

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

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ABSTRACT: Penaeid prawns are targeted in the Thukela Bank shallow-water trawling grounds in south-eastern Africa. Based on previous studies, these targeted prawns are assumed to primarily use 2 large estuaries (St. Lucia and Richards Bay/Mhlathuze) as nurseries on the KwaZulu-Natal (KZN) coast, which comprise over 80 % of the estuarine habitat in the region. However, St. Lucia has been closed to the Indian Ocean since 2002 due to continued separation from the Mfolozi River, cessation of dredging required to open the inlet, reduced freshwater flow and drought conditions. To study the effects of prawn trawling and prawn nursery loss on the ecosystem, Ecopath with Ecosim models of the Thukela Bank were constructed. Models were fitted to total catch (t) for 1990 to 2009, and biomass trends were estimated by scaling Ecosim feeding interaction parameters to prey trophic level. Prawn trawling was modelled using fishing effort data. Prawn recruitment was modelled via the 'hatchery stocking' function in Ecosim simulating nursery loss along the KZN coast. Various prawn recruitment and trawling effort levels were simulated from 2010 to 2040. Decreasing prawn recruitment positively affected benthic fish and carnivorous benthos biomass and negatively affected prawn, commercial crustacean and benthopelagic fish biomass. Negative effects were exacerbated and positive effects were decreased by high versus low trawling effort. The results suggest that indirect anthropogenic and environmental factors, such as recruitment from estuarine nursery areas, can impact offshore fisheries catches. Therefore, when modelling and managing marine ecosystems, it is important to couple processes between adjacent systems, particularly for critical life-history stages.

KEY WORDS: Ecosystem modelling · Nursery habitat · Anthropogenic impact · Fishing effects · Prawn trawling · Ecopath with Ecosim

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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 & 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. 2003). For example, mangrove-lined creeks or rivers are

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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 & Kingsford 2002). 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 & 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 & 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 Kwa-Zulu-Natal (KZN) Bight, South Africa, is affected by fishing within the system and by anthropogenic changes to rivers and estuaries which flow into the system (Flemming & Hay 1988, Fennessy 1994a,b, Bosman et al. 2007, Lamberth et al. 2009, Turpie & Lamberth 2010). Penaeid prawns (*Penaeus indicus*, *Metapenaeus monoceros*, *P. monodon*) occur on the mudbank and have been targeted by prawn trawlers since the mid 1960s, although regular trawling only began in the late 1970s (Fennessy & Groeneveld 1997). The life-cycle of penaeid prawns is short (12–18 mo) and includes marine adult and larval stages and estuarine postlarval and juvenile stages (Dall et al. 1990). Postlarvae of the 3 species migrate to nurseries in spring and recruit as juveniles to the marine environment from the end of summer (Joubert & Davies 1966). The Thukela Bank prawn population is assumed to primarily use the St. Lucia estuary and/or Richards Bay/Mhlathuze estuary as

nursery areas (Forbes & Cyrus 1991, Forbes et al. 1994, Forbes & 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 & Stretch 2011). However, the inlets were separated in the 1950s, and the St. Lucia mouth needed to be continuously dredged open (Whitfield & 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 6 mo in 2007 (Whitfield & Taylor 2009, Lawrie & 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 KZN 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, we modelled the effects that prawn trawling and reduced prawn recruitment, due to the loss of St. Lucia as a prawn nursery, have had on the Thukela Bank ecosystem. In addition, the effects of a complete loss or full restoration of prawn nurseries in the region were investigated as a simulation exercise. We focused on the changes in biomass of groups that are targeted, retained as bycatch or discarded by prawn trawlers, to investigate the potential effects of reduced recruitment due to nursery loss on trawl catches.

