, and the southern Bight had the lowest. In addition, the demersal community had higher biomasses than the pelagic community for all nutrients. Nutrient dynamics and limitations within the Bight were explored through the construction and analysis of trophic flow networks of carbon, nitrogen and phosphorus for the southern, central and northern Bight. Network analyses suggest nutrient cycling was lowest in the central Bight, and highest in the southern Bight. Cycling of nitrogen was highest in all areas due to the dominance of benthos, in terms of biomass, which was nitrogen-limited. Higher trophic levels were found to be phosphorus-limited. However many pelagic groups were co-limited by nitrogen and phosphorus, probably due to the oligotrophic nature of the bight. This suite of ecosystem models provides the first holistic view of the KZN Bight and an understanding of ecosystem functioning in the southern, central and northern Bight.

PREFACE

The experimental work described in this PhD thesis was carried out in the School of Life Sciences, University of KwaZulu-Natal, Westville, from April 2009 to November 2012, under the supervision of Dr. Ursula Scharler.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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DECLARATION 1 – PLAGIARISM

I, **Morag Jane Ayers** declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research;

2. This thesis has not been submitted for any degree or examination at any other university;

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

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DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis are as follows:

Publication 1

Ayers, M.J. and Scharler, U.M. (2011) Use of sensitivity and comparative analyses in constructing plausible trophic mass-balance models of a data-limited ecosystem – The KwaZulu-Natal Bight, South Africa. *Journal of Marine Systems*. 88: 289-311.

Publication 2

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Publication 3

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Publication 4

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Contribution from co-authors other than my supervisor Dr. U.M. Scharler:

This thesis is a sub-component of the project "Ecosystem processes within the KwaZulu-Natal Bight: linking geographical and physical processes to understand ecosystem functioning" under the African Coelacanth Ecosystem Program (ACEP) II and was originally designed to use data generated during the project to construct ecosystem models.

Dr. Sean Fennessy (Oceanographic Research Institute, Durban) provided KZN prawn trawl catch and effort data, advice and editorial comments for Ayers et al. (in press) and samples for phosphorus analyses and biomasses of demersal taxa for Chapter 3.

Dr. Ray Barlow and Dr. Tarron Lamont (Department of Environmental Affairs, Cape Town) provided inorganic nutrient concentrations and phytoplankton biomass data.

Dr. Jenny Huggett and Mrs Michelle Pretorius (Department of Environmental Affairs, Cape Town) provided zooplankton biomass data.

Dr. Dave Muir and Mr Travis Kunnen (University of KwaZulu-Natal, Westville) provided bacteria biomass data.

Dr AJ Smit and Ms. Aadila Omarjee (University of KwaZulu-Natal, Westville) provided organic nutrient concentrations.

Dr. Ander de Lecea (University of KwaZulu-Natal, Westville) provided carbon and nitrogen content of demersal organisms.

Signed: ....

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General Introduction

Marine ecosystems are subjected to increasingly frequent negative impacts such as fishing, decreasing river outflow and climate change. Therefore when considering global issues such as food security, freshwater storage, and ecosystem responses to climate change it is important to be able to identify how marine ecosystems function and react to natural and human-induced changes.

The analysis of ecosystems as functional entities becomes necessary given the complex direct and indirect interactions between and among biotic and abiotic components. This whole-system view is the focus of network ecology, an extension of systems ecology, which uses weighted models to study the structure and flows of nutrients and energy through the system. Ecological network analysis (ENA) is a tool commonly used to analyse mass-balanced foodwebs (Wulff et al., 1989, Christensen and Pauly, 1993, Kay et al., 1989, Ulanowicz, 1986). The constraint of mass-balance, where inflows to a group equal the outflows, is based on the assumption that the system is in a steady-state. This allows the construction of ecological networks with mutually compatible inputs of information on the size of nodes (biomass), links between nodes (trophic flows or diet compositions) and imports and exports across the system boundary. ENA is commonly used to characterise ecosystem functioning and to investigate the effects of anthropogenic impacts. In marine ecosystems, Ecopath with Ecosim (EwE) (Christensen and Walters, 2004) has been used extensively to study the impacts of fishing on ecosystems around the world, including South Africa (e.g. Jarre-Teichmann et. al. (1998), Shannon et al. (2003)). Another software, NETWRK (Ulanowicz and Kay, 1991), and the Windows-compatible version WAND (Allesina and Bondavalli, 2004), has been used to characterise ecosystems and compare them to others (e.g. Heymans and Baird (1995), Scharler and Baird (2005)).

For ENA studies, most networks have been constructed using biomass and trophic flows in terms of wet weight because the use of wet weight biomass is sufficient for answering fisheries-related questions which are the focus of EwE applications (e.g. Freire et al. (2008), Gribble (2003), Heymans et al. (2010) and Pinnegar and Polunin (2004)). Fewer studies use biomass and trophic flows in terms of nutrients, with most focusing on carbon (e.g. Heymans and Baird (2000a), Sandberg et al. (2000), Scharler and Baird (2005), and Christian et al.(2009)) and nitrogen (e.g. Borrett et al. (2006), Christian et al. (1996), Christian and Thomas (2003), Fores et al. (1994)). Very few studies have conducted ENA on networks constructed in terms of phosphorus (Baird, 1998, Kaufman and Borrett, 2010).

Networks based on nutrient flows can provide an increased understanding of ecosystem functioning, particularly when networks based on different nutrients are studied concurrently. Ecological stoichiometry considers how the elemental compositions of prey and predator affects ecosystem processes (Sterner and Elser, 2002). Studies have shown that organism stoichiometry can affect nutrient cycling (e.g. Elser and Urabe (1999)), population dynamics (e.g. Andersen et al. (2004)) and the trophic role of species in an ecosystem (e.g. Vanni et al. (2002)). Despite this, very few studies have investigated the dynamics of these nutrients concurrently and none have focused on oligotrophic marine systems.

The KwaZulu-Natal (KZN) Bight is located on the east coast of South Africa which is typically oligotrophic due to the warm southward-flowing Agulhas Current moving close to the coast (Fig. 1). The KZN Bight is slightly less oligotrophic than the surrounding waters and this is thought to be due to three major nutrient sources – a lee eddy in the south caused by the Agulhas Current flowing along the edge of the continental shelf (Pearce 1977, Pearce et al 1978, Carter et al 1988, Meyer et al 2002), a sporadic topographically-induced upwelling cell in the north (Meyer et al., 2002, Pearce, 1977, Lutjeharms et al., 1989), and riverine outflow, particularly from the Thukela River in the central Bight (Meyer et al., 2002). Historical quantitative data for biotic and abiotic components in the Bight is scarce and was last collated by Schumann (1988a). Since then, quantitative research has been primarily confined to oceanographic and primary production studies (e.g. Barlow et al. (2008), Barlow et al. (2010)), important linefish species (e.g. Chale-Matsau et al. (1999), Fennessy (2000a), Mann et al. (2002)) and large sharks and cetaceans caught in the KZN Sharks Board shark nets (e.g. Cliff and Dudley (1989), Dudley and Simpfendorfer (2006), Wintner (1993)). The completion of two multi-disciplinary research cruises in the KZN Bight in 2010 under the Africa Coelacanth Ecosystem Programme (ACEP II) provided the opportunity and data to study ecosystem functioning within the Bight and the potential role of riverine nutrient sources in ecosystem functioning.

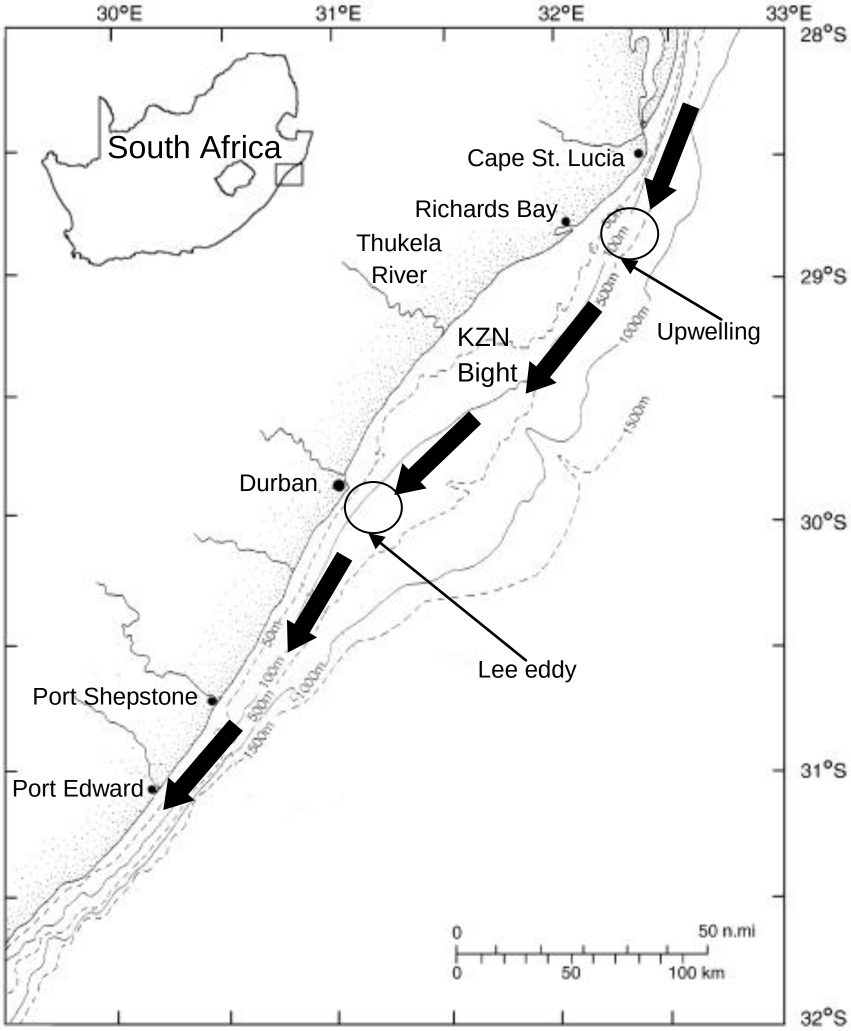

Figure 1. Map of the KZN Bight. Arrows indicate the path of the Agulhas Current. Circles indicate major oceanographic events. Adapted from Meyer et al. (2002).

The focus of this PhD study is to explore the functioning of the KZN Bight ecosystem through the use of marine ecosystem modelling. Because quantitative literature data for the Bight are sparse there is a poor understanding of how the ecosystem functions. There are many data-poor ecosystems in Africa and around the world and therefore there is a need to explore the potential for constructing ecosystem models of these systems so that an understanding of general ecosystem functioning can be provided. This is a challenging task and therefore few studies have examined methods that can be employed in modelling data-poor areas. In Chapter 1, a framework is developed for constructing marine ecosystem models of data-poor systems and applied to the KZN Bight to identify general trends in system functioning.

Most quantitative literature data, particularly fisheries-oriented data, are available for the central KZN Bight as this area comprises the southernmost prawn trawling ground in Africa – the Thukela Bank. This fishery began in the 1970's (Fennessy and Groeneveld, 1997) and is one of the most important fisheries on the east coast of South Africa. However since 2002, the fishery has collapsed following the closure of the mouth of the large St. Lucia estuary due to natural and human-induced factors. This estuary was one of two major prawn nurseries for the Thukela Bank population, highlighting the sensitivity of estuarine-dependent marine species which rely on multiple ecosystems during their life cycles. Studies have been conducted on the effects of the prawn trawl fishery in terms of bycatch rates (Fennessy, 1994a, Fennessy, 1994b). However no studies have investigated the ecosystem effects of this fishery or the effect of a decrease in prawn recruitment, via the closure of St. Lucia, on the marine ecosystem. Ecosystem effects of fishing have been studied extensively using the Ecopath with Ecosim approach (e.g. Bundy and Pauly (2001), Heymans et al. (Heymans et al., 2010), Pinnegar and Polunin (2004), Shannon et al. (2000), Wolff (1994)). Although Ecopath models have been constructed representing estuaries and coastal ecosystems separately, no models deal with questions of connectivity between them. Therefore, in Chapter 2, the ecosystem effects of prawn trawling and changes in marine-estuarine connectivity via changes in prawn recruitment on the central bight ecosystem are investigated using Ecopath with Ecosim models.

Although Chapters 1 and 2 demonstrate the potential for a data-poor ecosystem to be modelled, additional data are needed for an in-depth understanding of system functioning. Prior to the ACEP II research cruises, the elemental composition of taxa had not been measured within the Bight, although nitrate, nitrite and phosphate has been measured throughout the water column across the Bight in 1989 (Meyer et al., 2002). Therefore, Chapter 3 documents carbon, nitrogen and phosphorus content and stoichiometry of taxa sampled in the southern, central and northern regions of the Bight during the ACEP II cruises. Carbon, nitrogen and phosphorus biomasses are calculated to compare the distribution of these nutrients through the foodweb and across the Bight.

Because the Bight is nutrient-poor the system relies on various outside nutrient sources. However it is unknown how this oligotrophic nature is transferred to nutrient limitations within the foodwebs. Understanding the role of carbon, nitrogen and phosphorus in foodwebs within the oligotrophic Bight would provide a more in-depth understanding of ecosystem functioning. Moreover, studies which analyse the dynamics of carbon, nitrogen and phosphorus concurrently are rare. Therefore in Chapter 4 ecological network analysis (ENA) is used to characterise ecosystem functioning of the southern, central and northern KZN Bight in terms of carbon, nitrogen and phosphorus flows, identify nutrient limitations and explore the importance of riverine nutrient sources.

Overall, this study documents the construction and analyses of marine ecosystem models/networks to gain an understanding of ecosystem functioning within the KZN Bight. Results from this study will provide the first holistic view of the KZN Bight ecosystem.

In summary, the main objectives of this study were:

1) demonstrate that plausible representations of data-poor systems can be constructed, to better understand how the KZN Bight functions by gaining a holistic overview of the system;
2) model the effects of prawn trawling and reduced prawn recruitment on the central bight ecosystem and simulate the effects of complete loss or full restoration of prawn nurseries in the region;
3) document carbon, nitrogen and phosphorus content, stoichiometry and biomass within taxa in various regions of the KZN Bight;
4) investigate the nutrient limitations and the importance of riverine nutrient sources to the functioning of the KZN Bight ecosystem.

Use of sensitivity and comparative analyses in constructing plausible trophic mass-balance models of a data-limited marine ecosystem – The KwaZulu-Natal Bight, South Africa

1.1 INTRODUCTION

Understanding how marine ecosystems function as a whole is a challenge for data-poor systems. However, a holistic overview of an ecosystem is necessary for understanding how they function and how anthropogenic activities could potentially impact them. Bays and bights are ecosystems often influenced by anthropogenic activities due to their proximity to the coast. Firstly, most are affected by commercial, recreational and/or subsistence fisheries (Jennings and Kaiser, 1998, Pauly et al., 1998, Pauly et al., 2005). Secondly, some are influenced by the outflow of large rivers (Diaz and Rosenberg, 2008, Gillanders and Kingsford, 2002, Lamberth et al., 2009).

River-influenced bays and bights are usually more productive than the adjacent ocean due to an inflow of nutrients and detritus from topographical upwelling and rivers (Wollast, 1998). However, there is an increasing need to place impoundments onto large rivers for inland water-use, and to increase inshore fisheries catches for local consumption and export. Therefore it is important to understand how these ecosystems function at present in order to predict what effects these activities will have on production in the system.

The KwaZulu-Natal Bight (KZN Bight) on the east coast of South Africa is an example of a river-influenced bight (Fig. 1.1). It is also a data-poor ecosystem with sparse quantitative data on biotic and abiotic components. Biomasses are available for plankton groups and other quantitative data are available for important linefishing species, large sharks, and cetaceans only. Oceanic waters off south-east Africa are typically oligotrophic (Lutjeharms, 2006a). However, the waters of the bight are slightly less so than the bordering Agulhas Current (Lutjeharms et al., 2000, Meyer et al., 2002). This is due to nutrient inputs from an episodic upwelling off Richards Bay, a lee eddy off Durban and rivers along the coast, particularly the Thukela (Carter and D'Aubrey, 1988, Lutjeharms et al., 1989, Pearce et al., 1978). The Thukela River is the third largest river in southern Africa and has a sediment output of 6.79×10^3 m^3 y^{-1} (Birch, 1996). This outflow creates a turbid area in the central bight which is home to South Africa’s only prawn fishery (Fennessy and Groeneveld, 1997). The rivers and estuaries along the coast aid the recruitment of many targeted fisheries species by providing nursery grounds

(Wallace et al., 1984, Lamberth et al., 2009, Wallace and van der Elst, 1975, Whitfield, 1998). To understand and predict the impact of current and future anthropogenic activities (e.g. fishing and water impoundments on the Thukela River (DWAF, 2004)) on this ecosystem as a whole it is important to understand the functioning of this ecosystem as a whole.

Ecosystem modelling allows a system to be studied as a whole. The system can be constructed as a network using information on nodes (biomasses), links between nodes i.e. trophic flows (diet compositions), production, consumption, and fisheries landings of biotic groups. If biomass, production or consumption are missing for a group then this can be estimated using the mass-balance approach, most commonly used in Ecopath with Ecosim (EwE) software (Christensen and Pauly, 1992). Thus this approach lends itself to the modelling of ecosystems such as the KZN Bight where many biomasses are unknown. For example, EwE has been used to model coral reef ecosystems and historical representations of ecosystems (Morato and Pitcher, 2005, Heymans and Pitcher, 2002, Polovina, 1984). From this network system metrics can be calculated which describe the system in terms of energy flows, energy cycling and ecosystem services provided by the system (Ulanowicz, 1986). These metrics enable an understanding of how the ecosystem functions and the identification of system level characteristics. In addition, comparisons of marine ecosystems from different areas and of different spatial scales can be carried out. These comparisons can aid the modelling of a data-limited ecosystem if functional differences to another ecosystem are known *a priori*.

The east coast of South Africa is typically oligotrophic with low fisheries catches and is known to be influenced by the many rivers/estuaries flowing into coastal waters. This is in contrast to the west coast of South Africa, comprising the Southern Benguela upwelling ecosystem, which is nutrient rich with large plankton biomass and fisheries landings (Shannon et al., 2003). A direct comparison of models of these systems would aid in assessing the plausibility of models of the data-limited KZN Bight since plausible models would produce known differences in functioning to the Southern Benguela.

In this paper, the development and analysis of models of the KZN Bight are described. The aims of this study are to demonstrate that plausible representations of data-poor river-influenced bights can be constructed, to better understand how the KZN Bight functions by gaining a holistic overview of the system and to build a framework for future models of the KZN Bight. Comparisons are made between:

a) several versions of KZN Bight models to determine the levels of uncertainty associated with non-local input data,

b) the KZN Bight models and a model of the southern Benguela, an upwelling system on the west coast of South Africa, to determine if the KZN Bight models reproduce known differences in functioning between these systems.

1.2 METHODS

1.2.1 Modelling approach

Mass-balanced models of the KZN Bight were constructed and analysed using Ecopath with Ecosim software, version 5.1 (Christensen and Walters, 2004). Underlying Ecopath with Ecosim are two equations ensuring the mass-balance or energy-balance of each biotic group. The first describes the production of a group:

$$\left(\frac{P}{B}\right)_i B_i = Y_i + \sum \left(\frac{Q}{B}\right)_j B_j DC_{ij} + E_i + BA_i + \left(\frac{P}{B}\right)_i B_i(1 - EE_i) \qquad (1.1)$$

P/B_i is the production/biomass ratio of group *i*; B_i is the biomass of group *i*; Y_i is the total catch of group *i*; Q/B_j is the consumption/biomass ratio of predator *j*; B_j is the biomass of predator group *j*; DC_{ij} is the proportion of prey *i* in the diet of predator *j*; E_i is the net migration rate of group *i*; BA_i is the biomass accumulation rate of group *i* and EE_i is the ecotrophic efficiency of group *i* which represents the proportion of production utilised in the system and.

Energy balance within individual functional groups is modelled as the fate of all consumed energy (Christensen and Walters, 2004).

$$\text{Consumption} = \text{production} + \text{respiration} + \text{non-assimilated food} \qquad (1.2)$$

Respiration is the assimilated consumption not used for production and is used for adjusting the system balance (Christensen and Walters, 2004). Non-assimilated food is the proportion of food that is excreted. Thus the input data required for each functional group in Ecopath are biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), ecotrophic efficiency (EE), diet composition and total catch. When B, P/B, Q/B or EE are missing, the parameterization routine estimates the missing parameters iteratively and sets up linear equations for each group which are solved for one of the following parameters – B, P/B, Q/B and EE (Christensen and Walters, 2004). Once solved, the system of equations provide a ‘snapshot’ of the trophic flows in the system from the biomass, production and consumption estimates suggesting a possible configuration of quantified trophic flows in the ecosystem.

1.2.2 Construction of KZN Bight models

1.2.2.1 Boundary of model

The KZN Bight ecosystem was defined as the continental shelf from Durban (29˚53’S 31˚03’E) to Richards Bay (28˚48’S 32˚06’E), totalling 5096km^2 (Cockcroft and Peddemors, 1990) (Fig. 1.1). It extends from the subtidal region at the landward boundary to the 200m isobath, corresponding to the continental shelf break and boundary of the Agulhas Current (Lutjeharms et al., 2000, Pearce, 1977, Schumann, 1988b). The KZN Bight is the widest area of shelf off the east coast of South Africa (Lutjeharms, 2006b) and thus is a unique area in the KZN province and the South African east coast.

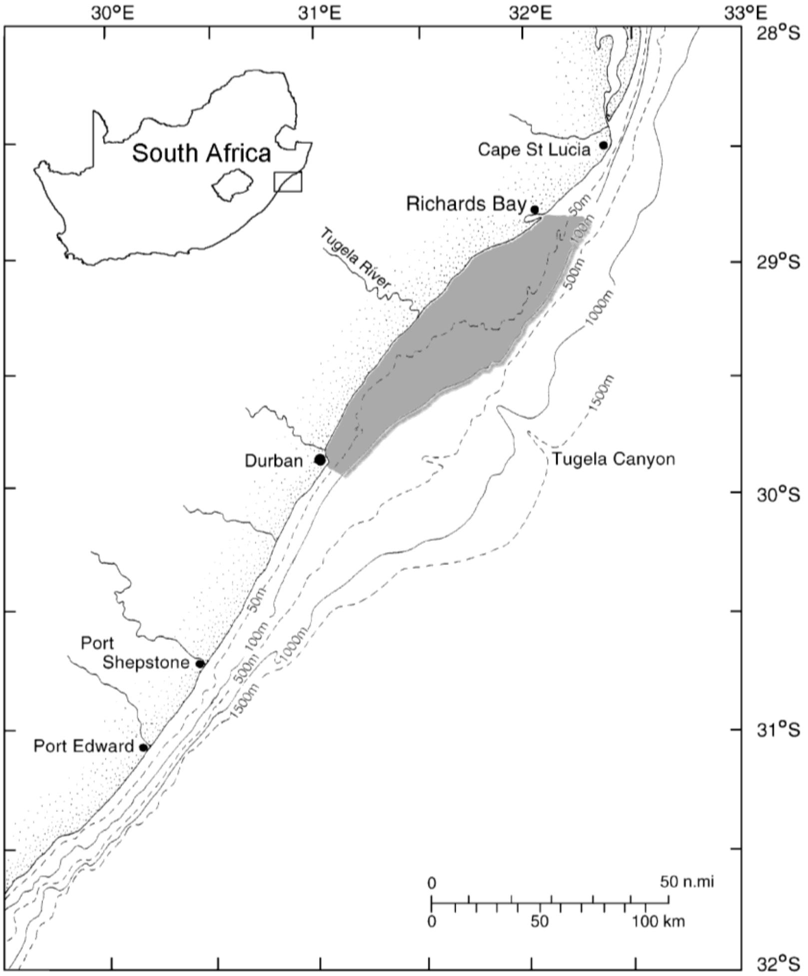

Figure 1.1. Map of the KZN Bight and South Africa. Adapted from Meyer et al. (2002).

1.2.2.2 Model groups

Following a literature search it was found that quantitative data were available for a larger number of parameters and groups for the period 1980-1989 in the KZN Bight compared to other years. The choice of the number and type of functional groups in the KZN Bight models was based on groups included in the 1980's Southern Benguela model (Shannon, 2000). This was to facilitate a comparison between the two models since functional groups needed to be similar for a direct comparison (Kremer, 1989, Mann et al., 1989). However the KZN Bight model included the additional groups 'prawns and shrimp', 'pelagic-feeding reef fish' and 'benthic-feeding reef fish' in order to represent groups which occur in the KZN Bight but not in the Southern Benguela. Species, for which quantitative data were available, were placed into functional groups based on information on habitats and feeding modes from literature (Smith and Heemstra, 1986, van der Elst, 1993).

Appendix 1.1 shows the functional groups and representative species included in both models. Differences include sardines, anchovy and redeye which were separated in the Southern Benguela model but combined into a small pelagic fish group in the KZN Bight models due to a lack of local quantitative data on each species. Zooplankton was separated into micro-, meso-, macro- and gelatinous zooplankton groups in the Southern Benguela but included as one zooplankton group in the KZN Bight models due to a lack of local data on each size class. Seabirds were not included in the KZN Bight model as they do not have a large enough biomass in the region for the majority of the year (D. Allan, pers. comm.). Juvenile horse mackerel, adult horse mackerel and chub mackerel, included in the Southern Benguela model as separate groups, were caught in large quantities in the Southern Benguela system (Shannon, 2000, Maggs, 2010) but not in the KZN Bight (Maggs, 2010) and therefore were included in the pelagic fish group. The following groups in the Southern Benguela model do not occur in the KZN Bight system: snoek (*Thrysites atun*), small *Merluccius capensis*, large *Merluccius capensis*, small *Merluccius paradoxus*, large *Merluccius paradoxus* (van der Elst, 1993).

1.2.2.3 Input parameters

Basic input data of B, P/B, Q/B, EE and/or diet compositions were collected from published and grey literature (listed in Appendices 1.2 and 1.3). Due to the scarcity of data for the KZN Bight it was not possible to gather data for all groups from the model area and time period. Therefore data for the area but another time period were used, or data for a similar area e.g. Maputo Bay, Mozambique (Paula E Silva et al., 1993) were used (see Appendix 1.2). In the final models, 54% of basic input parameters were from KZN; the remaining 46% were termed “non-local parameters”. When input parameters were available for more than one representative species in a group, the average of these was calculated and used as the final input parameter for that group. Ideally, the parameter of each species would be weighted by its biomass in order to produce a final input parameter representative of the group. However this was not possible due to the unavailability of biomasses for individual species.

Published biomass estimates were scarce for the KZN Bight. Only estimates for phytoplankton and zooplankton were found in the published literature. Detritus biomass was calculated using the model of Pauly et al. (1993):

$$\log_{10}D = -2.41 + 0.954 \log_{10}PP + 0.863 \log_{10}E \tag{1.3}$$

where D is detritus biomass (gC m^{-2}), PP is the rate of primary production (gC m^{-2} y^{-1}) and E is euphotic depth (m). A euphotic depth of 10 - 30m and primary production rate of 42 - 603gC m^{-2} y^{-1} from Burchall (1968) gave a detritus biomass of 0.001 – 0.46t km^{-2} for the KZN Bight. However, the primary productivity was measured in 1967 and no data representing the whole KZN Bight in the 1980’s were available. The only other available measurement of primary production was from 2006/07 (Barlow et al., 2010). Chlorophyll-a values of 20 - 70mg m^{-2} measured in 2005 by Barlow et al. (2008) were used to calculate phytoplankton biomass since the study covered the entire KZN Bight and no value for the 1980’s was available. Values were converted to carbon using a chlorophyll-a:carbon ratio of 40 then converted to wet weight using a carbon:wet weight ratio of 14.25 (Jarre-Teichmann et al., 1998). This resulted in a phytoplankton biomass of 0.011 - 0.04 t km^{-2}. Zooplankton biomass (dry weight) was available from a study off Richards Bay (Carter, 1973). This was converted to a wet weight of 0.002 - 0.006t km^{-2} using a dry weight:carbon ratio of 0.33 and a carbon:wet weight ratio of 14.25 (Wiebe et al., 1975). Tentative biomass estimates were available for cetaceans and small pelagic fish. Abundance of common dolphins (*Delphinus delphis*) in the Bight was available (Cockcroft and Peddemors, 1990) and converted to t km^{-2} using an average individual weight of 100kg (Collet and Girons, 1984). This gave a range of 0.059-0.078t km^{-2} of which 0.059t km^{-2} was used for the cetacean group. The biomass of pilchard (*Sardinops sagax*) in the KZN Bight from a 1987 cruise was 3.5t km^{-2} (Armstrong et al., 1991) and this was used for the biomass of the small pelagic fish group.

Local P/B values were available in the literature for most fish groups. Values for other groups were taken from models of other areas at similar latitudes such as Mozambique and Brazil. Sources can be found in Appendix 1.2.

For the fish groups, Q/B was calculated using the Fishbase life-history tool (Froese and Pauly, 2010). Local length and weight data from literature and mean sea surface temperature supplied by KZN Sharks Board (G. Cliff pers. comm.) were used. Q/Bs for the remaining groups were taken from models of areas at similar latitudes (Appendix 1.2).

Due to the lack of biomass data, EEs were used to balance the models. EE values are not directly measured and therefore do not represent a functional group as accurately as biomasses. Therefore, as a guide, EEs of similar functional groups in models of coastal areas at similar latitudes were used (Appendix 1.2). However, EE values may not be transferable between systems due to differences in production, biomass and predation mortality of a group. Moreover, the Maputo Bay model (Paula E Silva et al., 1993), used for 38% of the EEs, and the East Brazil model (Freire et al., 2008), used for 25% of the EEs, did not state how EEs were estimated. Therefore a subsequent sensitivity analysis was carried out to determine the effects of EEs on the KZN Bight models (see Section 1.2.4). Initially, the EE of apex chondrichthyans was based on the EE for the same group in the Southern Benguela model however it was increased to 0.1 because the group is caught in the KZN shark nets. These are deployed for 18.3 km at popular recreational sites along the KZN bight coast (Shelmerdine and Cliff, 2006).

Diet data from KZN or South Africa were available for cetaceans, chondrichthyan groups, benthic-feeding demersal fish and reef fish groups with 63% of the diets from KZN. Diets were based on information from Young and Cockroft (1994), Cockcroft and Ross (1990), de Bruyn et al. (2005), Aitken (2003), Cliff et al. (1989), Dudley and Cliff (1993), Porter (2006), Cliff and Dudley (1991a), Allen and Cliff (2000), Dudley et al. (2005), Cliff (1995), Cliff and Dudley (1991b), Cliff et al. (1990), Griffiths and Hecht (1995b), Griffiths (1997a), Joubert and Hanekom (1980) and Garratt (1984). Percentage diet compositions for these groups were calculated by averaging the percentage diet compositions of representative species. However, if the Q/Bs of all representative species were known for a group then the diets were weighted by these Q/Bs and summed. Zooplankton and large pelagic fish diets were taken from the KZN reef model (Toral-Granda et al., 1999). Macrobenthos, prawns & shrimp, cephalopod and small pelagic fish diets were taken from the East Brazil Large Marine Ecosystem model (Freire et al., 2008). The initial diet compositions can be found in Appendix 1.3.

A detritus import value needed to be calculated since detritus is transported into the KZN Bight from rivers and estuaries. No value for detritus import could be found in literature therefore particulate organic carbon (POC) flowing from the Thukela River was calculated. First, total suspended solids (TSS) in mg L^{-1} was calculated using the annual sediment yield ($9x10^{6}$ t) and annual river flow ($5m^{3}$ s^{-1}) from the Thukela (DWAF, 2004). POC was assumed to be 6.25% of TSS (Meybeck, 1982) and therefore the detritus import was calculated as 114t km^{-2} y^{-1}.

Major fisheries occurring in the KZN Bight include trawling and linefishing. Crustacean trawlers fish in the inshore and offshore areas in the central KZN Bight (Fennessy and Groeneveld, 1997). Both commercial and recreational linefishing occur throughout the KZN Bight (van der Elst and Adkin, 1991). Landings by crustacean trawlers were published for the years 1980-1987 Sea Fisheries Research Institute (1981, 1982, 1983, 1984, 1985, 1986, 1987). Unfortunately, fish species were aggregated into one group in the report. However, bycatch data by weight for this fishery was available for 2003 and this was used to assign the aggregated fish landings to model groups (Persad, 2005). Landings for the commercial linefishery were available from the National Marine Linefish System (NMLS), Department of Agriculture, Forestry and Fisheries, Cape Town (DAFF) (unpub. data) from 1982 - 1987 for the area from Durban Harbour to Richards Bay. These were assigned to model groups based on their habitat and feeding modes in literature (Smith and Heemstra, 1986, van der Elst, 1993). Recreational skiboat landings were also available from the NMLS for the area from Durban Harbour to Richards Bay. Data for 1980 - 1984 were provided by DAFF (unpub. data) and data from 1984 - 1989 were provided by Maggs (2010). In commercial and recreational data, landings of the aggregated group “others (mainly, sharks, skates and rays)” were assigned to ‘benthic-feeding chondrichthyans’. The KZN Sharks Board shark nets were included in the model as a type of fishery. Landings of sharks by these nets were provided for 1980-1989 (G. Cliff, KZN Sharks Board, pers. comm.). Landings included only dead specimens brought back to shore rather than those released alive. Species were assigned to model groups based on their habitat and feeding modes (Smith and Heemstra, 1986). Discards from all fisheries were not included in the Southern Benguela model and therefore were not included in the KZN Bight models. Landings for the 1980’s for each functional group can be found in Appendix 1.2.

1.2.3 Parameterisation of KZN models

In total ten models of the 1980’s KZN Bight were constructed. Five models were constructed and parameterised using combinations of minimum, maximum and mean biomasses of detritus, phytoplankton and zooplankton from literature (Table 1.1). These models represented various states of phytoplankton and detritus biomass the system could experience, and accounted for the variability in the dataset. Two models were constructed and parameterised using only detritus and phytoplankton biomasses while two other models were constructed using only detritus biomass (Table 1.1). These were constructed to test if models could estimate similar phytoplankton and zooplankton biomasses to those used in the first five models, i.e. literature data. An additional model was constructed and parameterised using maximum detritus, phytoplankton and zooplankton biomasses along with tentative biomass estimates of cetaceans and small pelagic fish (Table 1.1). This model was constructed to test whether the use of speculative biomasses would decrease model plausibility despite increasing the number of inputs constraining the model. Speculative biomasses were only available for cetacean and small pelagic fish groups. Maximum detritus biomass was used for many of the models as it was assumed that the equation used to calculate detritus biomass would be a low estimate since it only takes into account detritus from primary production.

Table 1.1. Biomass (t km^{-2}) and detritus import (t km^{-2} y^{-1}) values used in various 1980's KZN Bight models. Gaps indicate when Ecopath was used to calculate the biomass using EE. Detritus import was the minimum detritus import required to balance the model.

Model	Detritus	Phyto-plankton	Zoo-plankton	Other biomasses	Detritus import	Model description
1	0.001	0.011	0.002	-	200	Low plankton & detritus biomass. 3 biomass inputs.
2	0.46	0.040	0.006	-	158	High plankton & detritusbiomass. 3 biomass inputs.
3	0.011	0.025	0.004	-	169	Average plankton & detritus biomass. 3 biomass inputs.
4	0.46	0.025	0.004	-	162	Average plankton, high detritus biomass. 3 biomass inputs.
5	0.46	0.011	0.002	-	145	Low plankton, high detritus biomass. 3 biomass inputs.
6	0.011	-	-	-	174	Average detritus, unknown plankton biomass. 1 biomass input.
7	0.46	-	-	-	173	High detritus, unknown plankton biomass. 1 biomass input.
8	0.46	0.025	-	-	175	Average plankton, high detritus biomass. 2 biomass inputs.
9	0.46	0.011	-	-	174	Low plankton, high detritus biomass. 2 biomass inputs.
10	0.46	0.040	0.006	Cetaceans 0.06; Small pelagic fish 3.5	114	High plankton and detritus biomass. 5 biomass inputs.

Initially, none of the models were balanced. EEs of pelagic-feeding demersal fish, zooplankton, phytoplankton, detritus or a combination of these were greater than one. Therefore detritus import and diet compositions were adjusted until all EEs were between zero and one. The minimum amount of detritus import required to balance the models ranged between 114-200t km^{-2} y^{-1} (Table 1.1). The detritus import for model 10 (high plankton and detritus biomass, 5 biomass inputs) did not need to be changed from the initial value. Diet compositions that needed to be changed varied between models. Model 1 required the most changes to diet compositions in order to balance and model 10 the least. Of these changes, the most unrealistic was the complete removal of zooplankton in the diet of small pelagic fish in models 1 and 10 to balance the model. However, due to a lack of data on the diet of small pelagic fish in this oligotrophic region these changes were not altered. Adjustments to diet compositions were as follows:

Zooplankton was removed from the diets of:

- Benthic-feeding chondrichthyans and added to macrobenthos and cephalopods in all models.
- Small pelagic fish and added to macrobenthos and detritus in model 1; macrobenthos, phytoplankton and detritus in model 10.
- Benthic-feeding demersal fish and added to macrobenthos in all models.
- Benthic-feeding reef fish and added to macrobenthos in all models.
- Prawns and shrimp and added to prawns and shrimp (cannibalism) in model 1; macrobenthos and detritus in models 2, 3, 4, 5, 7, 8, 9, 10; detritus in model 6.
- Macrobenthos and added to detritus in all models.

Zooplankton was decreased in the diets of:

- Large pelagic fish and added to large pelagic fish, small pelagic fish and benthic-feeding reef fish in model 1; large pelagic fish, small pelagic fish, pelagic-feeding reef fish and macrobenthos in model 2, large pelagic fish, small pelagic fish, pelagic-feeding demersal fish, pelagic-feeding reef fish and macrobenthos in model 3; large pelagic fish, small pelagic fish, macrobenthos and import in models 4, 5; large pelagic fish, small pelagic fish, pelagic-feeding demersal fish, pelagic-feeding reef fish, macrobenthos and import in model 6, 7, 8, 9; small pelagic fish in model 10.
- Small pelagic fish and added to macrobenthos and phytoplankton in model 2; macrobenthos and detritus in models 6, 7, 8, 9; detritus and import in models 3, 4, 5.
- Pelagic-feeding reef fish and added to small pelagic fish, cephalopods and detritus in model 1, small pelagic fish in model 2, small pelagic fish and import in model 3, small pelagic fish, pelagic-feeding reef fish, cephalopods, and macrobenthos in model 4, small pelagic fish, macrobenthos and import in model 5, small pelagic fish, pelagic-feeding reef fish, cephalopods, macrobenthos, detritus and import in model 6, 7, 8, 9; benthic-feeding reef fish in model 10.
- Cephalopods and added to benthic-feeding demersal fish, benthic-feeding reef fish, cephalopods and prawns and shrimp in models 1, 2, 3, 4, 5, 6, 7, 8, 9; macrobenthos in model 10.

Phytoplankton was removed from the diets of:

- Cephalopods and added to macrobenthos in models 1, 3; macrobenthos and prawns and shrimp in models 4, 5.

- Prawns and shrimp and added to detritus in models 1, 2, 3, 4, 5, 7, 8, 9; prawns and shrimp in model 6.
- Macrobenthos and added to detritus in all models.

Phytoplankton was decreased in the diets of:

- small pelagic fish and added to detritus in model 1, 2, 3, 4, 5, 7, 8.
- Cephalopods and added to macrobenthos in models 6, 7, 8, 9.

Detritus was decreased in the diets of:

- Zooplankton and added to zooplankton in model 1.

1.2.4 Sensitivity analysis

A sensitivity analysis was conducted on each balanced model to determine which input parameters each model was sensitive to. The sensitivity analysis also served as a proxy for the resilience of the various network configurations. The routine varies all basic input parameters (i.e. those that were taken/calculated from literature data) in 10% increments from -50% to +50% and the outputs represent relative changes in the 'missing' basic parameters (i.e. those that were calculated in the mass balance approach, mainly biomass) for each group (Christensen et al., 2005). The results from the sensitivity analysis of each model were compared to determine if the models behaved differently to each other. Only changes in missing parameters that were greater than the change in input parameters, e.g. when missing parameters changed by more than 10% when the input parameter was changed by +/-10%, were included in the results. This comparison was carried out in two parts. The first determined how each of the models behaved when input parameters were changed by the smallest amount (+/-10%) i.e. which parameters the models were most sensitive to. The second determined how each of the models behaved when parameters taken from other models/areas were changed by -50% to +50% i.e. the effect of the most uncertain parameters.

1.2.5 System metrics

System metrics were compared between KZN Bight models and the Southern Benguela model. To show the size and productivity of the system the following trophic flow indices were calculated using Ecopath:

- such as sum of all consumption (Christensen et al., 2005)
- sum of all exports (Christensen et al., 2005)
- sum of all respiratory flows (Christensen et al., 2005)
- sum of flows into detritus (Christensen et al., 2005)
- total system throughput (the total sum of trophic flows) (Ulanowicz, 1986)
- net primary production (Christensen et al., 2005)
- net system production (difference between total primary production and total respiration) (Christensen et al., 2005)

Flows from detritus showed whether the systems were detritus- or primary producer-based. To show the extent of recycling in the system the following cycling indices were calculated using Ecopath:

- Finn's cycling index (the amount of throughput that is recycled) (Finn, 1976)

  $$FCI = \sum_i T_i(S_{ii} - 1)/S_{ii} \tag{1.4}$$

  where T_i is the total throughput through group *i* and (S_{ii} -1) is the throughput through group *i* resulting from cycling.
- predatory cycling index (the amount of recycling when detritus was excluded)

To illustrate selected ecosystem services provided by the systems the following fisheries indices were calculated using Ecopath:

- total catches (Christensen et al., 2005)
- mean trophic level of catches (Ulanowicz, 1986), where the trophic level of each fished group was calculated by

  $$TL_j = 1 + \sum(TL_i)(DC_{ij}) \tag{1.5}$$

  where TL_i is the trophic level of prey group *i* and DC_{ij} is the entire diet of group *j* (Ulanowicz, 1986). Primary producers were assumed to have a TL of one.

1.3 RESULTS

1.3.1 KZN Bight models

1.3.1.1 Parameterization

Ecopath routines allowed missing parameters, biomasses and EEs, to be estimated. These were similar, if not the same, between models for all groups except macrobenthos which ranged between 25.6 – 38.9t km^{-2} (Fig. 1.2). The system was clearly dominated by macrobenthos in terms of biomass.

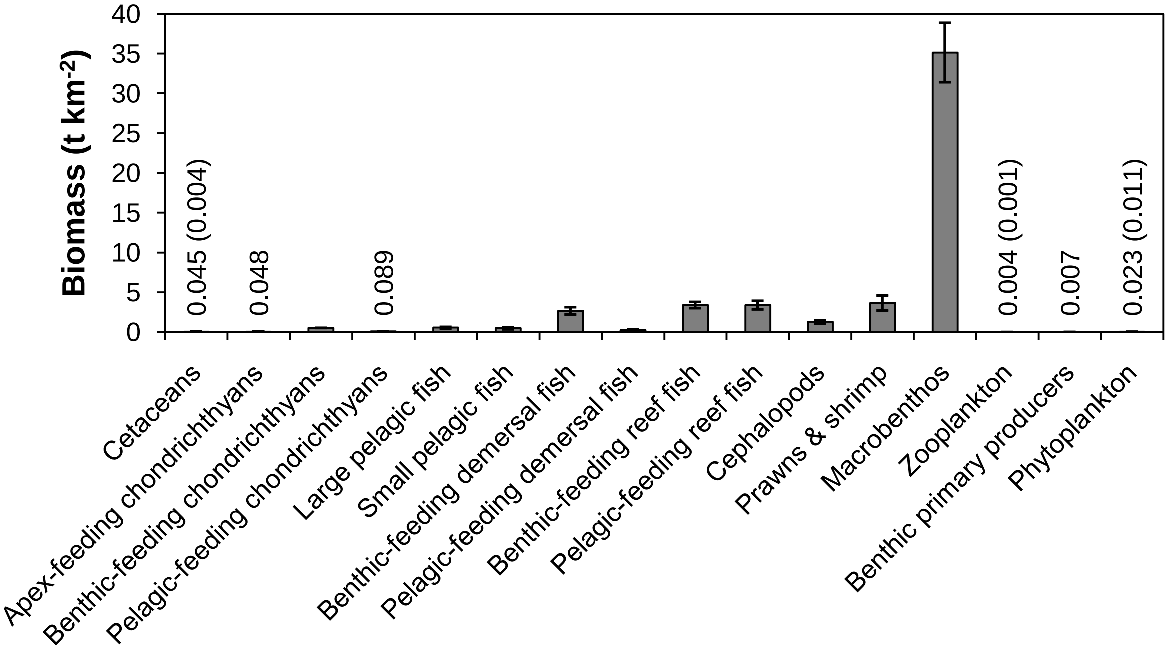

Figure 1.2. Biomasses (t km^{-2}) of groups in the KZN Bight averaged over all 10 models. Bars and numbers in brackets represent 1 SD.

1.3.1.2 Sensitivity of models

KZN Bight models were most sensitive to changes in the input parameters of apex and benthic-feeding chondrichthyans. Small changes (+/-10%) of these parameters caused the largest number of missing parameters (biomasses or EEs) to change by over +/-10% (Table 1.2). Models were also sensitive to small changes in the input parameters of large pelagic fish and benthic-feeding reef fish although the numbers of missing parameters changed was less than half that of the chondrichthyan groups (Table 1.2). Model 10 (high plankton and detritus biomass, 5 biomasses used) was not sensitive to small changes in large pelagic fish inputs (Column 10, Table 1.2).

Small changes in apex chondrichthyans parameters affected the biomasses of benthic- and pelagic-feeding chondrichthyans in all models (Table 1.2). Cetacean, large pelagic fish, pelagic-feeding demersal fish, benthic-feeding reef fish and cephalopod biomasses were affected by small changes in apex chondrichthyans parameters in all models except Model 10 (high plankton and detritus biomass, 5 biomass inputs). Small changes in benthic-feeding chondrichthyans affected pelagic-feeding chondrichthyans, large pelagic fish, benthic-feeding reef fish and pelagic-feeding reef fish biomasses in all models (Table 1.2). Biomasses of cetaceans, small pelagic fish and pelagic-feeding demersal fish were affected in all models except Model 10 (high plankton and detritus biomass, 5 biomass inputs) and cephalopod biomass was affected in all models except Model 5 (low plankton, high detritus biomass, 3 biomass inputs). Small changes in large pelagic fish P/B and EE affected benthic-feeding reef fish, pelagic-feeding reef fish and cephalopod biomasses in all models except Model 10 (high plankton and detritus biomass, 5 biomass inputs) (Table 1.2). Cephalopod biomass was affected by small changes in pelagic-feeding reef fish parameters in all models (Table 1.2). Other effects which did not occur in all models are detailed in (Table 1.2).

Overall sensitivity of a model, in terms of the number of missing parameters affected by a small change in input parameters, differed between models (Table 1.2). Model 10 (high plankton and detritus biomass, 5 biomass inputs) was the least sensitive to small changes in inputs with 16 missing parameters affected in total. The most sensitive was Model 8 (low plankton, high detritus biomass, 2 biomass inputs) with 38 missing parameters affected in total.

In the second part of the sensitivity analysis there were a number of differences between models in terms of which missing parameters were affected by changes in non-local inputs and the % change of these inputs required to produce a change. These can be viewed in detail in Appendix 1.4. The KZN Bight models were most sensitive to changes in non-local inputs of certain apex predator groups. These were the EE of apex chondrichthyans, benthic-feeding chondrichthyans, large pelagic fish, and pelagic-feeding reef fish and the Q/B pelagic-feeding reef fish (Table 1.3). A minimum change (+/-10-20%) of these parameters caused a change in missing parameters in all models (Appendix 1.4). However, this was most likely due to the top-down balancing routine in Ecopath with Ecosim which uses the consumption of higher trophic groups to determine the amount of primary production and detritus needed to sustain them (Steele, 2009).

Table 1.2. Effects (> +/-10%) of small changes in input parameters (+/-10%) on missing parameters in the 10 KZN Bight models. A "+" indicates the missing parameter was only affected when the input parameter was changed by +10%. A "-" indicates the missing parameter was only affected when the input parameters was changed by -10%. Grey squares indicate a change > +/-10% in the missing parameter when the input parameter was changed by +/-10%. Blank squares indicate no change or a change less than or equal to +/-10% when the input parameters was changed by +/-10%.

Group	**Input parameter**	**Missing parameter**	**Model number**									
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Apex chondrichthyans	Q/B, P/B, EE	Benthic –feeding chondrichthyans B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B, P/B, EE	Pelagic feeding chondrichthyans B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B, P/B, EE	Cetacean B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Large pelagic fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Small pelagic fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Pelagic-feeding demersal fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Benthic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Pelagic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Cephalopod B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B	Zooplankton EE		+	▨	+	+	▨	▨	▨	▨	
	P/B, EE	Zooplankton EE		-	-	-	-	▨	▨	▨	▨	
	Q/B, P/B, EE	Cetacean EE										▨
Benthic-feeding chondrichthyans	Q/B, P/B, EE	Pelagic feeding chondrichthyans B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B, P/B, EE	Large pelagic fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B	Benthic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	P/B, EE	Benthic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	+	▨	▨
	Q/B, P/B, EE	Pelagic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B, P/B, EE	Cetacean B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B, P/B, EE	Small pelagic fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	

Table 1.2 continued

Group	Input parameter	Missing parameter	Model number									
			1	2	3	4	5	6	7	8	9	10
Benthic-feeding chondrichthyans	Q/B, P/B, EE	Pelagic-feeding demersal fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	Q/B	Cephalopod B	▨	▨	▨	▨		▨	▨	▨	▨	▨
	Q/B, P/B, EE	Zooplankton EE	▨	▨	▨	▨	▨					
	Q/B, P/B, EE	Zooplankton B						▨	▨	▨	▨	
	P/B, EE	Benthic-feeding demersal fish B			+					+		
	P/B, EE	Prawns and shrimps B			+					+		
	P/B, EE	Macrobenthos B			+					+		
	Q/B, P/B, EE	Cetacean EE										▨
	Q/B, P/B, EE	Small pelagic fish EE										▨
	P/B, EE	Benthic-feeding reef fish B	▨	▨	▨	-	-	-	-	-	-	
	P/B, EE	Pelagic-feeding reef fish B	▨	▨	▨	-	-	-	-	-	-	
Large pelagic fish	Q/B	Benthic-feeding reef fish B	+	+	▨		+	▨	▨	▨	▨	
	Q/B	Pelagic-feeding reef fish B	▨	▨	▨		+	▨	▨	▨	▨	
	P/B, EE	Cephalopod B	▨	▨	▨		-	-	-	-	-	
	Q/B	Cephalopod B			▨			+	+	+	+	
	Q/B	Zooplankton B						+	+	+	+	
	PB, EE	Zooplankton B						-	-	-	-	
Pelagic-feeding reef fish	Q/B, P/B, EE	Cephalopod B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Q/B	Small pelagic fish B		▨	+	+		+	+	+	+	
	P/B, EE	Small pelagic fish B		-	-	-		-	-	-	-	
	P/B, EE	Zooplankton EE		-				-	-	-	-	
	Q/B	Zooplankton EE						+	+	+	+	

Table 1.3. Effects of changes (-50 to +50%) to non-local parameters on missing parameters which occurred in all 10 KZN Bight models, and in <10 of the KZN Bight models. B = biomass (wet weight); P/B = production/biomass; Q/B = consumption/biomass; and EE = ecotrophic efficiency. A '-' indicates the missing parameters were not affected by changes in input parameters taken from other models/areas.