MATERIALS AND METHODS

Model area

The Thukela Bank is an area of mud in the KZN Bight off the east coast of South Africa (Fig. 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 45 m depth, covering 560 km² (Fennessy & 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. 1). The rivers flowing into these estuaries have a combined catchment area of more than 30 500 km²

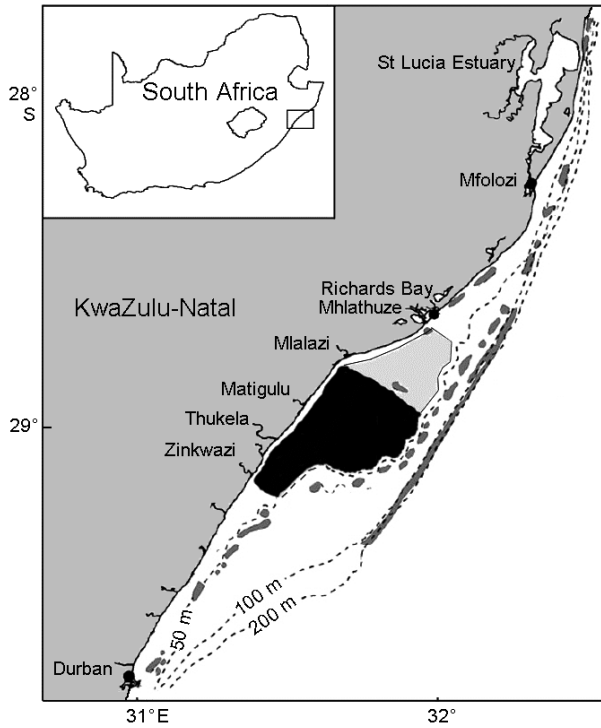


Fig. 1. Thukela Bank model area (black shading), un-trawlable reef area (light grey shading), known high-profile reefs (dark grey shading) and rivers/estuaries within the KwaZulu-Natal Bight. Adapted from Lamberth et al. (2009)

with an estimated mean annual runoff of 2.65×10^9 m³ (Division of Water, Environment and Forestry Technology 2001, Lamberth et al. 2009).

Mass-balance model construction

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). To ensure mass balance or energy balance, 2 equations are used in Ecopath to parameterise the model. The first describes the production of a functional group and its components (Christensen et al. 2008):

$$\begin{aligned} \text{Production} = & \text{catches} + \text{predation mortality} + \\ & \text{biomass accumulation} + \text{net migration} + \\ & \text{other mortality} \end{aligned} \quad (1)$$

which can be rewritten as:

$$\begin{aligned} \left(\frac{P}{B}\right)_i B_i = & Y_i + \sum_{j=1}^n \left(\frac{Q}{B}\right)_j B_j DC_{ij} + E_i + BA_i + \\ & \left(\frac{P}{B}\right)_i B_i (1 - EE_i) \end{aligned} \quad (2)$$

where $(P/B)_i$ 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 j ; DC_{ij} is the proportion of prey i in the diet of predator j ; E_i is the net migration rate; BA_i is the biomass accumulation rate for i ; and EE_i is the ecotrophic efficiency of group i . Thus, if 1 of the 4 input parameters above (B , P/B , Q/B , EE) is unknown, it can be estimated using this equation which ensures mass balance between groups.

The second equation describes the energy balance within a functional group as the fate of all consumed energy (Christensen & Walters 2004):

$$\begin{aligned} \text{Consumption} = & \text{production} + \text{respiration} + \\ & \text{non-assimilated food} \end{aligned} \quad (3)$$

where respiration is the assimilated consumption not used for production (Christensen et al. 2008), and non-assimilated food is the proportion of food that is excreted. These equations allow the identification of mutually incompatible flow estimates and produce a snapshot of groups and the flows between them in the ecosystem (Christensen et al. 2008). Thus the foodweb was constructed using diet composition, fisheries catch by gear and 3 of the following input parameters for each functional group: biomass (B , t km⁻²), production/biomass ratio (P/B , yr⁻¹), consumption/biomass ratio (Q/B , yr⁻¹), ecotrophic efficiency (EE , proportion), which represents the proportion of production utilised in the system (e.g. consumed, biomass accumulation, migration, export).

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). We therefore constructed 3 Thukela Bank models for this purpose based on maximum, minimum and mean biomass values available from literature and recent research trawls: the max B , min

B and mean B models. The models were based on data from the year 1990, the first year of reliable prawn trawl catch and effort statistics. Nineteen functional groups modelled as aggregates of their constituent species were chosen (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m479p143_supp.pdf). These included detritus, phytoplankton, 7 invertebrate groups (zooplankton, detritivorous benthos, carnivorous benthos, commercial crustaceans, juvenile prawns, adult prawns and cephalopods), 5 fish groups, 4 elasmobranch groups and 1 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).

Prawn input parameters

All 3 prawn species (*Penaeus indicus*, *Metapenaeus monoceros*, *P. monodon*) were aggregated into 1 multi-stanza group because catch data from prawn trawlers were reported as an aggregated group. Eco-path assumed that body growth followed a von Bertalanffy curve and that the population had reached a stable age-size distribution (Christensen & Walters 2004). The biomass of juvenile prawns (B_{juv}) was calculated using:

$$B_{\text{juv}} = b_{\text{juv}} \frac{B_{\text{adult}}}{b_{\text{adult}}} \quad (4)$$

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

$$b_s = \frac{\sum_{a=a_{s,\min}}^{a_{s,\max}} l_a w_a}{\sum_{a=1}^{a_{\max}} l_a w_a} \quad (5)$$

where $a_{s,\min}$ and $a_{s,\max}$ 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 . l_a can be calculated using:

$$l_a = e^{-\left(\sum Z_a - a \frac{BA}{B}\right)} \quad (6)$$

where $\sum Z_a$ 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:

$$w_a = (1 - e^{-K_a})^3 \quad (7)$$

where K_a is the von Bertalanffy growth parameter for age a . Q/B of the juvenile stanza is calculated in a similar way. Thus input parameters for the multi-stanza groups are B_{adult} , Z_{adult} , Z_{juv} , K , BA/B , Q/B_{adult} . Since no prawn biomasses were available in the literature, we constructed replicate models 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 3.44 t 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 1. The total mortality of juveniles was set at 0.001 yr⁻¹ so that density-dependent juvenile survival could be varied as a recruitment or 'stocking' rate detailed in 'Prawn recruitment time series' below (Christensen et al. 2008). The relative biomass accumulation rate (BA/B) was unknown and therefore the default value of 0 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 3 K parameters were used in the min B, mean B and max B models, and biomass predictions were compared.

Other input parameters

Riverine detritus import was calculated by first calculating the sediment concentration in the Thukela

Table 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	Source
a	6 mo	Benfield et al. (1990)
Z_{adult}	2.73, 5.38, 7.57 yr ⁻¹	Gribble (2003), Okey et al. (2004), Freire et al. (2008)
Z_{juvenile}	0.001 yr ⁻¹	Christensen et al. (2008)
Q/B_{adult}	37.9 yr ⁻¹	Gribble (2003)
K	1.6, 1.9, 2.73	Jayawardane et al. (2002), Gribble (2003)
BA/B	0	Christensen et al. (2008)

River outflow using an average annual sediment yield of 9.3 million t yr⁻¹ (Taljaard et al. 2004) and a total flow in 1990 of 2.174×10^{12} l (DWAf 2004) which gave 4.28 g l⁻¹. This was assumed to be total suspended solids (TSS). Using the relationship between TSS and particulate organic carbon (POC) reported by Meybeck (1982), we assumed that POC was 8.4 % of TSS, which gave a POC concentration of 0.359 g 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 1666 t km⁻² yr⁻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 unpubl. 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 3 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 (see Table 7 for biomasses). Other parameters (*P/B*, *Q/B*, *EE*) can be found in Table 2, and diets in Table 3. Diets of cetaceans, apex sharks, benthic-feeding sharks and pelagic-feeding sharks were available for the KZN Bight (see Table 3 for data sources). Prey that did not occur in the model area, e.g. reef fish, were assigned as import in diets.