Group #	Missing parameters affected	Group # and parameter that affected missing parameters in all models	Group # and parameter that affected missing parameters in <10 models
1	Cetacean B or EE	2EE, 3EE, 4EE	10Q/B, 13Q/B and EE.
2	Apex chondrichthyans B	-	-
3	Benthic-feeding chondrichthyans B	2EE, 4EE	10Q/B, 13Q/B and EE and P/B.
4	Pelagic-feeding chondrichthyans B	2EE, 3EE	13Q/B.
5	Large pelagic fish B	2EE, 3EE, 4EE,	8EE, 10Q/B, 13Q/B and EE and P/B.
6	Small pelagic fish B or EE	2EE, 3EE, 4EE	5EE, 8EE, 10Q/B and EE, 13Q/B and EE and P/B.
7	Benthic-feeding demersal fish B	3EE	10Q/B, 13Q/B and EE and P/B.
8	Pelagic-feeding demersal fish B	2EE, 3EE, 4EE	10Q/B, 13Q/B and EE and P/B.
9	Benthic-feeding reef fish B	2EE, 3EE, 4EE,5EE, 8EE	10Q/B and EE, 11P/B and EE, 13Q/B and EE and P/B.
10	Pelagic-feeding reef fish B	2EE, 3EE, 4EE,5EE	8EE, 13Q/B and EE and P/B.
11	Cephalopod B	2EE, 3EE, 4EE, 5EE, 10Q/B and EE	8EE, 9EE, 13Q/B and EE and P/B.
12	Prawns and shrimps B	3EE	7EE, 10Q/B, 13Q/B and EE and P/B.
13	Macrobenthos B	3EE	-
14	Zooplankton B or EE	2EE, 3EE	4EE, 5EE, 8EE, 10Q/B and EE, 13Q/B and EE and P/B.
15	Benthic primary producers B	-	-
16	Phytoplankton B or EE	-	-

The overall sensitivity of models in terms of the number of missing parameters affected by non-local inputs differed between models. The model least sensitive to changes in non-local inputs was model 10 (high plankton and detritus biomass, 5 biomass inputs) with 37 missing parameters changed in total. The most sensitive was model 3 (high plankton and detritus biomass, 3 biomass inputs) with 74 missing parameters changed in total.

Non-local input parameters in certain models caused changes of over 1000% in missing parameters. A decrease in benthic-feeding chondrichthyans EE of 20% in model 10 (high plankton and detritus biomass, 5 biomass inputs) increased cetacean EE and pelagic-feeding chondrichthyans biomass by 1548% and 1112% respectively. An increase in Q/B of macrobenthos of 40% in model 1 (low plankton and detritus biomass, 3 biomass inputs) increased prawn and shrimp biomass by 1145% and in model 5 (low plankton, high detritus biomass, 3 biomass inputs) increased benthic-feeding demersal fish biomass by 1703%. While an increase in Q/B of macrobenthos of 50% in model 1 (low plankton and detritus biomass, 3 biomass inputs) caused benthic-feeding demersal fish biomass to increase by 2016% and prawn and shrimp biomass to increase by 1145%.

1.3.1.3 System metrics

System metrics differed between the ten KZN Bight models (CV column, Table 1.4). The largest variation was predicted for total net primary production which had a coefficient of variation (CV) of 44% and ranged between 1.84 to 6.24t km^{-2} y^{-1}(Table 1.4). The highest net primary production was produced by models 2 and 10 (high plankton and detritus biomass, 3 or 5 biomass inputs). The lowest net primary production was produced by models 1 and 5 (low plankton, low or high detritus and 3 biomass inputs). The second largest variation was predicted for sum of all exports which had a CV of 29% (Table 1.4). However this metric is directly linked to the detritus import which differed between models. The smallest variation was predicted for the proportion of total flows from detritus which had a CV of 0.74% and a range of 98 – 100% (Table 1.4). Cycling indices were similar between models. Predatory cycling index had a CV of 4% and ranged between 23.3% in model 10 (high plankton and detritus biomass, 5 biomass inputs) to 25.8% in model 5 (low plankton, high detritus biomass, 3 biomass inputs) (Table 1.4). Similarly Finn’s cycling index had a CV of 6% and ranged between 29.8% in model 10 (high plankton and detritus biomass, 5 biomass inputs) to 36.1% in model 5 (low plankton, high detritus biomass, 3 biomass inputs) (Table 1.4). The remaining metrics had CV’s ranging between 11 – 16%. Total biomass, excluding detritus, ranged between 27.5 to 58.3t km^{-}

^{2} (Table 1.4). The highest total biomass was produced by model 1 (low plankton and detritus biomass, 3 biomass inputs). The lowest total biomass was in model 10 (high plankton and detritus biomass, 5 biomass inputs). Throughput of detritus ranged between 527t km^{-2} y^{-1} in model 10 (high plankton and detritus biomass, 5 biomass inputs) to 1004t km^{-2} y^{-1} in model 1 (low plankton and detritus biomass, 3 biomass inputs) (Table 1.4).

Table 1.4. Ecosystem metrics from the ten KZN Bight models. Units are t km^{-2} y^{-1} unless otherwise stated. CV = coefficient of variation.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Mean**	**CV**
Sum of all consumption	586	504	529	515	464	541	541	541	541	269	510	13%
Sum of all exports	0.4	0.8	1.4	1.0	1.4	1.1	1.4	0.9	1.2	28.4	1.08	29%
Sum of all respiratory flows	201	168	177	170	151	181	181	181	181	93	170	15%
Sum of all flows into detritus	330	284	299	292	268	305	305	305	305	192	289	12%
Sum of all production	271	243	250	247	223	254	254	255	253	130	971	13%
Total System Throughput	1123	957	1006	979	885	1028	1029	1028	1029	583	242	11%
Total net primary production	1.9	6.2	3.9	3.9	1.8	3.3	3.3	3.9	1.9	6.2	3.7	44%
Net system production	-199	-162	-173	-166	-149	-178	-178	-177	-179	-86	-166	16%
Total biomass (excluding detritus)	58.3	50.9	53.4	52.0	47.3	54.6	54.6	54.6	54.6	27.5	51.5	13%
Predatory cycling index (%)	23.5	24.3	24.4	24.8	25.8	24.2	24.2	24.2	24.3	23.3	24.7	4%
Finn’s cycling index (%)	31.2	34.2	33.8	34.7	36.1	33.6	33.7	33.6	33.5	29.8	34.4	6%
Proportion of total flows from detritus (%)	1	0.98	0.99	0.99	1	0.99	0.99	0.99	1	0.98	0.99	0.7%
Total consumption of detritus	469	398	419	408	367	429	429	430	431	220	862	13%
Total throughput from detritus	1005	844	892	867	785	913	913	912	917	528	405	13%

1.3.2 Comparison to the Southern Benguela

1.3.2.1 Biomasses

A comparison of biomasses in the KZN Bight models to those in the Southern Benguela model showed that the systems are dominated, in terms of biomass, by macrobenthos and phytoplankton respectively. The biomasses of all groups were smaller in the KZN Bight than the Southern Benguela with the exception of apex chondrichthyans (Table 1.5). In particular, biomasses of the lower trophic levels (phytoplankton, benthic primary producers, zooplankton and macrobenthos) were much smaller in the KZN Bight. However, cetacean and apex chondrichthyans biomasses were similar in both systems.

Table 1.5. Biomasses (t km^{-2}) of model groups. KZN Bight biomasses are averaged over all balanced models and standard deviation (1SD) is given. Bold and underlined indicates those estimated by Ecopath.

Group	**KZN Bight**	**1SD**	**Southern Benguela**
Phytoplankton	0.03	0.01	76.93
Benthic primary producers	**0.01**	0.00	**6.34**
Zooplankton	0.004	0.00	**33.35**[a]
Macrobenthos	**35.16**	3.73	**67.92**[b]
Prawns and shrimp	**3.65**	0.94	-
Cephalopods	**1.28**	0.21	1.36
Pelagic-feeding reef fish	**3.39**	0.54	-
Benthic-feeding reef fish	**3.40**	0.39	-
Pelagic-feeding demersal fish	**0.26**	0.08	**3.45**
Benthic-feeding demersal fish	**2.67**	0.49	**3.51**
Small pelagic fish	**0.48**	0.14	11.72[c]
Large pelagic fish	**0.55**	0.10	3.78[d]
Pelagic-feeding chondrichthyans	**0.09**	0.00	0.58
Benthic-feeding chondrichthyans	**0.52**	0.00	0.87
Apex chondrichthyans	**0.05**	0.00	0.05
Cetaceans	**0.05**	0.00	0.07

a: Sum of zooplankton groups; b: Sum of meio- and macrobenthos; c: Sum of 'other small pelagic fish', sardine, redeye and anchovy; d: Sum of 'other large pelagic fish', 'chub mackerel, 'adult horse mackerel', 'snoek', 'large *M. capensis*', 'Large *M. paradoxus'*.

1.3.2.2 System metrics

A comparison of system metrics showed that the KZN Bight was a less productive system and smaller, in terms of total biomass, than the Southern Benguela. Total system throughput was 34-65 times smaller in the KZN Bight models than the Southern Benguela model (Table 1.6). In addition, production, in terms of primary production and net system production (the difference between total primary production and total respiration), was lower in the KZN Bight models than the Southern Benguela with net system production being negative in the KZN Bight models (Table 1.6). Cycling indices showed that recycling is more important in the KZN Bight models than in the Southern Benguela. The fraction of throughput recycled (Finn's cycling index) and the predatory cycling index were 1.6 - 2 and 1.6 - 1.8 times larger respectively in the KZN Bight models than the Southern Benguela model (Table 1.6). Fisheries catch was 7.2 times smaller in the KZN Bight models than in the Southern Benguela (Table 1.6). A comparison of flows from detritus showed that detritus is more important in the KZN Bight models than the Southern Benguela. The total consumption and total throughput of detritus were 15 – 29 and 15 - 31 times smaller respectively in the KZN Bight models than in the Southern Benguela. However, the proportion of total flows was 99% from detritus and 1% from primary producers in the KZN Bight. In the Southern Benguela total flows from detritus was 45% and 55% from primary producers (Table 1.6).

Table 1.6. Ecosystem indices for the 1980's KZN Bight (this study) and Southern Benguela (Shannon, 2000) models. Indices for the KZN Bight are averaged over all balanced models. The same landings data were used in all KZN Bight models and therefore no SD is given.

Indices	KZN Bight	1SD	Southern Benguela	Units
Sum of all consumption	511.0	68.0	17,230.0	t km^{-2} y^{-1}
Sum of all exports	1.0	0.3	2,559.0	t km^{-2} y^{-1}
Sum of all respiratory flows	170.0	26.0	9,416.0	t km^{-2} y^{-1}
Sum of all flows into detritus	289.0	35.0	8,551.0	t km^{-2} y^{-1}
Sum of all production	242.0	27.0	16,233.0	t km^{-2} y^{-1}
Total system throughput	971.0	128.0	37,975.0	t km^{-2} y^{-1}
Total net primary production	3.7	1.6	11,974.0	t km^{-2} y^{-1}
Net system production	-166.0	27.0	2,559.0	t km^{-2} y^{-1}
Total landings	0.4		3.0	t km^{-2} y^{-1}
Mean TL of landings	3.0		4.7	-
Tot B (excl detritus)	52.0	7.0	221.0	t km^{-2}
Predatory cycling index	25.0	1.0	14.0	%
Finn’s cycling index	34.0	2.0	18.0	%
Proportion of total flows from detritus	99	0	45	%
Total consumption of detritus	405	54	7,025	t km^{-2} y^{-1}
Total throughput from detritus	862	115	15,795	t km^{-2} y^{-1}

1.4 DISCUSSION

1.4.1 KZN Bight models

This was the first set of ecosystem models of the entire KwaZulu-Natal Bight on the South African east coast. Due to the scarcity of local data, non-local data were used for many functional groups. In cases of high uncertainty or several poorly defined functional groups, the development of multiple models spanning the range of potential system states is important (Fulton et al., 2003, Essington, 2007). It should be noted however that due to limited data this set of models may not necessarily cover the full range of system states. Multiple models were developed using various published zooplankton biomasses, estimated phytoplankton and detritus biomasses, and speculative cetacean and small pelagic fish biomasses as input parameters. Sensitivity analyses of these models revealed those parameters which may be important drivers of system variability.

Different input parameters created a need to change detritus import and diet compositions in different ways to obtain mass-balanced models. The increase in detritus import required to balance some of the models was deemed realistic due to the calculated detritus import using only data from the Thukela River. Thus the calculated detritus import initially did not account for the other 16 rivers/estuaries that flow into the KZN Bight. Changes to initial diet compositions were needed in all models as the phytoplankton and zooplankton biomasses used as inputs were not large enough to sustain the grazing and predation on these groups. The changes to small pelagic fish diet in models 1 and 10 were deemed unrealistic as they involved the complete removal of zooplankton which is an important food source in many other systems (Heymans and Baird, 2000b, Shannon et al., 2003, Freire et al., 2008, Gasalla and Rossi-Wongtschowski, 2004). However these changes were used in the models since diet composition for this group was not available for the KZN Bight. A study of the diet compositions of small pelagic fish in the KZN Bight is necessary to confirm which changes in small pelagic fish diet were valid for this oligotrophic region.

Despite the differences in biomass inputs between models, the biomasses predicted in models 1-9 were similar. This could be attributed to P/B, Q/B, EE and landings being constant across models with ranges in biomass inputs of phytoplankton and zooplankton as laid out in Table 1.1. The biomasses predicted by model 10 (high plankton and detritus biomass, 5 biomass inputs) were different to those predicted by models 1 - 9 due to two additional biomass inputs. The speculative small pelagic fish biomass was almost three times lower than that predicted by the other models. This group was difficult to model due to the influence of the annual KZN sardine run which usually occurs during June-August (Baird, 1971). The speculative biomass of *S. sagax* used was calculated from a survey during the sardine run (Armstrong et al., 1991). However the biomass of small pelagic fish, other than sardine, for the rest of the KZN Bight is unknown and thus an improved biomass estimate for this group would verify whether the small biomass used in model 10 is more accurate than the larger biomass predicted by models 1-9.

All models were most sensitive to changes in parameters of apex predators with missing biomasses and EEs changing when inputs of apex chondrichthyans, benthic-feeding chondrichthyans, large pelagic fish and pelagic-feeding reef fish were changed. The P/B and Q/B of apex chondrichthyans, benthic-feeding chondrichthyans, and large pelagic fish along with P/B of pelagic-feeding reef fish were system-specific and therefore the sensitivity to these parameters would be understandable. On the other hand, EEs and the Q/B of pelagic-feeding reef fish were not system-specific and therefore there is a need for research on these groups to determine the Q/B of pelagic-feeding reef fish and biomass estimates of these groups to substitute for EEs to determine if the EEs used are similar to those predicted by models using biomass inputs.

In contrast to biomass values, system metrics differed between models with model 10 consistently producing different quantitative results to the rest of the models. However this model still required diet compositions to be changed in order to balance, was sensitive to the same input parameters as other models and produced similar general trends. Many flow indices differed due to differences in weighted diet compositions between models. Total system throughput had the largest variation between models due to the cumulative effect of variations in flow magnitudes. Model 10 had a much higher sum of all exports due to the initial calculated detritus import being higher than the minimum needed to balance the model (114t km^{-2} rather than 103t km^{-2}). Flow indices from the 10 KZN Bight models were higher than those for Kuosheng Bay, Taiwan (Lin et al., 2004), Tongoy Bay, Chile (Wolff, 1994) and San Miguel Bay, Philippines (Bundy and Pauly, 2001) but lower than Maputo Bay, Mozambique (Paula E Silva et al., 1993), South Brazil Bight, Brazil (Gasalla and Rossi-Wongtschowski, 2004), Bay of Mont St Michel, France (Arbach Leloup et al., 2008), San Pedro Bay, Philippines (Campos, 2003) and the Mid Atlantic Bight, USA (Okey, 2001) and thus fall within the range of other bays and bights.

The variation in net system production and net primary production between models can be attributed to the differences in phytoplankton biomass between models. However, net system production in model 10 was significantly different to other models due to using the initial calculated detritus import rather than the minimum required to balance. When compared to models of other bays and bights, the maximum net primary production was lower, however models 2 (high plankton and detritus, 3 biomass inputs) and 10 predicted a maximum net primary production similar to that of Kuosheng Bay, Taiwan (Lin et al., 2004). Perhaps one of the most interesting findings of the model is that net system production (the difference between total primary production and total respiration) is negative in the KZN Bight models in contrast to all other bays and bights models which are positive. However, negative net system production is possible for systems with very low primary production and large imports (Christensen et al., 2008), which in the case of the KZN Bight is detritus import.

System metrics varied the most between the models that included three biomass inputs (models 1 - 5) i.e. the models representing the range of possible states of the system given by the detritus, phytoplankton and zooplankton biomasses in literature. This variation in results gave an explanation of the functioning of the KZN Bight at different levels of phytoplankton biomass. If the system was experiencing the minimum phytoplankton biomass from the literature the demand for detritus in terms of consumption and throughput was higher than when there was maximum phytoplankton biomass (Table 1.4). If this amount of detritus was available (through detritus import) then the system had a higher total system throughput and total biomass and continued to function (Table 1.4). If the system was experiencing the maximum phytoplankton biomass from the literature the demand for detritus was slightly lower in terms of consumption and throughput than when there was minimum phytoplankton biomass. If this smaller amount of detritus was available then the system continued to function but had a lower total system throughput and total biomass but higher cycling within the system since detritus imports were lower. Despite these variations, the ten KZN Bight models predicted an ecosystem reliant on detritus, specifically detritus import and cycling, with low primary production and thus negative net system production. Therefore model configurations seem plausible since known ecosystem characteristics, e.g. detritus-based and low primary production, were reproduced (Schleyer, 1981).

The general trends predicted by the KZN Bight models have potential implications for river and fisheries management in the area. The KZN Bight has higher cycling than any other bays and bights mentioned and in particular high detritus recycling. Vasconcellos et al. (1997) found that high levels of recycling were correlated with increased resilience. However because the KZN Bight is reliant on a large amount of detritus imported from the Thukela River and other rivers/estuaries in the area it is more likely to have a lower resilience as suggested by Odum (1969) and Christensen (1995). Proposed impoundments on the Thukela River would decrease the amount of water flowing into the bight and therefore the amount of detritus. This could cause a decrease in primary consumers of detritus, e.g. macrobenthos and prawns and shrimp, and therefore secondary consumers, e.g. reef fish, demersal fish, pelagic fish and benthic chondrichthyans. Both primary and secondary consumers of detritus include important fisheries species, e.g. prawns and shrimp and linefish species, and therefore river management will impact fisheries management. Effects of river management on the linefish slinger

(*Chrysoblephus puniceus*) and squaretail kob (*Argyrosomus thorpei*) have already been suggested by Lamberth et al. (2009).

1.4.2 Ecosystem functioning on the east vs. west coasts of South Africa

A comparison of the KZN Bight and Southern Benguela models showed the KZN Bight models reproduced known differences between the two systems. These differences stem from the differences in nutrient concentrations in each system. Upwelling systems, such as the Benguela, are one of the most productive types of ecosystems due to the upwelling of water increasing the nutrients in surface waters and subsequently increasing primary production. For example, nitrate concentrations can range between 1-2μmol L^{-1} in the south and central areas of the KZN Bight and 9 μmol L^{-1} during upwelling events in the north of the Bight (Meyer et al., 2002). In the southern Benguela, however, nitrate concentrations are usually >20 μmol L^{-1} throughout the system (Giraudeau and Bailey, 1995). These differences in nutrient concentrations cause the difference in primary production between the two systems. Subsequently, biomasses and fisheries landings are lower in the KZN Bight models than the Southern Benguela (Shannon et al., 2003). These differences were clearly shown in the comparison between the models of the two systems. In addition, the relative importance of detritus inputs versus nutrient inputs was shown with low primary production and high detritus biomass causing the KZN Bight models to be detritus driven. In contrast, the Southern Benguela was phytoplankton-driven. This was shown through the flow from detritus to the various other compartments which was 99% of all flows from trophic level 1 in the KZN Bight models and 45% in the Southern Benguela. Partitioning the detritus group in the KZN Bight models to pelagic and benthic detritus would increase the explanatory power of the model and further understanding of the reliance of the system on different types of detritus. Similarly, including the microbial loop would allow a more detailed analysis of the pathway from detritus to top consumers. These aspects could not be implemented in the current models due to a lack of quantitative data on benthic detritus and bacteria. Nevertheless, all 10 KZN Bight models were able to reproduce known differences between these two systems.

1.5 CONCLUSIONS

While it is not clear if the models have predicted ‘accurate numbers’, these numbers are constrained by the best available data and the models have provided an overview of system functioning. Moreover, construction and sensitivity analyses have identified data gaps in the literature for the KZN Bight, identifying useful research directions. Expanding on the steps for ecological network construction in Fath et al. (2007), the following summarises steps taken in this study to construct the KZN Bight models which can serve as recommendations on how models for data-limited ecosystems may best be achieved:

1. Define model domain (spatial boundary and time period).

2. Define functional groups based on expert opinion. If comparative analysis will be carried out with another ecosystem then functional groups should be similar and favour the better understood system.

3. Identify available quantitative information from the literature on biomass, production/biomass, consumption/biomass, diets and fisheries catch. Prioritise usefulness of literature data with the following criteria:

    i. the model area
    ii. the same region (except biomass and catch)
    iii. similar ecosystem types at similar latitudes (except biomass and catch)
    iv. similar ecosystem types with similar water temperatures (except biomass and catch)

4. For groups with unknown biomass to be estimated by the model, select appropriate ecotrophic efficiencies from:

    i. the surrounding area
    ii. similar ecosystem types at similar latitudes
    iii. similar ecosystem types at similar water temperatures

5. When ranges of biomasses are available in literature, construct a number of models using combinations of these.

6. Conduct sensitivity analysis on all models

7. Conduct comparative analysis between:

i. models of the same area
ii. models of the area and models of another system, if available.

The construction of models is useful for data-limited areas where ecosystem studies have not been carried out. Information on ecosystem functioning can give indications of possible impacts from anthropogenic activities which should be further investigated and serve for future reference.

The KZN Bight models demonstrated that mass-balance models of a data-poor river-influenced bay or bight could be constructed and parameterized with outputs converging on general trends of how the ecosystem functions. Despite the use of non-local data, the current models may act as a framework for future dynamic models to be populated with more system-specific data. These dynamic models can aid further understanding of ecosystem functioning and allow investigation of problems the KZN Bight may face in future such as the effect of river impoundments on ecosystem functioning and fisheries.

Modelling ecosystem effects of reduced prawn recruitment on the Thukela Bank trawling grounds, South Africa, following nursery loss

2.1 INTRODUCTION

Marine ecosystems have been impacted by anthropogenic activities for hundreds of years (Jackson et al., 2001). The effects of fishing in particular have been studied extensively during the past decades in terms of direct effects on target, bycatch and discard groups that include changes in biomass and community structure and indirect effects including changes in predator-prey interactions (Jennings and Kaiser, 1998, Pauly et al., 1998). Anthropogenic activities occurring in neighbouring systems can also directly and indirectly affect an ecosystem. In particular, activities impacting nursery habitats can have far-reaching effects because these habitats contribute recruits to the adult population. Juveniles of many marine invertebrate and fish species worldwide use inshore nursery habitats as they provide abundant prey and protection from predators (Beck et al., 2001). For example, mangrove-lined creeks or rivers are used by penaeid prawns in Australia and Mozambique (e.g. Hughes (1966), Loneragan & Bunn (1999)), mangrove-lined estuaries and lagoons are used by penaeid prawns and fish species in South Africa (e.g. Benfield et al. (1990)), seagrass beds are used by blue crabs in Chesapeake Bay, USA (e.g. Heck & Thoman (1984)), and estuarine mudflats are used by sole in Portugal and France (e.g. Cabral & Costa (1999), Leguerrier et al. (2004)). With their close proximity to human activities and as a link between land and ocean, these inshore areas are prone to anthropogenic impacts including outflows of sewage treatment plants, terrestrial runoff and water abstraction from rivers. In particular, water abstraction and dam construction reduce river flow into estuaries potentially exacerbating existing environmental conditions such as droughts, affecting estuarine and coastal habitats, and causing permanent closure of estuary inlets (Gillanders and Kingsford, 2002, van Ballegooyen et al., 2005). These estuaries thus become unavailable as nurseries and the overall availability of nursery habitats along a stretch of coast decreases. Consequently, recruitment to the adult population decreases (Cyrus and Vivier, 2006, Whitfield et al., 2006, Le Pape et al., 2007, Rochette et al., 2010). For adult populations targeted by fisheries, a decrease in recruitment could lead to a decrease in target species biomass potentially affecting not only catch but also other species in the ecosystem (Jennings and Kaiser, 1998). Thus it is important to study both the concurrent effects of reduced recruitment (e.g. due to nursery loss) and fisheries on the ecosystem as a whole, and specifically the potential effect on fisheries catches.

The Thukela Bank ecosystem in the central KwaZulu-Natal Bight, South Africa, is affected by fishing within the system and by anthropogenic changes to rivers and estuaries which flow into the system (Flemming and Hay, 1988, Fennessy, 1994a, Fennessy, 1994b, Bosman et al., 2007, Lamberth et al., 2009, Turpie and Lamberth, 2010). The Bank itself comprises the southernmost shallow-water prawn trawling grounds in Africa. Penaeid prawns (*Penaeus indicus, Metapenaeus monoceros, Penaeus monodon*) occur on the mudbank and have been targeted by prawn trawlers since the mid 1960’s, although regular trawling only began in the late 1970’s (Fennessy and Groeneveld, 1997). The life-cycle of penaeid prawns is short (12 - 18 months) and includes marine adult and larval stages and estuarine postlarval and juvenile stages (Dall et al., 1990). Postlarvae of the three species migrate to these nurseries in spring and recruit as juveniles to the marine environment from the end of summer (Joubert and Davies, 1966). The Thukela Bank prawn population is assumed to primarily use the St. Lucia estuary and Richards Bay/Mhlathuze estuary as nursery areas (Forbes and Cyrus, 1991, Forbes et al., 1994, Forbes and Demetriades, 2005). Historically the St. Lucia estuary had a combined inlet with the Mfolozi River which had a stabilising effect on the open mouth (Lawrie and Stretch, 2011). However the inlets were separated in the 1950’s and the St. Lucia mouth needed to be continuously dredged open (Whitfield and Taylor, 2009). In June 2002 the St. Lucia mouth was allowed to close naturally and due to overall reduced freshwater flow and drought the St. Lucia mouth has remained closed to date (March 2012) with the exception of an opening lasting for six months in 2007 (Whitfield and Taylor, 2009, Lawrie and Stretch, 2011). Thus, penaeid prawns have not been able to utilise this nursery area since 2002.

The Thukela Bank is important economically and socially for the KwaZulu-Natal region as it comprises the main shallow-water prawn trawling ground in South Africa (Sauer et al., 2002). Thus it is essential to understand the potential negative effects on the ecosystem due to reduced prawn recruitment. In this paper the effects prawn trawling and reduced prawn recruitment, due to the loss of St. Lucia as a prawn nursery, have had on the Thukela Bank ecosystem are modelled. In addition, the effects of a complete loss or full restoration of prawn nurseries in the region are investigated as a simulation exercise. The changes in biomass of groups that are targeted, retained as bycatch, and discarded by prawn trawlers are focused on to investigate the potential effects of reduced recruitment due to nursery loss on trawl catches.

2.2 METHODS

2.2.1 Model area

The Thukela Bank is an area of mud in the KwaZulu-Natal (KZN) Bight off the east coast of South Africa (Fig. 2.1). The mudbank is formed by the outflow of the Thukela River which has a high sediment load (McCormick et al., 1992). The modelled Thukela Bank area extends from Zinkwazi in the south to Mlalazi in the north and from beyond the surf zone to approximately 45m depth, covering 560km^2 (Fennessy and Groeneveld, 1997). The area between Mlalazi and Richards Bay is untrawlable due to extensive scattered reef, hence its exclusion from the modelled area. In addition, detritus and nutrients are provided to the area by the Thukela, Zinkwazi, Matigulu and Mlalazi estuaries (Fig. 2.1). The rivers flowing into these estuaries have a combined catchment area of more than 30500km^2 with an estimated mean annual runoff of 2.65x10^{9}m^3 (Division of Water Environment and Forestry Technology, 2001, Lamberth et al., 2009).

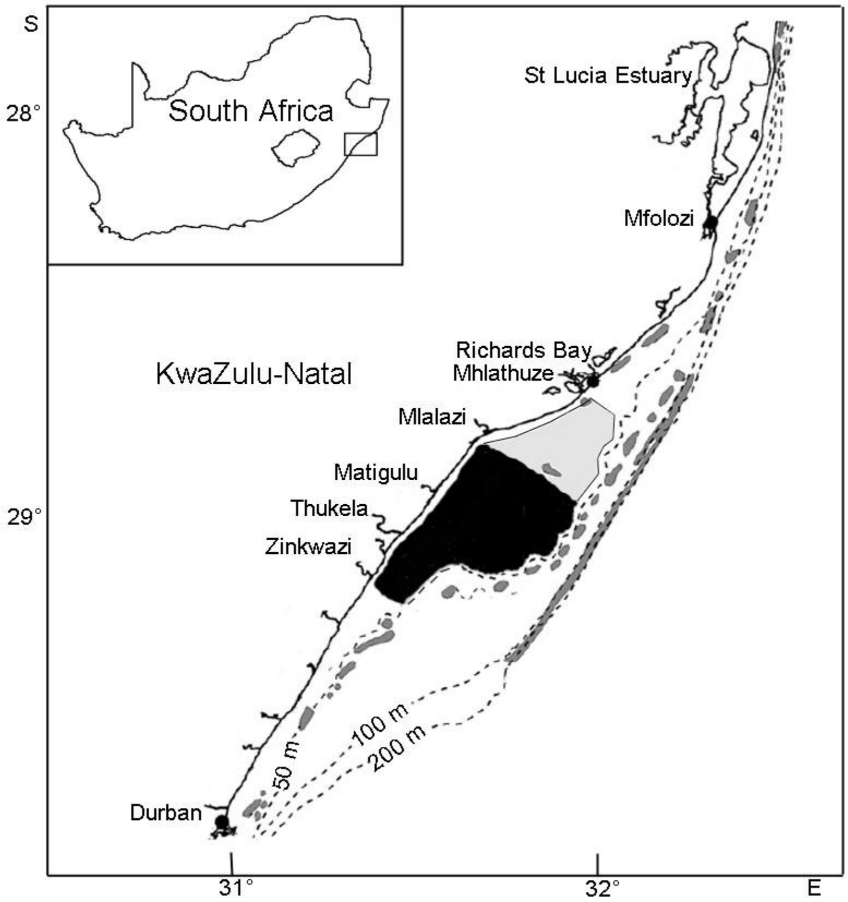

Figure 2.1. The Thukela Bank model area (black shading), untrawlable reef area (light grey shading), known high-profile reefs (dark grey shading) and rivers/estuaries within the KwaZulu-Natal Bight. Adapted from Lamberth et al. (2009).

2.2.2 Mass-balance models construction

2.2.2.1 Approach

Foodweb models of the Thukela Bank were constructed using the trophic mass-balance analysis tool, Ecopath, within the Ecopath with Ecosim (EwE) software package (version 6.2) (Christensen et al., 2008). Details of this approach can be found in Chapter 1, Section 1.2.1.

By constructing Ecopath models for the data-limited KZN Bight (incorporating the Thukela Bank), Ayers & Scharler (2011) showed through extensive sensitivity analyses that models constructed using data from similar ecosystem types at similar latitudes or with similar water temperatures, when local data were unavailable, can produce plausible ecosystem representations as shown through calculated characteristics and trends. The importance of testing the sensitivity of model outputs to input parameters is well known but rarely performed (Fulton et al., 2003, Essington, 2007). Therefore three Thukela Bank models were constructed for this purpose based on maximum, minimum and mean biomass values available from literature and recent research trawls – the max B model, min B model and mean B model. The models were based on the year 1990, the first year of reliable prawn trawl catch and effort statistics. However, due to the scarcity of quantitative data, only fisheries data were based on this year. Nineteen functional groups modelled as aggregates of their constituent species were chosen (Appendix 2.1). These included detritus, phytoplankton, seven invertebrate groups (zooplankton, detritivorous benthos, carnivorous benthos, commercial crustaceans, juvenile prawns, adult prawns and cephalopods), five fish groups, four elasmobranch groups and one marine mammal group. Prawns were split into multi-stanza groups of adult and juvenile prawns to enable modelling the effect of a decrease in juvenile prawn recruitment (due to nursery loss) on the adult population (Christensen et al., 2008).

2.2.2.2 Prawn input parameters

All three prawn species (*P. indicus, M. monoceros, P. monodon)* were aggregated into one multi-stanza group because catch data from prawn trawlers were reported as an aggregated group. Ecopath assumed body growth followed a von Bertalanffy curve and that the population had reached a stable age-size distribution (Christensen and Walters, 2004). The biomass of juvenile prawns (B_{juv}) was calculated using:

$$B_{juv} = b_{juv} \frac{B_{adult}}{b_{adult}} \tag{2.1}$$

where b_{juv} is the relative biomass of juveniles, B_{adult} is the biomass of the adult stanza and b_{adult} is the relative biomass of adults (Christensen and Walters, 2004). The relative biomass of stanza s can be calculated using:

$$b_s = \frac{\sum_{a=a_{s,min}}^{a_{s,max}} l_a w_a}{\sum_{a=1}^{a_{max}} l_a w_a} \tag{2.2}$$

where s, max and s, min are youngest and oldest age for stanza s, $a_{\max}$ is the oldest age overall, l_a is the population growth rate-corrected survivorship for age a and w_a is the relative body weight at age a (Christensen and Walters, 2004). l_a can be calculated using:

$$l_a = e^{-\left(\sum Z_a - a\frac{BA}{B}\right)} \tag{2.3}$$

where $\Sigma\ Z_a$ is the sum of total mortality over all ages up to age a and BA/B is the relative biomass accumulation rate. w_a can be calculated using:

$$w_a = (1 - e^{-K_a})^3 \tag{2.4}$$

where K_a is the von Bertalanffy growth parameter for age a. Q/B of the juvenile stanza is calculated in a similar way to biomass. Thus input parameters for the multi-stanza groups are B_{adult}, Z_{adult}, Z_{juv}, K, BA/B, Q/B_{adult}. No prawn biomasses were available in the literature. Therefore replicate models were constructed, without the juvenile prawn stanza, in order to estimate a biomass for adult prawns only. Using a prawn EE of 0.95 (Christensen et al., 2008), prawn biomasses of 1.55, 3.40 and 3.44t km^{-2} were estimated for the min B, mean B and max B models respectively. The diet of juvenile prawn was assigned to 100% import due to this group occurring outside the model area (Christensen et al., 2008). Input parameters and data sources for the multi-stanza prawn groups can be found in Table 2.1. The total mortality of juveniles was set at $0.001y^{-1}$ so that density-dependent juvenile survival could be varied as a recruitment or “stocking” rate detailed in “Prawn recruitment time series” (Christensen et al., 2008). The relative biomass accumulation rate (BA/B) was unknown and therefore the default value of zero was used (Christensen et al., 2008). Sensitivity analyses were carried out on adult prawn total mortality (Z_{adult}) and growth (K) parameters since these parameters were not sourced from the model area. Three Z and three K parameters were used in the min B, mean B and max B models and biomass predictions were compared.

Table 2.1. Input parameters for multi-stanza prawn groups. a = starting age of adult prawn group; Z = total mortality; Q/B = consumption/biomass ratio; K = von Bertalanffy growth parameter; BA/B = relative biomass accumulation rate.

Parameter	Value	Reference
a	6 months	Benfield et al. (1990)
Z_{adult}	2.73, 5.38, 7.57 y^{-1}	Freire et al. (2008) , Gribble (2003), Okey et al. (2004)
$Z_{juvenile}$	$0.001y^{-1}$	Christensen et al. (2008)
Q/B_{adult}	$37.9y^{-1}$	Gribble (2003)
K	1.6, 1.9, 2.73	Gribble (2003), Jayawardene et al. (2002)
BA/B	0	Christensen et al. (2008)

2.2.2.3 Other input parameters

Riverine detritus import was calculated by first calculating the sediment concentration in the Thukela River outflow using an average annual sediment yield of 9.3 million t y^{-1} and a total flow in 1990 of 2.174×10^{12}L (Taljaard et al., 2004) which gave 4.28g L^{-1}. This was assumed to be total suspended solids (TSS). Using the relationship between TSS and particulate organic carbon (POC) in Meybeck (1982), it was assumed the POC was 8.4% of TSS which gave a POC concentration of 0.359g L^{-1}. This was assumed to be the same for all estuaries flowing into the model area. The % mean annual runoff (MAR) for each estuary from Lamberth et al. (2009) was used to calculate total %MAR, and finally POC in tonnes. This was divided by the model area to derive a total riverine detritus import of 1666t km^{-2} y^{-1} and was used as total detritus import as it was not possible to calculate a marine detritus import across the model boundary.

Biomass data from the modelled area in 2010 (Oceanographic Research Institute, unpub. data) were used for skates and rays, benthopelagic carnivorous fish, benthic benthos-feeding fish and cephalopods. Zooplankton biomasses were calculated from Carter (1973) using conversion factors in Wiebe et al. (1975). Phytoplankton biomasses were calculated from Barlow et al. (2008) using a conversion factor from Jarre-Teichmann et al. (1998). Detritus biomass was calculated using the model of Pauly et al. (1993) and inputs from Barlow et al. (2010). This value was used in all three models. Remaining biomass values could not be based on those from other areas and therefore these were estimated with Ecopath by including EE values for each group. Biomasses are shown in Table 2.7. Other parameters (P/B, Q/B and EE) can be found in Table 2.2 and diets in Table 2.3. Diets of cetaceans, apex sharks, benthic-feeding sharks and pelagic-feeding sharks were available for the KZN Bight. Prey that did not occur in the model area, e.g. reef fish, were assigned as import in diets.

Table 2.2. Basic input parameters for trophic groups in the 1990 Thukela Bank models. P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency. Landings and discards are combined for all fisheries.

Groups	P/B (y^{-1})	Q/B (y^{-1})	EE	Landings ($t\ km^{-2}\ y^{-1}$)	Discards ($t\ km^{-2}\ y^{-1}$)
Cetaceans	0.60[a]	10.00[a]	0.76[v]		0.000
Apex sharks	0.13[b]	1.45[m]	0.1[w]	0.002	0.000
Benthic-feeding sharks	0.26[b]	2.55[n]	0.725[v]	0.005	0.004
Pelagic-feeding sharks	0.30[b]	2.80[o]	0.95[v]	0.001	0.000
Skates & rays	1.20[c]	3.50[p]		0.004	0.003
Large pelagic fish	1.66[d]	5.61[q]	0.78[e]	0.012	0.000
Small pelagic fish	2.00[e]	11.20[g]	0.999[v]	0.011	0.025
Benthopelagic carnivorous fish	1.41[f]	5.50[r]		0.040	0.121
Benthopelagic benthos-feeding fish	1.16[g]	7.15[s]	0.999[i]	0.000	0.153
Benthic benthos-feeding fish	1.20[h]	6.00[t]		0.002	0.018
Cephalopods	3.00[i]	10.88		0.003	0.013
Adult prawns	7.57[p]	37.90*		0.138	0.000
Juvenile prawns	0.001*				
Commercial crustaceans	1.38[j]	8.50[j]	0.9[j]	0.029	0.041
Carnivorous benthos	7.01[i]	27.14[i]	0.99[i]		0.048
Detritivorous benthos	7.50[k]	25.00[g]	0.95[x]		0.009
Zooplankton	40.00[l]	165.00[l]			
Phytoplankton	154.00[a]	n/a			
Detritus	n/a	n/a			

* see Table 2.1; a: Toral-Granda et al. (1999); b: Dudley & Simpfendorfer (2006); c: Cheung et al. (2002); d: Shannon et al. (2003); e: Paula E Silva et al. (1993); f: calculated using Olbers & Fennessy (2007); g: Gasalla & Rossi-Wongtschowski (2004); h: Sanchez & Olaso (2004); i: Okey et al. (2004); j: Okey & Meyer (2002); k: Rocha et al. (2007); l: Opitz (1996); m: Aitken (2003); n: calculated using b and Cliff et al. (1988); o: calculated using Allen & Wintner (2002) and Wintner (1993); p: Freire et al. (2008); q: calculated using van der Elst (1976); r: calculated using Olbers & Fennessy (2007) and van der Elst (1993); s: calculated using van der Elst & Adkin (1991) and Joubert (1981); t: Amorim et al. (2004); u: P/Q calculated from Buchan & Smale (1981); v: Shannon et al. (2000); w: Ayers & Scharler (2011); x: default value Christensen et al. (2008).

Table 2.3. Initial diet compositions for the Thukela Bank models. Groups 18 and 19 refer to primary producers and detritus and therefore do not require a predator column.

	Prey/Predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	Cetaceans		0.137	0.016	0.009													
2	Apex sharks		0.027	0.000	0.000													
3	Benthic-feeding sharks		0.336	0.143	0.095													
4	Pelagic-feeding sharks		0.011	0.019	0.009													
5	Skates and rays	0.007	0.222	0.112	0.018													
6	Large pelagic fish	0.061	0.048	0.034	0.048		0.042											
7	Small pelagic fish	0.397	0.019	0.088	0.457	0.027	0.200											
8	Benthopelagic carnivorous fish	0.069	0.005	0.095	0.118		0.071											
9	Benthopelagic benthos-feeding fish	0.163	0.036	0.055	0.101		0.550		0.770	0.010	0.010	0.347						
10	Benthic benthos-feeding fish	0.005		0.012	0.019	0.052				0.106	0.010							
11	Cephalopods	0.249	0.004	0.263	0.022	0.122	0.042					0.001						

Table 2.3 continued

	Prey/Predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
12	Adult prawn			0.001		0.010			0.170	0.206	0.050		0.005		0.010			
13	Juvenile prawn																	
14	Commercial crustaceans		0.000	0.007	0.002	0.105						0.179			0.005			
15	Carnivorous benthos		0.002	0.021		0.322	0.014	0.090	0.040	0.461	0.606	0.245	0.290		0.108	0.050		
16	Detritivorous benthos			0.062		0.320		0.010		0.202	0.277	0.229	0.345		0.655	0.386		
17	Zooplankton							0.780	0.020	0.016			0.010					0.050
18	Phytoplankton							0.030										0.950
19	Detritus							0.090			0.047		0.350			0.564	0.950	
	Import	0.049	0.154	0.071	0.103	0.042	0.081							1.000	0.222		0.050	

Calculated using 1: Young & Cockcroft (1994), Cockcroft & Ross (1990); 2: Cliff et al. (1989), Cliff & Dudley (1991a), Cliff & Dudley (1991b), Aitken (2003); 3: Smale & Compagno (1997), de Bruyn et al. (2005), Dudley et al. (2005), Porter (2006); 4: Dudley & Cliff (1993), Allen & Cliff (2000); 5: Mackinson (2002); 6: van der Elst (1976); 7: Toral-Granda et al. (1999); 8: Hajisamae (2009); 9: Rizkala et al. (1999), Hajisamae (2009); 10: Amorim et al. (2004); 11: Castro & Guerra (1990); 12: Gribble (2003); 13: see section 2.2.2.2; 14: Okey & Meyer (2002); 15: Okey et al. (2004); 16: Gasalla & Rossi-Wongtschowski (2004); 17: Toral-Granda et al. (1999).

2.2.3 Time-dynamic model

2.2.3.1 Approach

The ecosystem was dynamically modelled over time using the temporal simulations tool, Ecosim, in EwE. Ecosim expresses biomass dynamics over time using a series of coupled differential equations derived from the production equation of Ecopath:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \tag{2.5}$$

dB_i/dt is the growth rate during time interval dt of group i in terms of its biomass (B_i); g_i is the net growth efficiency (*Q/B* ratio); I_i is the immigration rate; M_i is the natural mortality rate due to factors other than predation; F_i is the fishing mortality rate ($F_i = Yield_i/B_i$); e_i is the emigration rate. In the absence of a time series of fishing mortality (F), relative fishing effort (f) can be used. Ecosim assumes that the base fishing effort (f_o), i.e. 1, is equal to the base fishing mortality rate from Ecopath (F_o=catch/Ecopath biomass) and therefore can drive the biomass dynamics of each group over time using the time series of relative fishing effort. The first summation in equation 2.5 represents the total consumption by group i and the second is the predation by all predators on group i. Consumption rates (Q_{ji}) are calculated based on the foraging arena theory (Walters et al., 1997) where B_i is divided into components that are either vulnerable or invulnerable to predation due to predator and prey behaviour. A transfer rate between the vulnerable and invulnerable states allows the exploration of predator control (top-down) and prey control (bottom-up) on the ecosystem. A feeding interaction (predator/prey) with a v value of 1 indicates bottom-up control where an increase in predator biomass will not cause an increase in predation mortality i.e. the prey is invulnerable to predation by that predator (Christensen and Walters, 2004, Christensen et al., 2008). A feeding interaction value (v) of 100 indicates top-down control where an increase in predator biomass will cause an almost equal increase in predation mortality i.e. the prey group is always vulnerable to that predator (Christensen and Walters, 2004, Christensen et al., 2008). The consumption rate of predator j feeding on prey i (Q_{ij}) is calculated by:

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i B_j P_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} P_j S_{ij} T_j / D_j} \tag{2.6}$$

where a_{ij} is the effective search rate of predator i for prey j, v is the feeding interaction value, P is abundance, T is relative feeding time, S_{ij} is user–defined long term forcing effects, M_{ij} is mediation forcing effects and D is the effect of handling time on consumption rate (Christensen and Walters, 2004). Because feeding interaction values cannot be easily calculated or measured they are estimated using a fitting routine in Ecosim which finds combinations of v that produce better fits to catch and biomass time series data. In summary, the input data required for the time-dynamic Ecosim model are fishing effort and prawn recruitment to drive the model forward in time, and catch and biomass time series to which the model predictions will be compared/fitted.

2.2.3.2 Fishing effort time series

Three fisheries operated in the model area in 1990 - the prawn trawl fishery, commercial linefishery and recreational linefishery. In addition, protective “shark nets” operated at Zinkwazi beach in the model area targeting sharks potentially dangerous to bathers. Prawn trawling effort data were available for 1990-2009 in terms of effective fishing time in days (Department of Agriculture, Forestry and Fisheries (DAFF), Oceanographic Research Institute (ORI), unpubl. data). Effort data for the recreational linefishery (hook and line) as number of angler outings per year was estimated from catch return cards, inspections and competition data (DAFF/National Marine Linefish System (NMLS), unpubl. data). Commercial linefishing effort in fishing hours was available for 1990-2009 (DAFF/NMLS, unpubl. data). A time series of relative effort for each fishery was calculated using 1990 as base effort rate (Fig. 2.2). The length of shark nets per year was deemed an unsuitable measure of fishing effort since CPUE varies widely and therefore was not included.

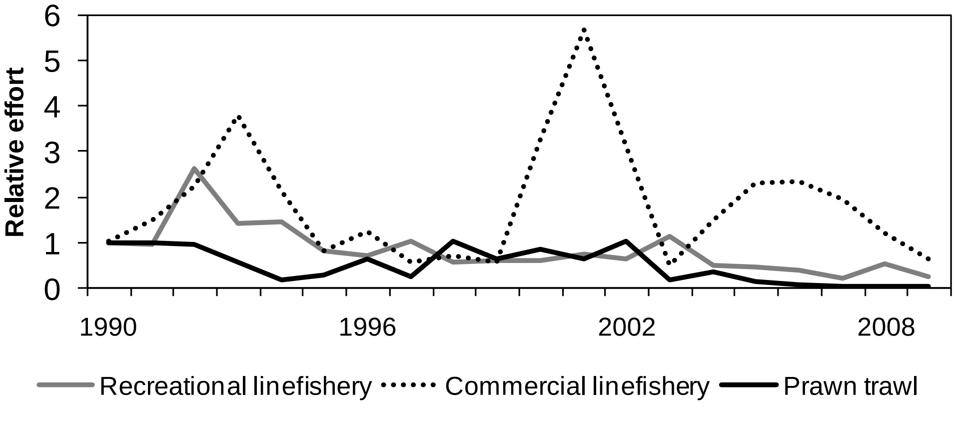

Figure 2.2. Effort of the prawn trawl, commercial linefishery and recreational linefishery, relative to their own base rate in 1990, for 1990 - 2009 in the modelled area. Prawn trawl effort ranged between 12 and 442 fishing days. Commercial linefishing effort ranged between 708 and 8432 fishing hours. Recreational linefishing effort ranged between 2864 and 36024 angler outings.

2.2.3.3 Prawn recruitment time series

To model the loss of access to the St. Lucia estuary from 2002, juvenile prawn recruitment was forced over time in Ecosim. In this study, St. Lucia and Richards Bay/Mhlathuze estuaries were considered the primary sources of recruits to the Thukela Bank and the proportions of recruits from each were assumed equal. This was based on a number of factors. Firstly, St. Lucia contributes the largest proportion to the total estuarine area along the KZN coast: ca. 80%, followed by Kosi Bay: ca. 9%, Richards Bay/Mhlathuze: ca. 7%, and Durban Bay: 2% (Begg 1978 Moreover, catches by the bait-fishery which operated in St. Lucia and Richards Bay were dominated by *P. indicus* with smaller catches of *P. monodon* and *M. monoceros*, all of which are targeted on the Thukela Bank (Forbes & Demetriades 2005). Secondly, postlarvae populations of Thukela Bank target species in Kosi Bay are almost absent (Forbes et al. 1994). Thirdly, Durban Bay postlarvae populations are dominated by *P. japonicus* (Forbes et al. 1994), and the area historically supported a small bait-fishery for this species only (Joubert 1965, Forbes & Cyrus 1991). Fourthly, the remaining estuarine area along the KZN coast (2%) is distributed over approximately 70 small estuaries, most of which are temporarily open/closed. They also lack suitable prawn habitat features such as muddy, mangrove-lined channels (Weerts et al., 2003). Due to their size they may harbour seed populations, but do not have the same carrying capacity as the larger KZN estuarine systems and therefore cannot produce the same number of recruits. Finally, in a tagging study 1.08% of prawns tagged in Richards Bay and 0.97% of prawns tagged in St. Lucia were caught on the Thukela Bank the following season (Forbes & Demetriades 2005). Therefore closing either St. Lucia or Richard Bay/Mhlathuze is assumed to almost halve the recruitment rate. During a simulation the base recruitment was multiplied by a forcing function value for each time step. The forcing function represented recruitment relative to a recruitment of 1.0 (i.e. 100%) in the Ecopath base year (Christensen et al., 2008). The forcing function was left at 1.0 for 1990 - 2001 and was decreased to 0.5, i.e. 50%, for 2002 - 2009 to represent the closure of the St. Lucia Estuary mouth.

To set the degree to which the juveniles outside the model area were subject to density-dependent mortality the “recruitment power” parameter was used (Christensen et al., 2008). This parameter is used by Ecosim to predict the stock/recruit relationship for the multi-stanza group. As suggested by Christensen et al. (2008), for juveniles that spend time outside the modelled area a low value of 0.1, in a range of 0.0 - 1.0, was set since juvenile prawn abundance can be limited by estuarine nursery availability, which makes juvenile abundance less dependent on adult prawn abundance.

2.2.3.4 Catch time series

Catches of specific species by each gear were assigned to model groups using habitat (e.g. benthic vs. benthopelagic) and diet information (e.g. carnivorous vs. benthos-feeding) from literature. Landings by prawn trawlers for 1990 - 2009 were provided by the DAFF (Fig. 2.3). Landings data were available from 1988 but prior to 1990 landings were reported as combined statistics for those made in Mozambique and South African waters (Sea Fisheries Research Institute, 1990) and therefore these were not included. Discards were calculated for 1990 - 2009 using the methods detailed in Appendix 2.2. Commercial linefishery landings for 1990 - 2009 were available from the NMLS (DAFF unpubl. data) (Fig. 2.3). Recreational linefishery landings were available for 1990 - 2009 (DAFF, NMLS) (Fig. 2.3) and incorporated catch return data, competition data and catch inspections covering unspecified shore fishing, marine shore fishing with rod, marine shore-based spearfishing, unspecified marine skiboat fishing, marine skiboat fishing with rod, marine skiboat, spearfishing and unspecified spearfishing. Shark net landings from Zinkwazi Beach for 1990 - 2009 were provided by the KZN Sharks Board (Fig. 2.3). Landings included only dead organisms brought to shore. For the model, weights of sharks which pose a threat to humans were classed as landings and other organisms were classed as discards. Further information on calculations of catch for the models can be found in Appendix 2.2.