Time-dynamic model

Approach

The ecosystem was dynamically modelled over time using the temporal simulations tool, Ecosim, in EwE. Ecosim expresses biomass dynamics over time

Table 2. Basic input parameters for trophic groups in the 1990 Thukela Bank models. *P/B*: production/biomass, *Q/B*: consumption/biomass, *EE*: ecotrophic efficiency, na: not applicable. Landings and discards are combined for all fisheries. (–) Parameters estimated by Ecopath

Groups	<i>P/B</i> (yr ⁻¹)	<i>Q/B</i> (yr ⁻¹)	<i>EE</i>	Landings (t km ⁻² yr ⁻¹)	Discards (t km ⁻² yr ⁻¹)
Cetaceans	0.60 ^a	10.00 ^a	0.76 ^v		<0.001
Apex sharks	0.13 ^b	1.45 ^m	0.1 ^w	0.002	<0.001
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	<0.001
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	<0.001
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	<0.001	0.153
Benthic benthos-feeding fish	1.20 ^h	6.00 ^t	–	0.002	0.018
Cephalopods	3.00 ⁱ	10.88 ^a	–	0.003	0.013
Adult prawns	7.57 ^p	37.90 ^y	–	0.138	<0.001
Juvenile prawns	0.001 ^y	–	–	–	–
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	na	–	–	–
Detritus	na	na	–	–	–

^aToral-Granda et al. (1999); ^bDudley & Simpfendorfer (2006); ^cCheung et al. (2002); ^dShannon et al. (2003); ^eDe Paula e Silva et al. (1993); ^fcalculated using Olbers & Fennessy (2007); ^gGasalla & Rossi-Wongtschowski (2004); ^hSanchez & Olaso (2004); ⁱOkey et al. (2004); ^jOkey & Meyer (2002); ^kRocha et al. (2007); ^lOpitz (1996); ^mAitken (2003); ⁿcalculated using Dudley & Simpfendorfer (2006) and Cliff et al. (1988); ^ocalculated using Allen & Wintner (2002) and Wintner (1993); ^pFreire et al. (2008); ^qcalculated using van der Elst (1976); ^rcalculated using Olbers & Fennessy (2007) and van der Elst (1993); ^scalculated using van der Elst & Adkin (1991) and Joubert (1981); ^tAmorim et al. (2004); ^ucalculated using *P/B* from Okey et al. (2004) and *P/Q* from Buchan & Smale (1981); ^vShannon et al. (2000); ^wAyers & Scharler (2011); ^xChristensen et al. (2008); ^ysee Table 1

Table 3. Initial diet composition (%) for the Thukela Bank models. Rows represent prey, and columns represent predators. Groups 18 and 19 refer to phytoplankton and detritus and therefore do not require a predator column. Values for each group (indicated by group number) were calculated using 1: Young & Cockcroft (1994), Cockcroft & Ross (1990); 2: Cliff et al. (1989), Cliff & Dudley (1991a,b), Aitken (2003); 3: Smale & Compagno (1997), de Bruyn et al. (2005), Dudley et al. (2006); 4: Dudley & Cliff (1993), Allen & Cliff (2000); 5: Mackinson (2002); 6: van der Elst (1976); 7: Toral-Granda et al. (1999); 8: Hajisamiae (2009); 9: Rizkala et al. (1999), Hajisamiae (2009); 10: Amorim et al. (2004); 11: Castro & Guerra (1990); 12: Gribble (2003); 13: see 'Prawn input parameters' section; 14: Okey & Meyer (2002); 15: Okey et al. (2004); 16: Gasalla & Rossi-Wongtschowski (2004); 17: Toral-Granda et al. (1999). Import: prey species that do not occur on Thukela Bank. (–) Prey not part of predator's diet