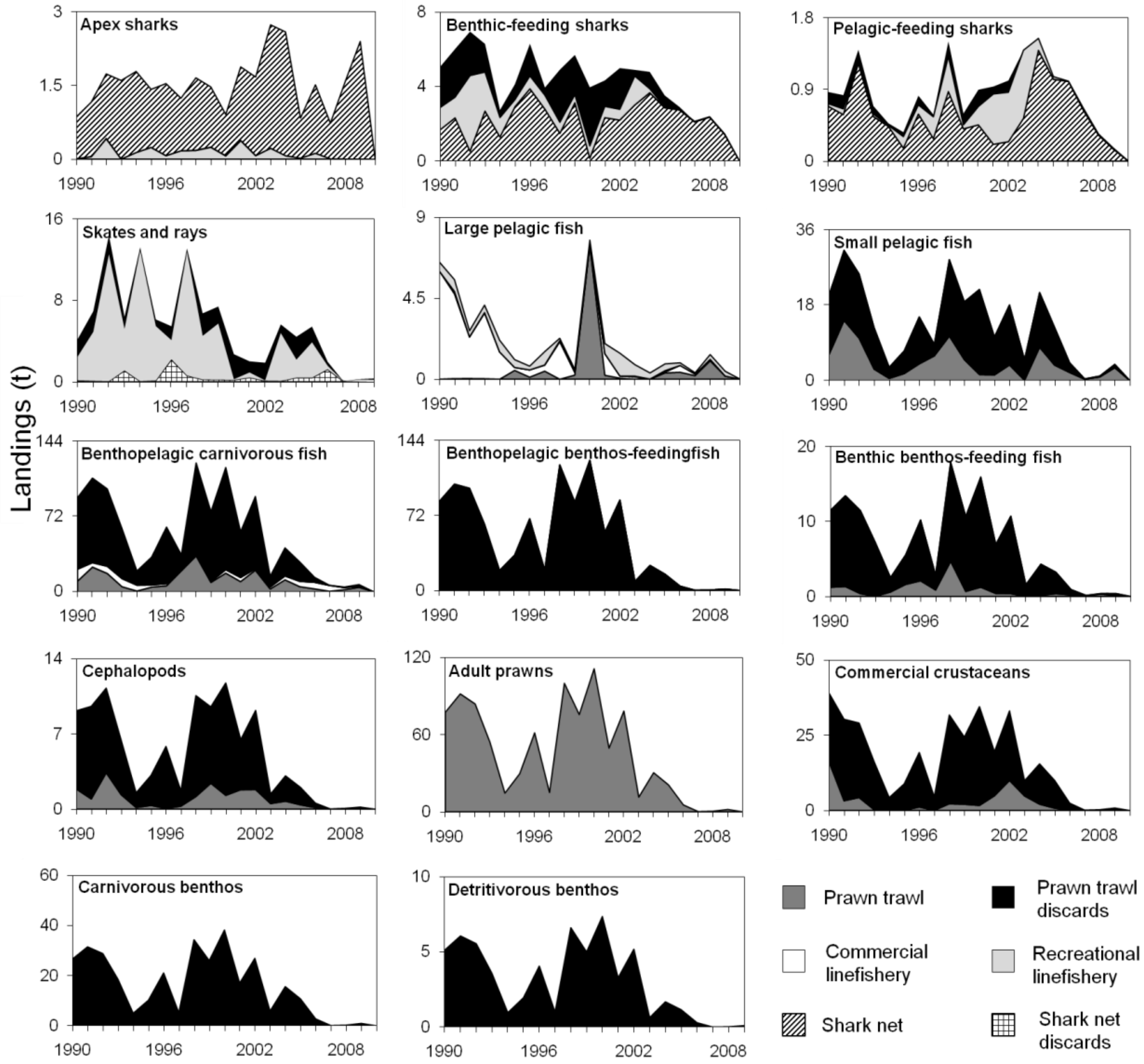

Figure 2.3. Landings (t) and discards by fishing gear for all fished groups included in the models. Note different scales on y axes.

2.2.4 Fitting the model

Catches predicted by each model were fitted to the time series of observed catches. This was done by including fishing effort and prawn recruitment time series' to drive the model and feeding interaction values (*v*). Cetaceans, apex sharks and pelagic sharks were caught most by shark nets for which effort (length of net per year) could not be used to accurately drive catch. Therefore, forced catches were used to remove the catch of these groups from the ecosystem similar to a stock reduction model (Kimura, 1985). As a measure of goodness of fit the weighted sum of squared deviations (SS) of log catches from log predicted catches for all groups was used.

Generally, *v* values are calculated via a fitting routine in Ecosim which chooses values that give the best fit, i.e. lowest SS, to observed catch and biomass time series. To choose values for the Thukela Bank models two methods were compared. The first was the “Ecosim fitting method” which chose values for the 30 most sensitive predator-prey interactions that improved fit to the catch time series (Table 2.4). The second method which has been termed the “TL scaling method”, used values for each predator-prey interaction which were scaled by the trophic level of each prey group (Table 2.5). This method has been used in other models which lack biomass time series with various scaling factors ranging between 1 - 4 and 1 - 15 (Cheung et al., 2002, Ainsworth, 2006, Brown et al., 2010, Li et al., 2010). In this study, values scaled between 1 and 5 were used, since scaling >5 resulted in Ecosim exhibiting oscillations and chaotic behaviour.

Table 2.4. Feeding interaction parameter values calculated by the Ecosim fitting routine for the 30 most sensitive predator-prey interactions in each model. Values >100 represent feeding interaction values calculated by Ecosim over 100.

	Predator	Prey	Min B	Mean B	Max B
1	Cetaceans	Small pelagic fish	>100	>100	>100
2	Apex sharks	Cetaceans	>100	>100	>100
		Benthic-feeding sharks	>100	2	2
		Skates and rays	1	2	2
		Large pelagic fish	2	2	>100
3	Benthic-feeding sharks	Cetaceans	1	1	1
		Skates and rays	>100	1	2
		Large pelagic fish	>100	>100	>100
		Benthopelagic carnivorous fish	2	2	>100
4	Skates and rays	Cephalopods	1	1	1
		Commercial crabs	>100	>100	>100
		Detritivorous benthos	>100	1	2
5	Large pelagic fish	Large pelagic fish	1	1	1
		Small pelagic fish	2.65	>100	>100
		Benthopelagic carnivorous fish	>100	>100	>100
		Benthopelagic benthos-feeding fish	>100	>100	>100

Table 2.4 continued

	Predator	**Prey**	**Min B**	**Mean B**	**Max B**
5	Large pelagic fish	Cephalopods	>100	2	>100
6	Small pelagic fish	Detritus	1	2	2
7	Benthopelagic carnivorous fish	Benthopelagic benthos-feeding fish	2	1	1
8	Benthopelagic benthos-feeding fish	Adult prawn	1	1	1
		Carnivorous benthos	>100	>100	>100
		Detritivorous benthos	1	>100	2
9	Benthic benthos-feeding fish	Benthopelagic benthos-feeding fish	1	1	1
		Carnivorous benthos	>100	2	2
		Detritivorous benthos	2	1.39	>100
10	Cephalopods	Benthopelagic benthos-feeding fish	1	1	1
		Commercial crabs	2	1	2
11	Adult prawn	Carnivorous benthos	>100	>100	>100
		Detritivorous benthos	2	1	1
		Detritus	>100	>100	>100
12	Commercial crabs	Carnivorous benthos	2	11	>100
		Detritivorous benthos	1	1	>100
13	Carnivorous benthos	Carnivorous benthos	>100	43	>100
		Detritivorous benthos	>100	>100	>100
		Detritus	1	2.84	1
14	Detritivorous benthos	Detritus	>100	>100	>100
15	Zooplankton	Phytoplankton	>100	>100	1

Table 2.5. Feeding interaction values calculated by the TL scaling method for each model. Values were used for all interactions in which the group was a prey.

	Group	**Min B**	**Mean B**	**Max B**
1	Cetaceans	4.51	4.56	4.56
2	Apex sharks	5.00	5.00	5.00
3	Benthic-feeding sharks	4.16	4.14	4.14
4	Pelagic-feeding sharks	4.18	4.19	4.17
5	Skates and rays	3.59	3.52	3.52
6	Large pelagic fish	4.37	4.42	4.44
7	Small pelagic fish	2.43	2.38	2.33
8	Benthopelagic carnivorous fish	4.27	4.35	4.37
9	Benthopelagic benthos-feeding fish	3.47	3.53	3.56
10	Benthic benthos-feeding fish	3.29	3.34	3.34
11	Cephalopods	3.81	3.87	3.88
12	Adult prawns	2.78	2.82	2.82
14	Commercial crabs	3.07	3.11	3.11
15	Carnivorous benthos	2.46	2.49	2.49
16	Detritivorous benthos	2.00	2.02	2.02
17	Zooplankton	2.05	2.08	2.08
18	Phytoplankton	1.00	1.00	1.00
19	Detritus	1.00	1.00	1.00

Predicted biomasses are sensitive to feeding interaction control values or vulnerabilities (*v*) in Ecosim. Therefore, because no biomass time series' were available for fitting, feeding interaction control values from each method were compared for each group and the best chosen for further analyses based on their ecological feasibility and the accuracy of predicted biomass dynamics. The following procedure was used to fit the models and the SS at each step was calculated to assess the improvement in fit:

1. The model was run from 1990 to 2009 with relative fishing effort time series.

2. The model was run with relative fishing effort and prawn recruitment time series'.

3. The model was run with both time series' and feeding interaction values calculated by the Ecosim fitting method.

4. The model was run with both time series' and feeding interaction values calculated by the TL scaling method.

2.2.5 Scenarios

Once the best fit to catch data was achieved and feasible *v* values were found, simulations were carried out to conduct a preliminary exploration of the effect of prawn nursery availability and prawn trawling on the ecosystem. Simulations were run for 50 years (1990-2040) under various scenarios (Table 2.6). Prawn trawling effort in 1990 (423 effective fishing hours) and 2009 (17 effective fishing hours) were used to test the effects of “high” and “low” trawling effort (Fig. 2.2) and were read into Ecosim from csv files. To simulate the loss of both major nurseries to prawns, a prawn recruitment level of 5% of the 1990 level was assumed. To simulate St. Lucia reopening it was assumed that prawn recruitment could return to the pre-closure level, i.e. 100%.

Table 2.6. Scenarios carried out in Ecosim involving changes to prawn recruitment level and prawn trawl effort from 2010 - 2040.

	Name	**Prawn recruitment level**	**Prawn trawl effort**
1	Current situation continues	50%	2009 level
2	St. Lucia opens, trawling constant	100%	2009 level
3	St. Lucia and Richards Bay/Mhlathuze nursery areas closed, trawling constant	5%	2009 level
4	St. Lucia closed, trawling stops	50%	zero
5	St. Lucia opens, trawling stops	100%	zero
6	St. Lucia and Richards Bay/Mhlathuze nursery areas closed, trawling stops	5%	zero
7	St. Lucia closed, trawling increases	50%	1990 level
8	St. Lucia opens, trawling increases	100%	1990 level
9	St. Lucia and Richards Bay/Mhlathuze nursery areas closed, trawling increases	5%	1990 level

2.3 RESULTS

2.3.1 The 1990 Thukela Bank mass-balance models

The three models (max, mean and min B) did not initially achieve mass-balance and therefore the following assumptions and changes were made to diet compositions to balance the models. To balance zooplankton energy flows, diet and biomass of small pelagic fish were changed. It was assumed that a proportion of the small pelagic fish in diets of cetaceans and large pelagic fish were from outside the model area since these organisms range over large distances e.g. Cockcroft & Peddemors (1990), Govender (1992). Therefore small pelagic fish were decreased in these diets and "import" was increased. This decreased the biomass of small pelagic fish estimated by Ecopath. Zooplankton was decreased in the diet until mass-balance was achieved and phytoplankton was increased along with import since, given their distributions beyond the modelled area (Smith and Heemstra, 1986), small pelagic fish partly feed outside the model area. Benthic benthos-feeding fish energy flows were balanced by decreasing their percentage in the diet of benthopelagic benthos-feeding fish and increasing carnivorous benthos. To balance the energy flows of cephalopods it was assumed, given their wide distribution (Manicom and Sauer, 2000), that skates and rays partly feed outside the model area and therefore the percentage of cephalopods in their diet was decreased and import was increased. These assumptions and changes were applied to each model; however the magnitude of percentage changes differed between models by up to 15%.

Once balanced, the missing biomasses were estimated from the models (Table 2.7). Diagrams depicting biomass flows for each model can be found in Appendix 2.3. Benthos groups (adult prawns, commercial crabs, carnivorous benthos and detritivorous benthos) dominated the ecosystem in terms of biomass in all models (65 - 69% of total biomass). Most group biomasses were lowest in the min B and highest in the max B model except top predators (Table 2.7). Consequently, a similar pattern was seen for total system biomass (excluding detritus). The net system production (the difference between total primary production and total respiration) was negative in all models and decreased from -521t km^{-2} y^{-1} in the min B model to -1358t km^{-2} y^{-1} in the max B model. Negative net system production is common in systems with very low primary production and large imports (Christensen et al., 2008). In the Thukela Bank models, large imports were provided by high riverine detritus levels. Each model estimated exactly the same Ecopath parameters when different prawn *Z* and *K* values (Table 2.1) were used in the sensitivity analyses. Thus the models were not sensitive to these prawn parameters.

Table 2.7. Biomasses (t km^{-2}) in the 1990 Thukela Bank models. Values in bold were estimated by Ecopath.

Group	Min B	Mean B	Max B
Cetaceans	**0.17**	**0.29**	**0.29**
Apex sharks	**0.15**	**0.15**	**0.15**
Benthic-feeding sharks	**0.92**	**1.74**	**1.74**
Pelagic-feeding sharks	**0.20**	**0.38**	**0.38**
Skates & rays	1.19	5.45	9.70
Large pelagic fish	**0.19**	**0.41**	**0.41**
Small pelagic fish	**0.53**	**1.25**	**1.47**
Benthopelagic carnivorous fish	0.97	2.09	3.21
Benthopelagic benthos-feeding fish	**6.48**	**13.28**	**18.19**
Benthic benthos-feeding fish	2.33	5.80	9.27
Cephalopods	0.51	0.76	1.01
Adult prawns	**1.55**	**3.40**	**3.44**
Juvenile prawns	**0.74**	**1.62**	**1.64**
Commercial crustaceans	**1.24**	**2.99**	**4.39**
Carnivorous benthos	**9.77**	**21.45**	**25.21**
Detritivorous benthos	**19.84**	**44.04**	**54.02**
Zooplankton	0.004	0.004	0.01
Phytoplankton	0.01	0.03	0.04
Detritus	0.10	0.10	0.10
Total (excluding detritus)	**47**	**106**	**135**

2.3.2 Fitting the time-dynamic models

To judge how well the models could reproduce observed catch trends, predicted catches were fitted to observed catches for each group. The goodness-of-fit of the models (expressed by SS) increased when fishing effort and prawn recruitment time series' were included (Table 2.8). The models produced similar fits to each other and were able to reproduce trends and, in general, magnitudes of observed catches from 1990 - 2009 (Fig. 2.4). Better fits were achieved for groups caught primarily by prawn trawlers (Fig. 2.4).

Table 2.8. SS of all functional groups after each step in the fitting procedure for the three Thukela Bank models.

		SS		
	Fitting procedure	**Min B**	**Mean B**	**Max B**
	Catch time series only	484.30	484.3	484.3
1.	With fishing effort time series	99.55	99.04	98.94
2.	With fishing effort & prawn recruitment time series’	97.57	97.75	97.32
3.	With both time series’ & *v*’s from Ecosim fitting method	80.15	81.61	85.68
4.	With both time series’ & *v*’s from TL scaling method	98.33	98.04	97.91

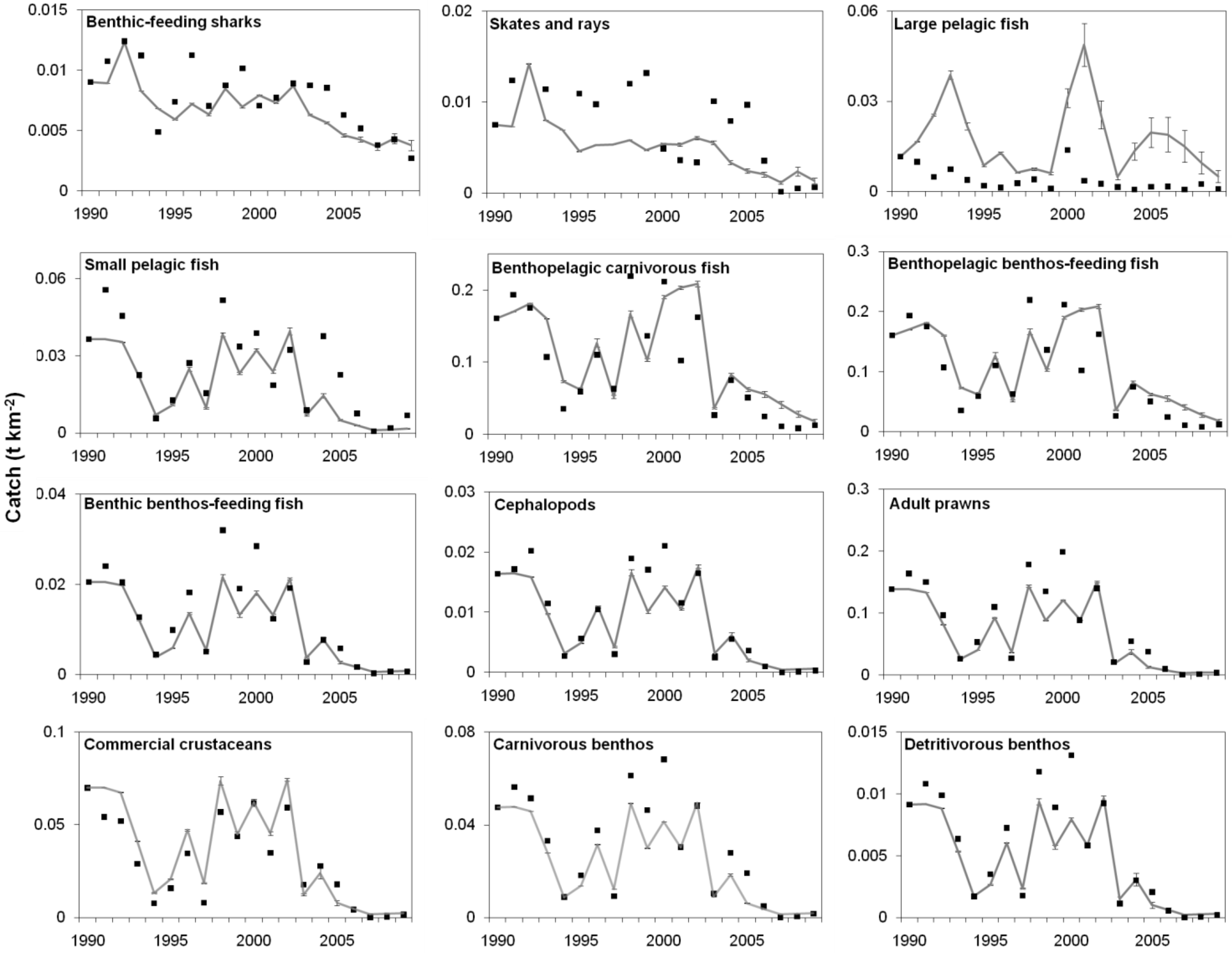

Figure 2.4. Fits to catch (t km^{-2}) data averaged over all fitting methods and models (n=6). Lines represent model predictions, squares represent observed catches and error bars represent 1SD. Note different scales on y axes.

To decide which feeding interaction control values (*v*) to use, biomass dynamics produced using *v* values from each method were compared. A number of *v* values caused differing biomass dynamics across all models. Detritivorous benthos, commercial crabs, skates and rays, and pelagic shark biomass dynamics were sensitive to the value of *v* across all models. The feeding interaction most groups were sensitive to was carnivorous benthos predation on detritivorous benthos. This interaction affected skates and rays, commercial crabs and detritivorous benthos in all models, benthic sharks in the mean B model and cephalopods in the mean B and max B models. The Ecosim fitting method allocated a value >100 to this interaction which allows carnivorous benthos to outcompete other groups with a lower *v* value for detritivorous benthos. In contrast, the TL scaling method allocated a value of 2 to all predators of detritivorous benthos which allows all predators equal access to detritivorous benthos. Detritivorous benthos were assumed to be equally accessible to all of its predators and therefore the value from the TL scaling method was preferred. Prawn predation on detritivorous benthos caused biomass dynamics of skates and rays and detritivorous benthos to differ between all models and cephalopods to differ between mean B and max B models. The Ecosim fitting method allocated a value of 1 which restricts access of prawns to prey on detritivorous benthos however, as above, detritivorous benthos was assumed equally accessible and therefore the value of 2 from the TL scaling method was preferred. Four other interactions caused differences in biomass dynamics in the mean B model only or mean B and max B models. Details of these and the previously mentioned interactions can be found in Appendix 2.4. Biomasses predicted using the TL scaling method matched expected biomass trends for 1990 to 2009. Biomasses had similar trends between models for all groups except benthopelagic carnivorous fish (Fig. 2.5). This group was thought to have recovered after the decrease in trawling effort in 2003 and this was predicted by the min B model. However, the mean B and max B models predicted a small decrease of 3.5% in biomass (Fig. 2.5). Most groups were predicted to increase in biomass from 1990 to 2009 by all models (Fig. 2.5). However, dynamics did not vary greatly from the 1990 value as the largest change was a 14% increase by benthic sharks. Biomasses of many groups changed most after 2003 when trawling effort and prawn recruitment decreased. Following this evaluation of the Ecosim and TL scaling methods for choosing *v* values, the TL scaling method were preferred for further analyses.

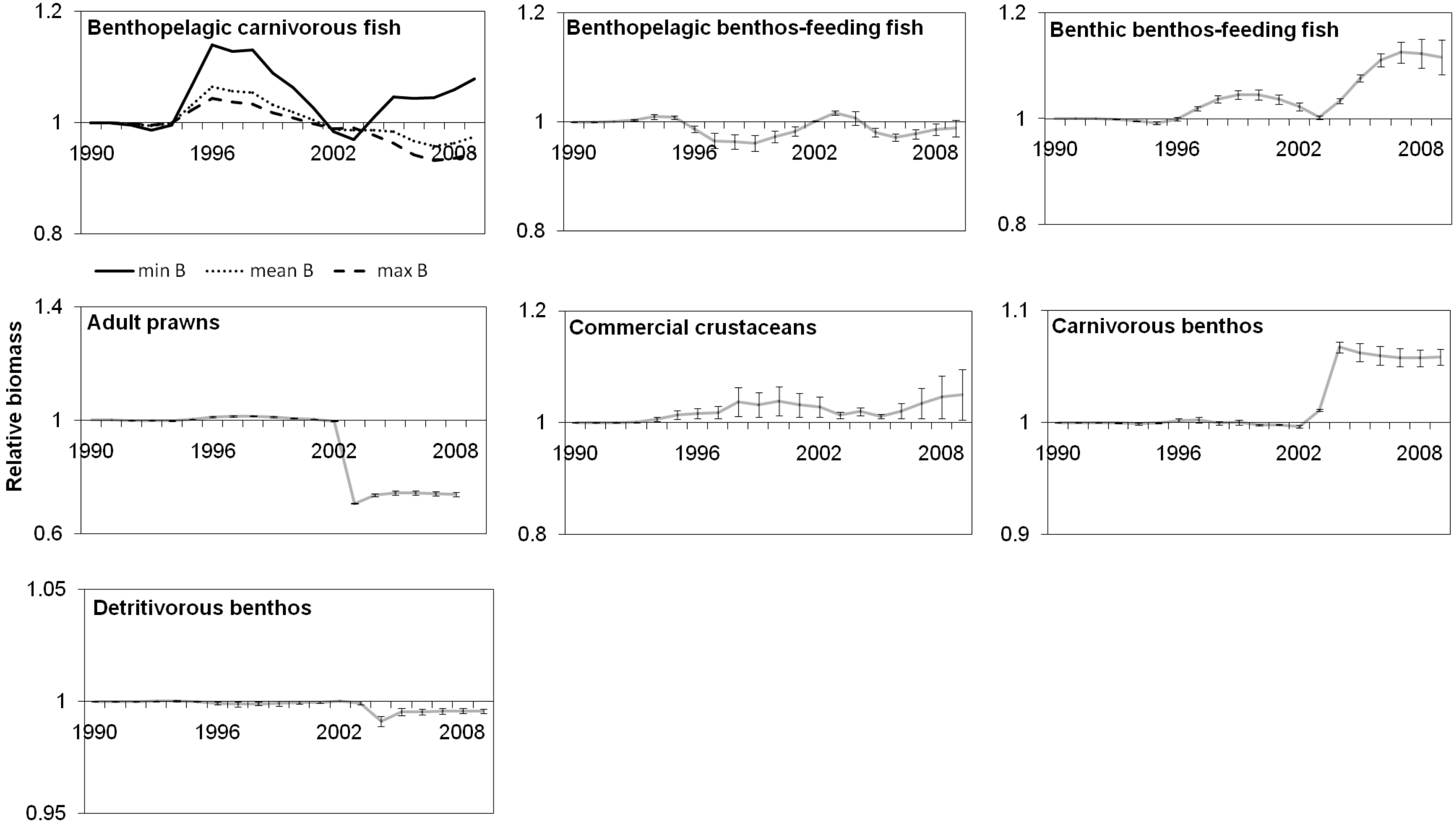

Figure 2.5. Relative biomass dynamics of prawn trawl target, bycatch and discard groups from 1990-2009 averaged over the three models fitted using the TL scaling method (±1SD). Note different scales on y axes. Dynamics which differed between models are shown separately on the benthopelagic carnivorous fish graph (black line indicates minimum B model result, dotted line indicates mean B model result and dashed line indicates maximum B model result).

2.3.3 Effects of reduced prawn recruitment (2010 - 2040 scenarios)

A comparison of relative biomass changes from 1990 to 2040 under all scenarios showed that most groups were affected by a combination of prawn trawling effort and prawn nursery availability (modelled as prawn recruitment rate). Prawn biomass was affected most by changes in prawn recruitment while detritivorous benthos biomass was unaffected in all scenarios (Fig. 2.6). Biomasses of groups remained relatively stable from 2009 - 2040 under the low trawling effort and St. Lucia estuary closed (50% prawn recruitment) scenario. The largest changes in relative biomass were a 4% increase in benthic benthos-feeding fish and 4% decrease in benthopelagic carnivorous fish (Fig. 2.6). However, when both prawn nurseries were lost (5% recruitment) simulations predicted a decrease in prawn biomass of 54% (Fig. 2.6). Simulations in which all prawn nurseries were available (100% recruitment) predicted a 36% increase in prawn biomass (Fig. 2.6).

Commercial crabs were impacted negatively by a decrease in prawn recruitment due to an increase in carnivorous benthos which competes with commercial crabs for detritivorous benthos (Fig. 2.6). Benthopelagic carnivorous and benthopelagic benthos-feeding fish were impacted negatively by a decrease in prawn recruitment as they both predate on prawns (Fig. 2.6). The negative impacts on benthopelagic carnivorous fish and benthopelagic benthos-feeding fish were the cause of the positive impact on benthic benthos-feeding fish due to a decrease in prawn recruitment. These groups are the greatest consumers of benthic-benthos feeding fish and therefore the decrease in their biomass, due to a decrease in prawn recruitment, caused an increase in benthic benthos-feeding fish biomass. Carnivorous benthos was also positively impacted by a decrease in prawn recruitment. This is because prawns are both a predator of carnivorous benthos and a competitor for detritivorous benthos. Thus, prawn biomass is hindered most by decreased prawn recruitment while benthic benthos-feeding fish and carnivorous benthos are benefited.

Total exploitable biomass was clearly driven by prawn recruitment (Fig. 2.7). Exploitable biomass was highest when St. Lucia was open (100% recruitment) and lowest when both St. Lucia and Richards Bay/Mhlathuze were lost (5% recruitment) (Fig. 2.7).

2.3.4 Effects of prawn trawling effort (2010 - 2040 scenarios)

Biomass dynamics predicted by all models were the same under low trawling effort (2009 level) and zero trawling effort. Therefore only results from the latter are shown, together with those from high trawling effort. Simulations showed that the negative effects of a decrease in prawn recruitment were exacerbated by high trawling effort and that positive effects were lower than for low trawling effort or became negative (Fig. 2.6). Differences in relative biomass change between low and high trawling effort were greatest for benthic benthos-feeding fish and benthopelagic carnivorous fish (Fig. 2.6). Biomass dynamics of carnivorous and detritivorous benthos were not affected by trawling effort due to their high biomasses and small percentage as discards. The increase in benthic benthos-feeding fish under decreasing prawn recruitment was less under high trawling effort and thus the biomass of benthic benthos-feeding fish was driven directly by predator-prey interactions and trawling effort and indirectly by prawn nursery availability.

Total exploitable biomass was affected by trawling effort level to a lesser extent than prawn recruitment levels (Fig. 2.7). Lower biomasses were predicted by all models in scenarios with high trawling effort compared to low trawling effort (Fig. 2.7).

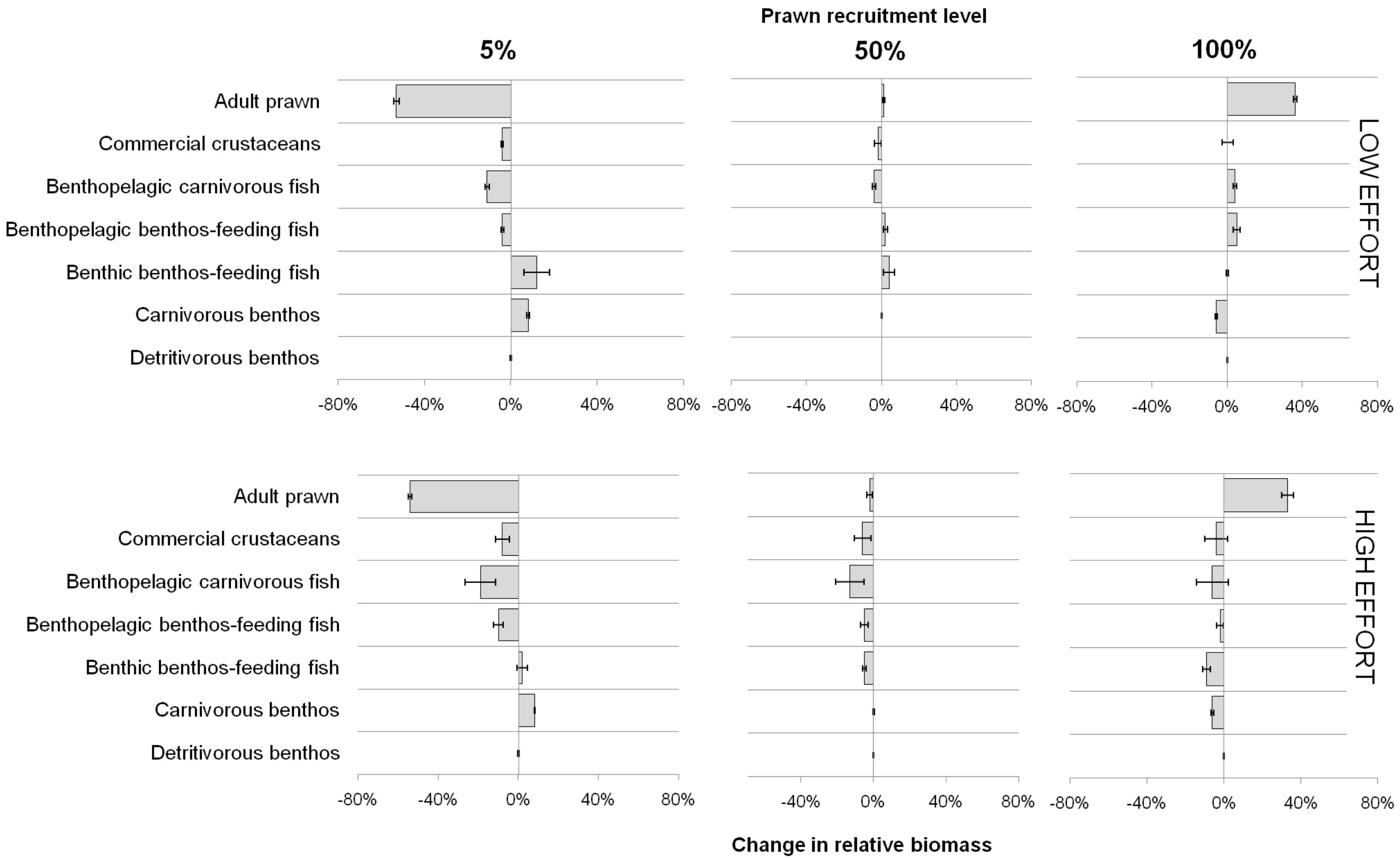

Figure 2.6. Biomass in 2040 relative to 2010 of groups caught by prawn trawlers in six scenarios of various prawn recruitment and trawling effort levels. Bars represent biomass averaged over the three models and error bars represent 1SD.

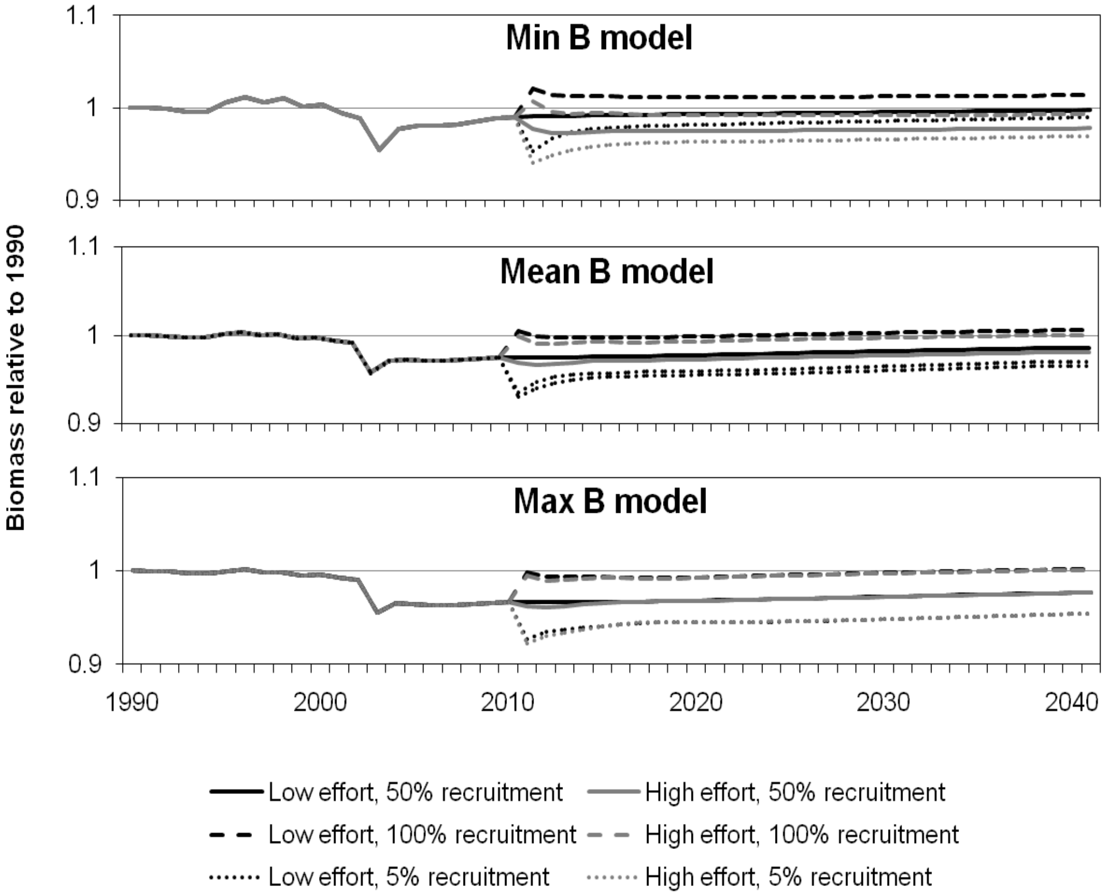

Figure 2.7. Change in relative total exploitable biomass between 1990 and 2040 for each model and scenario.

2.4 DISCUSSION

Anthropogenic activities occurring within and outside the Thukela Bank affected groups in the ecosystem. The three models of the 1990 Thukela Bank ecosystem based on minimum, maximum and mean biomasses predicted the system was dominated by benthos groups. This agrees with ecosystem models of the greater KZN Bight (Ayers and Scharler, 2011). However, the estimation of biomasses of high and low trophic level groups with Ecopath was not ideal as the biomass changes of these groups were not constrained well (Christensen and Walters, 2004). By fitting the models to catch data using fishing effort and prawn recruitment time series' and calculating feeding interaction control values (*v*) scaled by prey TL between 1 and 5 observed catches and expected biomass trends were able to be reproduced.

While the lack of biomass data for the Thukela Bank required the construction of multiple models and the analyses of *v* values, the methodology used in this study produced consistent trends in biomass dynamics across models. The difference in biomass dynamics of benthopelagic carnivorous fish in the min B model is due to the lower biomass causing the dynamics to be more extreme to changes in catch. Similarly, the min B model predicted different relative biomass changes to the mean and max B models for commercial crabs and benthopelagic carnivorous fish under high trawling effort with 100% recruitment. Scaling *v* values has been adequate for the needs of this study. This method has been favoured over using default values for systems lacking time series data for fitting (Cheung et al., 2002, Ainsworth, 2006). The use of the forcing function in Ecosim to model prawn nursery availability via changes in prawn recruitment is a first step in modelling this system. In future applications these models could incorporate recruitment of fish species to the Thukela Bank from estuaries along the KZN coast used as alternative nursery habitats. For example, the benthopelagic benthos-feeding fish *Johnius dorsalis*, which makes up a large part of the bycatch of prawn trawlers, also uses St. Lucia as a nursery area, albeit as a non-obligate estuarine associate (Whitfield, 1994), and could be modelled as a separate multi-stanza group.

Availability of alternative nurseries for the prawns targeted on the Thukela Banks trawl grounds is limited overall by estuarine habitat availability and specifically by the requirement of *P. indicus*, *P. monodon*, and to a lesser extent *M. monoceros* for muddy, mangrove-lined channels (de Freitas, 1986). With the exception of their demonstrated use of the Richards Bay/Mhlathuze estuary (Forbes et al., 1994), no research has been conducted on availability of alternative nurseries while St. Lucia is closed. Vivier & Cyrus (2009) suggest the Mfolozi River estuary, south of St. Lucia, functions as an alternative nursery for marine fish species. However the Mfolozi is now a temporarily open/closed swamp with a dredged channel (Cyrus et al., 2010) and therefore may not be suitable for prawn species discussed in this paper. Moreover the Mfolozi and other estuaries in the KZN Bight are too small to be able to provide the same amount of recruits as St. Lucia estuary. Therefore the decrease in prawn recruitment due to the loss of prawn nursery area is regarded as justified.

Simulations of 5% prawn recruitment between 2010 and 2040 were used to investigate the effects on the ecosystem if the St. Lucia and Richards Bay/Mhlathuze estuaries closed or became unusable by prawns. These showed that only benthic benthos-feeding fish and carnivorous benthos would increase and total system biomass would decrease by 1% under low trawling effort. Simulations of 100% prawn recruitment between 2010 and 2040, used to investigate the effects of reopening St. Lucia, showed that under low trawling effort, adult prawns, benthopelagic carnivorous fish and benthopelagic benthos-feeding fish would increase, but carnivorous benthos would decrease. The recovery to 100% prawn recruitment seems reasonable in light of the rapid growth rate of penaeid prawns (Benfield et al., 1990), and small populations in smaller neighbouring estuaries such as the Matigulu (Swemmer, 2010) and Thukela (DWAF, 2004) that may serve as seed populations. In addition, studies on the restoration of mangroves in Kenya show that replanted stands of mangroves have similar abundances of prawns to natural stands and higher abundances than degraded areas (Crona and Ronnback, 2005). Moreover, a study following the breaching of St. Lucia in 2007 showed rapid recruitment of marine fish species into the estuary (Vivier et al., 2010). However, it should be noted that our models only incorporate changes to the mouth status of the nurseries and not changes in river flow and associated sediment outflow to the Bank which may affect prawn recruitment rate.

From the changes in biomass predicted by the simulations the potential indirect effects of prawn nursery changes on trawl catches on the Thukela Bank were examined. Biomasses of the target groups (prawns) and bycatch groups (commercial crabs, benthopelagic carnivorous fish and benthopelagic benthos-feeding fish) were negatively affected by reduced prawn recruitment and therefore catches of these groups could decrease. On the other hand, benthic benthos-feeding fish, another bycatch group, increased following decreased prawn recruitment. However, this group is sensitive to trawling effort with a 9 - 10% drop in biomass from low to high trawling effort. Thus trawl catches of benthic benthos-feeding fish would be negatively impacted by reduced prawn recruitment. The degradation of the nursery habitat of kuruma prawn (*Penaeus japonicus*) in Japan has also been suggested as the cause of steady declines in prawn catch over the past 40 years (Hamasaki and Kitada, 2006). In addition to the negative impacts due to reduced recruitment from prawn nursery loss, Thukela Bank fisheries catches may be further affected by decreases in riverine inflow via other catchments (Turpie and Lamberth, 2010) due to a decrease in nutrient and detritus import which the system is reliant upon, as shown by the negative net system production. Thus the growing demand for water in South Africa needs to be considered in conjunction with issues of food security and employment due to the local importance of commercial, recreational and subsistence fisheries in the KZN Bight.

2.5 CONCLUSIONS

Model results suggest that reduced prawn recruitment not only affects prawns but also fisheries catches. In addition, due to potential interactions between bycatch and target species, one cannot assume that a decrease in fishing effort, due to a decrease in target species, will result in the recovery of bycatch species. Results also indicate that when modelling effects of anthropogenic activities on marine ecosystems, it is important to include processes external to the modelled system, particularly critical life-history stages. Moreover, management and modelling of adjacent ecosystems (riverine, estuarine and marine) must be coupled in order to understand the potentially wide-ranging effects of anthropogenic activities on any one of these systems.

Carbon, nitrogen and phosphorus distribution and stoichiometry within the KwaZulu-Natal Bight, South Africa

3.1 INTRODUCTION

The KwaZulu-Natal (KZN) Bight is an oligotrophic area off the east coast of South Africa (Lutjeharms, 2006a). However the waters of the Bight are slightly less oligotrophic than the surrounding Agulhas Current which flows southward from Mozambique (Lutjeharms et al., 2000, Meyer et al., 2002). This is thought to be the result of three major nutrient sources to the Bight. At the southern end of the Bight the shelf narrows causing a semi-permanent lee eddy via the warm Agulhas Current flowing along the edge of the continental shelf (Pearce, 1977, Pearce et al., 1978, Carter and Schleyer, 1988). This brings water with higher nutrient concentrations to the surface (Meyer et al., 2002). In the north of the Bight a sporadic topographically-induced upwelling occurs bringing water with higher nutrient concentrations onto the shelf (Meyer et al., 2002). In the centre of the Bight the Thukela River affects the coastal ecosystem via a subsurface outflow with higher nutrient concentrations than surrounding waters (Meyer et al., 2002). The Thukela River is the third largest river in southern Africa with a sediment output of $6.79x10^3m^3$ $year^{-1}$ (Birch, 1996).

The importance of riverine nutrient sources for ecosystem functioning in the KZN Bight has been shown through the analysis of a number of ecosystem models of the region (Chapters 1 and 2). However these models were based on literature data and therefore could only indicate that river outflow was important, in terms of detritus. It is not yet known how riverine nutrient sources may be important in terms of nutrients for the ecosystem functioning of the nutrient-limited Bight.

Nutrients such as carbon, nitrogen and phosphorus can become limiting in a system because of the requirements of individual organisms for growth, reproduction and maintenance. Nutrient content and thus requirements of organisms is determined by the bone and cellular structures within an organism (Elser et al., 1996). Because these structures differ between taxa nutrient requirements of taxa differ. This can cause nutrient imbalances and limitations when predators consume prey with nutrient compositions different to their own (Sterner and Hessen, 1994, Sterner, 1997, Frost and Elser, 2002).

Ecological stoichiometry focuses on understanding how processes at the ecosystem level are affected by nutrient compositions of predators and prey (Sterner and Elser, 2002). Predation rates can be affected by nutrient limitations through predators attempting to maintain adequate nutrient ratios (Sterner and George, 2000). Moreover, predators can influence dissolved nutrient ratios and nutrient recycling (Elser and Urabe, 1999). For example, the types and amounts of fish in a system can, via feeding and excretion, affect the transport of nutrients from demersal to pelagic systems (Vanni, 1996, Schindler et al., 1996, Schaus et al., 1997). Thus fisheries may affect nutrient cycling within a system through the removal of fish. For example, Hjerne and Hansson (2002) calculated that 1.4-7.0% of nitrogen and phosphorus loads were removed from the Baltic Sea by fisheries. Thus, in fished systems, particularly oligotrophic systems, riverine sources transported by oceanic currents may have increased importance for marine ecosystem functioning.

Most stoichiometric studies are conducted on freshwater systems. However there have been studies on marine phytoplankton following that of Redfield (1958). Moreover, studies examine nutrient content and stoichiometry at the species or community level, with most analysing freshwater pelagic (Sureda, 2003, Teubner et al., 2003, Frost et al., 2003) and freshwater benthic communities (Cross et al., 2003, Cross et al., 2005). Ecosystem-level studies are also needed to gain knowledge of the relative importance of limiting nutrients in aquatic systems. However, there is a severe lack of data on nutrient content of organisms spanning a wide range of trophic levels (Sterner and Elser, 2002, Sardans et al., 2012).

As a first step in understanding the role of nutrients in ecosystem functioning of the KZN Bight, the distribution of carbon, nitrogen and phosphorus in groups throughout the foodweb is compared across the Bight. To this end, carbon, nitrogen and phosphorus content (based on measurements in the southern, central and northern Bight and literature data) of pelagic and demersal organisms and nutrient pools are documented and used to calculate C:N:P ratios and biomasses. It is hypothesised that organisms in the central Bight will show higher nutrient contents due to the influence of the riverine nutrient source as suggested in Chapters 1 and 2.

3.2 MATERIALS AND METHODS

The lack of quantitative data for the KZN Bight led to the multidisciplinary, multi-institutional project “Ecosystem processes within the KwaZulu-Natal Bight: linking geographical and physical processes to understand ecosystem functioning” within the African Coelacanth Ecosystem Program (ACEP II). Overall aims were to investigate geological and oceanographic processes, oceanic vs. riverine inputs, biodiversity and ecosystem functioning. This thesis comprises the ecosystem modelling sub-component of this project, focusing on investigating ecosystem functioning. As part of this, one of the objectives was to construct ecosystem models/ecological networks based on abiotic and biotic data collected by other sub-components in the project during two research cruises in the Bight – one in February 2010 to coincide with the “wet” summer season and one in August 2010 to coincide with the “dry” winter season. In this chapter an ecosystem-level view of carbon, nitrogen and phosphorus content, stoichiometry and biomass of abiotic and biotic groups are documented. To this end, sample collection during both ACEP II cruises, sources of carbon and nitrogen data, phosphorus analysis and literature data are detailed.

3.2.1 Study sites

The KZN Bight, the widest area of continental shelf off the east coast of South Africa (Lutjeharms 2006), covers 5096km^2 (Cockcroft and Peddemors, 1990). Off the Thukela River mouth in the central bight the shelf extends for approximately 50km to the boundary of the Agulhas current at the 200m isobath (Fig. 3.1) (Pearce, 1977, Schumann, 1988b, Lutjeharms et al., 2000). Four focus areas were chosen for the ACEP II cruises based on areas which should reflect the major nutrient sources. In the southern Bight, in the vicinity of the lee eddy, the “Durban Eddy” (DE) site was located at the 200m isobath (Fig. 3.1). In the central Bight, off the Thukela River, the “Thukela Mouth” (TM) site was located between the 30m and 40m isobaths (Fig. 3.1). In the northern Bight two focus areas were sampled, one to the south of the upwelling cell and one to the north. However, because macrobenthos could not be sampled at the southern site due to reefs and thus an ecosystem-level view could not be achieved, only data from the northern site was included in this thesis. The “Richards Bay” (RB) site was located between the 30m and 40m isobaths (Fig. 3.1). It should be noted that nutrient and isotope analyses (de Lecea, 2012) and ADCP data showed that the Richards Bay upwelling did not occur during either research cruise.

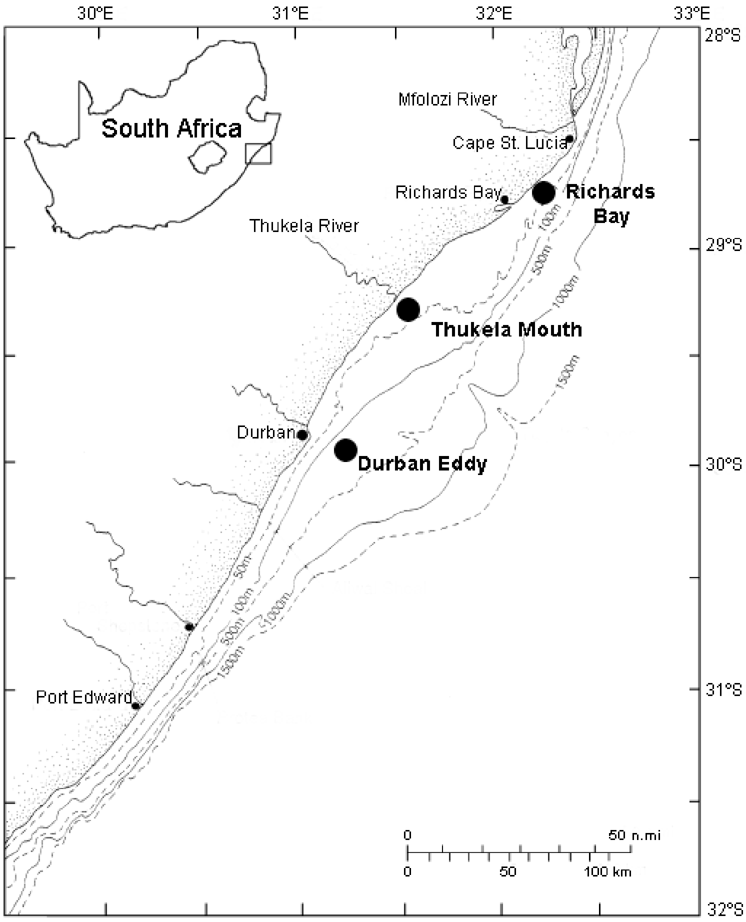

Figure 3.1. The KwaZulu-Natal (KZN) Bight and individual focus areas. Adapted from Meyer et al. (2002)

3.2.2 Data sources

3.2.2.1 Sample collection

Samples were collected by various researchers on board of the *FRV Algoa* at each study site during each cruise. Table 3.1 shows the researchers, affiliations, measurements and replicates provided for this thesis. Measurements from both cruises were pooled since no seasonal differences could be tested due to one cruise in each season. Nutrient analysis is detailed in section 3.2.2.3. For measurements not taken as part of ACEP II literature data were used as detailed in section 3.2.2.2.

Table 3.1. Data provided by ACEP II researchers and the number of replicates per site (n/site).

	Researcher	Data provided	n/site	Units
Pelagic community	Barlow, R. [a b] and Lamont, T. [a b]	Dissolved inorganic nitrogen (DIN: Nitrate + Nitrite)	12-20	μmol N L^{-1}
		Dissolved inorganic phosphorus (DIP: Phosphate)	12-20	μmol P L^{-1}
		Diatom and flagellate biomass	5-10	mg chl-*a* m^{-3}
	Smit, A., [c] and Omarjee, A. [c]	Particulate organic nitrogen (PON)	6-7	μg N L^{-1}
		Particulate organic phosphorus (POP)	3-4	μg P L^{-1}
	Muir, D., [c] and Kunnen, T [c]	Bacteria biomass	4-5	gC mL^{-1}
	Scharler, U., [c] and Moyo, R. [c]	Heterotrophic microplankton biomass	6	pgC mL^{-1}
	Huggett, J. [a] and Pretorius, M. [d]	Small, medium, large copepod and "other large" zooplankton biomass	12-20	mg dry weight m^{-3}
	Smit, A. [c] and de Lecea, A. [c]	Small, medium and large copepod carbon and nitrogen content	8-106	%C, %N
Demersal community	Fennessy, S.T. [e]	Demersal groups biomasses (large macrobenthos, cephalopods, bony fish, elasmobranchs)	4	kg wet weight km^{-2}
	Smit, A. [c] and de Lecea, A. [c]	Carbon content (sediment, demersal groups)	3-55	%C dry weight
		Nitrogen content (sediment, demersal groups)		%N dry weight

a: Department of Environmental Affairs, Cape Town, South Africa; b: Marine Research Institute, University of Cape Town, South Africa; c: School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa; d: Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa; e: Oceanographic Research Institute, Durban, South Africa.

Pelagic community

Dissolved inorganic nutrients (DIN: NO_3^-+NO_2^-; DIP: PO_4^{3-}) were determined from samples taken from each sampling occasion with 12 Niskin bottles of 5L capacity, attached to a Sea-Bird 911 *plus* CTD (Sea-Bird Electronics, Inc., Bellevue, Washington, USA). Samples were analysed using a standard Technicon Autoanalyser II method adapted to an Astoria Nutrient Analyser (Astoria-Pacific Int., Clackamas, USA) (Table 3.1). To determine particulate organic nitrogen and phosphorus (suspended PON and POP), water samples were collected at fluorescence maximum (F_{max}) and surface depths and filtered (500mL) through pre-combusted (4hr at 450ºC) 25mm diameter Whatman GF/F filters. These filters were frozen at -20ºC until digestion using a wet oxidation method according to Raimbault et al. (1999) and analysis on a Skalar SAN++ continuous flow analyser. Chlorophyll-*a* biomass was measured using a WET labs ECO-fluorometer (Philomath, USA), which was integrated with the CTD. These biomasses were proportioned into diatom, dinoflagellate, small flagellate and prokaryote contribution using pigment indices (see Barlow et al. (2008)). Samples for bacteria were collected at the surface, $\mathrm{F_{max}}$, and below $\mathrm{F_{max}}$ using water collected in the Niskin bottles attached to the CTD. Cells were counted using epifluorescent microscopy and biovolume and carbon biomasses were calculated based on Bratbak (1985) (Kunnen, 2012). Moyo (2011) counted and measured heterotrophic microplankton from samples collected at surface, $\mathrm{F_{max}}$ and bottom depths, calculated cell volumes and converted these to carbon based on the methods of Menden-Deuer and Lessard (2000). Zooplankton samples were collected using a double oblique bongo net (200µm and 300µm mesh) lowered to a few meters from the recorded bottom of the water column. Zooplankton collected in the 200µm mesh net were immediately preserved in 4% formalin and stored in plastic jars for later phosphorus analysis. Samples were sorted into four size classes: 200-500µm (“small copepods”), 500-750µm (“medium copepods”), 750-1600µm (“large copepods”) and 1600µm+ (“other large zooplankton” including chaetognaths, jellies, salps and fish larvae). These were dried and dry weight biomass was calculated based on the volume of water filtered by the bongo net.

Demersal community

Sediment samples were collected using a modified Van Veen grab. A sample was collected from the top layer of the grab, sealed in a bag and frozen at -20ºC for later isotope and phosphorus analyses to estimate benthic POM. Samples from the demersal system (large macrobenthos, cephalopods, bony fish and elasmobranchs) were collected on board the crustacean trawler *Ocean Spray* during March 2010 in the “wet” summer season and August 2010 in the “dry” winter season. Trawl locations were matched to the ACEP II focus areas. Wet weight biomass was estimated based on swept area. In this thesis, only data from trawls at similar depths as the study sites were used for biomass estimates. This was because there were large differences in the depths of each trawl and therefore differences in habitat types that, if included, would produce biomass estimates less representative of each study site.

To gain an understanding of community and ecosystem-level differences in nutrient content, stoichiometry and biomasses measurements at the species level were grouped into functional groups, i.e. species with similar habitat preferences, physiological characteristics and diet compositions. Phytoplankton biomasses were provided in terms of diatoms and flagellates (Table 3.1). Zooplankton biomasses were provided in terms of small copepods (250 - 500µm), medium copepods (500 - 750µm), large copepods (750 - 1600µm) and other large zooplankton (1600+µm) (Table 3.1). However for the demersal groups, species which dominated in terms of biomass were identified for each site. These were grouped into functional groups based on information from literature (Table 3.2) (Smith and Heemstra, 1986, van der Elst, 1993). Only species which dominated the biomass and for which three individuals could be collected at a site were included in analyses for this chapter. These were immediately frozen at -20ºC on board.

3.2.2.2 Literature data

Before biomasses of functional groups in terms of carbon, nitrogen and phosphorus could be calculated some measurements needed to be converted from wet to dry weight. Ratios were either calculated from this study (see section 3.2.2) or literature (Table 3.3). In addition, C:N, C:P and N:P ratios were used for groups for which wet weight or carbon biomass was calculated from ACEP II cruises or trawls but no carbon and/or nitrogen and/or phosphorus measurements were available (Table 3.3). These ratios were chosen from other oligotrophic marine areas where available.

Table 3.2. Demersal functional groups and representative species of each site where known.

Functional Group	**Durban Eddy**	**Thukela Mouth**	**Richards Bay**
Large suspension feeding benthos	Porifera spp	Crinoid spp	Mixed Porifera
Echinoderms	Phormosoma spp	Echinoidea spp	Asteroidea spp
Molluscs (non-cephalopod)	Phalium spp	*Sphenopus marsupialis*	*Phalium glaucum*
Prawns and shrimps	*Aristeomorpha foliacea*	*Harpiosquilla harpax*	*Penaeus japonicus*
Large crustaceans	*Scyllarides elizabethae, Munida incerta*	*Parthenope quemvis, Scyramathia spp*	*Portunus sanguinolinta*
Cuttlefish	*Sepia inserta, Sepia acuminata*	*Sepia vermicularis*	*Sepia acuminate, Sepia inserta*
Other cephalopods	*Ornithoteuthis volatilus, Notodarus hawaiiensis*	Cephalopoda spp	Cephalopoda spp
Flatfish	Pseudorhombus spp, *Citharoides macrolepis*	Pseudorhombus spp	*Pseudorhombus elevatus*
Gurnards	*Chelidonichthys queketti, Satyrichthys adeni*	*Lepidotrigla faurei*	*Lepidotrigla faurei*
Lizardfish	*Saurida undosquamis*	*Saurida undosquamis*	*Saurida undosquamis*
Other benthic carnivores	*Halieutaea fitzsimonsi, Hoplichthys acanthopleurus*	*Minous coccineus, Serranus knysnaensis*	*Cociella hemstraii*
Pinky	*Pomadasys olivaceum*	*Pomadasys olivaceum*	*Pomadasys olivaceum*
Red tjor-tjor	*Pagellus natalensis*	*Pagellus natalensis*	*Pagellus natalensis*
Other benthopelagic fish	*Polysteganus coeruleopunctatus, Neoscombrops annectens*	*Atrobucca nibe, Otolithes ruber*	*Upeneus vittatus, Lagocephalus guentheri*
Skates and rays	*Rhinobatus holcorhynchos*	*Raja miraletus, Dasyatis chrysonota*	not caught
Small benthic sharks	*Mustelus mosis, Pliotrema warreni*	*Halaelurus lineatus*	not caught

Table 3.3. Various ratios from literature data used to calculate carbon, nitrogen and phosphorus biomass when unavailable from ACEP II samples.

Group	Ratio	Value	Reference and study location
Dissolved inorganic carbon (DIC)	C:N	2880	calculated from Karl & Letelier (2008), N. Pacific gyre
Suspended POC	C:N	8.2	Diaz et al. (2001), NW Mediterranean Sea
Phytoplankton	chl-a:C C:N	40 8.2	Lenz (1974), Kiel Bight
Bacteria	C:N molar C:P molar	5.3 99	Gundersen et al. (2002), Sargasso Sea
Heterotrophic microplankton	C:N molar C:P molar	6.2 20	Le Borgne (1982) tropical E. Atlantic
Other large zooplankton	%C dry weight %N dry weight	19.6 5.2	Beers (1966), Sargasso Sea
Echinoderms	wet:dry weight %C %N %P	0.33 50.1 12.05 0.76	Ricciardi & Bourget (1998) Clarke (2008), Antarctica
Molluscs (non-cephalopods)	wet:dry weight %P	0.18 0.40	Segar et al. (1971), Celtic Sea Clarke (2008), Antarctica
Large crustaceans	wet:dry weight	0.25	Ricciardi & Bourget (1998)
Prawns and shrimp	wet:dry weight %P	0.2 1.26	Gulland & Rothschild (1989) Beers (1966), Sargasso Sea
Small benthic sharks	wet:dry weight	0.2	Cortés (2002)

3.2.2.3 Nutrient analysis

Carbon and nitrogen content (% dry weight) of sediment, zooplankton and demersal groups were measured by de Lecea (2012) via stable isotope analysis.

Phosphorus content (%P dry weight) was measured in sediment, zooplankton, large macrobenthos, cephalopods, bony fish and elasmobranchs. Sediment samples from two stations close to each study site were dried to a constant weight by placing in an oven at 60˚C for 48 hours. Zooplankton samples from each study site, which had been stored in 4% formalin, were rinsed with distilled water, dried to a constant weight, weighed, crushed and frozen until analysis. Muscle tissue of various species of large macrobenthos, cephalopods, bony fish and elasmobranchs caught in each study site were dried to a constant weight then weighed, crushed and frozen until analysis. Mean dry:wet weight ratios were calculated for a number of demersal groups. These can be found in Appendix 3.1.

Analyses were based on the method of Raimbault et al. (1999). Fresh reagent was prepared for each batch of samples for analysis by dissolving 30g disodium tetraborate in 250ml of distilled water heated at 40-50˚C, adding 15g of potassium peroxodisulphate and dissolving by stirring. Acid-washed Nalgene autoclave bottles were filled with 5-10mg of sample, 4ml of reagent and 30ml of distilled water. Blanks in triplicate were run with each batch. Samples were digested in an autoclave at 120˚C for 30min. The digestion mixture was diluted to 100ml in volumetric flasks and the orthophosphate concentrations were measured on a Skalar SAN++ continuous flow analyser.

Once carbon, nitrogen and phosphorus contents were calculated they were used to calculate biomasses. For wet weight biomasses provided in terms of volume, depth-integrated biomasses (g m^{-2}) were calculated based on ACEP II measurements mentioned in section 3.2.1.3 and depth measurements from CTD data at each site during the ACEP II cruises. However it should be noted that sampling efficiency was not taken into account in the biomasses provided by ACEP researchers. Suspended POM can include bacteria, micro- and phytoplankton along with detrital POM. Therefore suspended detrital POM was calculated by subtracting bacteria, microplankton and phytoplankton biomasses from total suspended POM. Carbon, nitrogen and phosphorus content were converted to molar weight to calculate C:N:P ratios.

3.2.3 Statistical analyses on nutrient content and biomass ratios

Carbon, nitrogen and phosphorus content (% dry weight) were compared between study sites for each group. Parametric statistical analyses were carried out using SPSS version 19 after data were confirmed to be normally distributed and homeoscedastic. A one-way ANOVA or

Kruskal-Wallis test was performed on each group. An independent-samples t-test or Mann-Whitney test was performed on groups that were only sampled at two sites.

A number of biomass ratios were calculated to compare the distribution of carbon, nitrogen and phosphorus biomass among trophic levels (low, mid and high) and certain predator-prey pairs (e.g. zooplankton and primary producers) between sites. Trophic levels were based on those of the same or similar groups in the models of Chapters 1 and 2 calculated by Ecopath.

3.3. RESULTS

3.3.1 Nutrient content

Carbon content (% dry weight) of zooplankton, benthic detrital POM and demersal groups were used to calculate carbon biomasses at each site. In the pelagic community carbon and nitrogen content of small and medium copepods sampled at the RB site were significantly lower than at the DE and TM sites (Figs. 3.2 and 3.3 Table 3.4). Phosphorus content of medium copepods also followed this trend (Fig 3.4, Table 3.4). However phosphorus content of large copepods at the DE site were significantly lower than at the TM and RB sites (Fig 3.4, Table 3.4).

Carbon and nitrogen content of sediment (benthic detrital POM) at the TM site were significantly higher than at the DE and RB sites (Figs 3.3 and 3.4, Table 3.4). Phosphorus content of sediment did not differ significantly between sites ($p>0.05$).

Of the demersal groups, significant differences in nutrient contents were found for large crustaceans, cuttlefish, flatfish, gurnards, other benthopelagic fish, skates and rays and small benthic sharks. Carbon, nitrogen and phosphorus content of cuttlefish were significantly higher at the TM site than the DE and RB sites (Figs 3.2, 3.3, 3.4, Table 3.4). Carbon and nitrogen content of flatfish were also significantly higher at the TM site than the DE and RB sites (Figs 3.2 and 3.3, Table 3.4). Nitrogen content of other benthopelagic fish was significantly lower at the RB site than at the DE and TM sites (Fig 3.3, Table 3.4). However the nitrogen content of skates and rays were significantly higher at the RB site than at the DE and TM sites (Fig 3.3, Table 3.4). Phosphorus content of large crustaceans was significantly higher at the TM site, gurnards at the RB site and small benthic sharks at the DE site (Fig 3.4, Table 3.4).

Of the biotic groups, large suspension feeders had the lowest carbon, nitrogen and phosphorus contents (Figs 3.2, 3.3, 3.4). However the highest nutrient contents varied with carbon content highest in zooplankton groups, nitrogen in sharks and rays, and phosphorus in Red tjor-tjor. (Figs 3.2, 3.3, 3.4). Moreover, the largest variability in nutrient content of groups was in carbon content, the highest of which was found among the large benthos groups and the lowest among the bony fish groups (Fig. 3.2).

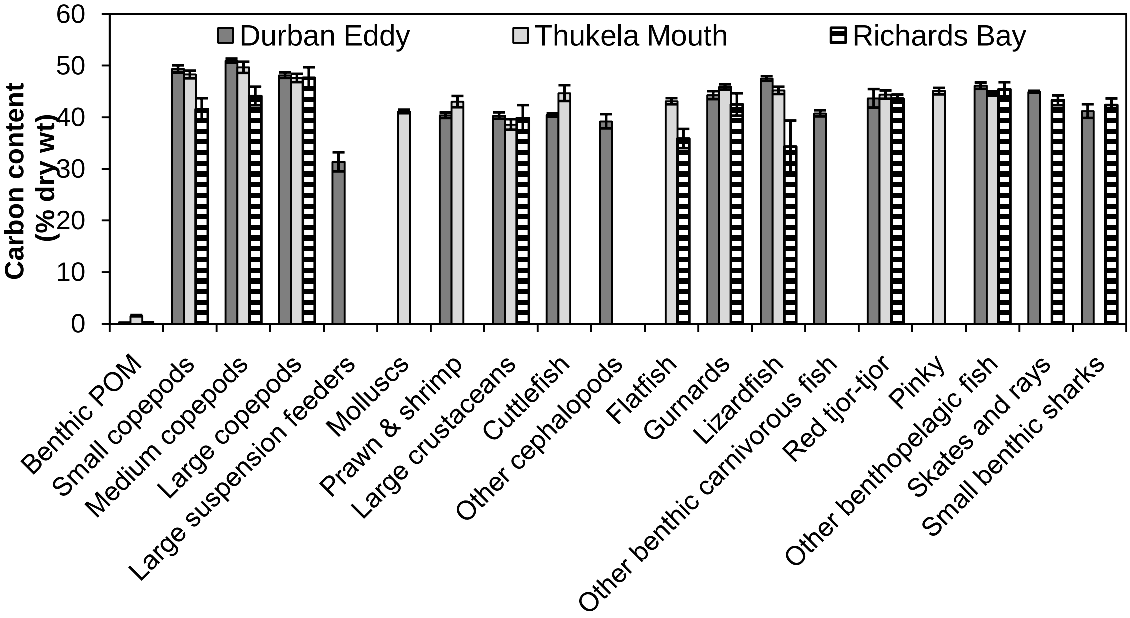

Figure 3.2. Mean carbon content (% of dry weight ±2SE) over all sites sampled. Light grey and striped bars represent significantly different results.

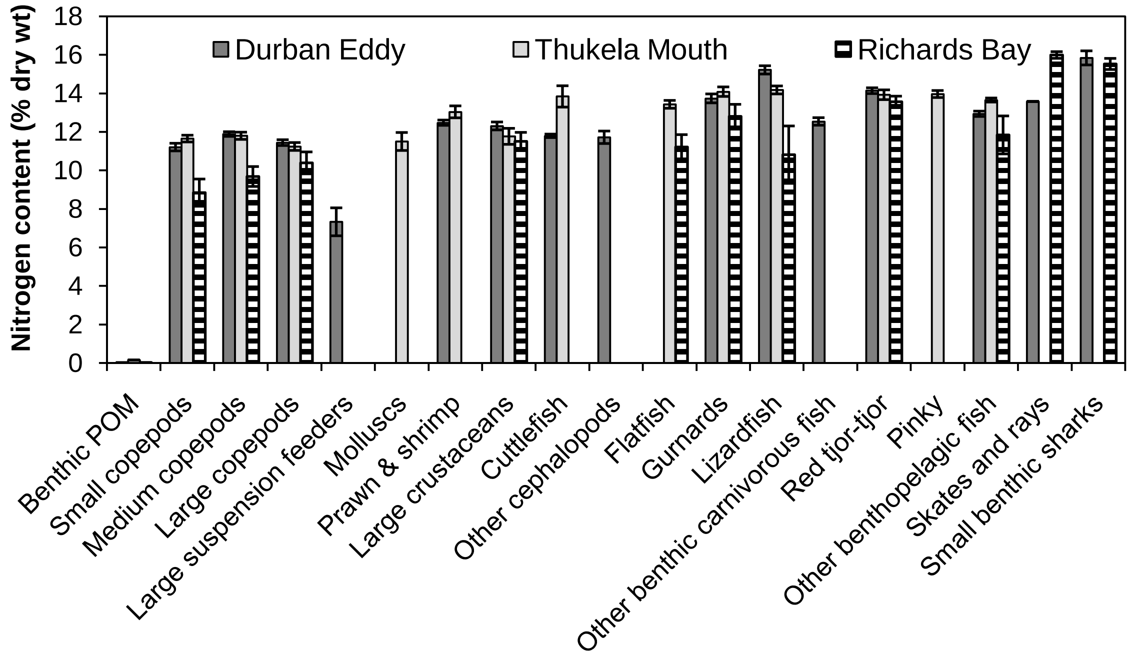

Figure 3.3. Mean nitrogen content (% of dry weight ±2SE) over all sites sampled. White, light grey and striped bars represent significantly different results.

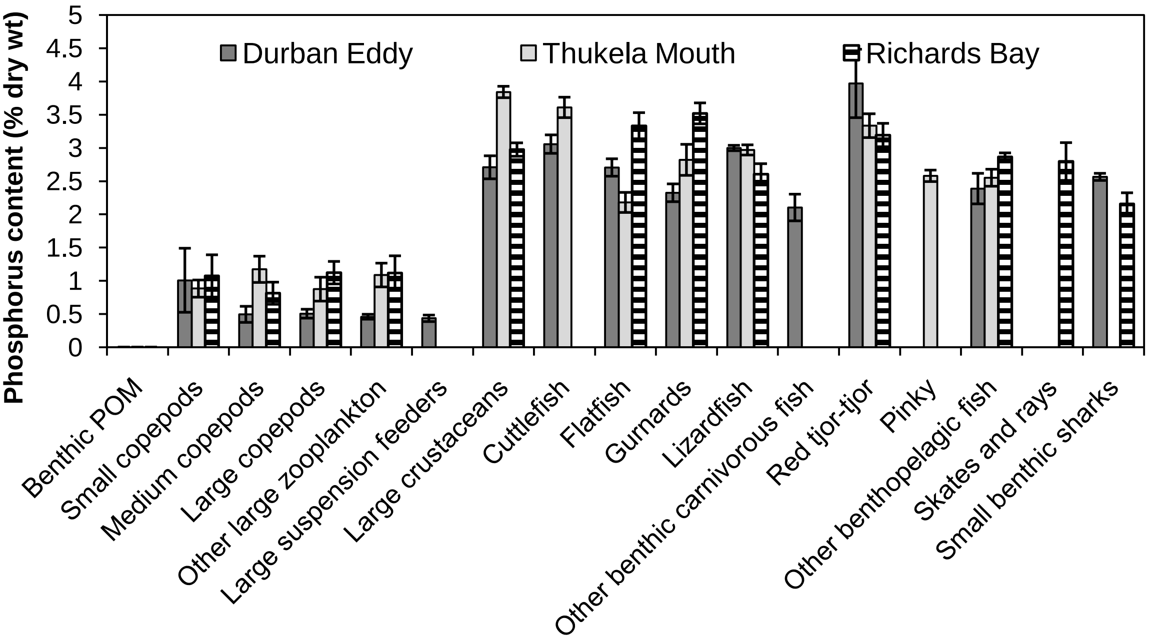

Figure 3.4. Mean phosphorus content (% of dry weight ±2SE) over all sites sampled. White, light grey and striped bars represent significantly different results.

Table 3.4 Analysis of variance and t-test results for the effects of site on carbon, nitrogen and phosphorus content of groups in the KZN Bight. df is the degrees of freedom, p is the probability with significant values in bold. DE is the Durban Eddy site, TM is the Thukela Mouth site and RB is the Richards Bay site. Blanks represent groups which were not sampled or only sampled at one site.

	Carbon content			**Nitrogen content**			**Phosphorus content**		
Group	df	p	Diff between sites	df	p	Diff between sites	df	p	Diff between sites
Benthic POM	8	**0.024**	TM>DE,RB	8	**0.000**	TM>DE,RB	5	0.091	
Small copepods	35	**0.000**	DE,TM>RB	35	**0.000**	DE,TM>RB	15	0.923	
Medium copepods	37	**0.000**	DE,TM>RB	38	**0.000**	DE,TM>RB	15	**0.035**	TM>RB>DE
Large copepods	153	0.69		153	0.071		15	**0.031**	TM,RB>DE
Other large zooplankton							14	0.060	
Prawn and shrimp	13			13	0.195				
Large crustaceans	29	0.505		29	0.251		7	**0.002**	TM>DE,RB
Cuttlefish	7	**0.047**	TM>DE	7	**0.014**	TM>DE	8	**0.037**	TM>DE
Lizardfish	14	**0.028**	DE,TM>RB	13	**0.018**	DE,TM>RB	13	0.058	
Flatfish	21	**0.001**	TM>RB	21	**0.004**	TM>RB	8	**0.011**	RB>DE>TM
Gurnards	38	0.296		38	0.057		15	**0.001**	RB>DE,TM
Red tjor-tjor	24	0.798		23	0.404		15	0.242	
Other benthopelagic fish	90	0.128		90	**0.000**	DE,TM>RB	6	0.192	
Skates and rays	7	0.439		7	**0.000**	RB>DE			
Small benthic sharks	15	0.548		15	0.505		12	**0.039**	DE>RB

3.3.2 Carbon, nitrogen and phosphorus biomass

The distribution of carbon, nitrogen and phosphorus biomass among abiotic and biotic groups differed between sites. Biotic groups of the pelagic community were the smallest biomass pools at all sites (Tables 3.4, 3.5, 3.6). Mean carbon, nitrogen and phosphorus biomass of DIM, suspended detrital POM, bacteria, flagellates and zooplankton groups were highest at the DE site and lowest at the RB site (Tables 3.4, 3.5, 3.6). The majority of carbon, nitrogen and phosphorus at all sites was located in the DIM pool (Tables 3.4, 3.5, 3.6). Of the biotic groups, diatoms dominated all sites in terms of carbon, nitrogen and phosphorus (Tables 3.4, 3.5, 3.6).

Of the demersal groups included in this study large crustaceans dominated at all sites in terms of carbon biomass (Table 3.4) and small benthic sharks dominated the DE site and Red tjor-tjor dominated the TM and RB sites in terms of nitrogen and phosphorus biomass (Tables 3.5 and 3.6).

Carbon, nitrogen and phosphorus biomasses of cuttlefish, flatfish, other benthopelagic fish and small benthic sharks were highest at the DE site (Tables 3.4, 3.5, 3.6). Nitrogen and phosphorus biomasses of large crustaceans were also highest at the DE site (Tables 3.5, 3.6). In contrast, carbon, nitrogen and phosphorus biomasses of gurnards and Pinky were highest at the TM site (Table 3.4, 3.5, 3.6). Nitrogen and phosphorus biomasses of other benthic carnivorous fish were also highest at the TM site (Tables 3.5, 3.6).

Of the three sites, total carbon and nitrogen biomass of the groups sampled was highest at the RB site, and phosphorus biomass was highest at the DE site (Tables 3.4, 4.5, 4.6). Lowest carbon and phosphorus biomass was found at the TM site (Table 3.4) but lowest total nitrogen biomass was found at the DE site (Tables 3.5, 3.6).

Table 3.5. Mean carbon biomass (gC m^{-2} ±2SE) of functional groups for each site. Groups which were not caught at a site are represented by n/a. Groups which have no SE were only caught in one of the ACEP II trawls.

Functional group	**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
	Mean	2SE	Mean	2SE	Mean	2SE
DIC	3.79E+04	4.04E+03	2.48E+03	8.50E+02	1.53E+03	1.17E+02
Suspended detrital POC	1.15E+01	1.39E+00	1.87E+00	6.03E-01	6.92E-01	3.31E-01
Benthic detrital POC	3.79E+02		1.89E+03		3.79E+02	
Bacteria	1.22E+00	4.56E-01	3.95E-01	9.36E-02	4.90E-01	1.24E-01
Heterotrophic microplankton	1.50E-03	1.80E-04	8.23E-04	1.22E-04	8.44E-04	1.75E-04
Diatoms	1.79E+00	4.10E-01	4.16E-01	4.26E-02	1.30E+00	3.02E-01
Flagellates	1.17E+00	1.27E-01	2.63E-01	2.65E-02	3.55E-01	1.86E-02
Small copepod	2.58E-01	5.58E-02	1.31E-01	2.59E-02	7.81E-02	1.71E-02
Medium copepod	1.54E-01	6.60E-02	9.03E-02	2.00E-02	4.59E-02	4.00E-03
Large copepod	1.11E-01	1.33E-02	7.61E-02	2.20E-02	6.49E-02	1.30E-02
Other large zooplankton	6.34E-03	1.11E-03	2.80E-03	4.80E-04	3.50E-03	5.70E-04
Large suspension feeders	2.00E+02	1.73E+02	2.97E+00	7.97E-01	1.98E+03	1.86E+03
Echinoderms	1.46E+01	1.84E+00	1.03E+01	3.60E+00	1.30E+02	1.29E+02
Mollusc (non-cephalopoda)	5.21E+01	4.69E+01	1.28E+00	5.80E-02	1.45E+00	
Prawn and shrimp	n/a	n/a	6.82E+00	6.71E+00	1.61E+00	7.57E-01
Large crustaceans	8.35E+01	2.84E+01	3.91E+01	2.03E+01	1.96E+01	1.46E+01
Cuttlefish	2.46E+02	8.09E+01	8.18E+01	2.67E+01	1.16E+01	8.05E+00
Other cephalopods	3.10E+01	2.94E+01	n/a	n/a	n/a	n/a
Lizardfish	2.85E+02	1.06E+02	1.13E+02	4.48E+01	4.33E+01	2.93E+01
Other benthic carnivorous fish	3.49E+02	2.04E+01	3.69E+02	2.17E+02	8.09E+01	4.84E+01
Flatfish	2.38E+02	1.14E+02	1.01E+02	6.82E+01	5.54E+01	1.22E+01
Gurnards	4.50E+01	1.88E+01	6.75E+00	2.17E+00	8.08E+00	2.23E+00
Red tjor-tjor	1.01E+03	8.81E+02	1.29E+03	1.22E+03	1.62E+03	1.54E+03

Table 3.5 continued

Functional group	Durban Eddy		Thukela Mouth		Richards Bay	
	Mean	2SE	Mean	2SE	Mean	2SE
Pinky	n/a	n/a	7.01E+01	3.92E+01	3.08E+00	5.01E-01
Other benthopelagic fish	1.49E+02	4.66E+01	5.49E+02	3.82E+02	1.11E+02	6.76E+01
Skates & rays	1.03E+02		4.18E+02	2.28E+02	1.24E+02	
Small benthic sharks	3.18E+02	1.47E+02	2.32E+01	1.92E+01	2.36E+02	
TOTAL	3.13E+03		3.08E+03		4.43E+03	

Table 3.6. Mean nitrogen biomass (gN m^{-2} ±2SE) of functional groups for each site. Groups which were not caught at a site are represented by n/a. Groups which have no SE were only caught in one of the ACEP II trawls.

Functional group	Durban Eddy		Thukela Mouth		Richards Bay	
	Mean	2SE	Mean	2SE	Mean	2SE
DIN	1.31E+01	8.38E-01	8.60E-01	1.18E-01	5.20E-01	6.84E-02
Suspended detrital PON	1.23E+00	1.41E-01	1.84E-01	6.62E-02	6.00E-02	1.70E-02
Benthic detrital PON	4.71E+01		1.86E+02		4.71E+01	
Bacteria	1.56E-01	5.85E-02	6.27E-02	1.42E-02	5.06E-02	1.30E-02
Heterotrophic microplankton	2.85E-04	3.40E-05	1.55E-04	2.29E-05	1.59E-04	3.29E-05
Diatoms	3.15E-01	7.20E-02	7.30E-02	7.50E-03	2.28E-01	5.30E-02
Flagellates	2.07E-01	2.20E-02	4.64E-02	4.66E-03	6.25E-02	3.20E-03
Small copepod	5.86E-02	1.27E-02	3.14E-02	6.30E-03	1.66E-02	3.64E-03
Medium copepod	3.58E-02	3.46E-03	2.13E-02	4.77E-03	1.00E-02	8.89E-04
Large copepod	2.64E-02	3.10E-03	1.80E-02	5.20E-03	1.42E-02	1.02E-02
Other large zooplankton	1.75E-03	3.08E-04	7.76E-04	1.33E-04	9.74E-04	1.58E-04
Large suspension feeders	4.67E+01	4.05E+01	6.95E-01	1.86E-01	4.64E+02	4.34E+02
Echinoderms	3.50E+00	4.42E-01	2.47E+00	8.66E-01	3.13E+01	3.09E+01
Mollusc (non-cephalopoda)	1.46E+01	1.31E+01	3.58E-01	1.62E-02	4.06E-01	

Table 3.6 continued

Functional group	**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
	Mean	2SE	Mean	2SE	Mean	2SE
Prawn and shrimp	n/a	n/a	2.07E+00	2.03E+00	4.89E-01	2.29E-01
Large crustaceans	2.55E+01	8.65E+00	1.19E+01	6.20E+00	5.68E+00	4.21E+00
Cuttlefish	7.19E+01	2.36E+01	2.54E+01	8.29E+00	3.60E+00	2.50E+00
Other cephalopods	9.28E+00	8.80E+00	n/a	n/a	n/a	n/a
Lizardfish	8.76E+01	3.26E+01	3.53E+01	1.40E+01	1.35E+01	9.17E+00
Other benthic carnivorous fish	1.07E+02	6.24E+00	1.13E+02	6.68E+01	2.44E+01	1.46E+01
Flatfish	7.60E+01	3.64E+01	3.16E+01	2.14E+01	1.75E+01	3.86E+00
Gurnards	1.38E+01	5.80E+00	2.08E+00	6.68E-01	2.49E+00	6.86E-01
Red tjor-tjor	3.20E+02	2.78E+02	4.05E+02	3.82E+02	5.05E+02	4.79E+02
Pinky	n/a	n/a	2.17E+01	1.22E+01	9.54E-01	1.55E-01
Other benthopelagic fish	4.23E+01	1.33E+01	1.68E+02	1.17E+02	2.89E+01	1.76E+01
Skates & rays	3.11E+01		1.26E+02	6.88E+01	3.76E+01	
Small benthic sharks	1.22E+02	5.67E+01	8.72E+00	7.23E+00	8.65E+01	
TOTAL	1.03E+03		1.14E+03		1.32E+03	

Table 3.7. Mean phosphorus biomass (gP m^{-2}±2SE) of functional groups for each site. Groups which were not caught at a site are represented by n/a. Groups which have no SE were only caught in one of the ACEP II trawls.

Functional group	**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
	Mean	2SE	Mean	2SE	Mean	2SE
DIP	2.86E+00	2.20E-01	3.96E-01	2.85E-02	2.46E-01	6.03E-02
Suspended detrital POP	5.72E-01	6.78E-02	6.07E-02	2.67E-03	1.39E-01	1.22E-01
Benthic detrital POP	6.54E+00		2.58E+01		6.54E+00	
Bacteria	3.18E-02	1.19E-02	1.28E-02	2.90E-03	1.00E-02	2.73E-03
Heterotrophic microplankton	3.15E-05	3.76E-06	1.71E-05	2.54E-06	1.76E-05	3.64E-06

Table 3.7 continued

Functional group	**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
	Mean	2SE	Mean	2SE	Mean	2SE
Diatoms	4.36E-02	9.97E-03	1.01E-02	1.00E-03	3.16E-02	7.30E-03
Flagellates	2.86E-02	3.00E-03	6.40E-03	6.00E-04	8.65E-03	4.54E-04
Small copepod	5.28E-03	1.14E-03	2.44E-03	4.70E-04	2.01E-03	4.40E-04
Medium copepod	1.50E-03	1.46E-04	2.10E-03	4.77E-04	8.43E-04	7.44E-05
Large copepod	1.18E-03	1.41E-04	1.39E-03	4.05E-04	1.53E-03	3.17E-04
Other large zooplankton	1.49E-04	2.62E-05	1.56E-04	2.67E-05	2.01E-04	3.27E-05
Large suspension feeders	2.80E+00	2.43E+00	4.17E-02	1.12E-02	2.79E+01	2.61E+01
Echinoderms	2.21E-01	2.79E-02	1.56E-01	5.46E-02	1.97E+00	1.95E+00
Mollusc (non-cephalopoda)	5.07E-01	4.57E-01	1.25E-02	5.64E-04	1.41E-02	
Prawn and shrimp	n/a	n/a	2.00E-01	1.96E-01	4.73E-02	2.22E-02
Large crustaceans	5.61E+00	1.91E+00	3.90E+00	2.02E+00	1.47E+00	1.09E+00
Cuttlefish	1.87E+01	6.13E+00	6.61E+00	2.16E+00	9.38E-01	6.51E-01
Other cephalopods	2.42E+00	2.30E+00	n/a	n/a	n/a	n/a
Lizardfish	1.68E+01	6.25E+00	5.72E+00	2.27E+00	4.02E+00	2.72E+00
Other benthic carnivorous fish	1.78E+01	1.04E+00	3.22E+00	1.90E+00	6.71E+00	4.01E+00
Flatfish	1.59E+01	7.63E+00	6.63E+00	4.49E+00	4.21E+00	9.28E-01
Gurnards	2.32E+00	9.71E-01	3.48E-01	1.12E-01	4.16E-01	1.15E-01
Red tjor-tjor	9.13E+01	7.93E+01	9.61E+01	9.05E+01	1.19E+02	1.13E+02
Pinky	n/a	n/a	4.02E+00	2.25E+00	1.76E-01	2.87E-02
Other benthopelagic fish	7.76E+00	2.43E+00	3.14E+01	2.19E+01	6.98E+00	4.26E+00
Skates & rays	6.38E+00		2.60E+01	1.41E+01	7.72E+00	
Small benthic sharks	1.98E+01	9.17E+00	0.00E+00	0.00E+00	1.20E+01	
TOTAL	2.18E+02		1.87E+02		2.00E+02	

3.3.3 C:N:P stoichiometry

As one of the aims was to gain an ecosystem-level view of carbon, nitrogen and phosphorus content, stoichiometry and biomass, and because nutrient content was not measured for all groups, C:N, C:P and N:P ratios were calculated from %C, %N and %P measurements of ACEP II samples and compared to literature ratios of the groups not measured. Of the living groups, bacteria (9.25) had the highest C:N ratio and small benthic sharks the lowest (3.48) (Fig. 3.5). There was low variability in C:N ratios among most groups (Fig. 3.5). Variability was higher among C:P and N:P ratios of groups (Figs 3.6 and 3.7). Molluscs (non-cephalopods) (217) had the highest C:P ratios and cephalopods groups(cuttlefish 32.79, other cephalopods 32.74) the lowest (Fig. 3.6). With the exception of large crustaceans, benthos groups had much higher C:P ratios than cephalopod and fish groups (Fig. 3.6). The same trend was found for N:P ratios (Fig. 3.7). Molluscs (non-cephalopods) (49.34) had the highest N:P ratio and cephalopod groups (cuttlefish 8.48, other cephalopods 8.49) the lowest (Fig. 3.7). Overall, C:N ratios were highest in low trophic level groups (diatoms, flagellates, bacteria, heterotrophic microplankton) but C:P and N:P ratios were highest in zooplankton and benthos groups (gastropods, prawn and shrimp) (Figs 3.5, 3.6, 3.7).

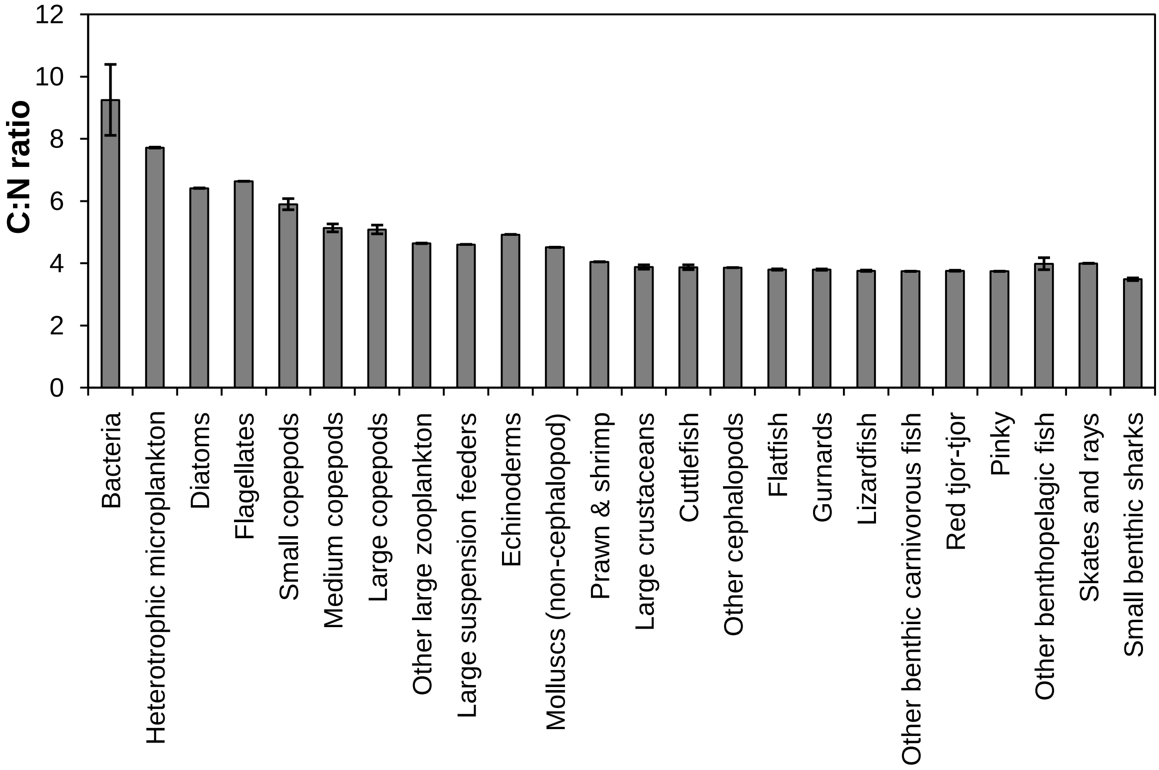

Figure 3.5. C:N ratios of groups sampled in KZN Bight calculated from mean carbon, nitrogen and phosphorus biomasses. Error bars represent ±2SE.

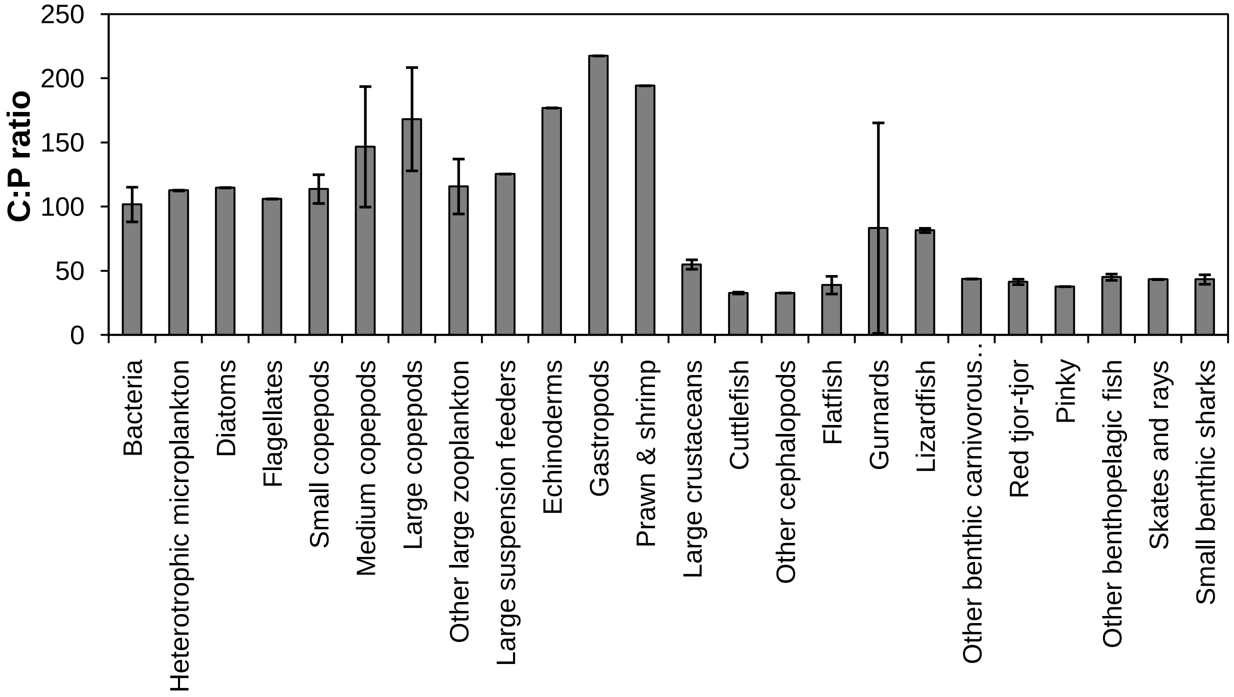

Figure 3.6. C:P ratios of groups sampled in KZN Bight calculated from mean carbon, nitrogen and phosphorus. Error bars represent ±2SE.

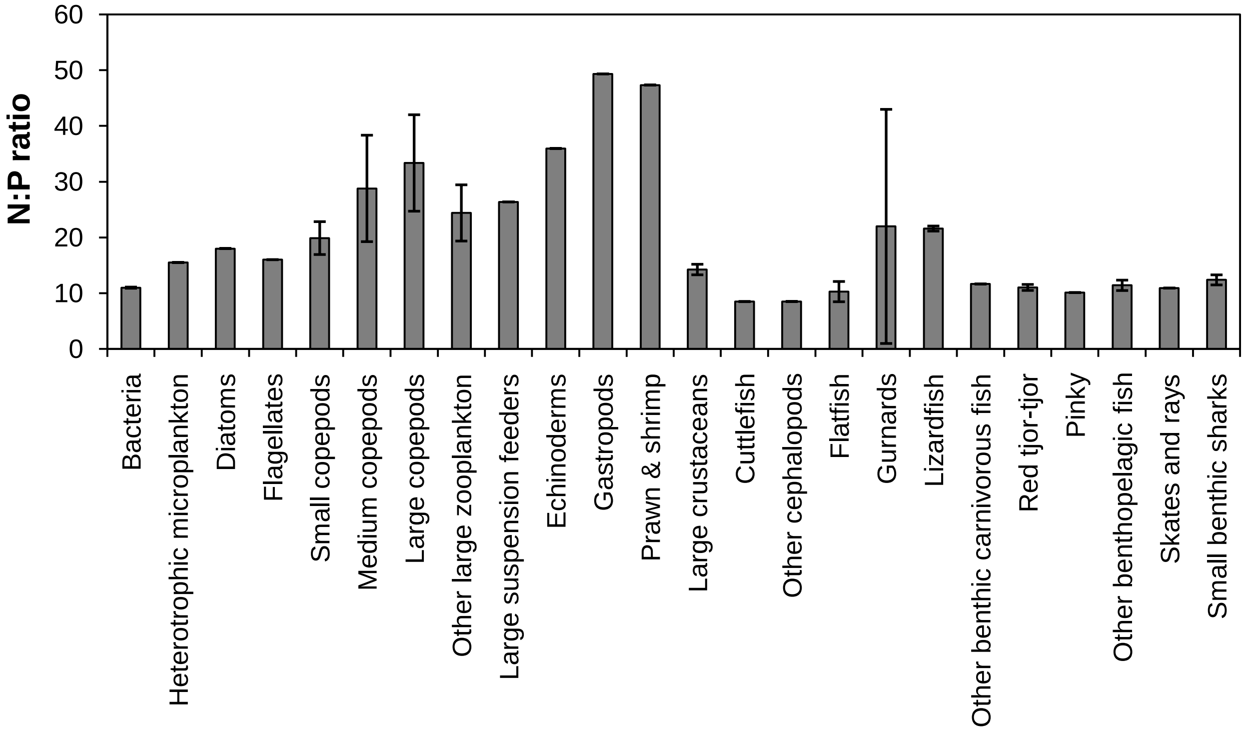

Figure 3.7. N:P ratios of groups sampled in KZN Bight calculated from mean carbon, nitrogen and phosphorus. Error bars represent ±2SE.

3.3.4 Biomass ratios

Biomass ratios were calculated to compare the distribution of carbon, nitrogen and phosphorus biomass among trophic levels (low, mid and high) and predator/prey pairs (e.g. zooplankton and primary producers) between sites. The trophic level ratios showed the proportion each trophic level contributed to total biomass in terms of carbon, nitrogen and phosphorus. Skates and rays and small benthic shark groups were assumed to be high trophic levels and diatoms, flagellates, bacteria and heterotrophic microplankton were assumed to be low trophic levels. The remaining groups were assumed to be mid trophic levels. Low trophic level biomass:total biomass was highest for nitrogen at the DE and RB sites and highest for nitrogen and phosphorus equally at the TM site (Table 3.7). Among sites, the ratio was highest for nitrogen and phosphorus at the DE site but highest for carbon at the RB site (Table 3.7). Mid trophic level biomass:total biomass was highest for phosphorus at each site. Among sites, the ratio was highest at the RB site for carbon, nitrogen and phosphorus (Table 3.7). High trophic level biomass:total biomass was highest for phosphorus at the DE site and highest for nitrogen at the TM site (Table 3.7). Among sites, the ratio was highest for carbon at the TM site but highest for nitrogen and phosphorus at the DE site (Table 3.7).

Biomass ratios of predator/prey pairs indicated whether nutrients in prey biomass were abundant in terms of predator demand for carbon, nitrogen and phosphorus. In the pelagic community, the zooplankton biomass:primary producer biomass ratio was highest for nitrogen at each site (Table 3.7). Among sites, the ratio was highest at the TM site for carbon, nitrogen and phosphorus (Table 3.7). In the demersal community large benthos biomass:benthic detrital POM biomass was highest for nitrogen at the DE site and highest for phosphorus at the TM and RB sites. Among sites, the large benthos biomass:benthic detrital POM biomass ratio was highest for nitrogen at the DE site but highest for carbon and phosphorus at the TM and RB sites (Table 3.7). Demersal fish biomass:large benthos biomass was highest for carbon at the DE site but highest for phosphorus at the TM and RB sites (Table 3.7). Among sites, the ratio was highest at the TM site for carbon, nitrogen and phosphorus (Table 3.7).

3.4 DISCUSSION

To gain a community and ecosystem-level view of nutrient stoichiometry and distribution within the KZN Bight, carbon, nitrogen and phosphorus content and biomass of functional groups from the pelagic and demersal communities were calculated and used to derive C:N:P ratios and various biomass ratios.

In the pelagic community lower carbon and nitrogen content of small and medium copepods was found at the RB site compared to the other two sites. De Lecea (2012) suggests that zooplankton in the region are influenced by the Agulhas current and drift in a southward direction. It is possible that the small and medium copepods sampled at the RB site had been recently swept onto the Bight from the Agulhas Current and had therefore not been exposed to prey on the Bight with a higher quality (%C) than within the Agulhas Current. Future research on phytoplankton carbon and nitrogen content on the Bight and in the Agulhas Current may resolve the cause of this difference between sites.

The lower carbon contents measured at the RB site were within the range found for copepod groups in the oligotrophic Sargasso Sea (Beers, 1966) but content from the DE and RB sites were slightly higher. However carbon content of zooplankton groups from the DE and RB sites were only slightly lower than the carbon content of copepods in the North Pacific Ocean (Omori, 1969). Thus carbon and nitrogen content of zooplankton groups throughout the KZN Bight were similar to samples from other oligotrophic regions.

No differences in phosphorus content were found between sites for zooplankton groups. Phosphorus content was similar to the maximum phosphorus content of copepod groups in the Sargasso Sea (Beers, 1966), within the range for zooplankton from the Inland Sea of Japan (Uye and Matsuda, 1988) but lower than for crustacean zooplankton in the eutrophic Baltic Sea (Walve and Larsson, 1999). Isotopic studies in the Bight suggest that at the time of sampling the pelagic community across the entire Bight was driven by marine nutrient sources rather than riverine (de Lecea, 2012). This could explain the homogeneity of zooplankton phosphorus content across the Bight.

Elemental composition of most pelagic and demersal groups in terms of %C, %N and %P was not significantly different between sites across the Bight. Similarly, in the Baltic Sea, nitrogen and phosphorus content of sprat and herring did not differ between seasons and areas (Hjerne and Hansson, 2002). The KZN Bight is a small area and despite riverine outflow into the TM site, migration between sites of most groups in the system is accepted. Thus, homogeneity in nutrient content between sites within the Bight would be expected.

Carbon and nitrogen content (%) of sediment was significantly higher at the TM site than DE and RB sites. Isotopic studies at these sites indicate that riverine TSS dominates the surface sediment at the TM site (de Lecea, 2012). Thus riverine outflow is responsible for increased carbon and nitrogen content in the sediments of the central Bight. This has implications for the functioning of the ecosystem at the TM site and in particular the benthic system for which detritus is the primary source of food.

In the demersal community, significant differences in carbon, nitrogen and phosphorus content (%) were found between sites in cuttlefish and flatfish. This could be due to the difference in species caught at each site. Samples from the Thukela Mouth site were taken from Common cuttlefish (*Sepia officianalis)* and samples from the Durban Eddy site were taken from *S. incerta* and *S. acuminata*. However there are no other studies in the literature, to the best of my knowledge, on *Sepia* nitrogen content to confirm this. A study by Lourenco et al. (2009) off Portugal gives phosphorus content for octopus, squid and cuttlefish. The phosphorus content of cephalopod samples from the Bight (3.06 - 3.61%P) were much higher than samples from Portugal (1.0 - 1.14%P, calculated from Lourenco et al. (2009) using wet:dry weight from this study). Many of the same species of flatfish were included in samples from all sites, however the RB site included Largescale flounder (*Citharoides macrolepis*) which was not included in samples from the DE and TM sites. Carbon and phosphorus content values of all demersal fish were similar to Gadiformes, Perciformes and Mugiliformes species from the Bay of Biscay (Czamanski et al., 2011). However nitrogen content of fish groups in the Bight were similar to the highest values found in the Bay of Biscay (Czamanski et al., 2011).

In the benthos groups the carbon content of molluscs was lower than samples from the Antarctic (Clarke, 2008) but similar to levels measured in freshwater molluscs sampled in streams in two regions of the U.S. (Evans-White et al., 2005). Nitrogen contents of molluscs were within the range for molluscs sampled in the Antarctic (Clarke, 2008) but higher than freshwater molluscs from streams in the US (Evans-White et al., 2005). In contrast, carbon content of large crustaceans in the Bight was higher than in freshwater crustaceans sampled in U.S. streams (Evans-White et al., 2005). Overall, large suspension feeders had the lowest phosphorus content. However samples, which were primarily from sea pens, were in the range for Anthozoa sampled from the Irish Sea (Riley & Segar (1970).

Skates and rays had higher nitrogen content at the RB site. The reason for this remains unknown as samples from each site were from Roughbelly skate (*Raja springeri*) individuals of similar sizes. In addition, no studies of Rajidae nitrogen content were available from the literature for comparison.