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Cetaceans	–	13.7	1.6	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–
2 Apex sharks	–	2.7	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–
3 Benthic-feeding sharks	–	33.6	14.3	9.5	–	–	–	–	–	–	–	–	–	–	–	–	–
4 Pelagic-feeding sharks	–	1.1	1.9	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–
5 Skates and rays	0.7	22.2	11.2	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–
6 Large pelagic fish	6.1	4.8	3.4	4.8	–	4.2	–	–	–	–	–	–	–	–	–	–	–
7 Small pelagic fish	39.7	1.9	8.8	45.7	2.7	20.0	–	–	–	–	–	–	–	–	–	–	–
8 Benthopelagic carnivorous fish	6.9	0.5	9.5	11.8	–	7.1	–	–	–	–	–	–	–	–	–	–	–
9 Benthopelagic benthos-feeding fish	16.3	3.6	5.5	10.1	–	55.0	–	77.0	1.0	1.0	34.7	–	–	–	–	–	–
10 Benthic benthos-feeding fish	0.5	–	1.2	1.9	5.2	–	–	–	10.6	1.0	–	–	–	–	–	–	–
11 Cephalopods	24.9	0.4	26.3	2.2	12.2	4.2	–	–	–	–	0.1	–	–	–	–	–	–
12 Adult prawn	–	–	0.1	–	1.0	–	–	17.0	20.6	5.0	–	0.5	–	1.0	–	–	–
13 Juvenile prawn	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14 Commercial crustaceans	–	0	0.7	0.2	10.5	–	–	–	–	–	17.9	–	–	0.5	–	–	–
15 Carnivorous benthos	–	0.2	2.1	–	32.2	1.4	9.0	4.0	46.1	60.6	24.5	29.0	–	10.8	5.0	–	–
16 Detritivorous benthos	–	–	6.2	–	32.0	–	1.0	–	20.2	27.7	22.9	34.5	–	65.5	38.6	–	–
17 Zooplankton	–	–	–	–	–	–	78.0	2.0	1.6	–	–	1.0	–	–	–	–	5.0
18 Phytoplankton	–	–	–	–	–	–	3.0	–	–	–	–	–	–	–	–	–	95.0
19 Detritus	–	–	–	–	–	–	9.0	–	–	4.7	–	35.0	–	–	56.4	95.0	–
Import	4.9	15.4	7.1	10.3	4.2	8.1	–	–	–	–	–	–	100	22.2	–	5.0	–

using a series of coupled differential equations derived from the production equation of Ecopath:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) B_i \quad (8)$$

where 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 ($F_i = \text{Yield}_i/B_i$); and 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_0), i.e. 1, is equal to the base fishing mortality rate from Ecopath ($F_0 = \text{catch}/\text{Ecopath biomass}$) and therefore can drive the biomass dynamics of each group over time using the time series of relative fishing effort. The first summation in Eq. (8) 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 feeding interaction value (v) 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. A v -value 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. The consumption rate of predator j feeding on prey i (Q_{ji}) is calculated by:

$$Q_{ij} = \frac{u_{ij}v_{ij}B_iB_jT_iT_jS_{ij}M_{ij}/D_j}{v_{ij} + v_{ij}T_iM_{ij} + u_{ij}M_{ij}B_jS_{ij}T_j/D_j} \quad (9)$$

where u_{ij} is the effective search rate of predator j for prey i , v is the feeding interaction value, T is relative feeding time, S_{ij} is the user-defined long-term forcing effect, M_{ij} is the mediation forcing effect, and D is the effect of prey handling time on predator consumption rate. 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.

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' were in operation at Zinkwazi beach in the model area, targeting sharks potentially dangerous to bathers. Prawn trawling effort data were available for 1990 to 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 were 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 to 2009 (DAFF/NMLS unpubl. data). A time series of relative effort for each fishery was calculated using 1990 as base effort rate (Fig. 2). The length of shark nets per year was deemed an unsuitable measure of fishing effort (since CPUE varies widely) and was therefore not included.