Molluscs (non-cephalopods) had the highest C:P and N:P ratios of all biotic groups sampled. The C:N, C:P and N:P ratios for molluscs from the KZN Bight were lower than for samples from Antarctica (Clarke, 2008). Ratios were also lower than freshwater molluscs from US streams (Evans-White et al., 2005). The ratios for crustacean groups from the KZN Bight (prawns and shrimp, large crustaceans) were also lower than freshwater crustaceans from US streams, particularly the C:P ratio (Evans-White et al. (2005).

Calculation of biomass ratios revealed how carbon, nitrogen and phosphorus were distributed through the foodweb in different areas of the Bight. Most of the biomass sampled was distributed in the mid trophic level groups in terms of carbon, nitrogen and phosphorus at all sites.

In the demersal community the ratio of benthos:benthic detrital POM biomass at the DE and RB sites indicated that nitrogen and phosphorus biomass of benthos was 1.2 - 1.4 times larger than benthic detrital POM. However at the TM site nitrogen and phosphorus biomass of benthos was nine times smaller than benthic detrital POM. This indicates the effect of river outflow on sediment nutrient concentrations. The ratio of demersal fish: benthos biomass was greater than one at all sites for carbon, nitrogen and phosphorus, indicating that demersal fish biomass is greater than their main prey group, benthos. The ratio of demersal fish biomass:benthos biomass was extremely high at the TM site and indicates that demersal fish biomass was 137, 113 and 209 times greater than benthos carbon, nitrogen and phosphorus biomass respectively. The biomass of demersal fish groups is potentially most limited by benthos carbon biomass at the DE site and benthos phosphorus biomass at the TM and RB sites. The high ratios of demersal fish:benthos indicate that fish biomass was greater than benthos biomass. Despite the lack of small macrobenthos and meiofauna data, which are potential prey for demersal fish, a high demersal fish:benthos ratio could indicate the necessity of omnivory (consumption from more than one trophic level) throughout the Bight since the biomass of benthos was 5-200 times lower than demersal fish biomass. The importance of omnivory in the Bight has also been suggest by isotope studies in each of the sites (de Lecea, 2012).

This study has provided, to the best of my knowledge, the most complete ecosystem-level study of nutrient contents and distributions throughout the KZN Bight to date. However some data gaps remain and therefore future studies in the region should aim to include meiofauna, small macrobenthos, pelagic fish, large sharks and cetaceans. Moreover, replicates in the wet and dry seasons would allow the confirmation of the seasonal impact of riverine outflow on ecosystem functioning. In addition, sampling when upwelling is occurring in the northern Bight would increase understanding of how this nutrient source affects the pelagic community. Nevertheless, the ACEP II programme (research cruises) has allowed the documentation of carbon, nitrogen and phosphorus pools in the southern, central and northern Bight in various taxa.

3.5. CONCLUSIONS

This study has taken the first steps in understanding the size of the carbon, nitrogen and phosphorus pools and distribution of carbon, nitrogen and phosphorus in groups throughout the foodweb across the KZN Bight ecosystem. Carbon, nitrogen and phosphorus biomasses and ratios suggest the pelagic community was more nutrient poor than the demersal community. Moreover, biomass ratios indicated that the southern Bight was the most nutrient poor compared to the central and northern Bight. In contrast, the central Bight had higher sediment nutrient content and higher total nitrogen biomass than other sites indicating the importance of river inflow, which is known to affect the site (Meyer et al., 2002). The results of this study provide a basic ecosystem-level view of nutrient distribution, in terms of biomasses, within the KZN Bight and showed that mid trophic level groups contain most of the carbon, nitrogen and phosphorus biomass in the Bight, particularly benthic fish groups. This high biomass and the high ratio of fish:benthos, indicating the biomass of fish was up to 200 times greater than benthos biomass, suggests that throughout the Bight. Benthic and benthopelagic fish may be omnivorous consuming other fish in addition to benthos. Biomasses documented in this chapter are valuable for extended ecosystem-level analyses required in understanding the role of each nutrient in ecosystem functioning (Chapter 4). While this study (Chapter 3) did not include all functional groups in the ecosystem it has, to the best of my knowledge, been one of the most comprehensive within a marine ecosystem to date.

Nutrient limitations and the importance of riverine nutrient sources within the oligotrophic KwaZulu-Natal Bight, South Africa

4.1 INTRODUCTION

The need for organisms to consume, transform, recycle and excrete nutrients for growth and reproduction has consequences for the functioning of the entire ecosystem (Elser et al., 1996, Vanni et al., 2002, Elser et al., 2000). In ecosystems carbon, nitrogen and phosphorus are important nutrients across various levels of organisation from the cellular level to the ecosystem level. Ecological stoichiometry theory focuses on how differences in the elemental composition of organisms affect ecosystem processes. In particular, ratios of carbon, nitrogen and phosphorus in autotrophs can be different to metazoans due to the difference in body composition (Sterner and Elser, 2002). Stoichiometric studies at the species level have been commonly conducted on freshwater autotrophs and zooplankton (e.g. Andersen & Hessen (1991), Hessen (1992)). Subsequently, community level studies have focused on freshwater pelagic communities (e.g. Elser & George (1993), Sterner et al (1992)). They suggest that the growth of organisms can be limited by low nutrient concentrations which can affect population dynamics (Elser et al., 1998) and interspecific interactions (DeMott and Gulati, 1999, Denno and Fagan, 2003) within communities. In addition, nutrient limitations can affect key ecosystem processes such as nutrient cycling (Sterner et al., 1997) and the structure of the ecosystem via the number of food chains that can be supported (Armstrong, 1994). For fisheries that target species at the top of the food chain, nutrient limitation of organisms, populations and ecosystems could extend to fisheries yields and thus food security in oligotrophic coastal regions in the tropic and subtropics.

Despite this, few studies have been conducted to investigate nutrient dynamics at the ecosystem-level (e.g. Elser et al. (1998)), although there are studies focusing on stoichiometrically explicit population dynamics (e.g. Andersen et al. (2004), Vrede et al. (2004), Andersen et al. (2005)). Most of the studies at the ecosystem level have been conducted using ecological network analysis where the system is constructed as a foodweb using information on nodes (biotic groups) and links between nodes (weighted trophic flows). By constructing networks of carbon, nitrogen or phosphorus flows the entire food web can be analysed, including direct and indirect interactions, in terms of these nutrients. Networks of carbon flows (e.g. Heymans and Baird (2000a), Sandberg et al. (2000), Scharler and Baird (2005), and

Christian et al. (2009)), nitrogen flows (e.g. Borrett et al. (2006), Christian et al. (1996), Christian and Thomas (2003), Fores et al. (1994)), and phosphorus flows (e.g. Baird (1998), Kaufman and Borrett (2010)) have been constructed and analysed separately. The dynamics of all three nutrients have been studied in the eutrophic mesohaline community of Chesapeake Bay, USA by Ulanowicz and Baird (1999) and the mesotrophic Sylt-Rømø Bight, Denmark/Germany by Baird et al. (2008). These studies constructed networks representing carbon, nitrogen and phosphorus trophic flows through the ecosystem and examined nutrient dynamics and limitations using ENA.

In nutrient-deficient systems, there is a greater difference between the elemental composition of autotrophs and heterotrophs (Sterner and Elser, 2002). However no studies have yet been conducted on an oligotrophic marine ecosystem. The KwaZulu-Natal (KZN) Bight is the widest area of continental shelf off the oligotrophic east coast of South Africa (Lutjeharms 2006). Off the Thukela River mouth in the central bight the shelf extends for approximately 50km to the boundary of the Agulhas current at the 200m isobath (Pearce, 1977, Schumann, 1988b, Lutjeharms et al., 2000). This area is slightly more nutrient-rich than the Agulhas Current (Lutjeharms et al., 2000, Meyer et al., 2002) and this is thought to be due to riverine and oceanic nutrient sources. In the southern area of the Bight a semi-permanent lee eddy caused by the warm Agulhas current flowing along the edge of the continental shelf, brings cold, nutrient-rich water to the surface (Pearce, 1977, Carter and Schleyer, 1988, Meyer et al., 2002, Pearce et al., 1978). The central Bight is affected by subsurface outflow from the Thukela River, the third largest river in southern Africa, causing higher nutrient concentrations (Meyer et al., 2002). River outflow throughout the region is generally higher in the summer “wet” season. In the northern area of the Bight a sporadic topographically-induced upwelling occurs, bringing nutrient-rich water onto the shelf (Meyer et al., 2002, Pearce, 1977, Lutjeharms et al., 1989). In addition, river outflow from the Mfolozi River reaches this area due to ocean currents (Flemming and Hay, 1988). Meyer et al (2002) suggested that the upwelling cell is the main source of nutrients to the Bight.

Considering issues such as food security, increased river water abstraction, runoff of terrestrial pollutants and climate change affecting oceanic currents, it is important to understand the behaviour and role of nutrients in coastal systems. In this paper, networks representing carbon, nitrogen and phosphorus flows within the KZN Bight are constructed and analysed using ENA to investigate the nutrient dynamics, limitations and the importance of nutrient sources to ecosystem functioning.

4.2 METHODS

4.2.1 Study areas

The KZN Bight extends from Durban in the south to Cape St. Lucia in the north and to the edge of the Agulhas current at the 200m isobath (Fig. 4.1) (Pearce 1977, Schumann 1988, Lutjeharms et al 2000). Three subsystems were chosen for analyses based on sampling areas of the ACEP II research cruises in February (summer) and August (winter) 2010 and the hypothesised locations of three major nutrient sources to the bight. The “Durban eddy” subsystem (DE) is located at the 200m isobath in the southern area of the bight (Fig. 4.1). The “Thukela Mouth” subsystem (TM) is located between the 30m and 40m isobaths in the central area of the bight (Fig. 4.1). Lastly, the “Richards Bay” subsystem (RB) is located between the 30m and 40m isobaths in the northern area of the bight (Fig. 4.1). It should be noted that nutrient and isotope analyses (de Lecea, 2012) and ADCP data showed that the Richards Bay upwelling did not occur during either research cruise.

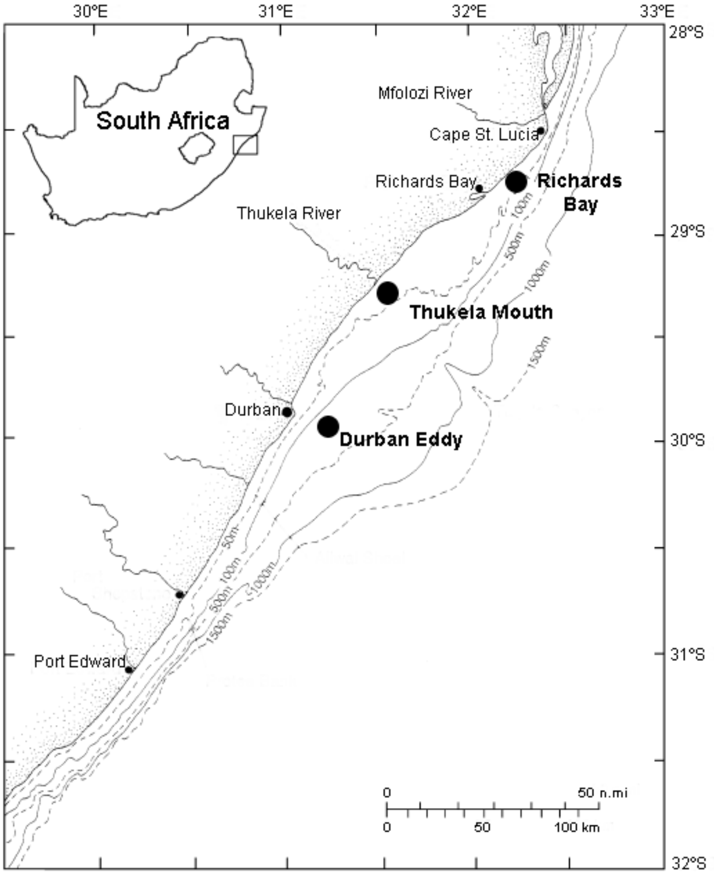

Figure 4.1. The KwaZulu-Natal Bight and location of subsystems. Adapted from Meyer et al. (2002).

4.2.2 Modelling approach

To carry out ecological network analysis, ecological networks were constructed using information on the size of nodes, links between nodes and flows across the system boundary. In this case, nodes represent species or functional groups, the size of nodes represents biomass, links between nodes represents trophic flows, and flows across the system boundary represent imports, exports, respiration and migration.

The ecosystem was divided into functional groups which were used in networks of all three subsystems and both seasons (summer 2010 and winter 2010). Many of these groups were based on biomasses measured during ACEP II research cruises and trawls (Barlow, R. pers. comm.; Fennessy, S.T. pers. comm.). A “large sharks” group was included in all networks and a cetacean group was included in the TM and RB networks. Cetaceans were not included in the DE network because resident dolphin species, which dominate the biomass of this group, do not occur beyond the 50m isobath (Cockcroft and Peddemors, 1990, Cockcroft et al., 1990). As suggested in Chapter 1, microbial groups were included and detritus was partitioned into suspended particulate organic matter (POM), sediment POM, dissolved organic matter (DOM) and dissolved inorganic matter (DIM). Input data for each functional group, in terms of carbon, nitrogen and phosphorus, were calculated from measurements taken during ACEP II cruises and trawls or from literature sources (Sections 4.2.3.2 and 4.2.4.2).

Carbon networks were constructed and parameterised first (Section 4.2.3). Nitrogen and phosphorus networks were constructed based on the mass-balanced carbon networks (Section 4.2.4). Once all networks were mass-balanced, ecological network analysis was carried out (Section 4.2.5).

4.2.3 Construction and parameterisation of carbon networks

4.2.3.1 Approach

Six carbon networks representing each subsystem in each season were constructed using biomasses, trophic flows, respiration and imports and exports across the system boundary. To estimate missing biomasses, carbon networks were initially constructed using Ecopath with Ecosim (EwE) software (Christensen and Pauly, 1992). Details of this approach can be found in Chapter 1, Section 1.2.1. Input parameters used to construct Ecopath networks include diet composition, biomass (gC m^{-2}), production/biomass ratio (P/B, year^{-1}), consumption/biomass ratio (Q/B, year^{-1}) and ecotrophic efficiency (EE, proportion) which represents the proportion of production utilised in the system. If one of either B, P/B, Q/B or EE is unknown, it is estimated using two mass-balance equations which ensure the inflows of each group in the system are equal to the outflows (Christensen and Walters, 2004).

4.2.3.2 Data sources

Carbon biomasses of most model groups were calculated from samples collected during the February and August ACEP II research cruises (detailed in Chapter 3, section 3.2.2). Other basic input data, needed to construct Ecopath networks (P/B, Q/B, EE) were collected from published and grey literature (Table 4.1). These were used in all networks since not all input data were available for the KZN Bight. The exceptions to this were the P/B ratios of diatoms, flagellates and prawn and shrimp. Ratios for diatoms and flagellates were calculated from biomass measurements in each subsystem and season (Barlow, R. pers. comm.). Due to a lack of production measurements during the August (winter) cruise, P/B ratios were based on measurements from the February (summer) cruise (Barlow, R. pers. comm.). Diatom P/B was 199y^{-1}, 242y^{-1} and 490y^{-1} in the DE, RM and RB subsystems respectively. Flagellate P/B was 208y^{-1} in the DE subsystem, 406y^{-1} in the TM subsystem and 410y^{-1} in the RB subsystem. In the DE networks, which represents a site at the 200m isobath, a P/B of 2.5y^{-1} was used for prawn and shrimp based on deep-water prawns (Heymans et al., 2010), and in the TM and RB networks, which represent sites between 30m and 40m isobaths, a P/B of 2.73y^{-1} was used based on shallow-water prawns (Freire et al., 2008).

An isotopic study, using samples collected during the ACEP II cruises, documents diet compositions for a number of demersal groups (de Lecea, 2012). However, because the study did not include samples from throughout the entire foodweb, diet compositions of the initial unbalanced networks were based on literature (Table 4.2). However, isotope diets were used to guide changes in diet compositions needed to balance the network. Because the networks contained more than one non-living group, the fate of biomass not consumed in the systems needed to be assigned to these groups.

Unused production of diatoms, flagellates, bacteria, heterotrophic microplankton and zooplankton groups was assumed to flow to suspended POC (Table 4.1). Unused production of the remaining groups in the network was assumed to sink and therefore 100% was assigned to sediment POC (Table 4.1).

Imports in the form of suspended POC, DOC and DIC were included in the TM and RB networks due to significant river inflow to the study areas. In the TM networks, suspended POC import was calculated using a sediment concentration for the Thukela River of 4.28g L^{-1}, the area of the Thukela mudbanks (561km^{2}, see Chapter 2, section 2.2.2.3) and flow rates based on a January flow rate of 429m^{3} s^{-1} and a June flow rate of 25m^{3} s^{-1} (Taljaard et al., 2004). Values of DOC import were calculated based on an average global estimate for rivers of 6mg L^{-1} (Meybeck, 1982) and the flow rates and area mentioned above. DIC imports for the TM networks were calculated using DIN values from the Thukela River estuary (see below) and a DIC:DIN ratio of 8.2 (Diaz et al., 2001). In the RB networks, a sediment concentration of 0.425g L^{-1} was calculated based on a sediment yield for the Mfolozi River of 6.8x10^{5}t y^{-1} and a mean annual flow of 1.6x10^{12}L y^{-1} (Grenfell and Ellery, 2009). A POC concentration of 2.57x10^{10}g y^{-1} was calculated using the sediment concentration and the assumption that POC was 8.4% of TSS (Meybeck, 1982). DOC imports were calculated based on an average global estimate of 6mg L^{-1} (Meybeck, 1982), a January flow rate of 6x10^{10}L and a June flow rate of 6x10^{9}L for the Mfolozi River (Grenfell and Ellery, 2009). A summary of imports can be found in Table 4.3). Unfortunately, nutrient imports from oceanic sources could not be included due to a lack of data.

Table 4.1. Input data for Ecopath carbon networks of DE, TM and RB subsystems. P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency. Flows to detritus and EE are proportions.

	Groups	P/B (y^{-1})	Q/B (y^{-1})	EE	Flows to detritus[*]		
					Suspended POC	Sediment POC	DOC
1	Diatoms	199-490[*]	n/a		1.00		
2	Flagellates	208-410[*]	n/a		1.00		
3	Bacteria	119.00[a]	215.00[p]	0.95[aa]	1.00		
4	Heterotrophic microplankton	100.00[b]	215.00[p]	0.95[aa]	1.00		
5	Small copepods	40.00[c]	165.00[c]		1.00		
6	Medium copepods	40.00[c]	165.00[c]		1.00		
7	Large copepods	40.00[c]	165.00[c]		1.00		
8	Other large zooplankton	8.70[d]	29.00[d]		1.00		
9	Small macrobenthos	6.32[e]	70.20[e]	0.95[aa]		1.00	
10	Large suspension feeders	0.25[f]	0.50[f]	0.95[aa]		1.00	
11	Echinoderms	1.20[g]	4.00[g]	0.95[aa]		1.00	

Table 4.1 continued

	Groups	**P/B (y^{-1})**	**Q/B (y^{-1})**	**EE**	**Flows to detritus***		
					Suspended POC	Sediment POC	DOC
12	Molluscs (non-cephalopod)	2.50^{g}	8.20^{g}			1.00	
13	Prawn and shrimp	2.50-2.73*	6.10^{q}	0.95^{aa}		1.00	
14	Large crustaceans	1.60^{h}	10.00^{h}			1.00	
15	Cuttlefish	1.10^{g}	3.50^{g}	0.95^{aa}		1.00	
16	Other cephalopods	1.95^{i}	3.90^{i}	0.95^{aa}		1.00	
17	Flatfish	1.17^{g}	6.80^{r}			1.00	
18	Gurnard	0.57^{j}	3.50^{s}			1.00	
19	Lizardfish	2.13^{k}	6.20^{t}			1.00	
20	Other benthic carnivorous fish	2.13^{k}	7.30^{v}			1.00	
21	Red tjor-tjor	2.70^{l}	6.90^{t}			1.00	
22	Pinky	0.65^{d}	4.80^{t}	0.95^{aa}		1.00	
23	Other benthopelagic fish	2.31^{k}	6.20^{v}			1.00	
24	Small pelagic fish	2.00^{m}	11.20^{w}	0.95^{aa}		1.00	
25	Large pelagic fish	0.87^{n}	8.98^{x}	0.43^{ab}		1.00	
26	Skates and rays	0.92^{g}	2.60^{t}	0.66^{g}		1.00	
27	Small benthic sharks	0.50^{g}	3.10^{y}			1.00	
28	Large sharks	0.10^{o}	1.75^{z}	0.10^{ac}		1.00	
29	Cetaceans	6.00^{c}	10.00^{c}			1.00	
30	Suspended POM	n/a	n/a			0.50	0.50
31	Sediment POM	n/a	n/a				1.00
32	DOM	n/a	n/a				1.00

References: * see section 4.2.2.3; a: Kunnen (2012); b: Opitz (1996); c: Toral-Granda et al. (1999); d: Okey et al. (2004); e: Rocha et al. (2007); f: “bottom-living structures” in Cheung et al. (2002); g: Amorim et al. (2004); h: Morato and Pitcher (2005); i: “squid” in Gasalla and Rossi-Wongtschowski (2004); j: Stanford and Pitcher (2004); k: Duan et al. (2009); l: Angelini and Vaz-Velho (2011); m: Paula E Silva et al. (1993); n: Govender (1995); o: intrinsic rate of increase of *S. lewini* from Dudley and Simpfendorfer (2006); p: Opitz (1996); q: Maynou and Cartes (1997); r: average of *Citharoides macrolepis* and *Pseudorhombus natalensis* calculated using Fishbase (Froese and Pauly, 2010); s: average of *Satirichthys adeni* and *Chelidonithys quecketti* calculated using Fishbase (Froese and Pauly, 2010); t: Fishbase (Froese and Pauly, 2010); u: average of *Hoplichthys acanthopleurus* and *Halieutaea fitzsimonsi* calculated using Fishbase (Froese and Pauly, 2010); v: average of *Neoscombrops annectens*, *Histiopterus typus* and *Polysteganus coeruleopunctatus* calculated using Fishbase (Froese and Pauly, 2010); w: Vasconcellos (2000); x: average of *Scomberomorus commerson*, *Thunnus albacares*, *Coryphaena hippurus*, *Euthynnus affinis* in Fishbase (Froese and Pauly, 2010); y: average of *Squalus megalops* and *Pliotrema warreni* using Fishbase (Froese and Pauly, 2010); z: average of *Sphyrna mokorran*, *Sphyrna lewini* and *Isurus oxyrinchus* using Fishbase (Froese and Pauly, 2010); aa: Christensen et al. (2008); ab: Freire et al. (2008); ac: Ayers and Scharler (2011).

Table 4.2. Diet compositions used in initial unbalanced Ecopath carbon networks. Group numbers refer to those in Table 4.1. Rows represent prey and columns represent predators. Groups 1 and 2 refer to primary producers and therefore do not require a predator column. I = imports. The first value in the column for group 28 was used in the DE networks and the second value was used in the TM and RB networks.

	3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
1	0.015	0.015	0.467	0.216	0.216	0.058	0.057	0.042	0.012		0.050											0.018					
2	0.015	0.015	0.333	0.154	0.154	0.042	0.041	0.030	0.008		0.050											0.013					
3			0.130	0.399	0.399	0.639	0.360	0.927	0.130	0.050																	
4			0.000	0.001	0.001	0.001			0.000	0.000																	
5			0.020	0.120	0.120	0.120					0.033											0.344					
6				0.010	0.010	0.057					0.033											0.204					
7						0.043					0.033										0.283	0.151					
8						0.012									0.030	0.001			0.049	0.045	0.025	0.084	0.000				
9							0.050		0.301	0.189	0.200	0.543	0.286	0.460	0.630	0.287	0.275	0.275	0.069	0.105	0.550	0.100	0.003	0.117	0.204		
10									0.103	0.100		0.188	0.041				0.029	0.029	0.002	0.399				0.303			
11									0.002	0.001		0.020			0.057				0.025	0.001				0.021			
12												0.019			0.080	0.001								0.014			
13												0.010	0.049	0.080	0.050	0.041	0.196	0.196	0.004	0.257	0.088	0.001	0.002	0.085	0.053		
14												0.005	0.333	0.241	0.116	0.131	0.127	0.127	0.009	0.113			0.006		0.204	0.002, 0.002	
15													0.091			0.007	0.039	0.039		0.068			0.010	0.028	0.016	0.011, 0.009	0.170
16													0.017	0.138		0.004	0.029	0.029		0.001			0.023	0.171	0.166	0.055, 0.028	0.075
17															0.010	0.401	0.059	0.059						0.118		0.012, 0.002	0.004
18																0.002	0.098	0.098						0.014		0.003, 0	
19																										0.007, .001	0.002
20													0.183			0.036							0.000		0.129	0.006, 0.025	0.043
21																							0.042			0.005, 0.003	0.020
22																							0.001			0.006, 0.005	0.060
23															0.010		0.147	0.147	0.842	0.011			0.085	0.052	0.085	0.175, 0.073	0.117
24														0.080	0.010	0.009							0.719		0.145	0.007, 0.162	0.428
25																							0.101			0.0478, 0.056	0.054
26																0.081								0.019		0.275, 0.148	0.007
27																										0.092. 0.068	
28																										0.271, 0.2	
29																										0, 0.076	
30	0.040	0.040	0.050	0.040	0.040	0.028	0.033		0.123	0.300												0.076					
31	0.010	0.010		0.060	0.060		0.458		0.320	0.360	0.600	0.215			0.007						0.055	0.010		0.057			
32	0.920	0.920																									
I																							0.008			0.0246,0.135	0.020

Calculated using: 3-12: Okey (2004); 13: Rainer (1992); 14: Okey and Meyer (2002); 15: Castro and Guerra (1990); 16: de Lecea (2012) 17: Amorim et al. (2004); 18: Meyer and Smale (1991); 19: Duan et al. (2009).; 20: Duan et al. (2009); 21: Morato et al. (2005); 22: Joubert and Hanekom (1980); 23: Hajisamae (2009); 24: Okey (2004); 25: Potier et al. (2007); 26: Amorim et al. (2004); 27: Ebert et al. (1992); 28 (DE): Cliff (1995), Cliff et al. (1990), de Bruyn et al. (2005); 28 (TM and RB): Aitken (2003), Cliff et al. (1989), Cliff and Dudley (1991a), Cliff and Dudley (1991b), Allend and Cliff (2000), Dudley and Cliff (1993), Dudley et al. (2005); 29: Young & Cockcroft (1994), Cockcroft & Ross (1990).

4.2.3.3 Parameterisation of carbon networks

In total, six carbon networks representing each of the three subsystems in summer 2010 and winter 2010 were constructed. Ecopath was used to estimate missing carbon biomasses in each network (Table 4.5) and check each group was mass-balanced. Initially, none of the six carbon networks were balanced. The proportion of the production utilised in the system (EE) was greater than one for many groups because outflows, in the form of predation, were greater than inflows. To balance the networks, biomasses of groups which were undersampled by the ACEP II trawling gear (Fennessy, S.T. pers. comm.) were replaced with biomass estimates from Ecopath. The biomasses of the groups other cephalopods, cuttlefish, molluscs (non-cephalopods), echinoderms, large suspension feeders and heterotrophic microplankton were removed from one or all of the carbon networks and estimated using an EE of 0.95 (Christensen et al., 2008) in Ecopath (Table 4.5). The proportions of unbalanced groups in the diets of predators with nonsystem-specific diets were decreased or removed and replaced by other groups. These replacements were based on diets from isotope studies on the same species/groups in each subsystem of the Bight (de Lecea, 2012). Diets identified by this isotope study were not used in initial diet compositions because they did not span all potential prey groups as identified in literature. In addition, the proportion of cannibalism was decreased (as suggested by Christensen et al. (2008)) in large sharks and replaced with diet import. Diet compositions were adjusted until all groups were balanced (EE<1). Final diet compositions for the six carbon networks can be found in Appendix 4.1.

The following decreases (greater than 5%) in the proportions of unbalanced groups in predator diets were made in all networks:

- Large crustaceans in the diets of Lizardfish, Flatfish, Gurnards, other cephalopods and cuttlefish were decreased and replaced with small macrobenthos.
- Other large zooplankton were decreased in the diet of small pelagic fish and added to diatoms and flagellates.
- Large copepods, medium copepods and small copepods were decreased in the diet of small pelagic fish and replaced with diatoms and flagellates.

The following changes to unbalanced groups were carried out in more than one network which are noted in brackets e.g. Thukela Mouth Summer network =TMS:

- Small pelagic fish were decreased in the diets of:

  - cetaceans (TMW) and large pelagic fish (TMW, RBS) and replaced with import.
  - small benthic sharks (DES, DEW) and replaced with small macrobenthos.

- Other benthopelagic fish were decreased in the diets of:

  - Red tjor-tjor (DES, DEW, RBW) and replaced with small macrobenthos and molluscs (non-cephalopods).
  - Lizardfish (TMS, TMW, RBW) and replaced with small macrobenthos.

- Flatfish were decreased in the diets of:

  - Gurnards (DES, DEW, TMS, TMW, RBN and replaced with small macrobenthos.

- Large crustaceans were decreased in the diets of:

  - Small benthic sharks (DES, DEW, TMW, RBS, RBN), Pinky (TMS, TMW), other benthic carnivorous fish (DES, DEW, TMW, RBS, RBN) and replaced with small macrobenthos.

- Prawn and shrimp were decreased in the diets of:

  - Skates and rays (TMS, TMW, RBS, RBN), other benthopelagic fish (TMS, TMW, RBS, RBN), Pinky (TMS, TMW, RBS, RBN), other benthic carnivorous fish (TMS, TMW, RBS, RBN), Lizardfish (TMS, TMW, RBS, RBN), other cephalopod (TMS, TMW, RBS, RBN) and replaced with small macrobenthos.

- Molluscs (non-cephalopods) were decreased in the diets of Flatfish (RBS, RBN) and replaced with small macrobenthos.

- Large suspension feeders were decreased in the diets of skates and rays (TMS, TMW), Pinky (TMS, TMW), molluscs (non-cephalopods) (TMS, TMW) and echinoderms (TMS, TMW) and replaced with small macrobenthos.

- Large copepods were decreased in the diets of other benthopelagic fish (TMS, TMW) and replaced with molluscs (non-cephalopod).

Biomasses, trophic flows and respiration calculated by Ecopath along with initial biomasses, imports and exports were used to construct final carbon networks. Ecopath does not include the uptake of DIM by primary producers. Therefore DIC was added to the carbon networks using a biomass calculated based on DIN measured in each subsystem during ACEP II cruises (Barlow, R. pers. comm.) and a C:N ratio of 8.2 (Diaz et al., 2001). Flows from DIC to primary producer groups were calculated based on demand, so that the inflow into each primary producer group balanced the outflow from each primary producer group. The DIC group was also balanced based on demand by adding imports or exports across the system boundary.

4.2.3.4 Comparative analysis of carbon networks

A basic comparative analysis was conducted to check how the networks in this study, which were based on more system-specific data, compared to ten networks of the KZN Bight (Chapter 1) and three networks of the Thukela Bank (Chapter 2) which were both based on literature data and for which sensitivity analyses were conducted. Because the previous networks represented wet weight biomass flows direct comparisons could not be made. However, a number of biomass ratios were calculated. These were used to compare the TM networks with the Thukela Bank networks and the DE, TM and RB networks with the KZN Bight networks. Due to differences in functional groups between the previous and current networks, ratios based on trophic levels (high and low), depths in the water column (demersal and pelagic) and predator/prey groupings (zooplankton/primary producers and demersal fish/benthos) were used. Low trophic level groups were those with a trophic level of one and high trophic level groups were those with a trophic level greater than 4.5.

4.2.4 Construction and parameterisation of nitrogen and phosphorus networks

4.2.4.1 Approach

Nitrogen and phosphorus networks were constructed based on the mass-balanced carbon networks. Input parameters (biomass, import, export and trophic flows) in terms of nitrogen and phosphorus were calculated using values from the carbon networks and C:N and C:P ratios calculated in Chapter 3 and from literature (see section 4.2.4.2). These networks were mass-balanced by adding imports or exports to unbalanced groups depending on availability and demand while preserving the C:N:P stoichiometry between networks.

4.2.4.2 Data sources

Biomasses, imports and exports in the nitrogen and phosphorus networks were calculated based on the corresponding carbon data for each network and C:N and C:P molar ratios calculated in Chapter 3 or from literature (Table 4.4). Seasonal DIN and DIP imports were calculated for the TM and RB networks using the flow rates and area mentioned in section 4.2.2.2 and nitrate and phosphate concentrations from the Thukela River estuary (Taljaard et al., 2004) (Table 4.3).

Table 4.3 Imports (g m^{-2} y^{-1}) of non-living groups into the Thukela Mouth (TM) and Richards Bay (RB) networks.

Detritus group		**Thukela Mouth**		**Richards Bay**	
		Summer	Winter	Summer	Winter
Suspended POM	C	8671358	501964	45900	4582
	N	1057483.	61215	5598	559
	P	433135	25073	2293	229
DOM	C	144789	8381	7701	770
	N	7239	419	385	39
	P	144	8	8	1
DIM	C	62332	1306	3315	120
	N	7601	159	404	15
	P	531	17	28	2

Table 4.4 C:N and C:P ratios used in the nitrogen and phosphorus networks. Non-bold values indicate ratios calculated in Chapter 3. DE = Durban Eddy, TM = Thukela Mouth, RB = Richards Bay.

	Functional group/species	**C:N**			**C:P**		
		DE	**TM**	**RB**	**DE**	**TM**	**RB**
1	Diatoms	**8.20**[a]	**8.2**[a]	**8.2**[a]	**20.00**[a]	**20.00**[a]	**20.00**[a]
2	Flagellates	**8.20**[a]	**8.2**[a]	**8.2**[a]	**20.00**[a]	**20.00**[a]	**20.00**[a]
3	Bacteria	**7.80**[a]	**7.8**[a]	**7.8**[a]	**38.36**[a]	**38.36**[a]	**38.36**[a]
4	Heterotrophic microplankton	**5.31**[b]	**5.31**[b]	**5.31**[b]	**48.05**[b]	**48.05**[b]	**48.05**[b]
5	Small copepods	5.14	4.87	5.49	126.11	138.19	100.22
6	Medium copepods	5.00	4.95	5.36	264.24	110.98	140.52
7	Large copepods	4.91	4.94	5.34	242.98	141.09	109.62
8	Other large zooplankton	**3.62**[c]	**3.62**[c]	**3.62**[c]	**22.27**[c]	**22.27**[c]	**22.27**[c]
9	Small macrobenthos	**4.67**[d]	**4.67**[d]	**4.67**[d]	**87.00**[j]	**87.00**[j]	**87.00**[j]
10	Large suspension feeders	4.99	4.99	4.99	183.83	183.83	183.83
11	Echinoderms	**4.16**[e]	**4.16**[e]	**4.16**[e]	**182.00**[e]	**182.00**[e]	**182.00**[e]
12	Molluscs (non-cephalopod)	4.19	4.19	4.19	265.12	265.12	265.12
13	Prawn and shrimp	3.85	3.85	3.85	88.08	88.08	88.08
14	Large crustaceans	3.82	3.83	4.03	38.38	25.92	34.56
15	Cuttlefish	4.00	3.76	3.76	34.07	31.92	31.92
16	Other cephalopods	3.90	3.90	3.90	33.06	33.06	33.06
17	Flatfish	3.80	3.74	3.73	43.86	51.01	27.78
18	Gurnard	3.81	3.80	3.87	50.60	295.76	31.12
19	Lizardfish	3.65	3.72	3.70	38.54	39.25	33.99
20	Other benthic carnivorous fish	3.79	3.79	3.79	50.07	50.07	50.07
21	Red tjor-tjor	3.70	3.72	3.75	26.69	34.69	35.25
22	Pinky	3.76	3.76	3.76	45.05	45.05	45.05
23	Other benthopelagic fish	4.10	3.81	4.47	49.44	45.12	40.997
24	Small pelagic fish	**3.83**[f]	**3.83**[f]	**3.83**[f]	**23.15**[f]	**23.15**[f]	**23.15**[f]
25	Large pelagic fish	**3.16**[f]	**3.16**[f]	**3.16**[f]	**10.89**[f]	**10.89**[f]	**10.89**[f]
26	Skates and rays	3.86	3.86	3.86	41.53	41.53	41.53
27	Small benthic sharks	3.03	3.11	3.18	41.51	50.56	50.56
28	Large sharks	**3.24**[g]	**3.24**[g]	**3.24**[g]	**16.38**[g]	**17.91**[g]	**19.44**[g]
29	Cetaceans	**3.2**[h]	**3.2**[h]	**3.2**[h]	**12.80**[k]	**12.80**[k]	**12.80**[k]
30	Suspended POM	**8.2**[a]	**8.2**[a]	**8.2**[a]	**20.00**[a]	**20.00**[a]	**20.00**[a]
31	Sediment POM	8.03	10.19	8.03	57.84	73.36	57.84
32	DOM	**3.40**[i]	**3.40**[i]	**3.40**[i]	**44.00**[l]	**44.00**[l]	**44.00**[l]

References: a: Diaz et al. (2001); b: Le Borgne (1982)1982; c: Beers (1966)1966; d: Newell (1982); e: Clarke (2008); f: Czamanski et al. (2011); g: Hussey et al. (2010); h: Ruiz-Cooley et al. (2004); i: Baird et al. (1995); j: Vink and Atkinson (1985); k: Portnoy (1990); l: Baird (1998).

4.2.4.3 Parameterisation of nitrogen and phosphorus networks

Because nitrogen and phosphorus networks were based on the balanced carbon networks, few groups were initially unbalanced. It was assumed that these imbalances were the result of the lack of data on migration to/from the model area. Therefore imports and exports were increased or decreased to balance these groups (Table 4.5). In all nitrogen and phosphorus networks exports of small macrobenthos were added. In order to achieve mass balance, imports and exports were added to selected groups in all nitrogen and phosphorus networks. Balanced carbon, nitrogen and phosphorus networks for each subsystem can be found in Appendix 4.2.

Table 4.5. Groups to which imports and exports were added in the nitrogen and phosphorus networks in order to achieve mass-balance. DE = Durban Eddy, TM = Thukela Mouth, RB = Richards Bay. Letters in bracket represent imports or exports of groups which were only added to the summer (S) or winter (W) networks.

Sub-system	**Imports**		**Exports**	
	Nitrogen	**Phosphorus**	**Nitrogen**	**Phosphorus**
DE	Bacteria Heterotrophic microplankton Large suspension feeders Suspended PON Sediment PON (W) DON	Bacteria Prawn and shrimp (S) Cuttlefish Other cephalopods Suspended POP	DIN	Prawn and shrimp (W)
TM	Large suspension feeders	Cuttlefish Other cephalopods Other benthopelagic fish	Suspended PON Sediment PON DON DIN	Suspended POP Sediment POP DOP DIP
RB		Cuttlefish Other cephalopods Flatfish DIP (W)	DON DIN (S)	Suspended POP DOP DIP

4.2.5 Ecological Network Analyses

The eighteen networks were analysed using ENA to determine carbon, nitrogen and phosphorus limitations and cycling in each subsystem. To identify the nutrient limiting to each biotic group, the method of Ulanowicz and Abarca-Arenas (1997) was used. First the biomass inclusive average mutual information (AMI_B) was calculated and used to calculate the biomass inclusive ascendency of each network. Then, the sensitivity of system ascendency to turnover times of carbon, nitrogen and phosphorus was calculated for each group to identify the limiting nutrient for each group. Finally, the sensitivity of system ascendency to individual flows of carbon, nitrogen and phosphorus was calculated to identify the limiting flow. This is the flow depleting its source faster compared to the other two nutrients.

Within the flow network of an ecosystem a quantum of biomass is more likely to flow along a route with high material transfer than along a route with low material transfer. Therefore the probability of a quantum of biomass leaving group i and entering group j (B_iB_j/B^2) will be different for a network where all routes transfer the same amount of biomass (unconstrained) and a network where the amount of biomass transferred varies along the different routes (constrained). Difference in probability is calculated as the information gained (I_B) by subtracting the amount of uncertainty that a quantum of biomass leaves group i and enters group j (T_{ij}) from the uncertainty a quantum of biomass passes along a route according to biomass availability (B_i/B and B_j/B),

$$I_B = -k\ log\left(\frac{B_iB_j}{B^2}\right) - \left[-k\ log\left(\frac{T_{ij}}{T_{..}}\right)\right] \tag{4.1}$$

where k is a constant, B_i is the biomass of prey group i, B_j is the biomass of predator group j, B is the total system biomass, T.. is total system throughput, or the sum of flows over all combinations of T_{ij} and $T_{ij}/T_{..}$ is the conditional probability of the actual flow from i to j.

The biomass inclusive average mutual information (AMI_B) is then calculated by summing over all realised combinations of i and j and weighted by the joint probability of occurrence

$$AMI_B = k\sum_{ij}\frac{T_{ij}}{T_{..}}log\left(\frac{T_{ij}B^2}{T_{..}B_iB_j}\right) \tag{4.2}$$

The biomass inclusive ascendency is then calculated by scaling AMI_B by the total system throughput (T..),

$$A_B = T_{..}\sum_{ij}\frac{T_{ij}}{T_{..}}log\left(\frac{T_{ij}B^2}{T_{..}B_iB_j}\right) \tag{4.3}$$

or

$$A_B = \sum_{ij} T_{ij} log\left(\frac{T_{ij}B^2}{T_{..}B_iB_j}\right) \tag{4.4}$$

To calculate a group's contribution in terms of a nutrient, *k*, to system ascendency then equation 4.4 becomes

$$A_B = \sum_{ijk} T_{ijk} log\left(\frac{T_{ijk}B^2}{T_{..}B_{ik}B_{jk}}\right) \tag{4.5}$$

The sensitivity of system ascendency to turnover times of carbon, nitrogen and phosphorus can be calculated by the differential of A_B regarding any group *z*

$$\frac{\partial A_B}{\partial B_{zk}} = 2\left(\frac{T_{..}}{B} - \frac{1}{2}\frac{T_{\cdot zk} + T_{z.k}}{B_{zk}}\right) \tag{4.6}$$

In addition, the limiting flow of the controlling nutrient can be calculated by including the sensitivity of system ascendency to individual flows from *i* to *j*,

$$\frac{\partial A}{\partial T_{ij}} = log\left(\frac{T_{ij}B^2}{T_{..}B_iB_j}\right) \tag{4.7}$$

Cycling in proportion to a systems size was determined using the Finn Cycling Index (FCI), which measures the fraction of throughput recycled (Finn, 1980). This was calculated using WAND (Allesina and Bondavalli, 2004) as follows

$$FCI = \sum_i T_i(S_{ii} - 1)/S_{ii} \tag{4.9}$$

where T_i is the total throughput through group *i* and (S_{ii} -1) is the throughput through group *i* resulting from cycling.

To determine how effectively carbon, nitrogen and phosphorus are transported between different trophic levels in the systems, trophic levels and transfer efficiencies were calculated using WAND, a software package for ecological network analysis (Allesina and Bondavalli, 2004). These were calculated by first calculating the trophic level of each species (TL_j) as the mean TL of its prey (TL_i), summed for its entire diet (DC_{ij}) plus one (Ulanowicz, 1986). Primary producers were assumed to have a TL of one.

$$TL_j = 1 + \sum(TL_i)(DC_{ij}) \quad (4.10)$$

Transfer efficiencies of discrete trophic levels were calculated as the fraction of input that is passed on to the next level, via predation.

$$TE_n = (Q_{n+1} + EX_n)/Q_n \quad (4.11)$$

where n is the number of trophic levels, Q is total consumption and EX is exports (Lindeman, 1942).

4.3 RESULTS

4.3.1 Comparative analysis of carbon networks

A network was deemed similar to another when a part of its error bar ranges were within that of the other. At least one of the seasonal TM networks was similar to the Thukela Bank networks (Fig. 4.2). The summer TM network had similar low TL B:total living B, demersal B:pelagic B and zooplankton:primary producer ratios (Fig. 4.2). The winter TM networks had similar high TL B:total living B to the Thukela Bank networks (Fig. 4.2). Both TM networks had similar demersal fish B:benthos B ratios to the Thukela Bank networks (Fig. 4.2).

Since the current networks represented different subsystems in the Bight, ratios differed between them (Fig. 4.2). However the KZN Bight networks (Chapter 1) represented the entire Bight and therefore it was important that they were similar to at least some of the current networks. All ratios were similar to the current networks except that of low TL B:total living B (0.0005) which was slightly higher than the current networks (mean 0.0002) (Fig 4.2). The ratio of high TL:total living biomass and demersal fish:benthos biomass of the KZN Bight networks were similar to both DE networks (Fig. 4.2). The ratio of demersal:pelagic biomass was similar to the TMS and RBS networks (Fig. 4.2). The ratio of zooplankton:producer biomass was similar to all current networks except TMW (Fig. 4.2). Thus the distribution of biomass among trophic levels, depth zones and predator/prey pairs was similar between the KZN Bight and current networks and the Thukela Bank and TM networks.

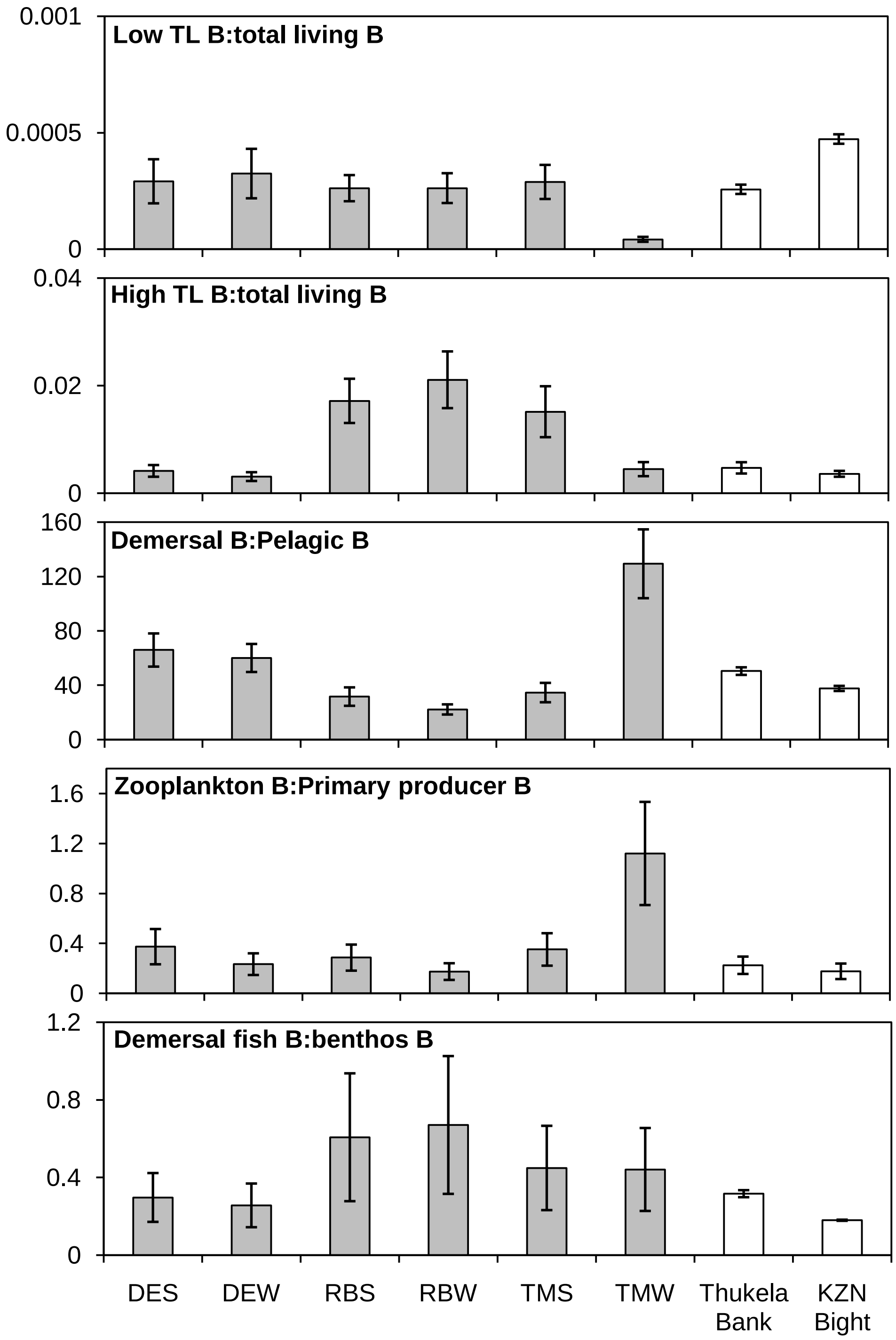

Figure 4.2. Mean biomass (B) ratio of subsystem networks (this chapter, light grey bars), Thukela Bank networks (Chapter 2, white bar) and KZN Bight networks (Chapter 1, white bar). DES = Durban Eddy summer, DEW = Durban Eddy winter, RBS = Richards Bay summer, RBW=Richards Bay winter, TMS = Thukela Bank summer, TMW = Thukela Bank winter.

4.3.2 Carbon, nitrogen and phosphorus biomass and turnover

Using the mass-balance approach in Ecopath and C:N and C:P ratios, carbon nitrogen and phosphorus biomasses (g m^{-2}) were calculated for each subsystem and season (Table 4.6). In the DE subsystem DIM dominated the biomass overall and small macrobenthos dominated the biotic groups (Table 4.6). The TM subsystem was dominated by DIM, sediment POM, small macrobenthos and large suspension feeders (Table 4.6). Similarly, the RB subsystem was dominated by DIM and small macrobenthos (Table 4.6). In all subsystems, demersal groups dominated pelagic groups (Table 4.6). Total system biomass (g m^{-2}) in terms of carbon, nitrogen and phosphorus was highest in the DE subsystem and lowest in the RB subsystem (Table 4.6). This was attributed to the depth-integrated biomass of DIM being higher at the DE site due to differences in depth between subsystems where the DE subsystem was at a depth of 200m and the TM and RB subsystems were between 30-40m. The size of each system in terms of flows (T..) made for a more accurate comparison of the size of the systems. The TM summer networks (C, N and P) were 44-87 times larger than the DE summer networks and 78-103 times larger than the RB summer networks. However the TM winter networks were only 2-4 times larger than the DE winter networks and 9-17 times larger than the RB winter networks (Table 4.7). Within systems, T.. was 11 - 16 times larger in the TM summer networks than the winter network and 2 – 3 times larger in the RB summer network than the winter network (Table 4.7).

Table 4.6. Carbon, nitrogen and phosphorus biomasses (g m^{-2}) of groups in each network. Bold values represent biomasses estimated by Ecopath.