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 estuary were assumed to be 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 *Penaeus indicus* with smaller catches of *P. monodon* and *Metapenaeus monoceros*, all of which were targeted on the Thukela Bank (Forbes & Demetriades 2005). Secondly, postlarvae populations of Thukela Bank target species in Kosi Bay have been shown to be almost absent (Forbes et al. 1994). Thirdly, Durban Bay postlarvae populations been shown to be 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. These estuaries 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, of the ~2% of tagged prawns recovered on the Thukela Bank, 1.08% of prawns had been tagged in Richards Bay and 0.97% of prawns had been tagged in St. Lucia the previous season (Forbes & Demetriades 2005). Therefore closing either St. Lucia or Richard Bay/Mhlathuze is assumed to almost halve the recruit-

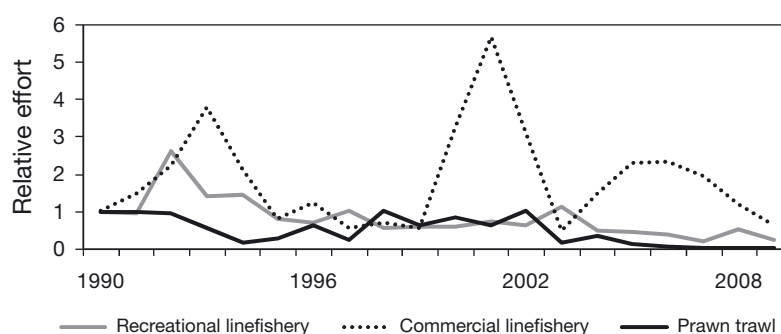


Fig. 2. Effort of the prawn trawl, commercial linefishery and recreational linefishery, relative to their own base rate in 1990, for 1990 to 2009 in the modelled area. Prawn trawl effort ranged between 12 and 442 fishing days. Commercial linefishing effort ranged between 708 and 8432 fishing hours. Recreational linefishing effort ranged between 2864 and 36 024 angler outings

ment rate of prawns to the Thukela Bank. 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 of 1991 (Christensen et al. 2008). The forcing function was left at 1.0 for 1990 to 2001 and was decreased to 0.5, i.e. 50%, for 2002 to 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, we used the 'recruitment power' parameter (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 to 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.

Catch time series

Catches of specific species by each gear type were assigned to model groups using habitat (e.g. benthic versus benthopelagic) and diet information (e.g. carnivores versus benthivores) from the literature (see Table 3 for sources). Landings by prawn trawlers for 1990 to 2009 were provided by DAFF (Fig. 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 to 2009 using the methods detailed in Supplement 2. Commercial linefishery landings for 1990 to 2009 were available from the NMLS (DAFF unpubl. data) (Fig. 3). Recreational linefishery landings were available for 1990 to 2009 (DAFF/NMLS) (Fig. 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 to 2009 were provided by the KZN Sharks Board (Fig. 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 organ-

isms were classed as discards. Further information on calculations of catch for the models can be found in Supplement 2.

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 mostly 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, we compared 2 methods. 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 4). The second method, which we term the 'TL scaling method', used values for each predator–prey interaction which were scaled by the trophic level (TL) of each prey group (Table 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.

Predicted biomasses are sensitive to feeding interaction values (v) in Ecosim. Therefore, because no biomass time series were available for fitting, feeding interaction values from each method were compared for each group, and the best were 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 for the years 1990 to 2009 with relative fishing effort time series.

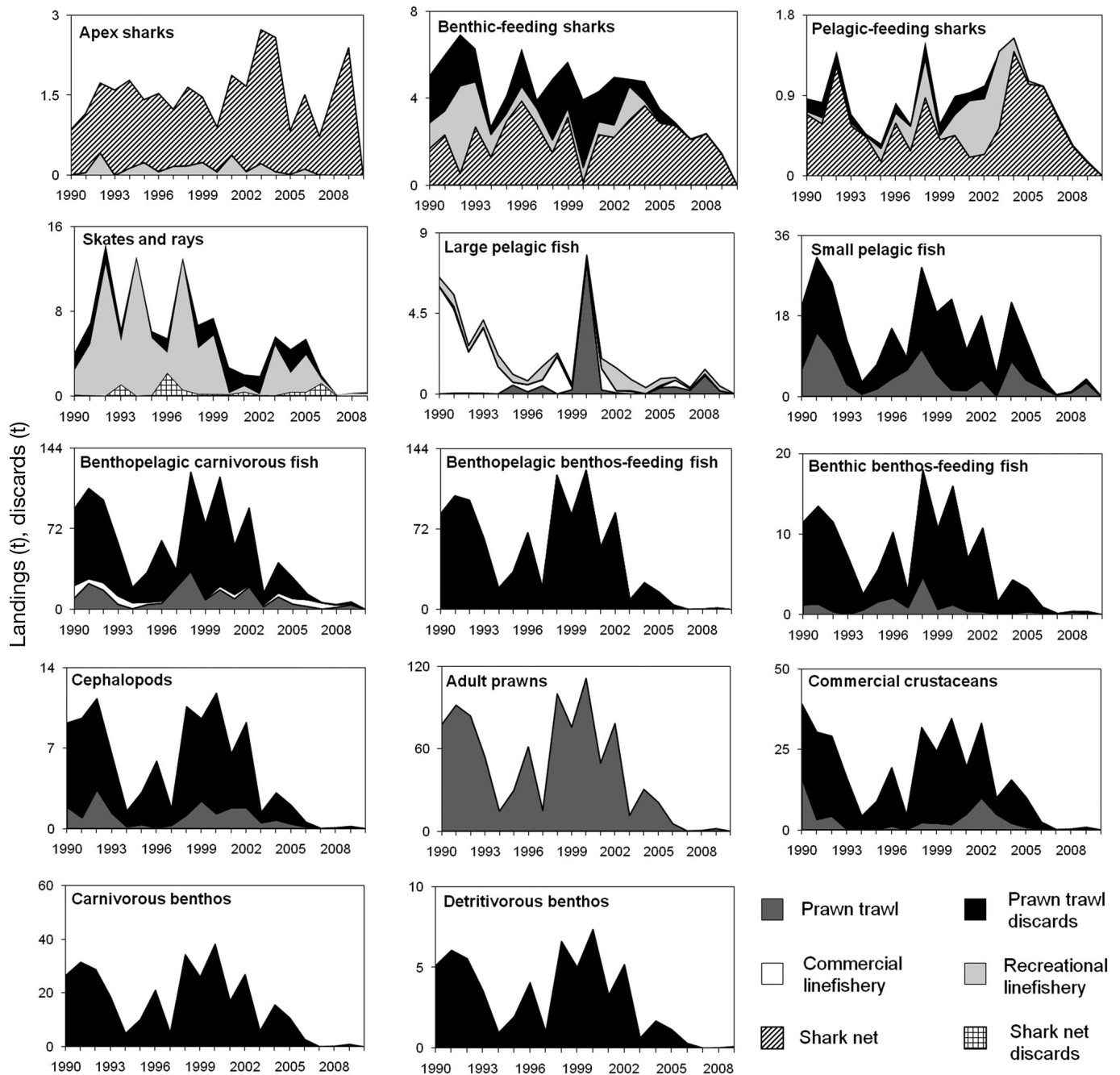


Fig. 3. Landings (t) and discards by fishing gear for all fished groups included in the models. Note different scales on y-axes

(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.

Scenarios

Once the best fit to catch data was achieved and plausible 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 the 50 yr period 1990–2040 under various scenarios

Table 4. Feeding interaction values calculated by the Ecosim fitting routine for the 30 most sensitive predator–prey interactions in each model. A v-value of 1 indicates bottom-up control while a v-value of 100 indicates top-down control. Values >100 represent feeding interaction values calculated by Ecosim over 100. B: biomass