	Functional groups/species		**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
			Summer	Winter	Summer	Winter	Summer	Winter
1	Diatoms	C	1.15	2.43	0.46	0.39	0.50	1.93
		N	0.14	0.30	0.06	0.06	0.06	0.24
		P	0.06	0.12	0.02	0.02	0.03	0.10
2	Flagellates	C	1.23	1.12	0.46	0.26	0.34	0.37
		N	0.15	0.14	0.06	0.03	0.04	0.04
		P	0.06	0.06	0.02	0.01	0.02	0.02
3	Bacteria	C	1.84	0.60	0.69	0.29	0.52	0.31

Table 4.6 continued

	Functional groups/species		**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
			Summer	Winter	Summer	Winter	Summer	Winter
3	Bacteria	N	0.24	0.08	0.09	0.04	0.07	0.04
		P	0.05	0.02	0.02	0.01	0.01	0.01
4	Heterotrophic microplankton	C	**0.20**	**0.20**	**0.08**	**0.244**	**0.08**	**0.06**
		N	0.04	0.05	0.01	0.05	0.02	0.01
		P	0.004	0.06	0.002	0.005	0.002	0.001
5	Small copepods	C	0.37	0.15	0.11	0.16	0.04	0.11
		N	0.08	0.03	0.02	0.04	0.01	0.03
		P	0.007	0.003	0.002	0.003	0.001	0.002
6	Medium copepods	C	0.17	0.13	0.06	0.12	0.05	0.05
		N	0.04	0.03	0.01	0.03	0.01	0.01
		P	0.003	0.002	0.001	0.002	0.001	0.001
7	Large copepods	C	0.07	0.15	0.03	0.13	0.03	0.10
		N	0.02	0.03	0.01	0.03	0.01	0.02
		P	0.001	0.003	0.001	0.002	0.001	0.002
8	Other large zooplankton	C	0.03	0.09	0.02	0.03	0.03	0.04
		N	0.01	0.03	0.01	0.01	0.01	0.01
		P	0.002	0.004	0.001	0.001	0.001	0.002
9	Small macrobenthos	C	**3515.17**	**4751.11**	**1376.05**	**4392.53**	**1482.28**	**1064.64**
		N	752.71	1017.37	294.66	940.58	317.41	227.98
		P	40.40	54.61	15.82	50.49	17.04	12.24
10	Large suspension feeders	C	**2122.76**	**2658.02**	**1239.95**	**3858.49**	**435.90**	**586.82**
		N	496.33	621.49	289.92	902.17	101.92	137.21
		P	29.54	36.98	17.25	53.69	6.06	8.16
11	Echinoderms	C	**154.39**	**282.23**	14.88	4.91	1.01	1.13
		N	37.11	67.84	3.58	1.18	0.24	0.27
		P	0.85	1.55	0.08	0.03	0.01	0.01

Table 4.6 continued

	Functional groups/species		**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
			Summer	Winter	Summer	Winter	Summer	Winter
12	Molluscs (non-cephalopod)	C	138.3	**271.33**	**128.92**	**363.66**	1.22	**4.22**
		N	40.28	79.02	37.54	105.91	0.35	1.23
		P	3.43	6.73	3.20	9.02	0.03	0.10
13	Prawn and shrimp	C	**335.05**	**470.08**	0.10	**0.33**	0.59	2.67
		N	102.94	144.42	0.03	0.10	0.18	0.82
		P	25.23	35.40	0.01	0.02	0.04	0.20
14	Large crustaceans	C	88.01	83.26	24.08	2.92	8.08	48.11
		N	27.23	25.76	7.45	0.90	2.50	14.88
		P	6.30	5.96	1.72	0.21	0.58	3.44
15	Cuttlefish	C	**720.60**	**606.01**	**104.07**	**318.03**	**385.78**	**79.60**
		N	209.67	176.33	33.57	102.59	112.25	23.16
		P	51.35	43.18	8.76	26.75	27.49	5.67
16	Other cephalopods	C	**233.29**	**400.96**	**67.25**	**412.35**	**39.64**	**31.33**
		N	69.49	119.43	20.03	122.82	11.81	9.33
		P	20.98	36.06	6.05	37.09	3.56	2.82
17	Flatfish	C	130.33	254.13	66.29	239.37	34.77	150.93
		N	40.37	78.71	2.053	74.14	10.77	46.75
		P	7.91	15.42	4.02	14.53	2.73	11.86
18	Gurnard	C	336.31	287.76	146.72	568.66	5.55	179.14
		N	102.75	87.92	44.83	173.74	1.70	54.73
		P	19.29	16.50	8.42	32.62	0.44	14.06
19	Lizardfish	C	73.61	25.69	88.64	291.77	6.57	10.48
		N	22.69	15.54	0.72	1.45	2.06	3.28
		P	3.53	2.42	0.15	0.31	0.44	0.69
20	Other benthic carnivorous fish	C	52.75	255.94	2.28	4.64	44.06	26.20
		N	16.53	8.05	27.32	89.92	97.56	19.78
		P	3.50	1.70	1.95	13.99	2.11	3.08
21	Red tjor-tjor	C	83.21	169.73	137.44	137.44	22.55	22.55

Table 4.6 continued

	Functional groups/species		**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
			Summer	Winter	Summer	Winter	Summer	Winter
21	Red tjor-tjor	N	26.03	80.07	43.00	43.00	7.06	7.06
		P	6.58	20.24	10.87	10.87	1.78	1.78
22	Pinky	C	**13.95**	**9.81**	82.96	175.09	3.57	2.57
		N	4.34	3.05	25.81	54.48	1.11	0.80
		P	0.70	0.49	4.16	8.78	0.18	0.13
23	Other benthopelagic fish	C	232.27	169.73	30.17	266.46	345.60	26.20
		N	71.22	47.92	8.52	75.22	97.56	7.40
		P	16.33	10.98	1.95	17.24	22.36	1.70
24	Small pelagic fish	C	**83.21**	**133.23**	**68.39**	**59.60**	**48.38**	**68.89**
		N	21.72	34.82	17.87	15.58	12.64	18.00
		P	3.59	5.76	2.95	2.57	2.09	2.98
25	Large pelagic fish	C	**5.64**	**5.64**	**9.81**	**9.71**	**9.14**	**9.14**
		N	1.78	1.78	3.10	3.07	2.89	2.89
		P	0.52	0.52	0.90	0.89	0.84	0.84
26	Skates and rays	C	**15.63**	**15.63**	118.73	970.68	**17.13**	**17.13**
		N	4.96	4.96	41.02	335.32	5.44	5.44
		P	1.02	1.02	7.75	63.39	1.12	1.12
27	Small benthic sharks	C	238.45	766.05	4.04	43.20	**7.60**	**7.60**
		N	87.82	282.11	1.49	15.91	2.80	2.80
		P	14.56	46.78	0.23	2.41	0.39	0.39
28	Large sharks	C	18.00	18.00	18.00	18.00	18.00	18.00
		N	5.56	5.55	5.56	5.56	5.56	5.56
		P	1.01	1.01	1.01	1.01	0.93	0.93
29	Cetaceans	C	n/a	n/a	**7.13**	**7.05**	**6.64**	**6.64**
		N	n/a	n/a	2.23	2.20	2.08	2.08
		P	n/a	n/a	0.56	0.55	0.52	0.52
30	Suspended POM	C	7.28	7.28	1.33	0.19	0.33	0.33
		N	0.89	0.89	0.16	0.02	0.04	0.04
		P	0.36	0.36	0.07	0.01	0.02	0.02

Table 4.6 continued

	Functional groups/species		**Durban Eddy**		**Thukela Mouth**		**Richards Bay**	
			Summer	Winter	Summer	Winter	Summer	Winter
31	Sediment POM	C	378.60	378.60	1890.00	1890.00	378.55	378.55
		N	47.12	47.12	185.92	185.92	47.12	47.12
		P	6.54	6.54	25.82	25.82	6.54	6.54
32	DOM	C	378.60	378.60	271.20	271.20	271.20	271.20
		N	0.89	0.89	4.34	4.34	4.34	4.34
		P	0.36	0.36	0.34	0.34	0.34	0.34
33	DIM	C	28600.00	10641.66	2796.53	1375.27	1360.00	1190.00
		N	11.7	13.68	1.15	0.57	0.57	0.49
		P	2.11	3.62	0.35	0.45	0.39	0.24
	TOTAL	C	37873.00	22818.64	8726.26	15745.00	4939.89	4245.28
		N	2206.28	2968.86	1125.99	3256.97	764.18	643.83
		P	266.22	354.47	127.03	373.11	98.09	79.97

Table 4.7. Total system throughput (gC m^{-2} y^{-1}) for each network.

	Durban Eddy		**Thukela Mouth**		**Richards Bay**	
	Summer	**Winter**	**Summer**	**Winter**	**Summer**	**Winter**
C	688557	931066	30813856	1942292	391888	217848
N	65552	90809	2188817	192697	39702	20607
P	10012	12369	870785	57673	8374	3275

4.3.3 Nutrient limitations within the KZN Bight

The sensitivity of system ascendency to changes in carbon, nitrogen or phosphorus biomass turnover time of each group was calculated for all networks. Essentially, this calculated the nutrient with the slowest turnover rate (Ulanowicz and Abarca-Arenas, 1997). The largest sensitivity value between carbon, nitrogen and phosphorus for a group represented the nutrient with the slowest turnover rate and therefore was the limiting nutrient for that group. Negative sensitivities occurred (Fig. 4.3) when the turnover rate of a group $((T_{\cdot zk}+T_{z\cdot k})/B_{zk})$ was higher than the turnover rate of the network $(T_{\cdot\cdot}/B)$ (see equation 4.6).

Negative sensitivities occurred in the low trophic level groups with fast turnover times – phytoplankton, bacteria, heterotrophic microplankton, zooplankton groups and small macrobenthos (Fig. 4.3). Sensitivities of phytoplankton were lowest in the TM networks but similar in the DE and RB networks (Fig. 4.3). The other low trophic level groups showed similar sensitivity between networks (Fig. 4.3).

Between groups nutrient limitations differed between higher and lower trophic levels. Phytoplankton groups were phosphorus-limited in the TM and RB networks but co-limited by nitrogen and phosphorus in the other networks, as shown by the same sensitivity values for these nutrients (Fig. 4.3). Similarly, bacteria were co-limited by nitrogen and phosphorus in most networks with the exception of the DE winter network where they were phosphorus-limited (Fig. 4.3). Heterotrophic microplankton were co-limited by nitrogen and phosphorus in all networks except the DE winter network where they were phosphorus-limited and the TM winter network where they were nitrogen-limited (Fig. 4.3). Other low trophic level groups (small copepods, medium copepods, large copepods, other large zooplankton, small macrobenthos, large suspension feeders, echinoderms, molluscs and small pelagic fish) were nitrogen-limited in all networks (Fig. 4.3 and 4.4). Many higher trophic level groups (prawn and shrimp, large crustaceans, cephalopods, fish and skates and rays) were phosphorus-limited in all networks (Fig. 4.4). One exception to this was other benthic carnivorous fish which were nitrogen-limited in the DE networks (Fig. 4.4). However the differences in sensitivities to nitrogen and phosphorus in cephalopods, fish and skates and rays were very small and therefore co-limitation is probable (Fig. 4.4). Similarly, small benthic sharks were predominantly nitrogen-limited but differences in sensitivities to nitrogen and phosphorus were small (Fig. 4.4). Large sharks were co-limited by carbon and nitrogen in all networks (Fig. 4.4). Sensitivities of higher trophic level groups did not differ greatly between seasons (Fig. 4.4).

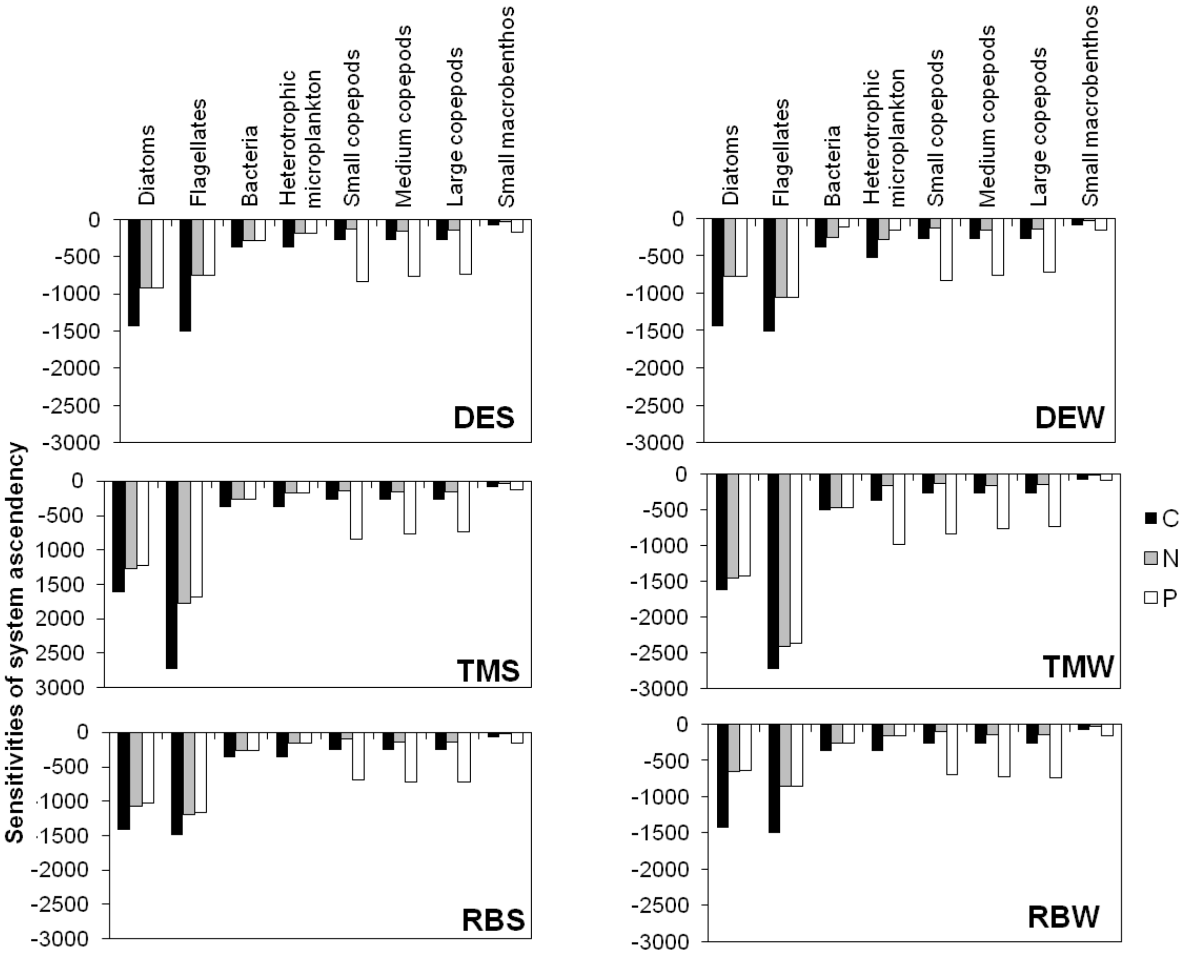

Figure 4.3. Negative sensitivities of system ascendency to changes to carbon, nitrogen and phosphorus turnover rates in each network calculated using equation 4.6.

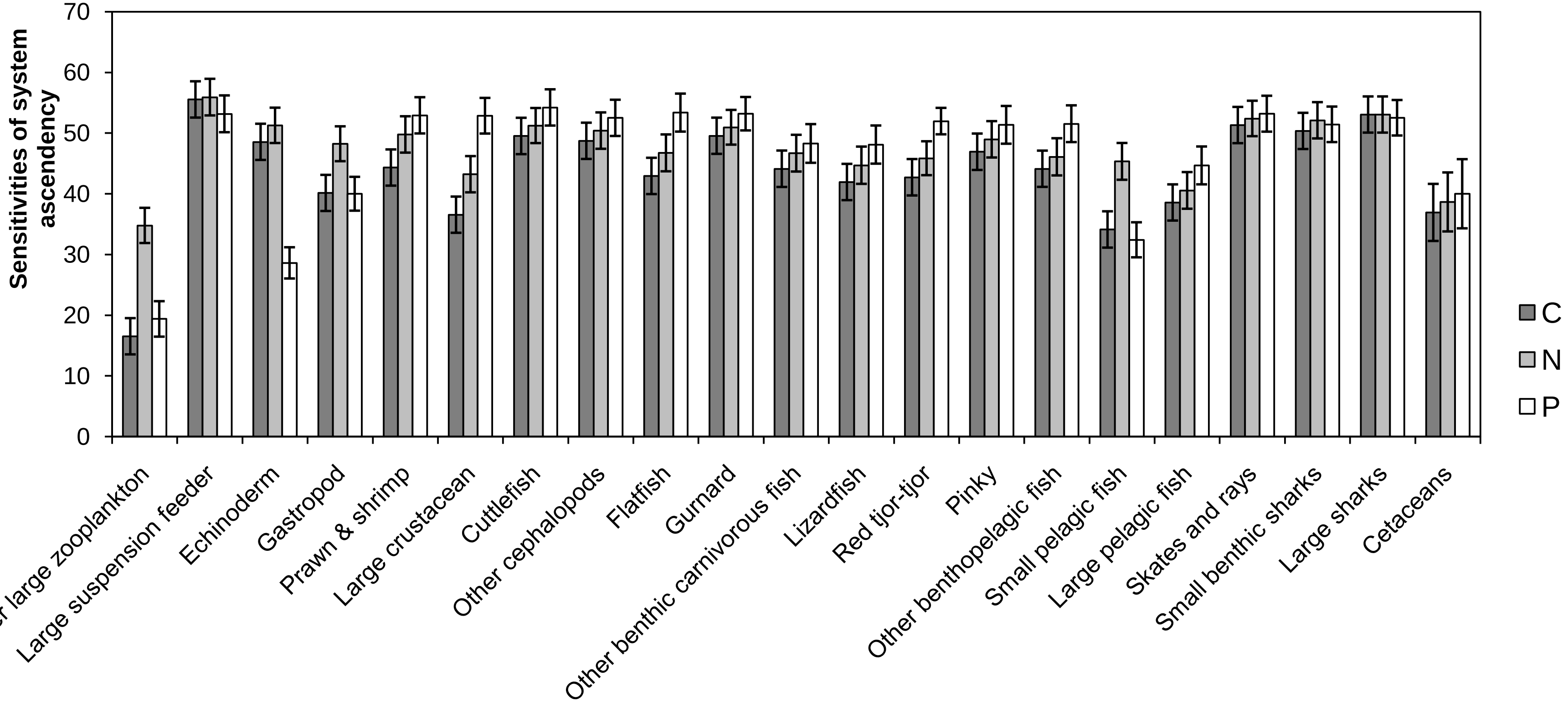

Figure 4.4. Mean positive sensitivities of system ascendency to changes to carbon, nitrogen and phosphorus turnover rates of all networks calculated using equation 4.6. Error bars represent SE.

The sensitivity of system ascendency to changes in carbon, nitrogen and phosphorus flows was calculated for all networks. This calculated the nutrient which was depleted fastest in relation to the available biomass, and for which flow (T_{ij}). The largest sensitivity value represented the limiting flow from each group.

All limiting flows identified were of phosphorus. This indicates that phosphorus was depleted fastest in relation to available biomass in the entire system. The highest sensitivities in all networks were for flows from pelagic planktonic (groups 1 – 7) and dissolved nutrient groups (groups 31 – 33) (Fig. 4.5). Therefore phosphorus was depleted faster in relation to available biomass in these groups than others. The flows from phytoplankton (groups 1 and 2) and zooplankton groups (5 and 6) were identified as most limiting to the greatest number of groups (Fig. 4.5). However, the flow from Lizardfish (group 20) was also limiting to more than one group in the TMS and RBW (Fig. 4.5).

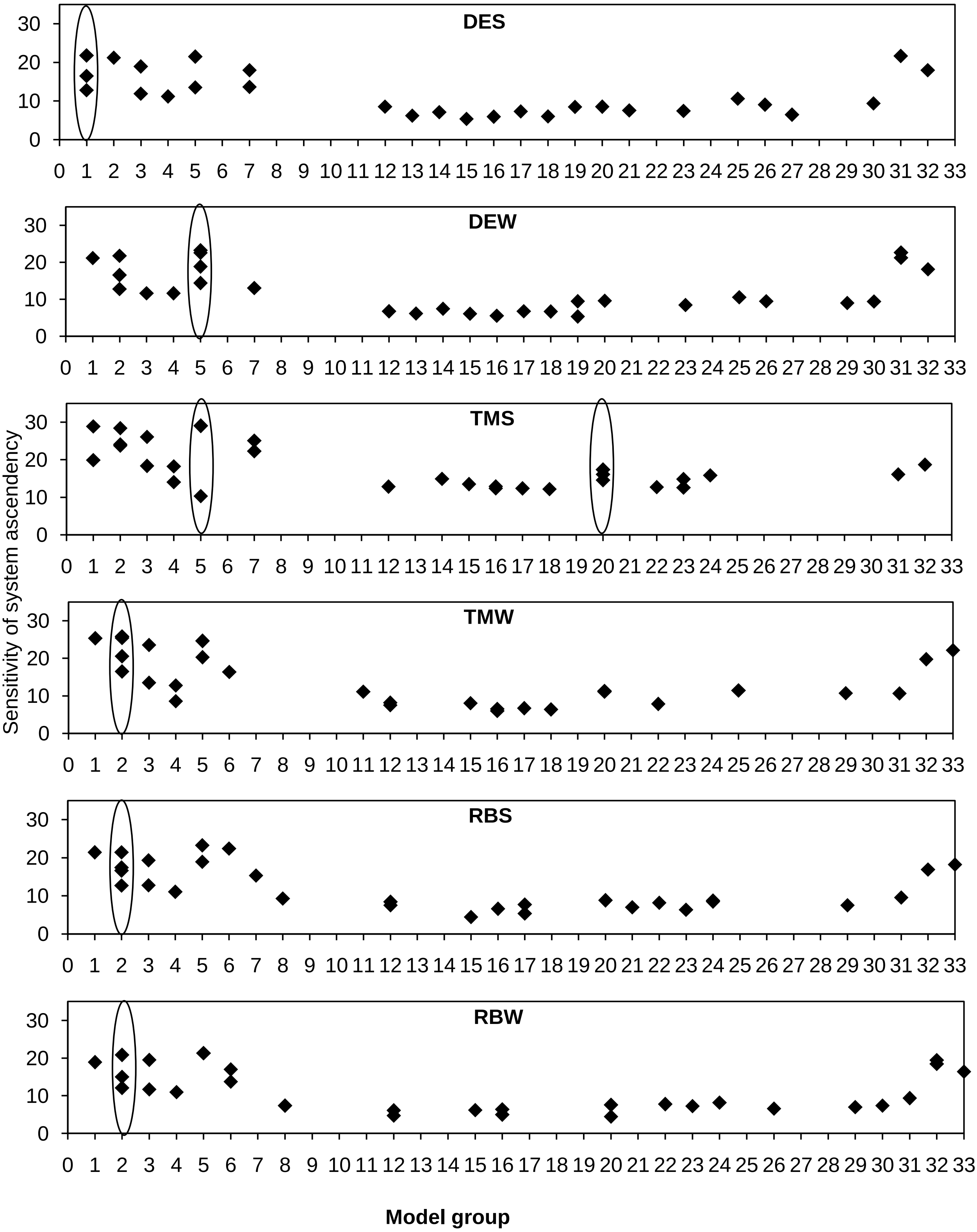

Figure 4.5. Sensitivities of system ascendency to changes in flows of carbon, nitrogen and phosphorus from one group to another in each network. The model group where the limiting flow originates is on the x-axis and group names can be found in Table 4.4. For clarity, circles have been placed around groups with the largest number of limiting flows across the network.

4.3.4 Nutrient cycling within the KZN Bight

The FCI was highest in nitrogen networks compared to carbon and phosphorus except in the DE winter network where the FCI for the phosphorus network was slightly higher (90% for phosphorus vs. 88% for nitrogen) (Fig. 4.6). This indicates that a larger fraction of the system throughput in terms of nitrogen was cycled (Fig. 4.6). The FCI was lowest for carbon networks of all subsystems (Fig. 4.6). Among the subsystems, FCI for all nutrients was highest in the DE and lowest in the TM. Cycling was lower in the summer TM and RB networks than the winter but not in the DE networks (Fig. 4.6).

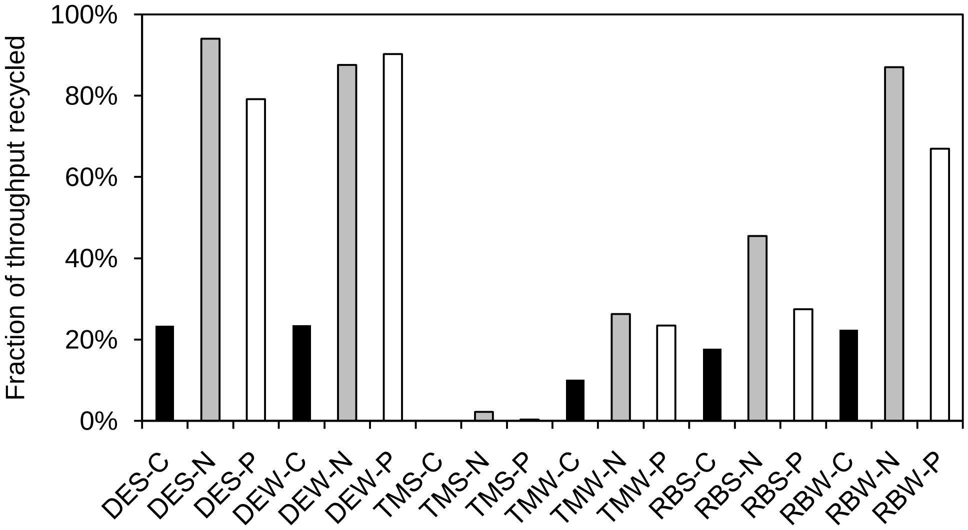

Figure 4.6. Finn Cycling Index (FCI) of each network. DES = Durban Eddy Summer, DEW = Durban Eddy winter, TMS = Thukela Mouth Summer, TMW = Thukela Mouth winter, RBS = Richards Bay summer, RBW = Richards Bay winter. C = carbon, N = nitrogen, P = phosphorus.

4.3.5 Transfer efficiencies within the KZN Bight

Trophic transfer efficiencies were highest from the nutrient and detritus groups (N+D) to the primary producers (TL 1) for all nutrients (Fig. 4.7). The exception to this was the TM summer network which had extremely low transfer efficiencies (Fig. 4.7). Efficiencies of 100% were calculated for transfers from the nutrient and detritus groups to TL1 in DE networks (Fig. 4.7). Large differences were found between seasons in the TM and RB networks at this level. Efficiencies decreased for transfers from discrete TL 2 to TL 3 compared to the previous level

(Fig. 4.7). Phosphorus efficiencies were highest and carbon efficiencies lowest for transfers from TL 3 and higher (Fig. 4.7). However, nitrogen transfer efficiency was higher than phosphorus from TL 1 to TL 2 (Fig. 4.7).

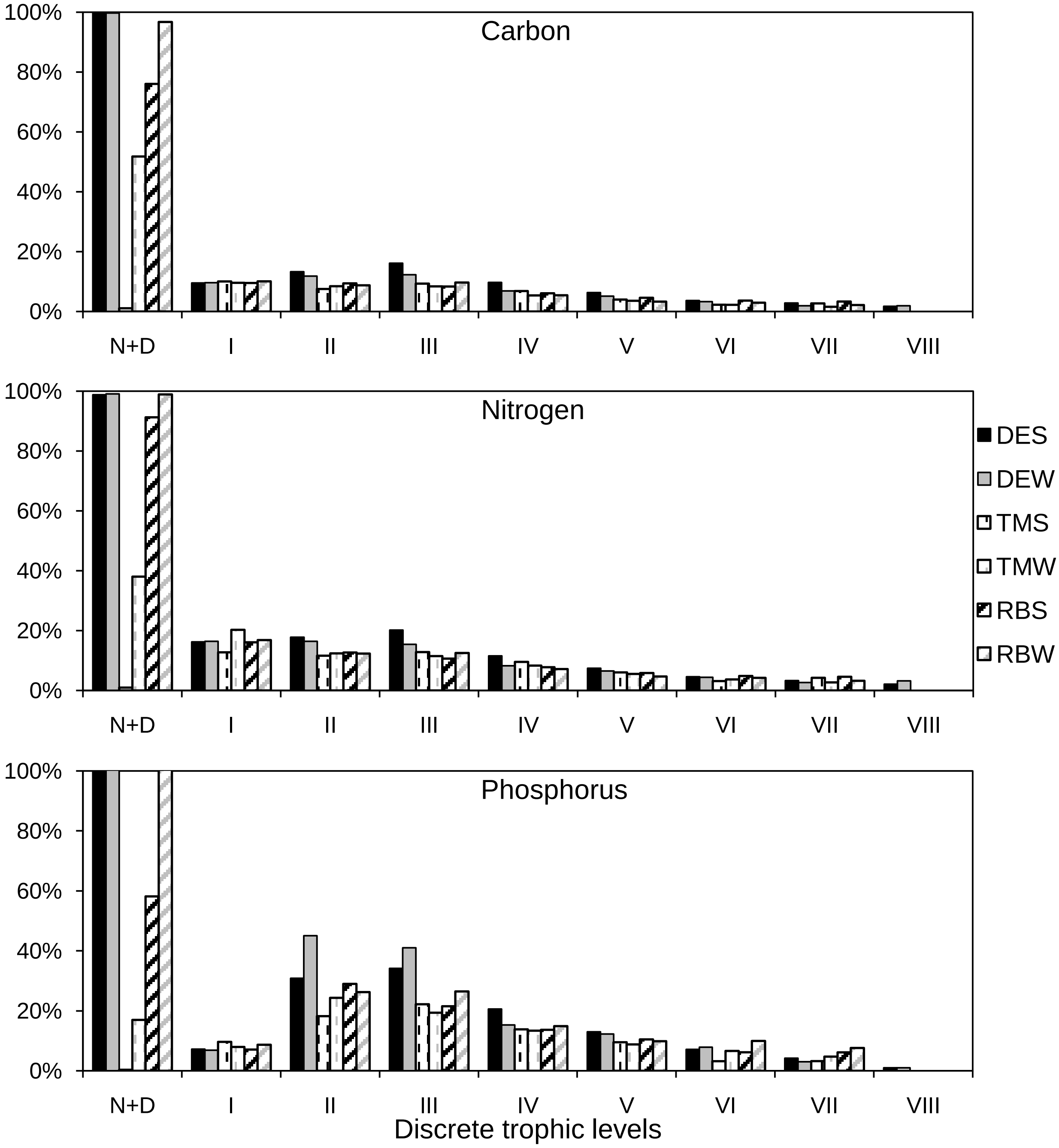

Figure 4.7. Trophic transfer efficiencies between discrete trophic levels of each nutrient in each network. N+D represents nutrient and detritus groups.

4.4 DISCUSSION

The construction and analysis of the eighteen flow networks revealed nutrient biomasses, turnover, limitations, cycling and transfer efficiencies within the KZN Bight.

Benthos dominated each subsystem in terms of biomass and subsequently demersal groups dominated pelagic groups. This is in agreement with literature models of the KZN Bight and Thukela Bank (Chapters 1 and 2). In terms of total system throughput (T..), the TM subsystem was the largest and DE subsystem the smallest in terms of carbon, nitrogen and phosphorus. In addition, T.. of the TM summer network was 11 – 16 times greater than the winter network. This was due to larger imports of suspended POM and DOM from higher precipitation in the summer “wet” season causing increased river outflow. This was also seen to a lesser extent in the RB subsystem where river outflow was much smaller. There was no significant river outflow into the DE subsystem. Recent isotopic studies also found seasonal differences for 2010 in the nearshore foodweb of the KZN Bight and suggest that the demersal system is controlled by riverine TSS (de Lecea, 2012). Riverine nutrient sources are therefore important in determining the size of the subsystems in the Bight in terms of biomass and total flows.

The sensitivity of system ascendency to nutrient turnover times identified differences between broad trophic level groups. Low trophic levels were co-limited by nitrogen and phosphorus, mid trophic levels were nitrogen-limited and higher trophic levels were phosphorus-limited. However, small benthic sharks were nitrogen-limited and large sharks were co-limited by carbon and nitrogen. Sharks are cartilaginous and therefore do not have the high phosphorus requirements that bony organisms do (Sterner and Elser, 2002). Thus the nitrogen-limitation is more likely in sharks and phosphorus-limitation more likely in fish groups, in this case the higher trophic level groups. These trends did not differ greatly between the two seasons in any subsystems. Moreover, the trend of phosphorus-limitation in nekton groups and nitrogen-limitation in benthos groups was found by Ulanowicz & Baird (1999) in the Chesapeake Bay mesohaline community. They did not find co-limitation by nitrogen and phosphorus which occurred in the KZN Bight. However this could be because the KZN Bight is oligotrophic while Chesapeake Bay is eutrophic.

The sensitivity of system ascendency to the nutrient depleted fastest in relation to biomass showed that system ascendency was most sensitive to flows of phosphorus, particularly from pelagic planktonic and dissolved nutrient groups. Thus system ascendency was most sensitive to nutrient limitations at the base of the foodweb. This is in agreement with the oligotrophic nature of the Bight, of which the pelagic community is particularly nutrient-poor. The sensitivity of system ascendency to individual flows has not been applied to other ecological networks in the literature and therefore no results are available for comparison. However, differences in nutrient compositions between groups at the base of the foodweb and metazoans is known to have consequences on trophic flow dynamics in ecosystems (Sterner and Elser, 2002).

Carbon, nitrogen and phosphorus dynamics were described by the FCI. The FCI was highest for nitrogen networks and lowest for carbon. This suggests that nitrogen is scarce in the Bight since the probability a nutrient is reused increases with its scarcity (Ulanowicz, 2004). Phosphorus cycling was higher in the DE winter network, however FCI in the nitrogen network was only 2% smaller. Despite the majority of groups in the networks being phosphorus-limited, the FCI of nitrogen networks were higher due to the high biomasses, and therefore flows, of small macrobenthos and large suspension feeders which were nitrogen-limited. Moreover, the sensitivity of system ascendency to nitrogen turnover in most groups was similar to the sensitivity to phosphorus turnover i.e. most groups were almost co-limited by nitrogen and phosphorus.

The high levels of nitrogen cycling in the southern Bight (87 - 94%) have been found in nitrogen networks of the open ocean (42 - 89%, Ducklow et al. (1989)) and the Neuse River estuary, USA (74 - 98%, Christian and Thomas (2003)). The amount of phosphorus cycling in the southern bight was similar to that in the Sylt-Rømø Bight (80.8%, Baird et al. (2008)). However unlike in the KZN Bight networks phosphorus cycling in the Sylt-Rømø Bight was 40% higher than nitrogen. The high levels of cycling of both nitrogen and phosphorus suggest that both are scarce in the Bight.

Among subsystems, the TM in the central Bight had the lowest FCI for all nutrients. This suggests they were not as scarce in this area than the southern and northern areas. In addition, lower levels of cycling found in the summer “wet” networks for the TM and RB networks suggests that river outflow, with its higher nutrient concentrations, caused the lower levels of cycling. A peak in cycling during the dry season was also found in nitrogen networks of Chesapeake Bay (Baird et al., 1995).

In terms of the way nutrients were transferred through the systems, phosphorus was transferred most efficiently throughout the majority of the food web. This supports the findings that the majority of consumers were limited by phosphorus. At the base of the food web phosphorus was transferred least efficiently. Specifically, the transfer of phosphorus between TL 1 (primary producers) and TL 2 (bacteria, heterotrophic microplankton, zooplankton, small macrobenthos, and large suspension feeders) was the lowest of all nutrients. This result is supported by the results that system ascendency was most sensitive to phosphorus flows originating from primary producer groups. Seasonal differences in transfer efficiencies from nutrient and detritus groups were most evident in the TM and RB networks with extremely low efficiencies for each nutrient in the TM summer network. This suggests that the central Bight receives an adequate supply of nutrients in the summer wet season.

To improve these networks for further analyses data gaps for groups, such as DOM, "small macrobenthos" and pelagic fish, and processes such as resuspension and settling of organic matter within the Bight need to be filled. Moreover, in order to investigate the role of oceanic nutrient sources the imports and exports across the system boundaries by currents need to be investigated. Another potential nutrient source is the annual KZN "sardine run", the winter migration of sardine (*Sardinops sagax*) to KZN from the southern coast of South Africa. Although the northern extent of the migration varies each year, it has been suggested to be a significant source of nitrogen and has the potential to affect the southern bight in the winter "dry" season (Hutchings et al., 2010).

Despite these remaining data gaps this study has increased the knowledge of ecosystem functioning within the Bight and the behaviour of carbon, nitrogen and phosphorus throughout the system. This kind of knowledge is essential in order to assess and manage ecosystems (Christensen et al., 1996, Reichman and Pulliam, 1996). In light of water security issues in South Africa causing an increase in freshwater impoundments inland, the oligotrophic nature of the bight and the reliance of coastal communities on various fisheries sectors, the results of this study and others which conclude the importance of nutrient sources to fisheries in the area (Lamberth et al., 2009, Turpie and Lamberth, 2010) and ecosystem functioning (de Lecea, 2012) have wide management implications.

4.5 CONCLUSIONS

The use of ENA to analyse carbon, nitrogen and phosphorus networks revealed the nutrient dynamics and importance of riverine nutrient sources in ecosystem functioning within the KZN Bight. Cycling indices showed that all the subsystems, and thus the Bight, were nitrogen-limited. Nutrient limitations of biotic groups showed that small macrobenthos and large suspension feeders were nitrogen-limited. Because the systems were dominated by these groups, in terms of biomass and total flows, cycling of nitrogen was highest. The Bight was oligotrophic at an ecosystem-level with many groups co-limited or close to co-limited by nitrogen and phosphorus.

Seasonal differences in ENA indices suggest the importance of riverine nutrient sources within the KZN Bight. Total system throughput, cycling and transfer efficiencies from dissolved and particulate nutrients to primary producers were lower in summer networks than winter networks for all nutrients in the central and northern Bight. Moreover, the central Bight was larger in terms of carbon, nitrogen and phosphorus biomasses and total flows than the southern and northern subsystems. In addition, the northern subsystem, which has lower imports from rivers, was larger than the southern subsystem which has almost no imports from rivers. Thus changes in the amount and elemental composition of river outflow could impact ecosystem functioning in the central and northern Bight.

General Conclusions

The suite of ecosystem models in this thesis has provided the first ecosystem-level view of the data-limited KZN Bight and an understanding of the structure and functioning of this oligotrophic system. Beginning with a broad overview of the functioning of the entire Bight, using models based on literature data, the ACEP II cruises allowed the progression to an understanding of nutrient dynamics and the importance of riverine nutrient sources in the southern, central and northern Bight, using networks based on carbon, nitrogen and phosphorus.

Plausible representations of the data-limited Bight were constructed using static mass-balance models and sensitivity and comparative analyses. This provided the first holistic overview of the system and showed that the system was dominated by benthos in terms of biomass. Outputs in the form of ecosystem-level indices converged on general trends of system functioning. High cycling, particularly of detritus, and negative net system production demonstrated that the Bight is detritus-driven rather than phytoplankton-driven and reliant on riverine detritus imports. Because the Bight was data-limited, there was a high degree of aggregation in these models. However, the results of these models suggests the need to partition detritus groups and include groups involved in the microbial loop to increase understanding of this detritus-driven system. Despite this, these models demonstrated that an overview of ecosystem functioning can be gained for data-limited ecosystems. For the KZN region, the results of this study indicate the sensitivity of the Bight ecosystem to river management.

Much of the riverine outflow into the Bight flows into the central region from the Thukela River, the third largest in southern Africa. This outflow forms the Thukela Bank mudbanks which is home to penaeid prawns and the prawn trawl fishery that targets them. Fisheries time series’ were therefore available for the central Bight and were incorporated into the framework from Chapter 1 to model the central Bight specifically, focusing on the effects of prawn trawling and decreased prawn recruitment following estuarine nursery loss. As in the models representing the entire Bight, the models of the central Bight showed the system to be dominated by benthos in terms of biomass, detritus-driven and reliant on river imports. Dynamic simulations showed that group biomasses in the central Bight were more sensitive to prawn recruitment levels than prawn trawling effort levels. Trawling exacerbated the negative and decreased the positive effects of changes in prawn recruitment. As in Chapter 1, this study showed that a data-limited system could be modelled using literature data, fisheries catch and effort data and sensitivity analyses of Ecosim tuning parameters. The models replicated catch dynamics and biomass trends of groups targeted by the prawn trawl fishery, caught as bycatch or discarded. Moreover, they indicated the need to include critical life-history stages in models and to couple processes between adjacent ecosystems for dynamic modelling and management.

The importance of riverine nutrient sources to ecosystem functioning was demonstrated in Chapters 1 and 3 in terms of an aggregated detritus group. To gain a more detailed understanding of the role of riverine nutrient sources and functioning of an oligotrophic system, stoichiometry, biomass and distribution of specific nutrients through the foodweb were required. Following the ACEP II cruises carbon, nitrogen and phosphorus contents, stoichiometric ratios and biomasses were documented for pelagic and demersal functional groups in the southern, central and northern Bight. Demersal groups sampled had higher biomasses for all nutrients than pelagic groups. Across the Bight, the total biomass of sampled groups was highest in the central Bight and lowest in the southern Bight for all nutrients. Thus riverine nutrient sources are important in determining the size of subsystems within the KZN Bight in terms of carbon, nitrogen and phosphorus.

To gain a more in-depth understanding of the role of carbon, nitrogen and phosphorus in ecosystem functioning ecological networks were constructed and analysed. Using data from Chapter 3 and literature less aggregated networks were constructed which included microbial groups and partitioned detritus groups as suggested in Chapter 1. Cycling indices showed that nitrogen was recycled to a greater extent than carbon or phosphorus through the entire Bight. Nutrient limitations of biotic groups showed similar trends throughout the Bight with high trophic levels limited by phosphorus, benthos limited by nitrogen and planktonic groups co-limited by nitrogen and phosphorus. Seasonal differences in cycling and transfer efficiencies between nutrients and primary producers indicated the importance of river nutrient sources to ecosystem functioning.

The models constructed and analysed in this thesis have certain limitations and levels of uncertainty and could be improved in a number of ways. It must be remembered that the models are based on the underlying assumption of being in steady-state. Thus the models are a “snapshot in time” of the ecosystems they represent and therefore uncertainty increases when drawing conclusions about the systems at other times. Moreoever, input data has certain uncertainties even when sourced from the model system. To deal with this sensitivity analyses were used in Chapter 1 and future work will include carring out sensitivity analyses of models in Chapter 4. In addition, a simple validation could be carried out using trophic level estimates from stable isotope analyses of the Bight by De Lecea (2012). Future research in the Bight should aim to fill data gaps identified by the models in this thesis such as the imports and exports of nutrients across the oceanic boundary of the Bight. Moreover, if time series data were available this would allow the dynamic models to be constructed, validated and used to answer questions on the effects of climate change or river management decisions on the functioning of the KZN Bight ecosystem.

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Appendices

Appendix 1.1: Comparable model groups and representative species/subgroups for the 1980's KZN Bight models (this study) and 1980's Southern Benguela model (Shannon, 2000). "Present" represents groups where the species compositions are unknown.

Model Group	**Representative species/subgroups**	
	KZN Bight	**Southern Benguela**
Detritus	present	present
Phytoplankton	present	present
Zooplankton	present	Microzooplankton Mesozooplankton Macrozooplankton
Benthic primary producers	present	present
Macrobenthos	present	Macrobenthos Meiobenthos
Prawns & Shrimp	*Penaeus indicus* *Metapenaeus monoceros* *Penaeus monodon*	n/a
Cephalopods	present	present
Pelagic-feeding reef fish	*Cheimerius nufar* *Pomadasys olivaceum* *Scomberoides tala* *Polysteganus undulosus*	n/a
Benthic-feeding reef fish	*Chrysoblephus puniceus* *Parablennius cornutus* *Scartella cristata* *Rhabdosargus sarba* *Acanthurus triostegus* *Pomadasys commersonni* *Epinephelus andersoni*	n/a
Pelagic-feeding demersal fish	*Atractoscion aequidens* *Argyrosomus japonicus*	*Brama brama* *Lepidopus caudatus* *Zeus capensis* *Emmelichthys nitidus nitidus* *Epigonus denticulatus* *Spicara axillaris* *Trichiurus lepturus* *Parascorpis typus*

Appendix 1.1 continued

Model Group	KZN Bight	Southern Benguela
Benthic-feeding demersal fish	*Sarpa salpa*	*Genypterus capensis*
	Diplodus sargus	*Lophius sp.*
	Dichistius multifasciatus	*Pterogymnus laniarius*
	Neoscorpis lithophilus	*Chelidonichthys capensis*
	Otolithes ruber	*Trigloporus l. africanus*
		Chirodactylus grandis
		Bassanago albescens
		Chelidonichthys queketti
		Cynoglossus zanazibarensis
		Gonorhynchus gonorhynchus
		Congipodus spinifer
		Congiopodus torvus
		Coelorinchus fasciatus
		Malacocephalus laevis
		Helicolenus dactylopterus
Small pelagic fish	*Sardinops sagax*	*Scomberesox saurus*
		Exocetidae
		Sufflogobius bibarbatus
Large pelagic fish	*Pomatomus saltatrix*	*Atractoscion aequidens*
	Lichia amia	*Thunnus* spp
	Scomberomorus commerson	*Seriola lalandi*
	Scomberomorus plurilienatus	*Argyrosomus inodorus*
	Elops machnata	
	Liza tricuspidens	
Pelagic-feeding chondrichthyans	*Carcharhinus brevipinna*	*Isurus oxyrinchus*
	Carcharhinus limbatus	*Prionace glauca*
		Carcharhinus brachyurus
		Sphyrna zygaena
		Squalus acanthias
		Squalus mitsukurii
		Torpedo nobiliana
		Other skates and rays
Benthic-feeding chondrichthyans	*Carcharhinus taurus*	*Carcharhias taurus*
	Carcharhinus plumbeus	*Torpedo fuscomaculata*
	Sphyrna lewini	*Raja wallacei*
	Carcharhinus obscurus	*Raja alba*
		Raja pullopunctata

Appendix 1.1 continued

Model Group	KZN Bight	Southern Benguela
Benthic-feeding chondrichthyans		*Pliotrema warreni*
		Galeorhinus galeus
		Squalus megalops
		Dasyatis thetidis
		Triakis megalopterus
		Haploblepharus edwardsii
		Poroderma africanum
		Poroderma pantherinum
		Scyliorhinus capensis
		Callorhincus capensis
Apex chondrichthyans	*Carcharadon carcharias*	*Carcharadon carcharias*
	Galeocerdo cuvier	*Hexanchus griseus*
	Carcharhinus leucas	*Notorhinchus cepedianus*
	Isurus oxyrinchus	
	Carcharinus amboinensis	
	Sphyrna mokorran	
Cetaceans	*Tursiops truncatus*	*Balaenoptera edeni*
	Sousa chinensis	*Lagenorhynchus obscurus*
	Delphinus capensis	*Delphinus delphis*
	Delphinus delphis	*Cephalorhynchus heavisidii*
Seabirds	n/a	*Spheniscus demersus*
		Morus capensis
		Phalacrocorax spp.
		Pelecanus onocrotalus
		Larus spp.
		Sterna spp.

Appendix 1.2: Basic input data for the 10 KZN Bight ecosystem models. B = biomass (wet weight); P/B = production/biomass; Q/B = consumption/biomass; and EE = ecotrophic efficiency. Values in bold are from the KZN Bight. Phytoplankton, zooplankton, small pelagic fish and cetacean EEs are used in model configurations that do not include the biomass of the group.

Group	**B (t km^{-2})**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**EE**	**Landings (t km^{-2})**
Detritus	**0.001-0.46***	-	-	-	**0**
Phytoplankton	**0.011-0.0399***	154[a]	-	0.9[c]	**0**
Zooplankton	**0.0015-0.006***	40[a]	165[a]	0.86[c]	**0**
Benthic primary producers		14[b]	-	0.5[c]	**0**
Macrobenthos		6.00[c]	10.00[a]	0.800[c]	**0.124**
Prawns & shrimp		2.73[d]	13.45[d]	0.999[d]	**0.122**
Cephalopods		4.15[d]	**14.56[k]**	0.900[d]	**0.011**
Pelagic-feeding reef fish		**0.33[e]**	5[l]	0.818[u]	**0.024**
Benthic-feeding reef fish		**1.48[f]**	**7.595[m]**	0.860[d]	**0.051**
Pelagic-feeding demersal fish	**0.053**	**0.68[g]**	**3.65[n]**	0.760[i]	**0.003**
Benthic-feeding demersal fish		**1.02[h]**	**13.34[o]**	0.798[c]	**0.048**
Small pelagic fish	**3.5**	4.41[i]	14.65[p]	0.725[d]	**0.000**
Large pelagic fish		**1.66[j]**	**5.30[q]**	0.780[c]	**0.02**
Pelagic-feeding chondrichthyans		**0.50[i]**	**4.08[r]**	0.990[i]	**0.003**
Benthic –feeding chondrichthyans		**1.00[i]**	**2.55[s]**	0.725[i]	**0.012**
Apex chondrichthyans		**0.53[a]**	**1.95[t]**	0.100*	**0.002**
Cetaceans	**0.059**	0.60[a]	10.00[a]	0.760[i]	**0**

*see section 2.2.3; a: Toral-Granda (1999); b: Vidal and Basurto (2003); c: Paula E Silva et al. (1993); d: Freire et al. (2008); e:Chale-Matsau (1996); f: average from Punt et al. (1993), Eyberg (1984), Joubert (1980), Mann et al. (2000), Fennessy (2000b), Mann et al. (2000); g: average of Griffiths (1988), Griffiths (1997b); h: average of Olbers and Fennessy (2007), van der Walt (1995), Mann et al. (2002) ; i: Shannon et al. (2003); j: average of Govender (1996), Smith (2008), Govender (1995); k: P/Q calculated from Buchan and Smale (1981); l: l-w data from Coetzee and Baird (1981), Chale-Matsau (1996); m: l-w data from Punt et al. (1993), Radebe et al. (2002), Mann et al. (2000), Bennett and Griffiths (1986), Wallace and Schleyer (1979)); n: l-w data from Griffiths (1988), Griffiths and Hecht (1995a); o: l-w data from Mann and Buxton (1997), Brash and Fennessy (2005), van der Walt and Beckley (1997), Mann et al (2002);p: l-w data from Torres and Pauly (1991); q: l-w data from van der Elst (1976), Smith (2008), Govender (1995), Chale-Matsau et al. (1999); r: l-w data from Allen and Cliff 2000 (2000), Dudley and Cliff (1993); s: l-w data from Dudley et al. (2005), de Bruyn et al. (2005), Cliff et al. (1988); t: l-w data from Aitken (2003), Cliff et al. (1989), Cliff and Dudley (1991a); u: Opitz (1996).

Appendix 1.3: Initial diet composition (%) for the 10 KZN Bight ecosystem models before balancing. Groups 1-3 refer to detritus and primary producers and therefore do not require a predator column. Changes of quantified diets necessary to obtain a balanced model are detailed in section 2.3. Values in bold are from KZN.

Prey/Predator	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1.Detritus	0.220	0.600	0.475											
2.Phytoplankton	0.727	0.050	0.001	0.050					0.320					
3. Benthic primary producers		0.125	0.066			**0.157**		**0.178**						
4.Zooplankton	0.053	0.010	0.133	0.210	**0.110**	**0.017**		**0.004**	0.680	0.124				
5.Macrobenthos		0.155	0.325	0.580	**0.410**	**0.714**	0.022	**0.817**		0.156	**0.001**	**0.155**	**0.001**	
6.Prawns & shrimp		0.030		0.080	**0.300**	**0.006**	0.075	**0.001**				**0.021**	**0.000**	
7.Cephalopods				0.050	**0.160**	**0.017**	0.057				**0.022**	**0.153**	**0.002**	**0.241**
8.Pelagic-feeding reef fish					**0.020**					0.160	**0.024**	**0.016**	**0.003**	**0.066**
9.Benthic-feeding reef fish				0.010		**0.056**	0.074			0.553	**0.035**	**0.096**	**0.040**	**0.075**
10.Pelagic-feeding demersal fish						**0.032**					**0.097**	**0.074**	**0.066**	**0.071**
11.Benthic-feeding demersal fish		0.030		0.020			0.013				**0.072**	**0.120**	**0.020**	**0.125**
12.Small pelagic fish							0.380			0.005	**0.397**	**0.053**	**0.011**	**0.270**
13.Large pelagic fish							0.377			0.002	**0.243**	**0.059**	**0.045**	**0.146**

Appendix 1.3 continued

	4	5	6	7	8	9	10	11	12	13	14	15	16	17
14.Pelagic-feeding chondrichthyans											**0.009**	**0.016**	**0.185**	
15.Benthic-feeding chondrichthyans											**0.077**	**0.214**	**0.535**	**0.006**
16.Apex chondrichthyans													**0.011**	
17.Cetaceans											**0.006**	**0.010**	**0.049**	
Import						**0.001**	0.002				**0.017**	**0.013**	**0.032**	

Appendix 1.4: Sensitivity of models to changes (-50% - +50%) in input parameters taken from other models/areas. Includes only changes in missing parameters greater than change in input parameter. Does not include effect of input parameters on own group. P/B = production/biomass, Q/B = consumption/biomass, B = biomass. Numbers refer to model numbers in Table 1. Shaded areas indicate a change in missing parameter greater than the change in input parameter. Unshaded areas indicate no change or a change less than or equal to the change in input parameter.

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Apex chondrichthyans EE	10-50% decrease and 10-20% increase	Cetacean B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Cetacean EE										▨
		Benthic-feeding chondrichthyans B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		Pelagic-feeding chondrichthyans B	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
		Small pelagic fish B	▨			▨	▨	▨	▨	▨	▨	
		Pelagic-feeding demersal fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Large pelagic fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
	10-50% decrease and 10% increase	Small pelagic fish B		▨	▨							
		Benthic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Pelagic-feeding reef fish B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Cephalopod B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Zooplankton B						▨	▨	▨	▨	
	10-50% decrease	Zooplankton EE		▨	▨	▨	▨					
	20-50% decrease	Large pelagic fish B										▨
		Small pelagic fish EE										▨
		Benthic-feeding reef fish B										▨
		Pelagic-feeding reef fish B										▨
		Cephalopod B										▨
		Zooplankton EE	▨									
	50% decrease	Zooplankton EE										▨
Benthic-feeding chondrichthyans EE	10-20% decrease, 10-50% increase	Cetacean B	▨	▨	▨	▨	▨	▨	▨	▨	▨	
		Cetacean EE										▨

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Benthic-feeding chondrichthyans EE	10-20% decrease, 10-50% increase	Pelagic-feeding chondrichthyans B	■	■	■	■	■	■	■	■	■	■
		Large pelagic fish B	■	■		■	■					
		Small pelagic fish B	■	■		■	■					
		Pelagic-feeding demersal fish B	■	■		■	■					
		Pelagic-feeding reef fish B	■	■		■	■					
		Cephalopod B			■			■	■	■	■	
	10-50% decrease, 10-20% increase	Benthic-feeding reef fish B										■
		Large pelagic fish B										■
		Cephalopod B			■			■	■	■	■	
	10% decrease, 10-50% increase	Large pelagic fish B			■			■	■	■	■	
		Small pelagic fish B			■			■	■	■	■	
		Pelagic-feeding demersal fish B			■			■	■	■	■	■
		Benthic-feeding reef fish B	■	■	■	■	■	■	■	■	■	
		Pelagic-feeding reef fish B			■			■	■	■	■	
		Cephalopod B	■	■		■	■					
		Zooplankton B						■	■	■	■	
	10-50% decrease, 10% increase	Pelagic-feeding reef fish B										■
	10-20% decrease, 10-30% increase	Zooplankton B	■	■	■	■	■					
	10-20% decrease, 10% increase	Small pelagic fish EE										■
	20-50% decrease	Benthic-feeding demersal fish B	■									
	20-40% decrease	Benthic-feeding demersal fish B		■		■	■	■	■		■	
	20-40% decrease, 10% increase	Benthic-feeding demersal fish B			■					■		
	20% decrease, 40-50% decrease	Prawn and shrimp B	■	■		■	■	■	■		■	
	30-50% decrease	Macrobenthos B		■		■		■	■		■	
	30-50% decrease, 10% increase	Macrobenthos B			■					■		

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Benthic-feeding chondrichthyans EE	20% decrease, 40-50% decrease, 10% increase	Prawn and shrimp B			■					■		
	30-40% decrease	Prawn and shrimp B										■
	40-50% decrease	Macrobenthos B	■				■					
	20% decrease	Zooplankton EE										■
	30% decrease	Benthic-feeding demersal fish B										■
	30% decrease	Macrobenthos B										■
Pelagic-feeding chondrichthyans EE	30-50% decrease	Small pelagic fish B	■				■					
	40-50% decrease	Large pelagic fish B	■	■	■	■	■	■	■	■	■	■
		Small pelagic fish B		■	■	■		■	■	■	■	
		Small pelagic fish EE										■
		Benthic-feeding demersal fish B	■	■	■	■	■	■	■	■	■	■
		Pelagic-feeding demersal fish B	■	■	■	■	■	■	■	■	■	
		Benthic-feeding reef fish B	■	■	■	■	■	■	■	■	■	
		Cephalopod B	■	■	■	■	■	■	■	■	■	
		Zooplankton B						■	■	■	■	
	50% decrease	Cetacean B	■	■	■	■	■	■	■	■	■	■
		Benthic-feeding chondrichthyans B	■	■	■	■	■	■	■	■	■	■
		Pelagic-feeding demersal fish B										■
		Benthic-feeding reef fish B										■
		Cephalopod B										■
	50% decrease	Zooplankton EE		■	■	■	■					
Large Pelagic fish EE	10-50% decrease	Benthic-feeding reef fish B	■	■	■	■	■	■	■	■	■	
		Pelagic-feeding reef fish B	■	■	■	■	■	■	■	■	■	
		Cephalopod B	■	■	■		■	■	■	■	■	
		Zooplankton B						■	■	■	■	
	20-50% decrease	Small pelagic fish B		■	■			■	■	■	■	

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Large Pelagic fish EE	20-50% decrease	Cephalopod B				▨						
		Zooplankton EE			▨							
	30-50% decrease	Small pelagic fish B	▨									
		Benthic-feeding reef fish B										▨
		Pelagic-feeding reef fish B										▨
		Zooplankton EE		▨			▨					
	40-50% decrease	Small pelagic fish B				▨	▨					
		Cephalopod B										▨
		Zooplankton EE	▨			▨						
Benthic-feeding demersal fish EE	50% increase	Prawns and shrimp B	▨									
Pelagic-feeding demersal fish EE	30-50% decrease	Large pelagic fish B			▨			▨	▨	▨	▨	
	40-50% decrease	Small pelagic fish B			▨			▨	▨	▨	▨	
		Benthic-feeding reef fish B			▨			▨	▨	▨	▨	
		Pelagic-feeding reef fish B			▨			▨	▨	▨	▨	
		Cephalopod B			▨			▨	▨	▨	▨	
		Zooplankton B						▨	▨	▨	▨	
	50% decrease	Large pelagic fish B	▨	▨		▨	▨					
		Small pelagic fish B	▨	▨		▨	▨					
		Benthic-feeding reef fish B	▨	▨		▨	▨					
		Zooplankton EE			▨							
Benthic-feeding reef fish EE	50% decrease	Cephalopod B	▨									
Pelagic-feeding reef fish EE	10-50% decrease, 10-20% increase	Cephalopod B				▨						
	10-50% decrease, 10% increase	Cephalopod B		▨	▨		▨	▨	▨	▨	▨	▨
	10-50% decrease	Small pelagic fish B		▨		▨		▨	▨	▨	▨	
		Zooplankton B						▨	▨	▨	▨	

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Pelagic-feeding reef fish EE	10-50% decrease	Zooplankton EE		■								
	20-50% decrease	Small pelagic fish B	■		■							
		Benthic-feeding reef fish B										■
		Zooplankton EE			■	■						
	30-50% decrease	Benthic-feeding reef fish B				■						
		Zooplankton EE					■					
	40-50% decrease	Zooplankton EE	■									
		Benthic-feeding reef fish B	■	■	■			■	■	■	■	
	50% decrease	Benthic-feeding reef fish B					■					
Pelagic-feeding reef fish Q/B	10-50% decrease, 10-50% increase	Cephalopod B				■		■	■	■	■	
	10-40% decrease, 10-50% increase	Cephalopod B	■	■	■							
	10-40% decrease, 10-40% increase	Cephalopod B					■					
	10-30% decrease, 10-50% increase	Cephalopod B										■
	10-50% increase	Small pelagic fish B		■	■	■		■	■	■	■	
		Zooplankton B						■	■	■	■	
	30-50% increase	Zooplankton EE		■	■	■						
	40-50% increase	Benthic-feeding reef fish B										■
	40% increase	Small pelagic fish B					■					
		cetacean B					■					
		Benthic-feeding chondrichthyans B					■					
		Large pelagic fish B					■					
		Small pelagic fish B	■									
		Benthic-feeding demersal fish B					■					
		Pelagic-feeding demersal fish B					■					
		Prawns & shrimp B					■					
Cephalopod EE & P/B	40-50% decrease	Benthic-feeding reef fish B	■		■							

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Cephalopod EE & P/B	50% decrease	Benthic-feeding reef fish B		▨		▨	▨	▨	▨	▨	▨	
Macrobenthos EE and P/B	40-50% decrease, 50% increase	Prawn & shrimp B		▨		▨	▨			▨	▨	
	50% decrease, 40-50% increase	Prawn & shrimp B			▨							
	40-50% increase	Benthic-feeding chondrichthyans B			▨							
		Large pelagic fish B			▨							
		Small pelagic fish B			▨							
		Benthic-feeding demersal fish B			▨							
		Pelagic-feeding demersal fish B			▨							
		Benthic-feeding reef fish B			▨							
		Pelagic feeding reef fish B			▨							
		Cephalopod B			▨							
		Zooplankton EE			▨							
	40% increase	Cetacean B			▨							
	50% increase	Benthic-feeding chondrichthyans B		▨		▨	▨			▨	▨	
	50% increase	Large pelagic fish B		▨		▨	▨			▨	▨	
		Small pelagic fish B		▨		▨	▨			▨	▨	
		Benthic-feeding demersal fish B		▨		▨	▨			▨	▨	
		Pelagic-feeding demersal fish B		▨		▨	▨			▨	▨	
		Benthic-feeding reef fish B		▨		▨	▨			▨	▨	
		Pelagic feeding reef fish B		▨		▨	▨			▨	▨	
		Cephalopod B		▨		▨	▨			▨	▨	
		Prawn & shrimp B						▨	▨			
		Zooplankton B								▨	▨	
		Zooplankton EE		▨		▨	▨					
Macrobenthos Q/B	30-50% decrease	Benthic-feeding demersal fish B			▨					▨	▨	
		Prawn & shrimp B			▨					▨	▨	
	30-40% decrease	Cetacean B			▨					▨	▨	

Appendix 1.4 continued

Input parameter changed	**% change**	**Missing parameter changed**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Macrobenthos Q/B	30-40% decrease	Benthic-feeding chondrichthyans B			▨					▨	▨	
		Large pelagic fish B			▨					▨	▨	
		Small pelagic fish B			▨					▨	▨	
		Pelagic-feeding demersal fish B			▨					▨	▨	
		Benthic-feeding reef fish B			▨					▨	▨	
		Pelagic feeding reef fish B			▨					▨	▨	
		Cephalopod B			▨					▨	▨	
		Zooplankton B								▨	▨	
		Zooplankton EE			▨							
	40-50% decrease	Benthic-feeding demersal fish B		▨		▨	▨	▨	▨			▨
		Prawn & shrimp B		▨		▨	▨	▨	▨			▨
	30% decrease	Pelagic-feeding chondrichthyans B			▨					▨	▨	
	40% decrease	Cetacean B						▨	▨			
		Benthic-feeding chondrichthyans B						▨	▨			
		Large pelagic fish B						▨	▨			
		Small pelagic fish B						▨	▨			
		Pelagic-feeding demersal fish B						▨	▨			
		Benthic-feeding reef fish B						▨	▨			
		Pelagic feeding reef fish B						▨	▨			
		Cephalopod B						▨	▨			▨
	50% decrease	Prawn & shrimp B	▨									
		Benthic-feeding demersal fish B	▨									

Appendix 2.1: Functional groups and representative species in the Thukela Banks models.

Functional groups	**Representative species**
Cetaceans	*Tursiops truncatus, Sousa chinensis, Delphinus delphis*
Apex sharks	*Carcharadon carcharias, Galeocerdo cuvier, Carcharhinus leucas, Carcharinus amboinensis*
Benthic-feeding sharks	*Carcharius taurus , Carcharhinus plumbeus, Sphyrna lewini, Carcharhinus obscurus, Halaeleurus lineatus*
Pelagic-feeding sharks	*Carcharhinus brevipinna, Carcharhinus limbatus*
Skates & Rays	*Dasyatis chrysonota, Raja miraletus*
Large pelagic fish	*Pomatomus saltatrix, Scomberomorus commerson, Scomberomorus plurilineatus*
Small pelagic fish	*Thryssa vitrirostris, Sardinops sagax, Decapterus* sp.
Benthopelagic carnivorous fish	*Otolithes ruber, Saurida undosquamis*
Benthopelagic benthos-feeding fish	*Pomadasys olivaceum, Pagellus natalensis, Johnius spp*
Benthic benthos-feeding fish	Flatfish (Pleuronectiformes), Gurnards (Chelidonichthys spp)
Cephalopods	*Sepia spp,*
Adult prawns	*Penaeus indicus, Metapenaeus monoceros, Penaeus monodon*
Juvenile prawns	*Penaeus indicus, Metapenaeus monoceros, Penaeus monodon*
Commercial crustaceans	*Portunus sanguinolentus*
Carnivorous benthos	*Parthenope quemvis,* Asteroidea, Polychaeta
Detritivorous benthos	Echinoidea, Zoantharia
Zooplankton	
Phytoplankton	
Detritus	

Appendix 2.2: Catch time series calculations.

Prawn trawl catch

Discard estimates from prawn trawlers were unavailable for the full time period. However, a discard:prawn ratio of 8.9:1 based on data from 2003-2004 (Mkhize, 2006) was used to calculate the total weight of discards using the landings of prawns for 1990-2002. Discard weights for each trophic group for 1990-2002 were calculated from Fennessy (1992) and for 2003-2009 from Mkhize (2006). Unfortunately the % contribution by mass to discards was unavailable and therefore % by number was used to assign discard weights to functional groups. Fennessy and Groeneveld (1997) state the composition of discards, based on data from 1989-2002, was 75% fish, 20% crustaceans, and 5% other (echinoderms and molluscs). For 1990-2002 "fish" were divided using % by number of fish species in discards from Fennessy (1992), "crustaceans" and "other" were split between commercial crustaceans (9%), carnivorous benthos (10%), cephalopods (3%) and detritivorous benthos (2%). For 2003-2004 % by number from Mkhize (2006) was used to assign discards to all functional groups (Fig. 2.3).

Commercial linefishery catch

To calculate landings in the model area only, locality codes were used with landings from Zinkwazi up to and including Mlalazi included in calculations of total catch (locality codes between 3829 and 3883). In addition, only landings with a "shore distance" of equal to or less than 16km (equivalent to the 45m isobath) were included. Landings with the generic label "fish" or "shark" were summed and allocated to each fish or shark group by calculating the % composition of these groups to the total landings.

Recreational linefishery catch

The same locality codes as the commercial linefishery were used to calculate landings in the model area and only landings equal to or less than 16km "shore distance" were included. When the number of fish caught in an outing was not given then a value of one was assigned as the number caught.

Shark net catch

When the weight of an organism was not given the length-weight relationships from local linefish status reports (Mann, 2000) or Fishbase (Froese and Pauly, 2010) were used to calculate mass from total length of the animal. For landings with the generic label "hammerheads" the length-weight relationship for scalloped hammerheads (*Sphyrna lewini*) was used to calculate weight as these were the most commonly caught hammerheads in the area. For landings with the generic label "mako", the length-weight relationship of shortfin mako (*Isurus oxyrinchus*) was used for the same reason. Where length-weight relationships were available for males and females of a species, the average of the two weights calculated using each length-weight relationship was used as the final weight of the organism. When no weights or lengths were given for an organism, the average from the known weights of that species was used. It was deemed more useful to estimate these missing values than leave them out.

Catches of species other than large sharks by the shark nets were classified as discards (Fig. 2.3). However only those brought back to shore were included in the weights. Discards at sea were unknown. When the weight of an animal was not given length-weight relationships from Mann (2000) or Fishbase (Froese and Pauly, 2010) were used. Weights of "tunas and bonitos" caught in the shark nets were calculated using the length-weight relationship of Eastern Little Tuna (*Euthynnus affinis*) as these were more commonly caught compared to other tunas, based on the landings data. For dolphin landings for which only fork lengths were provided, only length-weight relationships utilising total length were available, and no length-length relationships were available to convert the fork length, so the average weights for dolphins of similar fork lengths were used.

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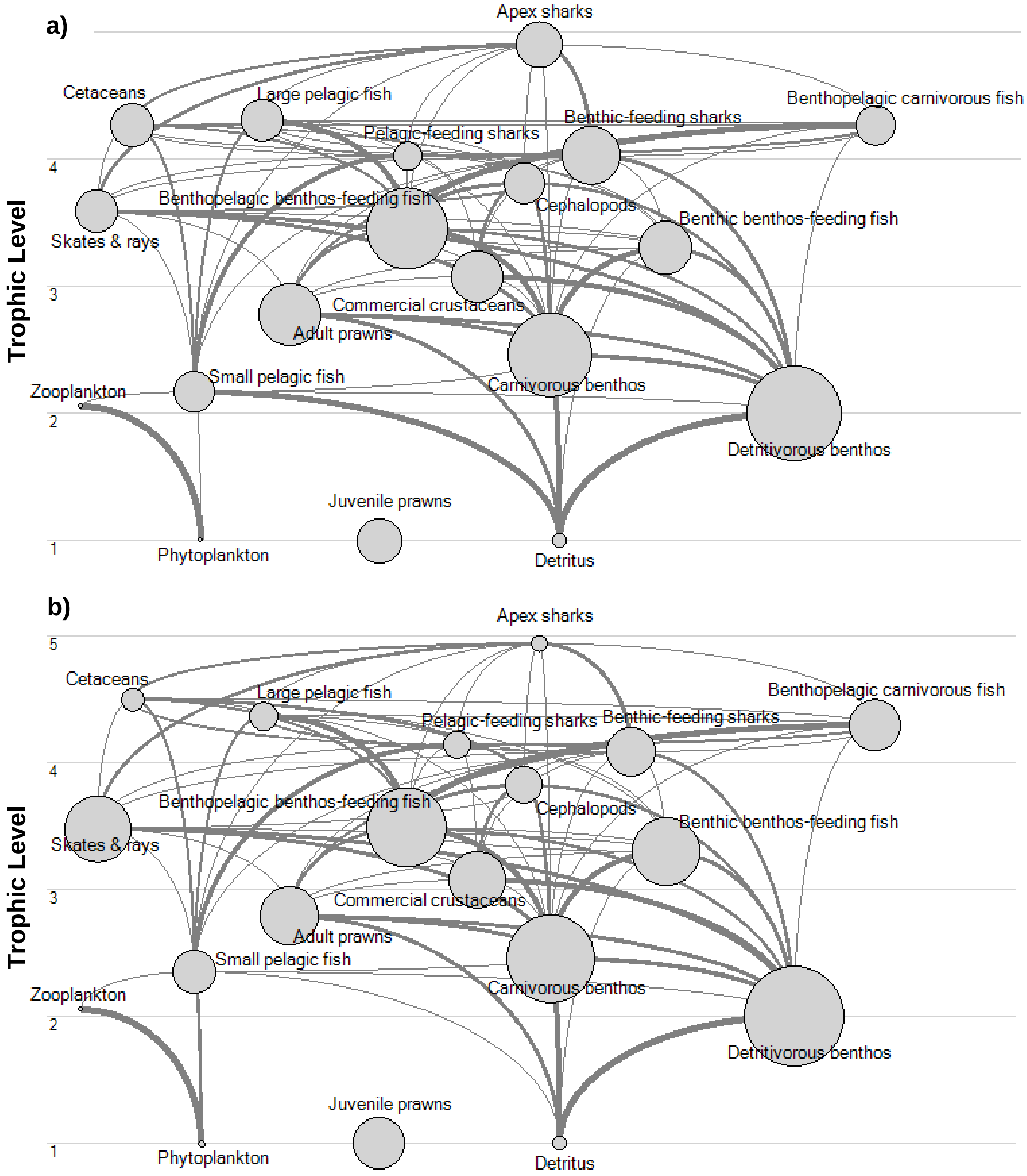
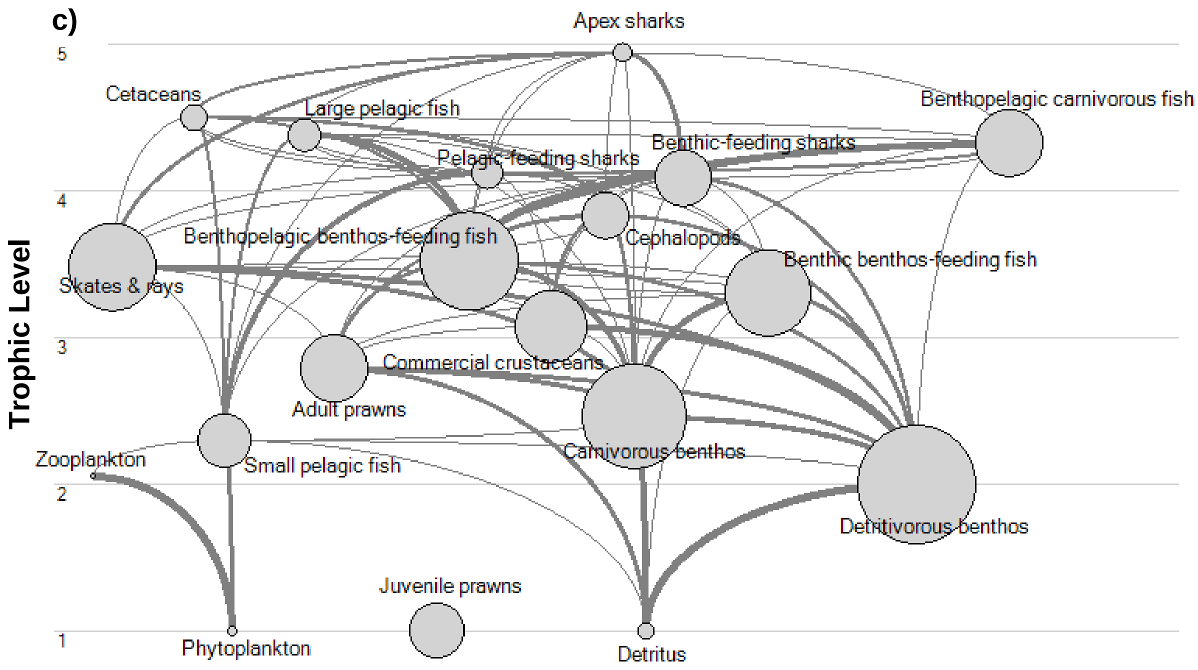
Appendix 2.3: Flow diagrams depicting the size of biomass pools (circle size) and biomass flows (line thickness size) of the a) min B, b) mean B and c) max B models.




c)
Trophic Level
5
4
3
2
1
Apex sharks
Cetaceans
Large pelagic fish
Benthopelagic carnivorous fish
Pelagic-feeding sharks
Benthic-feeding sharks
Cephalopods
Benthopelagic benthos-feeding fish
Benthic benthos-feeding fish
Skates & rays
Commercial crustaceans
Adult prawns
Carnivorous benthos
Zooplankton
Small pelagic fish
Detritivorous benthos
Juvenile prawns
Phytoplankton
Detritus

Appendix 2.4: Functional groups which were sensitive to feeding interaction values.

Predator/prey interaction	**TL Scaling method value**	**Ecosim fitting method value**	**Sensitive groups**	**Models**	**Assumptions**
Carnivorous benthos/detritivorous benthos	2	>100	Benthic sharks Skates and rays Cephalopods Commercial crustaceans Detritivorous benthos	mean B All mean B and max B All All	Detritivorous benthos would be equally accessible to all its predators and therefore the scaling method was preferred.
Prawn/detritivorous benthos	2	1	Skates and rays Cephalopods Detritivorous benthos	All mean B and max B All	It was assumed that detritivorous benthos would be equally accessible to all its predators and therefore the scaling method was preferred. In addition, due to trawling the prawn population would be less than carrying capacity and therefore a higher value predicts more accurate dynamics.
Benthopelagic carnivorous fish/Benthopelagic benthos-feeding fish	3.5	1	Large pelagic fish Benthopelagic benthos-feeding fish Cephalopods	mean B mean B and max B mean B and max B	It was assumed that benthopelagic carnivorous fish would not have restricted access to benthopelagic benthos-feeding fish. Therefore the scaling method was preferred.
Skates and rays/Detritivorous benthos	2	1	Skates and rays	mean B	It was assumed that detritivorous benthos would be equally accessible to all its predators and therefore the scaling method was preferred.
Benthic sharks/Skates and rays	3.6	>100	Skates and rays	min B	It was assumed that benthic sharks would be somewhat restricted in their access to the vulnerable portion of skates and rays and that the latter would be equally vulnerable to all predators. Therefore the scaling method was preferred.
Apex sharks/Skates and rays	3.6	1	Skates and rays	min B	It was assumed that apex sharks would be somewhat restricted in their access to the vulnerable portion of skates and rays and that the latter would be equally vulnerable to all predators. Therefore the scaling method was preferred.

Appendix 3.1. Dry:wet weight ratios of demersal species from ACEP II trawls, calculated during phosphorus analysis

Functional group	**Species**	**Site**	**n**	**Mean**	**2SE**
Cuttlefish	*Sepia acuminata*	DE	4	0.244	0.007
Flatfish	*Citharoides macrolepis*		1	0.191	-
Gurnard	*Satyrichthys adeni*	DE	6	0.212	0.003
Gurnard	*Lepidotrigla faueri*	RB	3	0.222	0.004
Other benthic carnivorous fish	*Chaunax pictus*	DE	3	0.174	0.002
Other benthopelagic fish	*Atrobucca nibe*	TM	1	0.196	-
Other benthopelagic fish	*Upeneus vittatus*	RB	3	0.219	0.004
Red tjor-tjor	*Pagellus natalensis*	RB	2	0.238	0.005
Lizardfish	*Saurida undoquamis*	TM	2	0.226	0.011
Large suspension feeders	*Sea Pen sp.*	DE	1	0.286	-
Skates and rays	*Rhinobatos holorhynchos*	RB	3	0.231	0.007

Appendix 4.3. Input data for carbon, nitrogen and phosphorus flow networks in each subsystem of the KZN Bight and season.

Table 1. Flow data for the Durban Eddy Summer carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			5.934	0.6333	28.22	6.1079	2.5917	0.0404			7.2084					
2 Flagellates			5.934	0.6333	20.124	4.3557	1.8482	0.0288			5.1404					
3 Bacteria					1.8129	2.7997	1.188	0.027		212.28						
4 HM plankton					0.0117	0.0168	0.0071	0.0007	18.415		0.1194	0.0843				
5 Small copepods					1.2086	3.3936	1.44	0.083								
6 Medium copepods						0.2828	0.12	0.0397								
7 Large copepods								0.0295								
8 Other lg zooplankton								0.0083								
9 Sm macrobenthos									12383		185.95	214.23	1842.8	608.8	2039.5	619.7
10 Lg suspension feeder											63.802	113.4	0.3208	210.53	50.42	
11 Echinoderm											1.3357	1.2266	0.5784	22.789		
12 Mollusc													17.824	21.704		
13 Prawn & shrimp													178.24	10.852	123.43	73.217
14 Large crustacean													4.0859	5.426	12.605	18.2
15 Cuttlefish															229.09	
16 Other cephalopod															41.842	125.51
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															25.21	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																73.217
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp POC			15.824	1.6888	9.0644	11.312	4.7999	0.4346	8255.6	849.11	76.151	340.19				
30 Sed POC			3.956	0.4222					226108		277.85	464.93				
31 DOC			363.95	38.842												
32 DIC	856.48	959.10														
B	1.1495	1.2276	1.84	0.1964	0.3662	0.1714	0.0727	0.0346	3515.2	2122.8	154.39	138.3	335.05	88.01	720.6	233.29
I																

Table 1 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	R	E
1 Diatoms								393.62					246.7				171.35	
2 Flagellates								350.82					384.27				191.88	
3 Bacteria													79.976				97.52	
4 HM plankton													9.4258				14.139	
5 Small copepods								6.5139					14.096				33.694	
6 Medium copepods								5.5833					6.4859				15.768	
7 Large copepods						0.67		1.3958					3.2136				6.6907	
8 Other lg zooplankton						0.067							0.3641				0.2526	
9 Sm macrobenthos	677.39	721.64	178.91	150.94	205.56	1.675	878.69	93.056		5.0249	297.89			50464			175196	
10 Lg suspension feeder			13.423	11.325	1.1461	26.719				13.073				238.81			318.41	
11 Echinoderm	50.895				14.326	0.0903	46.905			0.8988	36.959			132.78			308.78	
12 Mollusc	71.431	0.7131			114.84	7.6379	17.181			0.6128				320.62			561.5	
13 Prawn & shrimp	44.644	52.311	89.489	75.499	2.2922	17.21	85.907			3.6768	38.97			450.64			797.42	
14 Large crustacean	15.073	11.772	4.5639	3.8505	5.1574	7.5598	15.635				14.784	0.0565		198.07			563.26	
15 Cuttlefish		302.55	17.898	15.1		4.5735	154.63		15.997	1.2256	11.575	0.3878		544.05			1225	
16 Other cephalopod		4.5637	13.423	11.325		0.063	103.09		0.4471	7.3536	122.7	1.8593		204.71			272.95	
17 Flatfish	8.9289	23.545	26.847	22.65						5.1066	36.959	0.3935		204.65			557.15	
18 Gurnard		2.0689	44.745	37.75			51.544			0.6128		0.1094		290.29			749.98	
19 Other benthic carnivorous fish							40.09		3.5585		22.176	0.2325		182.03			208.33	
20 Lizardfish		45.959							1.9421		35.481	0.2164		80.557			195.7	
21 Red tjor-tjor							78.175					0.1778		261.14			234.65	
22 Pinky							7.8175		0.5931			0.2052		13.848			44.509	
23 Other benthopelagic fish	8.9289		67.117	56.625	230.82	0.7073	84.429		23.13	2.2469	62.583	5.9115		353.07			668.52	
24 Sm pelagic fish	8.9289	11.97							4.4578		59.135	0.2325	97.258	97.258			578.56	
25 Lg pelagic fish									0.4939			1.6149		12.919			35.592	
26 Skates and rays										0.8171		9.3271		12.369			18.136	
27 Sm benthic shark												3.1166		263.95			472.14	
28 Large sharks												0.0399		8.1141			23.346	
29 Susp POC								80.028										
30 Sed POC																		
31 DOC																		297
32 DIC																		
B	130.33	336.31	73.615	52.748	83.209	13.953	252.27	83.127	5.637	15.634	238.45	18	7.28	378.6	271.2	3.E+04	28600	
I												7.62	8800	173000	711	1820	1815	

Table 2. Flow data for the Durban Eddy Winter carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			1.935	0.8589	11.712	4.7041	5.3812	0.1074			13.18					
2 Flagellates			1.935	0.8589	8.352	3.3545	3.8374	0.0766			9.3988					
3 Bacteria					0.7524	2.1562	2.4666	0.0718		53.16						
4 HM plankton					0.0048	0.013	0.0148	0.0018	24.882		0.2182	0.1654				
5 Small copepods					0.5016	2.6136	1.9932	0.2208								
6 Medium copepods						0.2178	1.2458	0.1056								
7 Large copepods								0.0784								
8 Other lg zooplankton								0.0221								
9 Sm macrobenthos									16732		340	420.33	2586.4	575.94	1732.9	1080.5
10 Lg suspension feeder											116.66	222.49	0.4503	199.17	42.421	
11 Echinoderm											2.4422	2.4066	0.8118	21.559		
12 Mollusc													25.018	20.533		
13 Prawn & shrimp													250.18	10.266	103.85	125.82
14 Large crustacean													5.7349	5.1332	10.605	15.637
15 Cuttlefish															192.74	
16 Other cephalopod															35.204	215.69
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															4.2421	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																125.82
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp POC			1.29	0.5726	3.762	8.712	9.966	1.1555	11155	1275.9	139.23	667.48				
30 Sed POC			5.16	2.2903					305511		508.02	912.22				
31 DOC			118.68	52.678												
32 DIC	1808.8	875.00														
B	2.428	1.12	0.6	0.1964	0.152	0.132	0.151	0.092	4751.1	2658	282.23	271.33	470.08	83.26	606.01	400.96
I																

Table 2 continued

	17	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**R**	**E**
1 Diatoms								747.6					663.55				361.72	
2 Flagellates								458.11					216.01				175	
3 Bacteria													38.593				31.8	
4 HM plankton													12.783				14.139	5.06
5 Small copepods								0.7461					5.0207				13.984	
6 Medium copepods								2.9844					5.0824				12.144	
7 Large copepods						0.4711		5.2227					5.2509				13.892	
8 Other lg zooplankton						0.0471		0.5969					0.5023				0.6716	
9 Sm macrobenthos	1332.3	627.45	122.53	73.515	1162	1.1776	591.41	149.22		5.0249	992.65			68207			236795	
10 Lg suspension feeder			9.1935	5.5158	3.5249	18.785				13.073				299.03			398.7	
11 Echinoderm	99.195				44.061	0.0635	31.57			0.8988	118.74			242.72			564.47	
12 Mollusc	139.22	0.6101			441.49	5.37	11.564			0.6128				478.9			1101.6	
13 Prawn & shrimp	87.013	44.754	61.29	36.772	7.0497	12.1	57.82			3.6768	315.84			632.25			1118.8	
14 Large crustacean	17.281	10.071	3.1258	1.8754	15.862	5.3151	10.523				11.874	0.0565		186.64			532.86	
15 Cuttlefish		258.84	12.258	7.3544		3.2155	104.08		15.999	1.2256	37.187	0.3878		457.54			1030.2	
16 Other cephalopod		3.9044	9.1935	5.5158		0.0443	69.384		0.4472	7.3536	394.18	1.8593		351.84			469.12	
17 Flatfish	17.403	30.214	18.387	11.032						5.1066	208.98	0.3935		350.16			1086.4	
18 Gurnard		1.77	30.645	18.386			34.692			0.6128		0.1094		279.24			641.7	
19 Other benthic carnivorous fish							26.983		3.5589		71.243	0.2325		67.885			142.68	
20 Lizardfish		19.136							1.9424		23.748	0.2164		42.943			95.31	
21 Red tjor-tjor							52.616					0.1778		991.42			721.74	
22 Pinky							5.2616		0.5932			0.2052		9.7401			31.306	
23 Other benthopelagic fish	17.403		45.968	27.579	91.83	0.4973	56.826		23.133	2.2469	106.15	5.9115		225			449.78	
24 Sm pelagic fish	17.403	10.241							4.4583		94.99	0.2325	155.88	155.88			927.3	
25 Lg pelagic fish									0.4942			1.6149		12.921			35.596	
26 Skates and rays										0.8171		9.3271		12.369			18.136	
27 Sm benthic shark												3.1166		854.86			1516.8	
28 Large sharks												0.0399		7.9686			23.346	
29 Susp POC								128.33										
30 Sed POC																		
31 DOC																		238.3
32 DIC																		
B	254.13	287.76	50.416	25.69	255.94	9.8137	169.73	133.23	5.6377	15.634	766.05	18	7.28	378.6	271.2	10642		
I												7.43	12336	233567	414	2685		

Table 3. Flow data for the Thukela Mouth Summer carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			2.2253	0.2526	8.4367	2.2492	1.0043	0.0271			0.6947		0.0292			
2 Flagellates			2.2253	0.2526	6.0163	1.6039	0.7162	0.0193			0.4954		0.0292			
3 Bacteria					0.542	1.031	0.4604	0.0181		74.397						
4 HM plankton					0.0035	0.0062	0.0028	0.0004	7.339		0.0115	0.0786				
5 Small copepods					0.3613	1.2497	0.558	0.0557					0.0194			
6 Medium copepods						0.1041	0.0465	0.0266					0.0194			
7 Large copepods								0.0198					0.0194			
8 Other lg zooplankton								0.0056								
9 Sm macrobenthos									4935.2		24.1	305.49	0.1166	133.12	313.11	202.39
10 Lg suspension feeder														45.206		
11 Echinoderm											0.1287	1.1434		4.8934		
12 Mollusc														4.6604		
13 Prawn & shrimp														0.0048	0.0036	0.0026
14 Large crustacean														1.1651	12.015	2.6217
15 Cuttlefish															33.084	
16 Other cephalopod															6.0428	36.161
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																21.094
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POC			5.934	0.6737	2.7099	4.1655	1.86	0.2914	3290.1	545.58	7.3391	317.12				
31 Sed POC			1.4835	0.1684					90102		26.791	433.43	0.3499	51.749		
32 DOC			136.48	15.495												
33 DIC	385.25	636.51														
B	0.46	0.4564	0.69	0.0783	0.1095	0.0631	0.0282	0.0232	1401.2	1239.9	14.884	128.92	0.0956	24.08	104.07	67.249
I																

Table 3 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								258.13						37.377				77.05	
2 Flagellates								360.77						139.39				127.22	
3 Bacteria														35.332				36.57	
4 HM plankton														3.7602				5.6403	
5 Small copepods								1.9149						3.8339				10.073	
6 Medium copepods								1.9149						2.4957				5.8065	
7 Large copepods								0.9192						1.099				2.5928	
8 Other lg zooplankton								0.1532	0.0103					0.1256				0.1694	
9 Sm macrobenthos	396.35	438.62	400.12	7.8529	679.97	268.76	134.12	76.596	0.576	93.194	3.2045				20116			69836	
10 Lg suspension feeder			16.165	0.4904	78.713	79.235				74.679					139.49			185.99	
11 Echinoderm	4.5091					0.5364				6.4349					12.122			29.768	
12 Mollusc	36.327	0.2859			189.67	17.917	52.937			4.3874		0.0005			227.54			523.41	
13 Prawn & shrimp	0.009	0.0051	0.0055	0.0003	0.0095	0.008	0.0019			0.0062	0.0003	0.0003			0.1188			0.4073	
14 Large crustacean	4.5091	5.6497	5.4961	2.125					0.5676	0	2.5482	0.1015			49.889			154.11	
15 Cuttlefish		3.6597	21.553	0.6538		27.179			0.9287	8.7748	0.196	0.3696	12.356		78.575			176.92	
16 Other cephalopod		1.8298	16.165	0.4904		0.3746			2.167	52.649	2.0778	1.1717	5.45		59.011			78.681	
17 Flatfish	4.5409	21.058	21.325	0.9808						24.687		0.0907	0.313		94.393			283.4	
18 Gurnard		0.8295	53.884	1.6346						4.3874					125.61			327.2	
19 Other benthic carnivorous fish												0.0254	0.1565		298.53			250.84	
20 Lizardfish									0.0053		1.6106	1.0438	1.704		3.8392			8.4771	
21 Red tjor-tjor									4.0286			0.1305	1.4611		555.15			387.59	
22 Pinky									0.052			0.1924	5.775		127.55			264.65	
23 Other benthopelagic fish	4.5409		14.84	2.4519		4.2031			8.1167	16.087	1.0598	3.0918	8.4912		44.223			79.952	
24 Sm pelagic fish									69.042		1.8171	6.8721	31.115	80.016	80.016			475.99	
25 Lg pelagic fish									1.768			2.3737	3.9648		18.042			61.929	
26 Skates and rays		41.595								5.8499		6.2677	0.4755		116.79			137.73	
27 Sm benthic shark												1.436			3.0852			7.9929	
28 Large sharks												0.0398			8.1142			23.346	
29 Cetaceans												3.2158			15.312			52.734	
30 Susp POC								65.873							4E+06	4E+06			
31 Sed POC																4E+06			
32 DOC																			9E+06
33 DIC																			61278
B	66.293	146.72	88.637	2.2849	137.44	82.962	30.17	68.389	9.8082	118.73	4.0368	18	7.1263	1.3312	1894.2	271.2	2796.5		
I									0.816	17.6		5.08		9E+06		145000	62300		

Table 4. Flow data for the Thukela Mouth Winter carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.7999	0.4871	12.6	4.36	4.52	0.0367			0.229		0.101			
2 Flagellates			0.7999	0.4871	8.97	3.11	3.22	0.0261			0.164		0.101			
3 Bacteria					0.808	2	2.07	0.0245		48.2						
4 HM plankton					0.0052	0.012	0.0125	0.0006	23.3		0.0038	0.222				
5 Small copepods					0.539	2.42	2.51	0.0754					0.0674			
6 Medium copepods						0.202	0.209	0.0361					0.0674			
7 Large copepods								0.0267					0.0674			
8 Other lg zooplankton								0.0075								
9 Sm macrobenthos									15700	0	7.95	862	0.405	16.2	993	1260
10 Lg suspension feeder														5.48		
11 Echinoderm											0.0425	1.49		0.593		
12 Mollusc														0.565		
13 Prawn & shrimp														0.0006	0.0111	0.0161
14 Large crustacean														0.0292	0.111	0.161
15 Cuttlefish															101	
16 Other cephalopod															18.5	222
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																96.5
23 Other benthopelagic fish																
24 Sm pelagic fish																33
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POC			1.299	2.133	4.04	8.07	8.38	0.394	10400	1880	2.42	895				
31 Sed POC			0.3247	0.5332					286000		8.82	1220	1.21	6.27		
32 DOC			29.876	49.058												
33 DIC	327	357														
B	0.3898	0.256	0.29	0.248	0.1632	0.1223	0.1269	0.0314	4450.1	3858.5	4.91	363.66	0.3316	2.916	318.03	412.35
I			18.99													

Table 4 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								232						7.72				65.325	
2 Flagellates								260						9.78				71.424	
3 Bacteria														12.8				15.37	
4 HM plankton														11.9				17.857	
5 Small copepods								0.668						5.63				15.014	
6 Medium copepods								4.01						4.41				11.252	
7 Large copepods								4.67						4.5				11.675	
8 Other lg zooplankton								0.234	0.0102					0.147				0.2292	
9 Sm macrobenthos	1460	1720	1340	20.2	680	567	1180	66.8	1.14	815	59.7				63900			221795	
10 Lg suspension feeder			53.2	0.997	78.7	167				611					434			578.77	
11 Echinoderm	1.63					1.13									4.93			9.82	
12 Mollusc	131	1.11			190	37.8	468			35.9		0.0005			642			1476.5	
13 Prawn & shrimp	0.0326	0.0199	0.0181	0.0007	0.0095	0.0168	0.0165			0.0505	0.0027	0.0003			0.415			1.4127	
14 Large crustacean	0.163	1.99	0	0.0339							1.87	0.1			6.03			18.662	
15 Cuttlefish		14.2	70.9	1.33		57.4			0.92	71.8	2.1	0.366	12.2		240			540.65	
16 Other cephalopod		7.09	53.2	0.997		0.791			2.15	431	22.2	1.16	5.39		362			482.45	
17 Flatfish	16.4	81.6	70.2	1.99						101		0.0897	0.31		333			1023.3	
18 Gurnard		3.21	177	3.32						35.9					502			1268.1	
19 Other benthic carnivorous fish										101	10.7	0.0251	0.155		871			825.7	
20 Lizardfish									0.0052		6.56	1.03	1.69		7.39			17.229	
21 Red tjor-tjor									3.99			0.129	1.45		555			387.59	
22 Pinky									0.0515			0.19	5.71		179			558.55	
23 Other benthopelagic fish	16.4		48.8	4.99	0	8.87			8.04	132	11.3	3.06	8.4		704			706.11	
24 Sm pelagic fish									30.3		19.4	6.8	23.7	69.7	69.7			414.81	
25 Lg pelagic fish									1.75			2.35	3.92		17.9			61.285	
26 Skates and rays		161								47.8		6.2	0.47		1180			1126	
27 Sm benthic shark												1.76			46.6			85.538	
28 Large sharks												0.0398			7.98			23.346	
29 Cetaceans												3.18			15.2			52.199	
30 Susp POC								99.5				0			244000	244000			
31 Sed POC																27000			
32 DOC																			280000
33 DIC																			626
B	239.37	568.66	291.77	4.644	137.44	175.09	266.46	59.598	9.7062	970.68	43.201	18	7.0539	0.1941	1894.2	271.2	1375.3		
I									38.8	144		5.01	7.12	502000		8380	1310		

Table 5. Flow data for the Richards Bay Summer carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			1.677	0.264	2.89	1.8	0.894	0.0307			0.047		0.178			
2 Flagellates			1.677	0.264	2.06	1.23	0.638	0.0219			0.0335		0.178			
3 Bacteria					0.186	0.791	0.41	0.0205		58.8						
4 HM plankton					0.0012	0.0048	0.0025	0.0005	7.76		0.0008	0.0007				
5 Small copepods					0.124	0.878	0.207	0.0579					0.119			
6 Medium copepods						0.0799	0.331	0.0352					0.119			
7 Large copepods								0.0224					0.119			
8 Other lg zooplankton								0.0063								
9 Sm macrobenthos									5220		1.21	1.9	0.714	46.8	1100	119
10 Lg suspension feeder											0.416	0.999		15.2	56	
11 Echinoderm											0.0087			0.404		
12 Mollusc														0.646		
13 Prawn & shrimp														0.0081	0.135	0.0155
14 Large crustacean														0.391	1.35	1.55
15 Cuttlefish															123	
16 Other cephalopod															22.4	21.3
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															44.6	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																12.4
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POC			4.472	0.704	0.928	3.19	1.66	0.33	3480	159	0.496	3				
31 Sed POC			1.118	0.176					95300		1.81	4.09	2.14	17.4		
32 DOC			102.86	16.2												
33 DIC	372.8	267.9														
B	0.5011	0.3424	0.52	0.0818	0.0375	0.0484	0.0251	0.0263	1482.3	435.9	1.006	1.218	0.585	8.078	385.78	39.644
I																

Table 5 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								251						41.1				74.649	
2 Flagellates								188						22.1				53.438	
3 Bacteria								0						24				27.56	
4 HM plankton								0						3.93				5.892	
5 Small copepods								0.0542						1.3				3.45	
6 Medium copepods								1.08						1.88				4.4528	
7 Large copepods								0.542						1.15				2.3092	
8 Other lg zooplankton		0.0188			0.0156			0.152	0.0097					0.132				0.192	
9 Sm macrobenthos	228	8.87	197	30.8	22.7	7.83	1840	54.7	0.538	10.2	9.61				21300			73877	
10 Lg suspension feeder			8.03	1.41	0.31	6.83				14.3					49			65.384	
11 Echinoderm	0.236				0.156	0.0231				0.223					0.962			2.012	
12 Mollusc	1.18	0.0118								0.672		0.0005	0		2.53			4.9451	
13 Prawn & shrimp	0.0236	0.0019	0.0273	0.0048	0.0156	0.0017				0.0445	0.0471	0.0064	0		0.745			2.4921	
14 Large crustacean	0.236	0.836	1.37	1.3	1.4	1.08	1.07		0.534	0	1.18	0.0946	0		16.7			51.699	
15 Cuttlefish	0	0.151	10.7	1.88		1.17	252		0.874	1.34	0.369	0.344	11.5		291			655.82	
16 Other cephalopod	0	0.0754	8.03	1.41		0.0161			2.04	8.06	3.91	1.09	5.08		34.8			46.383	
17 Flatfish	2.38	8.49	7.87	2.82			10.7		0	5.6		0.0845	0.292		49.5			148.63	
18 Gurnard		0.0342	0.273	1.34					0	0.672					4.73			12.386	
19 Other benthic carnivorous fish							42.9					0.0236	0.146		60.9			124.68	
20 Lizardfish		0.759							0.005		3.03	0.973	2.92		15.9			24.382	
21 Red tjor-tjor									3.79			0.122	3.99		84.1			63.596	
22 Pinky									0.0489			0.179	1.43		4.09			11.385	
23 Other benthopelagic fish	2.38	0	40.2	7.05	131	0.181			7.64	2.46	1.99	2.88	7.92		1020			915.85	
24 Sm pelagic fish	2.38	0.198							38.1		3.42	6.4	29	56.6	56.6			336.75	
25 Lg pelagic fish									1.65			2.21	3.7		16.8			57.737	
26 Skates and rays										0.895		5.84	0.443		17.5			19.871	
27 Sm benthic shark												2.69			5.82			15.042	
28 Large sharks												0.0398			8.11			23.346	
29 Cetaceans												3			14.3			49.159	
30 Susp POC								46.6							21100	21100			
31 Sed POC																			
32 DOC																			28800
33 DIC																			2679
B	34.767	5.5544	44.056	6.5719	22.552	3.569	345.6	48.384	9.1443	17.13	7.5971	18	6.6431	0.3321	378.55	271.2	1364.2		
I									26.9			5.51		45800	51200	7700	3320		

Table 6. Flow data for the Richards Bay Winter carbon network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.9998	0.19	8.24	1.89	3.39	0.0486			0.0527		0.815			
2 Flagellates			0.9998	0.19	5.88	1.21	2.42	0.0346			0.0376		0.815			
3 Bacteria					0.53	0.83	1.55	0.0324		32.3						
4 HM plankton					0.0034	0.005	0.0093	0.0008	5.58		0.0009	0.0026				
5 Small copepods					0.353	1.01	1.88	0.0998					0.543			
6 Medium copepods						0.0838	0.157	0.0474					0.543			
7 Large copepods								0.0354					0.543			
8 Other lg zooplankton								0.01								
9 Sm macrobenthos									3750		1.36	6.58	3.26	280	225	94.2
10 Lg suspension feeder											0.466	3.46		90.4	11.6	
11 Echinoderm											0.0098			0.481		
12 Mollusc														3.85		
13 Prawn & shrimp														0.241	0.139	0.0611
14 Large crustacean														2.33	2.79	1.22
15 Cuttlefish															25.3	
16 Other cephalopod															4.62	16.8
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															9.19	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																9.83
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POC			2.666	0.507	2.65	3.35	6.28	0.522	2500	261	0.556	10.4				
31 Sed POC			0.6665	0.127					68500		2.03	14.2	9.78	103		
32 DOC			61.318	11.7												
33 DIC	1440	285														
B	1.9347	0.3652	0.31	0.0589	0.107	0.0508	0.0951	0.0416	1064.6	586.82	1.128	4.224	2.671	48.11	79.603	31.334
I																

Table 6 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								630						508				288.32	
2 Flagellates								139						78.8				57.03	
3 Bacteria								0						15				16.43	
4 HM plankton								0						2.83				4.2428	
5 Small copepods								0.0772						3.85				9.844	
6 Medium copepods								0.0772						2.8				4.6736	
7 Large copepods								2.31						4.05				8.7492	
8 Other lg zooplankton					0.0467			0.231	0.0097					0.23				0.3037	
9 Sm macrobenthos	979	412	298	43.7	141	5.64	133			10.2	8.43				15300			53062	
10 Lg suspension feeder			11.7	2.25	0.31	4.92				14.3					66			88.023	
11 Echinoderm					0.156	0.0166				0.223					1.37			2.256	
12 Mollusc	5.13	0.38								0.672		0.0005			7.46			17.149	
13 Prawn & shrimp	0.513	0.313	0.199	0.0382	0.0156	0.0062				0.0445	0.0471	0.0064			3.29			11.378	
14 Large crustacean	10.3	49.5	1.99	2.06	1.4	0.777	0.162		0.534		2.36	0.0946			97.7			307.9	
15 Cuttlefish		4.86	15.6	3		0.842	19.1		0.874	1.34	0.369	0.344	11.5		60.1			135.33	
16 Other cephalopod		2.43	11.7	2.25		0.0116			2.04	8.06	3.91	1.09	5.08		27.5			36.661	
17 Flatfish	10.3	125	11.5	4.5			0.812			5.6		0.0845	0.292		223			645.24	
18 Gurnard		1.1	39	7.5	3.11		9.55			0.672					167			399.48	
19 Other benthic carnivorous fish		11.9										0.0236	0.146		195			181.62	
20 Lizardfish		12.5							0.005		3.03	0.973	2.92		18.1			38.87	
21 Red tjor-tjor				3.59					3.79			0.122	4.32		80.2			63.596	
22 Pinky									0.0489			0.179	1.1		2.81			8.1957	
23 Other benthopelagic fish	10.3		7.96	7.65	9.65	0.13			7.64	2.46	1.99	2.88	7.92		34.4			69.44	
24 Sm pelagic fish	10.3	6.38							65.5		3.42	6.4	29	80.6	80.6			479.44	
25 Lg pelagic fish									1.65			2.21	3.7		16.8			57.737	
26 Skates and rays										0.895		5.84	0.443		17.5			19.871	
27 Sm benthic shark												2.69			5.82			15.042	
28 Large sharks												0.0398			8.11			23.346	
29 Cetaceans												3			14.3			49.159	
30 Susp POC															1250	1250			
31 Sed POC																			
32 DOC																			2240
33 DIC																			
B	150.93	179.14	64.178	10.477	22.552	2.5692	26.204	68.885	9.1442	17.13	7.5971	18	6.6431	0.33	379	271	1190		
I												5.51		4580	51200	1065	1730		

Table 7. Flow data for the Durban Eddy Summer nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1 Diatoms			0.7608	0.0771	3.433	0.7438	0.3153	0.0049			0.8777					
2 Flagellates			0.7608	0.0772	2.4512	0.5317	0.2256	0.0035			0.6268					
3 Bacteria					0.2322	0.3591	0.1526	0.0035		27.191						
4 HM plankton					0.0022	0.0032	0.0013	0.0001	3.4735		0.0225	0.0159				
5 Small copepods					0.2701	0.7567	0.3214	0.0185								
6 Medium copepods						0.0616	0.0261	0.0086								
7 Large copepods								0.0067								
8 Other lg zooplankton								0.0023								
9 Sm macrobenthos									2652.6		39.789	45.779	393.61	130.28	436.4	132.63
10 Lg suspension feeder											14.927	26.438	0.0751	49.366	11.792	
11 Echinoderm											0.3228	0.2963	0.1392	5.4927		
12 Mollusc													5.1981	6.337		
13 Prawn & shrimp													54.728	3.3513	37.818	22.506
14 Large crustacean													1.2642	1.6784	3.8945	5.6255
15 Cuttlefish															66.699	0
16 Other cephalopod															12.468	37.584
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															7.8899	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																19.115
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp PON			2.0287	0.2059	1.1039	1.3768	0.5848	0.053	1006.4	103.44	9.2843	41.426				
30 Sed PON			0.5072	0.0524					28086		34.548	57.788				
31 DON			46.661	0.6547												
32 DIN	68.677	60.069														
B	0.14	0.1497	0.2359	0.037	0.0817	0.0372	0.0164	0.0096	752.71	496.33	37.113	40.277	102.94	27.226	209.67	69.488
I			36.04	3.46						10.91						

Table 7 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	R	E
1 Diatoms								47.965					7.631			7.631		
2 Flagellates								42.805					6.6751			6.6711		
3 Bacteria													5.5866			5.5866		
4 HM plankton													0.502			0.502		
5 Small copepods								1.4532					2.3375			2.3334		
6 Medium copepods								1.2139					1.2611			1.2611		
7 Large copepods						0.1511		0.3158					0.5783			0.5743		
8 Other lg zooplankton						0.0185							0.0402			0.0361		
9 Sm macrobenthos	144.82	154.45	38.292	32.302	44.068	0.3572	188.04	19.916		1.0739	63.748			26378		24.701		
10 Lg suspension feeder			3.1351	2.6438	0.2691	6.2468				3.0649				11.796		11.792		
11 Echinoderm	12.262				3.445	0.0218	11.299			0.2166	8.9136			33.285		24.701		
12 Mollusc	20.851	0.2082			33.583	2.2311	5.0229			0.179				73.449		24.701		
13 Prawn & shrimp	13.713	16.08	27.518	23.213	0.7041	5.2884	26.411			1.1315	11.991			185.88		24.701		
14 Large crustacean	4.6673	3.6473	1.4095	1.19	1.5949	2.3367	4.8218				4.5745	0.0175		135.1		24.701		
15 Cuttlefish		88.252	5.2136	4.3981		1.3311	45.146		4.6602	0.3583	3.3786	0.113		332.63		24.701		
16 Other cephalopod		1.3602	3.997	3.3706		0.0188	30.723		0.1333	2.1924	36.689	0.5548		63.693		24.697		
17 Flatfish	2.7752	7.3031	8.3286	7.0234						1.588	11.498	0.1221		140.63		24.697		
18 Gurnard		0.6346	13.703	11.557			15.787			0.1879		0.0334		222.89		24.697		
19 Other benthic carnivorous fish							12.368		1.098		6.847	0.0719		75.491		24.697		
20 Lizardfish		14.402							0.6074		11.115	0.0676		42.909		24.697		
21 Red tjor-tjor							24.438					0.0556		99.758		24.697		
22 Pinky							2.4242		0.1838			0.0636		7.7635		7.7635		
23 Other benthopelagic fish	2.5231	0	18.958	15.992	65.267	0.1998	23.846		6.5267	0.6357	17.687	1.6698		212.34		24.697		
24 Sm pelagic fish	2.3319	3.1336							1.1646		15.433	0.0608	28.746	28.746		24.697		
25 Lg pelagic fish									0.1559			0.5081		6.9321		6.9321		
26 Skates and rays										0.2598		2.9665		3.8315		3.8275		
27 Sm benthic shark												1.151		166.05		24.697		
28 Large sharks												0.0123		4.9038		4.8998		
29 Susp PON								9.7473										
30 Sed PON																		
31 DON																		
32 DIN																		301.54
B	40.368	102.75	22.687	16.526	26.031	4.3416	71.217	21.724	1.783	4.9605	87.816	5.5556	0.887	47.12	4.34	11.70		
I												2.35	1122.2		1.31			

Table 8. Flow data for the Durban Eddy Winter nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.2481	0.1046	1.4252	0.5725	0.6553	0.013			1.6079					
2 Flagellates			0.2481	0.1051	1.0214	0.4098	0.4697	0.0094			1.1498					
3 Bacteria					0.0964	0.2768	0.3166	0.0092		6.8185						
4 HM plankton					0.0012	0.0033	0.0038	0.0004	6.3774		0.0558	0.0423				
5 Small copepods					0.112	0.5821	0.4438	0.0493								
6 Medium copepods						0.0472	0.2708	0.023								
7 Large copepods								0.0177								
8 Other lg zooplankton								0.0061								
9 Sm macrobenthos									3586.1		73.011	90.189	556.17	123.69	371.49	231.92
10 Lg suspension feeder											27.315	51.828	0.1051	46.458	9.8986	
11 Echinoderm											0.5866	0.5794	0.1952	5.1932		
12 Mollusc													7.2878	5.976		
13 Prawn & shrimp													76.596	3.1557	31.864	38.604
14 Large crustacean													1.7747	1.5889	3.2831	4.8317
15 Cuttlefish															56.053	
16 Other cephalopod															10.446	64.1
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															1.3281	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																32.968
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp PON			0.1654	0.0698	0.4581	1.0612	1.2148	0.1413	1364.6	155.96	16.936	81.268				
30 Sed PON			0.6615	0.2846					38028		63.131	113.34				
31 DON			15.215	0.2698												
32 DIN	122.77	76.098														
B	0.2961	0.1366	0.0769	0.0502	0.0339	0.0286	0.0341	0.0254	1017.4	621.49	67.844	79.02	144.42	25.756	176.33	119.43
I			10.96	7.5				0.03		13.99						

Table 8 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	R	E
1 Diatoms								91.114					13.642			13.642		
2 Flagellates								56.023					8.4547			8.4547		
3 Bacteria													1.5021	1.5021		1.5021		
4 HM plankton													0.9258			0.9258		
5 Small copepods								0.1664					0.8829			0.8767		
6 Medium copepods								0.6457					0.981			0.981		
7 Large copepods						0.1064		1.1788					1.0361			1.03		
8 Other lg zooplankton						0.013		0.1648					0.0613			0.0552		
9 Sm macrobenthos	285.6	134.64	26.413	15.783	249.09	0.2534	126.91	31.996		1.078	213.23			34710		34.981		2122.8
10 Lg suspension feeder			2.1455	1.2887	0.8218	4.389				3.0583				14.733		14.727		
11 Echinoderm	23.85				10.603	0.0153	7.5974			0.2161	28.611			71.344		34.981		
12 Mollusc	40.52	0.1778			128.56	1.5654	3.3816			0.1787				114.6		34.981		
13 Prawn & shrimp	26.655	13.726	18.781	11.275	2.16	3.7072	17.709			1.1275	96.817			264.95		34.981		
14 Large crustacean	5.3582	3.1282	0.9694	0.5823	4.9246	1.6477	3.2521				3.6857	0.0175		116.01		34.981		
15 Cuttlefish		75.221	3.5723	2.1347		0.9352	30.205		4.6469	0.3572	10.804	0.1127		265.32		34.981		
16 Other cephalopod		1.1574	2.7272	1.6381		0.0131	20.595		0.1327	2.1812	116.92	0.552		116.96		34.975		
17 Flatfish	5.3913	9.3572	5.7011	3.4083						1.5833	64.757	0.1218		271.52		34.975		
18 Gurnard		0.5402	9.3394	5.6158			10.591			0.1871		0.0333		185.3		34.975		
19 Other benthic carnivorous fish							8.3036		1.0948		21.897	0.0717		25.621		25.621		
20 Lizardfish		5.9827							0.6077		7.4235	0.0677		17.05		17.044		
21 Red tjor-tjor							16.458					0.0557		370.51		34.975		
22 Pinky							1.6354		0.1844			0.0637		5.4505		5.4505		
23 Other benthopelagic fish	4.9027		12.961	7.7767	25.866	0.14	16.004		6.5088	0.634	29.867	1.6652		121.32		34.975		
24 Sm pelagic fish	4.5528	2.6689							1.167		24.857	0.061	47.8	47.794		34.975		
25 Lg pelagic fish									0.1559			0.5081		6.9158		6.9158		
26 Skates and rays										0.2598		2.9665		3.8196		3.8134		
27 Sm benthic shark												1.1486		582.91		34.975		
28 Large sharks												0.0123		4.8987		4.8925		
29 Susp PON								15.596										
30 Sed PON																		
31 DON																		
32 DIN																		361.78
B	78.715	87.919	15.537	8.0488	80.067	3.0537	47.915	34.819	1.7832	4.9605	282.11	5.5556	0.887	47.12	4.3382	13.684		
I												2.35	1562	887.16	0.54			

Table 9. Flow data for the Thukela Mouth Summer nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1 Diatoms			0.285	0.031	1.029	0.274	0.122	0.003			0.085		0.004			
2 Flagellates			0.285	0.031	0.735	0.195	0.087	0.002			0.060		0.004			
3 Bacteria					0.070	0.132	0.059	0.002		9.543						
4 HM plankton					0.001	0.001	0.001	0.000	1.387		0.002	0.015				
5 Small copepods					0.081	0.280	0.125	0.012					0.004			
6 Medium copepods						0.023	0.010	0.006					0.004			
7 Large copepods								0.004					0.004			
8 Other lg zooplankton								0.002								
9 Sm macrobenthos									1059		5.164	65.357	0.025	28.500	67.071	43.286
10 Lg suspension feeder														10.571		
11 Echinoderm											0.031	0.274		1.175		
12 Mollusc														1.355		
13 Prawn & shrimp														0.001	0.001	0.001
14 Large crustacean														0.362	3.710	0.810
15 Cuttlefish															10.694	
16 Other cephalopod															1.798	10.774
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																5.522
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp PON			0.761	0.082	0.330	0.508	0.227	0.035	401	66.505	0.894	38.612				
31 Sed PON			0.190	0.017					8867		2.637	42.613	0.034	5.088		
32 DON			17.498	1.447												
33 DIN	37.139	50.862														
B	0.0561	0.0557	0.0885	0.0148	0.0244	0.0137	0.0064	0.0064	300.04	289.92	3.5779	37.545	0.0294	7.4491	33.572	20.031
I									6441.6	80.35						

Table 9 continued

	17	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**R**	**E**
1 Diatoms								31.465						4.126					
2 Flagellates								44.096						5.067					
3 Bacteria														1.962	1.960				
4 HM plankton														0.200					
5 Small copepods								0.428						1.316					
6 Medium copepods								0.415						0.956					
7 Large copepods								0.207						0.414					
8 Other lg zooplankton								0.042	0.003					0.021					
9 Sm macrobenthos	84.857	94.071	85.714	1.682	145.71	57.643	28.714	16.414	0.123	19.971	0.686				4638				
10 Lg suspension feeder			3.789	0.115	18.406	18.523				17.470					11.478				
11 Echinoderm	1.084					0.129				1.545					4.637				
12 Mollusc	10.552	0.083			55.233	5.203	15.378			1.276		2.E-04			57.790				
13 Prawn & shrimp	0.003	0.002	0.002	1.E-04	0.003	0.002	0.001			0.002	8.E-05	1.E-04			0.061				
14 Large crustacean	1.394	1.747	1.700	0.655					0.176		0.788	0.032			35.678				
15 Cuttlefish		1.182	6.978	0.211		8.788			0.300	2.833	0.063	0.120	4.006		48.097				
16 Other cephalopod		0.545	4.821	0.146		0.112			0.646	15.655	0.619	0.348	1.622		23.306				
17 Flatfish	1.404	6.524	6.586	0.303						7.637		0.028	0.097		77.995				
18 Gurnard		0.253	16.427	0.497						1.338					100.22				
19 Other benthic carnivorous fish												0.008	0.048		128.95				
20 Lizardfish									0.002		0.506	0.327	0.534		2.932				
21 Red tjor-tjor									1.265			0.041	0.458		216.71				
22 Pinky									0.016			0.060	1.797		89.712				
23 Other benthopelagic fish	1.281		4.175	0.691		1.185			2.291	4.542	0.299	0.872	2.395		26.361				
24 Sm pelagic fish									18.057		0.476	1.798	8.139	5.067	62.039				
25 Lg pelagic fish									0.559			0.749	1.251		20.878				
26 Skates and rays		14.333								2.016		2.160	0.164		55.618				
27 Sm benthic shark												0.531			2.906				
28 Large sharks												0.012			9.649				
29 Cetaceans												1.007			19.504				
30 Susp PON								8.027							4637	13227			1E+06
31 Sed PON																1269			
32 DON																			21720
33 DIN																			7512
B	20.534	44.829	27.316	0.7159	42.997	25.815	8.5172	17.873	3.1024	41.015	1.4866	5.5556	2.227	0.1623	185.92	4.3382	1.1549		
I									0.0003	0.0058		1.57		1E+06		7240	7600		

Table 10. Flow data for the Thukela Mouth Winter nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.103	1.000	1.535	0.531	0.551	0.004			0.028		0.012			
2 Flagellates			0.103	1.000	1.093	0.379	0.392	0.003			0.020		0.012			
3 Bacteria					0.104	0.257	0.266	0.003		6.183						
4 HM plankton					0.001	0.002	0.002	0.000	4.331		0.001	0.041				
5 Small copepods					0.120	0.540	0.561	0.017					0.015			
6 Medium copepods						0.044	0.045	0.008					0.015			
7 Large copepods								0.006					0.015			
8 Other lg zooplankton								0.002								
9 Sm macrobenthos									3320		1.681	182.28	0.086	3.426	209.98	266.44
10 Lg suspension feeder														1.281		
11 Echinoderm											0.010	0.358		0.143		
12 Mollusc														0.165		
13 Prawn & shrimp														0.000	0.003	0.005
14 Large crustacean														0.009	0.034	0.050
15 Cuttlefish															32.714	
16 Other cephalopod															5.523	66.277
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																30.053
23 Other benthopelagic fish																
24 Sm pelagic fish																8.638
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp PON			0.167	0.260	0.494	0.986	1.024	0.048	1271	229.67	0.296	109.34				
31 Sed PON			0.042	0.052					28146		0.868	120.06	0.119	0.617		
32 DON			3.830	2.691												
33 DIN	35.906	38.911														
B	0.048	0.0312	0.0372	0.0461	0.0364	0.0265	0.0286	0.0087	940.58	902.17	1.1803	105.91	0.1019	0.9021	102.59	122.82
I										13.97						

Table 10 continued

	17	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**R**	**E**
1 Diatoms								28.256						3.187					
2 Flagellates								31.688						3.187					
3 Bacteria														1.362	1.361				
4 HM plankton														0.624					
5 Small copepods								0.149						1.944					
6 Medium copepods								0.871						1.755					
7 Large copepods								1.052						1.767					
8 Other lg zooplankton								0.065	0.003					0.023					
9 Sm macrobenthos	308.73	363.71	283.36	4.272	143.79	119.90	249.52	14.126	0.241	172.34	12.624				14140				12944
10 Lg suspension feeder			12.432	0.233	18.391	39.024				142.78					35.689				
11 Echinoderm	0.392					0.272									1.728				
12 Mollusc	38.148	0.323			55.330	11.008	136.29			10.454		2.E-04			159.14				
13 Prawn & shrimp	0.010	0.006	0.006	2.E-04	0.003	0.005	0.005			0.016	0.001	1.E-04			0.213				
14 Large crustacean	0.050	0.615		0.010							0.578	0.031			4.262				
15 Cuttlefish		4.599	22.964	0.431		18.592			0.298	23.256	0.680	0.119	3.952		140.62				
16 Other cephalopod		2.117	15.883	0.298		0.236			0.642	128.67	6.628	0.346	1.609		143.09				
17 Flatfish	5.085	25.299	21.765	0.617						31.314		0.028	0.096		272.74				
18 Gurnard		0.982	54.127	1.015						10.978					385.10				
19 Other benthic carnivorous fish										31.096	3.294	0.008	0.048		388.80				
20 Lizardfish									0.002		2.050	0.322	0.528		5.385				
21 Red tjor-tjor									1.252			0.040	0.455		214.71				
22 Pinky									0.016			0.059	1.778		159.14				
23 Other benthopelagic fish	4.636		13.796	1.411		2.508			2.273	37.317	3.195	0.865	2.375		317.19				
24 Sm pelagic fish									7.931		5.078	1.780	6.203	3.187	55.541				
25 Lg pelagic fish									0.553			0.743	1.239		22.974				
26 Skates and rays		55.546								16.491		2.139	0.162		575.25				
27 Sm benthic shark												0.648			33.479				
28 Large sharks												0.012			9.670				
29 Cetaceans												0.992			19.683				
30 Susp PON								12.155							14140	418.44			45033
31 Sed PON																418.44			2539
32 DON																			1244
33 DIN																			84.18
B	74.142	173.74	89.918	1.455	42.997	54.484	75.221	15.575	3.0701	335.32	15.91	5.5556	2.2044	0.0237	185.92	4.34	0.5645		
I									12.3	45.6		1.55	2.23	61200		419	159		

Table 11. Flow data for the Richards Bay Summer nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.215	0.032	0.352	0.220	0.109	0.004			0.006		0.022			
2 Flagellates			0.215	0.032	0.252	0.150	0.078	0.003			0.004		0.022			
3 Bacteria					0.024	0.101	0.053	0.003		7.542						
4 HM plankton					2.E-04	0.001	5.E-04	9.E-05	1.461		0	0				
5 Small copepods					0.033	0.230	0.054	0.015					0.031			
6 Medium copepods						0.018	0.075	0.008					0.027			
7 Large copepods								0.005					0.027			
8 Other lg zooplankton								0.002								
9 Sm macrobenthos									1118		0.259	0.407	0.153	10.024	235.61	25.489
10 Lg suspension feeder											0.097	0.234		3.556	13.101	
11 Echinoderm											0.002			0.097		
12 Mollusc														0.188		
13 Prawn & shrimp														0.002	0.042	0.005
14 Large crustacean														0.121	0.418	0.480
15 Cuttlefish															35.689	
16 Other cephalopod															6.675	6.347
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															13.754	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																3.228
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp PON			0.573	0.086	0.113	0.389	0.203	0.040	424.52	19.396	0.061	0.366				
31 Sed PON			0.143	0.022					11843		0.225	0.508	0.266	2.162		
32 DON			13.187	1.499												
33 DIN	35.274	26.458														
B	0.06	0.0418	0.0667	0.0154	0.0098	0.011	0.0057	0.0073	317.41	101.92	0.2418	0.3547	0.1797	2.4989	112.25	11.808
I																

Table 11 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								30.611						2.983					
2 Flagellates								22.978						2.940					
3 Bacteria														1.545	1.544				
4 HM plankton														0.209					
5 Small copepods								0.014						0.396					
6 Medium copepods								0.245						0.735					
7 Large copepods								0.122						0.417					
8 Other lg zooplankton		0.005			0.004			0.042	0.003					0.023					
9 Sm macrobenthos	48.835	1.900	42.195	6.597	4.862	1.677	394.11	11.716	0.115	2.185	2.058				6281				5200
10 Lg suspension feeder			1.879	0.330	0.073	1.598				3.345					2.725				
11 Echinoderm	0.057				0.037	0.006				0.053					0.402				
12 Mollusc	0.343	0.003								0.196		1.E-04			0.784				
13 Prawn & shrimp	0.007	0.001	0.008	0.001	0.005	0.001				0.014	0.014	0.002			0.445				
14 Large crustacean	0.073	0.259	0.424	0.402	0.433	0.334	0.331		0.165		0.365	0.029			12.316				
15 Cuttlefish		0.044	3.105	0.545		0.339	73.119		0.254	0.389	0.107	0.100	3.337		188.06				
16 Other cephalopod		0.022	2.393	0.420		0.005			0.608	2.402	1.165	0.325	1.514		13.672				
17 Flatfish	0.739	2.635	2.442	0.875			3.321			1.738		0.026	0.091		39.478				
18 Gurnard		0.010	0.084	0.410						0.206					4.457				
19 Other benthic carnivorous fish							13.230					0.007	0.045		36.833				
20 Lizardfish		0.238							0.002		0.950	0.305	0.916		9.160				
21 Red tjor-tjor									1.184			0.038	1.246		39.898				
22 Pinky									0.015			0.056	0.445		3.494				
23 Other benthopelagic fish	0.671		11.340	1.989	36.953	0.051			2.155	0.694	0.561	0.812	2.234		425.13				
24 Sm pelagic fish	0.620	0.052							9.919		0.890	1.666	7.550	2.982	44.509				
25 Lg pelagic fish									0.522			0.699	1.170		21.060				
26 Skates and rays										0.285		1.858	0.141		9.222				
27 Sm benthic shark												0.991			5.121				
28 Large sharks												0.012			9.553				
29 Cetaceans												0.940			17.747				
30 Susp PON								5.685							4802	386.20			
31 Sed PON																			
32 DON																			759.58
33 DIN																			342.27
B	10.769	1.697	13.577	2.059	7.055	1.1106	97.564	12.645	2.8924	5.4351	2.7978	5.5556	2.076	0.0405	47.12	4.34	0.5707		
I									8.51			1.70		5590		385	404		

Table 12. Input data for the Richards Bay Winter nitrogen network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.128	0.023	1.008	0.231	0.415	0.006			0.006		0.100			
2 Flagellates			0.128	0.023	0.717	0.148	0.295	0.004			0.005		0.099			
3 Bacteria					0.068	0.106	0.199	0.004		4.136						
4 HM plankton					0.001	0.001	0.002	1.E-04	1.052		0.000	0.000				
5 Small copepods					0.093	0.265	0.494	0.026					0.143			
6 Medium copepods						0.019	0.036	0.011					0.124			
7 Large copepods								0.008					0.123			
8 Other lg zooplankton								0.003								
9 Sm macrobenthos									806.60		0.293	1.415	0.701	60.226	48.396	20.262
10 Lg suspension feeder											0.109	0.808		21.098	2.707	
11 Echinoderm											0.002			0.115		
12 Mollusc														1.122		
13 Prawn & shrimp														0.074	0.043	0.019
14 Large crustacean														0.722	0.864	0.378
15 Cuttlefish															7.374	
16 Other cephalopod															1.377	5.008
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															2.834	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																2.568
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp PON			0.342	0.062	0.323	0.409	0.766	0.064	304.97	31.839	0.068	1.269				
31 Sed PON			0.085	0.016					8513		0.252	1.765	1.215	12.800		
32 DON			7.861	1.082												
33 DIN	84.550	20.520														
B	0.24	0.0445	0.0397	0.0111	0.0281	0.0116	0.0215	0.0115	227.98	137.21	0.2712	1.2302	0.8206	14.883	23.162	9.333
I																

Table 12 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								77.036						5.729					
2 Flagellates								16.947						2.278					
3 Bacteria														0.903	0.901				
4 HM plankton														0.149					
5 Small copepods								0.020						1.167					
6 Medium copepods								0.018						0.971					
7 Large copepods								0.522						1.552					
8 Other lg zooplankton					0.013			0.064	0.003					0.044					
9 Sm macrobenthos	210.58	88.619	64.098	9.400	30.328	1.213	28.608			2.194	1.813				7736				514
10 Lg suspension feeder			2.731	0.525	0.072	1.148				3.337					3.613				
11 Echinoderm					0.037	0.004				0.053					0.520				
12 Mollusc	1.495	0.111								0.196		1.E-04			2.332				
13 Prawn & shrimp	0.158	0.096	0.061	0.012	0.005	0.002				0.014	0.014	0.002			2.005				
14 Large crustacean	3.191	15.334	0.616	0.638	0.434	0.241	0.050		0.165		0.731	0.029			72.764				
15 Cuttlefish		1.416	4.547	0.874		0.245	5.567		0.255	0.391	0.108	0.100	3.352		39.367				
16 Other cephalopod		0.724	3.488	0.671		0.003			0.608	2.403	1.166	0.325	1.514		10.947				
17 Flatfish	3.192	38.742	3.564	1.395			0.252			1.736		0.026	0.091		175.22				
18 Gurnard		0.336	11.918	2.292	0.950		2.918			0.205					136.00				
19 Other benthic carnivorous fish		3.670										0.007	0.045		86.714				
20 Lizardfish		3.905							0.002		0.947	0.304	0.912		13.019				
21 Red tjor-tjor				1.121					1.184			0.038	1.350		30.870				
22 Pinky									0.015			0.056	0.342		2.479				
23 Other benthopelagic fish	2.909		2.248	2.161	2.726	0.037			2.158	0.695	0.562	0.813	2.237		20.848				
24 Sm pelagic fish	2.691	1.667							17.112		0.893	1.672	7.576	5.729	54.698				
25 Lg pelagic fish									0.522			0.699	1.170		19.631				
26 Skates and rays										0.285		1.858	0.141		9.224				
27 Sm benthic shark												0.991			5.242				
28 Large sharks												0.012			9.559				
29 Cetaceans												0.940			17.788				
30 Susp PON															199.00	38.499			
31 Sed PON																			
32 DON																			70.01
33 DIN																			
B	46.75	54.732	19.779	3.2825	7.055	0.7995	7.3974	18.002	2.8923	5.4351	2.7978	5.5556	2.076	0.0405	47.12	4.34	0.49		
I												1.70		559		38.5	14.6		

Table 13. Input data for the Durban Eddy Summer phosphorus network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.1547	0.0316	1.4075	0.305	0.1293	0.002			0.3599					
2 Flagellates			0.1547	0.0315	1.0017	0.2173	0.0922	0.0014			0.2562					
3 Bacteria					0.0472	0.073	0.031	0.0007		5.5304						
4 HM plankton					0.0002	0.0004	0.0001	1.E-05	0.384		0.0025	0.0018				
5 Small copepods					0.0218	0.061	0.0259	0.0015								
6 Medium copepods						0.005	0.0021	0.0007								
7 Large copepods								0.0005								
8 Other lg zooplankton								0.0004								
9 Sm macrobenthos									142.32		2.1348	2.4561	21.118	6.9897	23.414	7.1159
10 Lg suspension feeder											0.8878	1.5724	0.0045	2.9361	0.7013	
11 Echinoderm											0.0074	0.0068	0.0032	0.1255		
12 Mollusc													0.4424	0.5394		
13 Prawn & shrimp													13.39	0.8199	9.2525	5.5064
14 Large crustacean													0.2928	0.3887	0.902	1.303
15 Cuttlefish															16.294	
16 Other cephalopod															3.7674	11.356
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															1.6688	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																3.1623
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp POP			0.4125	0.0836	0.448	0.5588	0.2374	0.0215	408.46	41.984	3.7681	16.813				
30 Sed POP			0.1031	0.0073					3899.8	0	4.7972	8.024				
31 DOP			9.4878	0.2312												
32 DIP	28.16	24.548														
B	0.06	0.0613	0.048	0.0041	0.0066	0.003	0.0013	0.0016	40.404	29.535	0.8483	3.4301	25.23	6.2999	51.348	20.981
I			6.87	0.11									33.76		8.36	17.65

Table 13 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	R	E
1 Diatoms								19.666					3.8465			2.4097		
2 Flagellates								17.493					3.0449			2.4097		
3 Bacteria													1.1369			1.1356		
4 HM plankton													0.0559			0.0546		
5 Small copepods								0.1172					1.3491			1.3491		
6 Medium copepods								0.0979					0.5577			0.5564		
7 Large copepods						0.0122		0.0254					0.2401			0.2388		
8 Other lg zooplankton						0.003							0.0127			0.0114		
9 Sm macrobenthos	7.7701	8.2866	2.0544	1.7331	2.3643	0.0192	10.089	1.0685		0.0576	3.4202			3699.7		2.4085		506.52
10 Lg suspension feeder			0.1865	0.1572	0.016	0.3715				0.1823				38.09		2.4085		
11 Echinoderm	0.2803				0.0787	0.0005	0.2583			0.005	0.2037			8.8349		2.4085		
12 Mollusc	1.7747	0.0177			2.8583	0.1899	0.4275			0.0152				20.2		2.4085		
13 Prawn & shrimp	3.355	3.9342	6.7325	5.6794	0.1723	1.2939	6.4617			0.2768	2.9337			6.7923		2.4085		
14 Large crustacean	1.081	0.8448	0.3265	0.2756	0.3694	0.5412	1.1168				1.0595	0.004		1.6463		1.6463		
15 Cuttlefish		21.559	1.2736	1.0744		0.3252	11.028		1.1384	0.0875	0.8254	0.0276		8.3179		2.4085		
16 Other cephalopod		0.411	1.2077	1.0185		0.0057	9.2833		0.0403	0.6624	11.086	0.1676		4.6823		2.4085		
17 Flatfish	0.5434	1.4299	1.6307	1.3751						0.3109	2.2513	0.0239		5.7938		2.4085		
18 Gurnard		0.1189	2.5676	2.1655			2.9582			0.0352		0.0063		29.905		2.4085		
19 Other benthic carnivorous fish							1.9233		0.1707		1.0648	0.0112		14.74		2.4085		
20 Lizardfish		3.0463							0.1285		2.3509	0.0143		7.5214		2.4085		
21 Red tjor-tjor							6.1846					0.0141		12.194		2.4085		
22 Pinky							0.3904		0.0296			0.0102		1.189		1.1877		
23 Other benthopelagic fish	0.5776		4.3402	3.661	14.942	0.0457	5.4592		1.4942	0.1455	4.0491	0.3823		18.075		2.4085		
24 Sm pelagic fish	0.3858	0.5184							0.1927		2.5532	0.0101	16.596	16.596		2.4085		
25 Lg pelagic fish									0.0453			0.1476		1.5231		1.5231		
26 Skates and rays										0.0534		0.61		0.5843		0.5831		
27 Sm benthic shark												0.1914		29.198		2.4085		
28 Large sharks												0.0024		1.0429	0	1.0416		
29 Susp POP								3.956										
30 Sed POP																		
31 DOP																		
32 DIP																		
B	7.9111	19.289	3.5286	3.4923	6.5797	0.6993	16.325	3.5908	0.5174	1.0211	14.56	1.0991	0.36	6.54	0.34	2.11		
I												0.47	450.27		0.46			

Table 14. Input data for the Durban Eddy Winter phosphorus network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.0504	0.0428	0.5826	0.234	0.2679	0.0053			0.6573					
2 Flagellates			0.0504	0.0429	0.4168	0.1672	0.1917	0.0038			0.4692					
3 Bacteria					0.0196	0.0562	0.0642	0.0019		1.3832						
4 HM plankton					0.0001	0.0004	0.0004	5.E-05	0.7038		0.0062	0.0047				
5 Small copepods					0.009	0.047	0.0359	0.004								
6 Medium copepods						0.0038	0.0219	0.0019								
7 Large copepods								0.0014								
8 Other lg zooplankton								0.001								
9 Sm macrobenthos									191.96		3.9082	4.8278	29.771	6.621	19.886	12.414
10 Lg suspension feeder											1.6274	3.088	0.0063	2.768	0.5898	
11 Echinoderm											0.0134	0.0132	0.0045	0.1187		
12 Mollusc													0.6208	0.5091		
13 Prawn & shrimp													18.83	0.7758	7.8332	9.4902
14 Large crustacean													0.41	0.367	0.7584	1.1162
15 Cuttlefish															13.758	0
16 Other cephalopod															3.1689	19.445
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish															0.2805	
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																5.4568
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Susp POP			0.0336	0.0283	0.1859	0.4307	0.493	0.0574	553.85	63.297	6.8736	32.984				
30 Sed POP			0.1345	0.0395					5280.3		8.766	15.737				
31 DOP			3.0938	0.0561												
32 DIP	50.19	30.914														
B	0.1213	0.0559	0.0156	0.0055	0.0027	0.0023	0.0028	0.0041	54.61	36.983	1.5507	6.7296	35.397	5.9599	43.183	36.06
I																

Table 14 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	R	E
1 Diatoms								37.246					7.9082			3.2444		
2 Flagellates								22.859					3.656			3.2444		
3 Bacteria													0.3064	0.3041		0.3041		
4 HM plankton													0.1029			0.1006		
5 Small copepods								0.0134					0.552			0.552		
6 Medium copepods								0.0522					0.4304			0.4281		
7 Large copepods						0.0086		0.0951					0.4842			0.4842		
8 Other lg zooplankton						0.0021		0.0268					0.0234			0.0211		
9 Sm macrobenthos	15.288	7.2072	1.4139	0.8449	13.334	0.0136	6.7934	1.7127		0.0577	11.414			4937.9		3.2444		236
10 Lg suspension feeder			0.1278	0.0768	0.049	0.2615				0.1822				52.659		3.2444		
11 Echinoderm	0.5452				0.2424	0.0003	0.1737			0.0049	0.6541			17.307		3.2444		
12 Mollusc	3.4519	0.0151			10.952	0.1334	0.2881			0.0152				37.425		3.2444		
13 Prawn & shrimp	6.5528	3.3743	4.6171	2.7717	0.531	0.9114	4.3534			0.2772	23.801			9.6978		3.242		3.16
14 Large crustacean	1.2378	0.7226	0.2239	0.1345	1.1376	0.3806	0.7513				0.8514	0.004		1.5321		1.5298		
15 Cuttlefish		18.463	0.8768	0.524		0.2295	7.4139		1.1406	0.0877	2.6519	0.0277		5.7915		3.242		
16 Other cephalopod		0.3511	0.8273	0.4969		0.004	6.2477		0.0402	0.6617	35.47	0.1674		8.9164		3.242		
17 Flatfish	1.055	1.831	1.1156	0.6669						0.3098	12.672	0.0238		9.0919		3.242		
18 Gurnard		0.1014	1.7531	1.0542			1.988			0.0351		0.0062		25.592		3.242		
19 Other benthic carnivorous fish							1.2964		0.1709		3.4187	0.0112		5.7915		3.242		
20 Lizardfish		1.2634							0.1283		1.5677	0.0143		2.552		2.5496		
21 Red tjor-tjor							4.1505					0.014		24.778		3.242		
22 Pinky							0.2638		0.0297			0.0103		0.8374		0.8351		
23 Other benthopelagic fish	1.1259		2.9765	1.7859	5.94	0.0322	3.6753		1.4947	0.1456	6.8588	0.3824		9.7352		3.242		
24 Sm pelagic fish	0.7536	0.4417							0.1932		4.1143	0.0101	27.065	27.063		3.242		
25 Lg pelagic fish									0.0453			0.1476		1.5251		1.5228		
26 Skates and rays										0.0534		0.61		0.5824		0.5824		
27 Sm benthic shark												0.1906		100.04		3.242		
28 Large sharks												0.0024		1.0432		1.0409		
29 Susp POP								6.3297										
30 Sed POP																		
31 DOP																		
32 DIP																		
B	15.426	16.504	2.4166	1.7009	20.238	0.4918	10.984	5.7552	0.5175	1.0211	46.776	1.0991	0.36	6.5444	0.3352	3.619		
I												0.47						

Table 15. Input data for the Thukela Mouth Summer phosphorus network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.058	0.013	0.422	0.113	0.050	0.001			0.035		0.001			
2 Flagellates			0.058	0.013	0.301	0.080	0.036	0.001			0.025		0.001			
3 Bacteria					0.014	0.027	0.012	5.E-04		1.941						
4 HM plankton					7.E-05	1.E-04	6.E-05	9.E-06	0.153		2.E-04	0.002				
5 Small copepods					0.007	0.023	0.010	0.001					4.E-04			
6 Medium copepods						0.002	0.001	5.E-04					3.E-04			
7 Large copepods								4.E-04					4.E-04			
8 Other lg zooplankton								2.E-04								
9 Sm macrobenthos									56.810		0.277	3.508	0.001	1.530	3.600	2.323
10 Lg suspension feeder														0.631		
11 Echinoderm											0.001	0.006		0.027		
12 Mollusc														0.116		
13 Prawn & shrimp														4.E-04	3.E-04	2.E-04
14 Large crustacean														0.084	0.856	0.187
15 Cuttlefish															2.788	
16 Other cephalopod															0.544	3.259
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																0.910
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POP			0.155	0.034	0.136	0.209	0.093	0.015	164.50	27.300	0.367	15.850				
31 Sed POP			0.039	0.002					1230		0.366	5.911	0.005	0.706		
32 DOP			3.558	0.116												
33 DIP	14.780	19.750														
B	0.023	0.0228	0.018	0.0016	0.002	0.0011	0.0005	0.001	16.106	17.252	0.0818	3.1974	0.0072	1.7237	8.7551	6.0481
I															2.3	5.56

Table 15 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								12.900						1.242					
2 Flagellates								18.050						1.242					
3 Bacteria														0.399	0.399				
4 HM plankton														0.022					
5 Small copepods								0.035						0.804					
6 Medium copepods								0.033						0.415					
7 Large copepods								0.017						0.184					
8 Other lg zooplankton								0.007	5.E-04					0.012					
9 Sm macrobenthos	4.554	5.049	4.600	0.090	7.820	3.094	1.541	0.881	0.007	1.072	0.037				656.73				697.8
10 Lg suspension feeder			0.226	0.007	1.098	1.105				1.042					25.132				
11 Echinoderm	0.025					0.003				0.035					0.973				
12 Mollusc	0.900	0.007			4.713	0.444	1.312			0.109		1.E-05			17.674				
13 Prawn & shrimp	0.001	4.E-04	4.E-04	3.E-05	0.001	0.001	0.000			5.E-04	0.000	3.E-05			0.005				
14 Large crustacean	0.322	0.403	0.393	0.151					0.041		0.182	0.007			0.466				
15 Cuttlefish		0.308	1.819	0.055		2.291			0.078	0.739	0.017	0.031	1.044		0.917				
16 Other cephalopod		0.165	1.458	0.044		0.034			0.195	4.736	0.187	0.105	0.491		1.020				
17 Flatfish	0.275	1.279	1.291	0.059						1.498		0.005	0.019		1.942				
18 Gurnard		0.048	3.087	0.093						0.251					6.489				
19 Other benthic carnivorous fish												0.001	0.008		13.822				
20 Lizardfish									0.000		0.107	0.069	0.113		0.370				
21 Red tjor-tjor									0.321			0.010	0.116		13.185				
22 Pinky									0.003			0.010	0.290		6.940				
23 Other benthopelagic fish	0.293		0.956	0.158		0.271			0.524	1.040	0.068	0.200	0.548		0.451				
24 Sm pelagic fish									2.976		0.078	0.296	1.341	1.242	28.370				
25 Lg pelagic fish									0.162			0.217	0.363		3.639				
26 Skates and rays		2.709								0.381		0.408	0.031		8.523				
27 Sm benthic shark												0.080			0.596				
28 Large sharks												0.002			2.003				
29 Cetaceans												0.252			4.112				
30 Susp POP								3.295							649.34	147.11			431997
31 Sed POP																139.73			66.42
32 DOP																			429.25
33 DIP																			496.47
B	4.0241	8.4155	4.2486	0.1513	10.868	4.1577	1.9524	2.9542	0.9003	7.7542	0.2254	1.0052	0.5567	0.0665	25.82	0.335	0.3478		
I							1.66		0.0749	1.15		0.31		433000		145	531		

Table 16. Input data for the Thukela Mouth Winter phosphorus network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.021	1.000	0.630	0.218	0.226	0.002			0.011		0.005			
2 Flagellates			0.021	1.000	0.449	0.156	0.161	0.001			0.008		0.005			
3 Bacteria					0.021	0.052	0.054	0.001		1.257						
4 HM plankton					0.000	0.000	0.000	0.000	0.479		0.000	0.005				
5 Small copepods					0.010	0.044	0.045	0.001					0.001			
6 Medium copepods						0.004	0.004	0.001					0.001			
7 Large copepods								5.E-04					0.001			
8 Other lg zooplankton								3.E-04								
9 Sm macrobenthos									178.17		0.090	9.782	0.005	0.184	11.269	14.299
10 Lg suspension feeder														0.076		
11 Echinoderm											0.000	0.008		0.003		
12 Mollusc														0.014		
13 Prawn & shrimp														4.E-05	0.001	0.001
14 Large crustacean														0.002	0.008	0.012
15 Cuttlefish															8.512	
16 Other cephalopod															1.666	19.991
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish																
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																4.842
23 Other benthopelagic fish																
24 Sm pelagic fish																1.423
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POP			0.034	0.107	0.202	0.404	0.419	0.020	520.00	94.000	0.121	44.750				
31 Sed POP			0.008	0.007					3904		0.120	16.654	0.017	0.086		
32 DOP			0.779	0.528												
33 DIP	14.360	15.450														
B	0.02	0.0128	0.0076	0.0051	0.0029	0.0021	0.0023	0.0014	50.489	53.686	0.027	9.0195	0.025	0.2087	26.754	37.085
I															9.34	34.53

Table 16 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								11.600						0.665					
2 Flagellates								13.000						0.665					
3 Bacteria														0.277	0.277				
4 HM plankton														0.665					1.49
5 Small copepods								0.012						0.665					0.53
6 Medium copepods								0.070						0.665					0.13
7 Large copepods								0.085						0.665					0.16
8 Other lg zooplankton								0.011	0.000					0.015					
9 Sm macrobenthos	16.569	19.519	15.207	0.229	7.717	6.434	13.391	0.758	0.013	9.249	0.677				2013				
10 Lg suspension feeder			0.740	0.014	1.095	2.323				8.500					82.381				
11 Echinoderm	0.009					0.006									0.324				
12 Mollusc	3.246	0.028			4.708	0.937	11.597			0.890		1.E-05			49.779				
13 Prawn & shrimp	0.002	0.001	0.001	5.E-05	0.001	0.001	0.001			0.004	2.E-04	3.E-05			0.020				
14 Large crustacean	0.012	0.142		0.002							0.134	0.007			0.046				
15 Cuttlefish		1.197	5.975	0.112		4.837			0.078	6.051	0.177	0.031	1.028		2.799				
16 Other cephalopod		0.638	4.791	0.090		0.071			0.194	38.811	1.999	0.104	0.485		6.258				
17 Flatfish	0.995	4.951	4.259	0.121						6.128		0.005	0.019		5.416				
18 Gurnard		0.184	10.141	0.190						2.057					24.600				
19 Other benthic carnivorous fish										4.842	0.513	0.001	0.007		38.905				
20 Lizardfish									3.E-04		0.434	0.068	0.112		0.467				
21 Red tjor-tjor									0.317			0.010	0.115		13.077				
22 Pinky									0.003			0.010	0.286		10.043				
23 Other benthopelagic fish	1.060		3.155	0.323		0.574			0.520	8.535	0.731	0.198	0.543		9.350				
24 Sm pelagic fish									1.307		0.837	0.293	1.022	0.665	24.965				
25 Lg pelagic fish									0.161			0.216	0.360		5.416				
26 Skates and rays		10.512								3.121		0.405	0.031		83.432				
27 Sm benthic shark												0.098			5.403				
28 Large sharks												0.002			2.001				
29 Cetaceans												0.249			5.540				
30 Susp POP								4.975							2013	8.379			22418
31 Sed POP																8.378			467
32 DOP																			22.8
33 DIP																			
B	14.53	32.616	13.985	0.3075	10.868	8.7751	17.243	2.5744	0.8909	63.394	2.4126	1.0052	0.5511	0.0097	25.82	0.3352	0.4448		
I									3.56	9.38		0.31	1.78	25100		8.38	16.8		

Table 17. Input data for the Richards Bay Summer phosphorus network. Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.044	0.013	0.144	0.090	0.045	0.002			0.002		0.009			
2 Flagellates			0.044	0.013	0.103	0.062	0.032	0.001			0.002		0.009			
3 Bacteria					0.005	0.021	0.011	0.001		1.538						
4 HM plankton					2.E-05	1.E-04	5.E-05	1.E-05	0.161		2.E-05	2.E-05				
5 Small copepods					0.003	0.019	0.004	0.001					0.003			
6 Medium copepods						0.001	0.006	0.001					0.002			
7 Large copepods								4.E-04					0.002			
8 Other lg zooplankton								3.E-04								
9 Sm macrobenthos									59.959		0.014	0.022	0.008	0.538	12.635	1.367
10 Lg suspension feeder											0.006	0.014		0.211	0.778	
11 Echinoderm											0.000			0.002		
12 Mollusc														0.016		
13 Prawn & shrimp														0.001	0.010	0.001
14 Large crustacean														0.028	0.097	0.111
15 Cuttlefish															8.763	
16 Other cephalopod															2.019	1.920
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															2.134	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																0.535
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POP			0.117	0.035	0.046	0.160	0.083	0.017	174.00	7.950	0.025	0.150				
31 Sed POP			0.029	0.003					1644		0.031	0.071	0.037	0.300		
32 DOP			2.681	0.120												
33 DIP	13.700	10.490														
B	0.03	0.0171	0.0136	0.0017	0.0008	0.0009	0.0005	0.0012	17.038	6.0649	0.0055	0.0302	0.0441	0.5782	27.49	3.5654
I															4.91	3.28

Table 17 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								12.525						0.873					
2 Flagellates								9.400						0.872					
3 Bacteria														0.315	0.314				
4 HM plankton														0.023					
5 Small copepods								0.001						0.270					
6 Medium copepods								0.020						0.321					
7 Large copepods								0.010						0.168					
8 Other lg zooplankton		0.001			0.001			0.007	0.000					0.013					
9 Sm macrobenthos	2.619	0.102	2.263	0.354	0.261	0.090	21.135	0.628	0.006	0.117	0.110				786.73				989.66
10 Lg suspension feeder			0.112	0.020	0.004	0.095				0.199					8.049				
11 Echinoderm	0.001				0.001	1.E-04				0.001					0.074				
12 Mollusc	0.029	3.E-04								0.017		1.E-05			0.194				
13 Prawn & shrimp	0.002	1.E-04	0.002	4.E-04	0.001	1.E-04				0.003	0.004	5.E-04			0.045				
14 Large crustacean	0.017	0.060	0.098	0.093	0.100	0.077	0.077		0.038		0.084	0.007			0.209				
15 Cuttlefish		0.011	0.762	0.134		0.083	17.953		0.062	0.095	0.026	0.025	0.819		2.612				
16 Other cephalopod		0.007	0.724	0.127		0.001			0.184	0.727	0.352	0.098	0.458		0.601				
17 Flatfish	0.187	0.666	0.617	0.221			0.839			0.439		0.007	0.023		0.375				
18 Gurnard		0.003	0.021	0.105						0.053					0.726				
19 Other benthic carnivorous fish							2.053					0.001	0.007		3.007				
20 Lizardfish		0.050							0.000		0.201	0.064	0.193		1.001				
21 Red tjor-tjor									0.299			0.010	0.314		8.226				
22 Pinky									0.002			0.009	0.072		0.276				
23 Other benthopelagic fish	0.154		2.603	0.456	8.481	0.012			0.495	0.159	0.129	0.186	0.513		28.869				
24 Sm pelagic fish	0.103	0.009							1.645		0.148	0.276	1.252	0.872	20.079				
25 Lg pelagic fish									0.151			0.203	0.340		4.660				
26 Skates and rays										0.059		0.383	0.029		1.398				
27 Sm benthic shark												0.138			0.916				
28 Large sharks												0.002			1.977				
29 Cetaceans												0.234			3.786				
30 Susp POP								2.330							786.58	7.699			1314
31 Sed POP																			
32 DOP																			13.2
33 DIP																			
B	2.732	0.4359	2.1117	0.4351	1.7833	0.1789	22.365	2.09	0.8393	1.1187	0.3909	0.9262	0.519	0.0166	6.5444	0.3352	0.394		
I	0.26								2.47			0.34		2290		7.7	28.2		

Table 18. Input data for the Richards Bay Winter phosphorus network. B Rows = prey, Columns = predators. B = biomass, I = import, R = respiration, E = export.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Diatoms			0.026	0.010	0.412	0.095	0.170	0.002			0.003		0.041			
2 Flagellates			0.026	0.009	0.293	0.060	0.121	0.002			0.002		0.041			
3 Bacteria					0.014	0.022	0.040	0.001		0.842						
4 HM plankton					0.000	0.000	0.000	0.000	0.117		0.000	0.000				
5 Small copepods					0.007	0.021	0.040	0.002					0.012			
6 Medium copepods						0.002	0.003	0.001					0.010			
7 Large copepods								0.001					0.010			
8 Other lg zooplankton								4.E-04								
9 Sm macrobenthos									43.160		0.016	0.076	0.038	3.223	2.590	1.084
10 Lg suspension feeder											0.006	0.048		1.257	0.161	
11 Echinoderm											0.000			0.003		
12 Mollusc														0.096		
13 Prawn & shrimp														0.018	0.010	0.005
14 Large crustacean														0.167	0.200	0.087
15 Cuttlefish															1.802	
16 Other cephalopod															0.416	1.514
17 Flatfish																
18 Gurnard																
19 Other benthic carnivorous fish															0.441	
20 Lizardfish																
21 Red tjor-tjor																
22 Pinky																
23 Other benthopelagic fish																
24 Sm pelagic fish																0.425
25 Lg pelagic fish																
26 Skates and rays																
27 Sm benthic shark																
28 Large sharks																
29 Cetaceans																
30 Susp POP			0.069	0.025	0.133	0.168	0.314	0.026	125.00	13.050	0.028	0.520				
31 Sed POP			0.017	0.002					1182		0.035	0.245	0.169	1.777		
32 DOP			1.598	0.087												
33 DIP	33.810	8.390														
B	0.0966	0.0182	0.0081	0.0012	0.0023	0.0009	0.0017	0.0019	12.237	8.1648	0.0062	0.1048	0.2011	3.4438	5.6724	2.818
I															0.84	2.58

Table 18 continued

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	R	E
1 Diatoms								31.533						1.550					
2 Flagellates								6.931						0.932					
3 Bacteria														0.184	0.183				
4 HM plankton														0.016					
5 Small copepods								0.002						0.775					
6 Medium copepods								0.001						0.350					
7 Large copepods								0.042						0.635					
8 Other lg zooplankton					0.002			0.010	0.000					0.022					
9 Sm macrobenthos	11.268	4.742	3.430	0.503	1.623	0.065	1.531			0.117	0.097				995.27				281.47
10 Lg suspension feeder			0.163	0.031	0.004	0.068				0.199					11.953				
11 Echinoderm					0.001	9.E-05				0.001					0.084				
12 Mollusc	0.128	0.009								0.017		1.E-05			0.639				
13 Prawn & shrimp	0.039	0.024	0.015	0.003	0.001	5.E-04				0.003	0.004	5.E-04			0.196				
14 Large crustacean	0.737	3.540	0.142	0.147	0.100	0.056	0.012		0.038		0.169	0.007			1.139				
15 Cuttlefish		0.346	1.111	0.214		0.060	1.361		0.062	0.095	0.026	0.025	0.819		0.538				
16 Other cephalopod		0.219	1.054	0.203		0.001			0.184	0.726	0.352	0.098	0.458		0.475				
17 Flatfish	0.812	9.851	0.906	0.355			0.064			0.441		0.007	0.023		1.637				
18 Gurnard		0.087	3.072	0.591	0.245		0.752			0.053					15.691				
19 Other benthic carnivorous fish		0.571										0.001	0.007		9.390				
20 Lizardfish		0.826							3.E-04		0.200	0.064	0.193		1.541				
21 Red tjor-tjor				0.283					0.299			0.010	0.340		1.671				
22 Pinky									0.002			0.009	0.055		0.192				
23 Other benthopelagic fish	0.668		0.516	0.496	0.626	0.008			0.496	0.160	0.129	0.187	0.514		0.379				
24 Sm pelagic fish	0.445	0.276							2.833		0.148	0.277	1.254	1.549	31.311				
25 Lg pelagic fish									0.151			0.203	0.340		3.372				
26 Skates and rays										0.059		0.383	0.029		1.401				
27 Sm benthic shark												0.138			0.986				
28 Large sharks												0.002			1.978				
29 Cetaceans												0.234			3.797				
30 Susp POP															94.789	0.770			
31 Sed POP																			
32 DOP																			0.31
33 DIP																			
B	11.86	14.058	3.0762	0.6937	1.7833	0.1288	1.6957	2.9756	0.8393	1.1187	0.3909	0.9262	0.519	0.0166	6.54	0.34	0.24		
I							0.46					0.34		229		0.77	42.2		