Predator	Prey	Min B	Mean B	Max B
Cetaceans	Small pelagic fish	>100	>100	>100
Apex sharks	Cetaceans	>100	>100	>100
	Benthic-feeding sharks	>100	2	2
	Skates and rays	1	2	2
	Large pelagic fish	2	2	>100
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
Skates and rays	Cephalopods	1	1	1
	Commercial crabs	>100	>100	>100
	Detritivorous benthos	>100	1	2
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
	Cephalopods	>100	2	>100
Small pelagic fish	Detritus	1	2	2
Benthopelagic carnivorous fish	Benthopelagic benthos-feeding fish	2	1	1
Benthopelagic benthos-feeding fish	Adult prawns	1	1	1
	Carnivorous benthos	>100	>100	>100
	Detritivorous benthos	1	>100	2
Benthic benthos-feeding fish	Benthopelagic benthos-feeding fish	1	1	1
	Carnivorous benthos	>100	2	2
	Detritivorous benthos	2	1.39	>100
Cephalopods	Benthopelagic benthos-feeding fish	1	1	1
	Commercial crabs	2	1	2
Adult prawn	Carnivorous benthos	>100	>100	>100
	Detritivorous benthos	2	1	1
	Detritus	>100	>100	>100
Commercial crabs	Carnivorous benthos	2	11	>100
	Detritivorous benthos	1	1	>100
Carnivorous benthos	Carnivorous benthos	>100	43	>100
	Detritivorous benthos	>100	>100	>100
	Detritus	1	2.84	1
Detritivorous benthos	Detritus	>100	>100	>100
Zooplankton	Phytoplankton	>100	>100	1

(Table 6). Prawn trawling effort in 1990 (423 effective fishing hours) and 2009 (17 effective fishing hours) was used to test the effects of 'high' and 'low' trawling effort (Fig. 2). 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, we assumed that prawn recruitment could return to the pre-closure level, i.e. 100 %.

RESULTS

1990 Thukela Bank mass-balance models

The 3 models (max B, mean B 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 & Heemstra 1986), small pelagic fish partly feed outside the model area. Energy flows of benthic benthos-feeding fish were balanced by decreasing

Table 5. Feeding interaction values calculated by the trophic level (TL) scaling method for each model. Values were used for all interactions in which the group was a prey. B: biomass

	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

the percentage of this group 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 & 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 7). Diagrams depicting biomass flows for each model can be found in Figure S1 in Supplement 1. Benthos groups (adult prawns, commercial crabs, carnivorous and detritivorous benthos) dominated the ecosystem in terms of bio-

mass in all models (65 to 69% of total biomass). Most group biomasses were lowest in the min B and highest in the max B model, except top predators (Table 7). Consequently, a similar pattern was seen for total system biomass (excluding detritus) (Table 7). The net system production (the difference between total primary production and total respiration) was negative in all models and decreased from $-521 \text{ t km}^{-2} \text{ yr}^{-1}$ in the min B model to $-1358 \text{ t km}^{-2} \text{ yr}^{-1}$ 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 1) were used in the sensitivity analyses. Thus the models were not sensitive to these prawn parameters.

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 8). The models produced similar fits to each other and were able to reproduce trends and, in general, magnitudes of observed catches from 1990 to 2009 (Fig. 4). Better fits were achieved for groups caught primarily by prawn trawlers (Fig. 4).

Table 6. Scenarios carried out in Ecosim involving changes to prawn recruitment level and prawn trawl effort from 2010 to 2040. The '1990 level' refers to the highest trawl effort, and the '2009 level' refers to the lowest trawl effort

	Scenario	Recruitment level (%)	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	No trawling
5	St. Lucia opens, trawling stops	100	No trawling
6	St. Lucia and Richards Bay/Mhlathuze nursery areas closed, trawling stops	5	No trawling
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

Table 7. Biomasses (B, 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

To decide which feeding interaction 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 to which most groups were sensitive 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 of >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 in Ecosim simulations. We assumed that detritivorous benthos was 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 among 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 detritivorous benthos in Ecosim simulations; 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 inter-

actions can be found in Table S2 in Supplement 1. 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. 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. 5). Most groups were predicted to increase in biomass from 1990 to 2009 by all models (Fig. 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. Thus v -values from the TL scaling method were preferred for further analyses.

Table 8. Sum of squared deviations (SS) of all functional groups after each step in the fitting procedure for the 3 Thukela Bank models. B: biomass, TL: trophic level

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

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

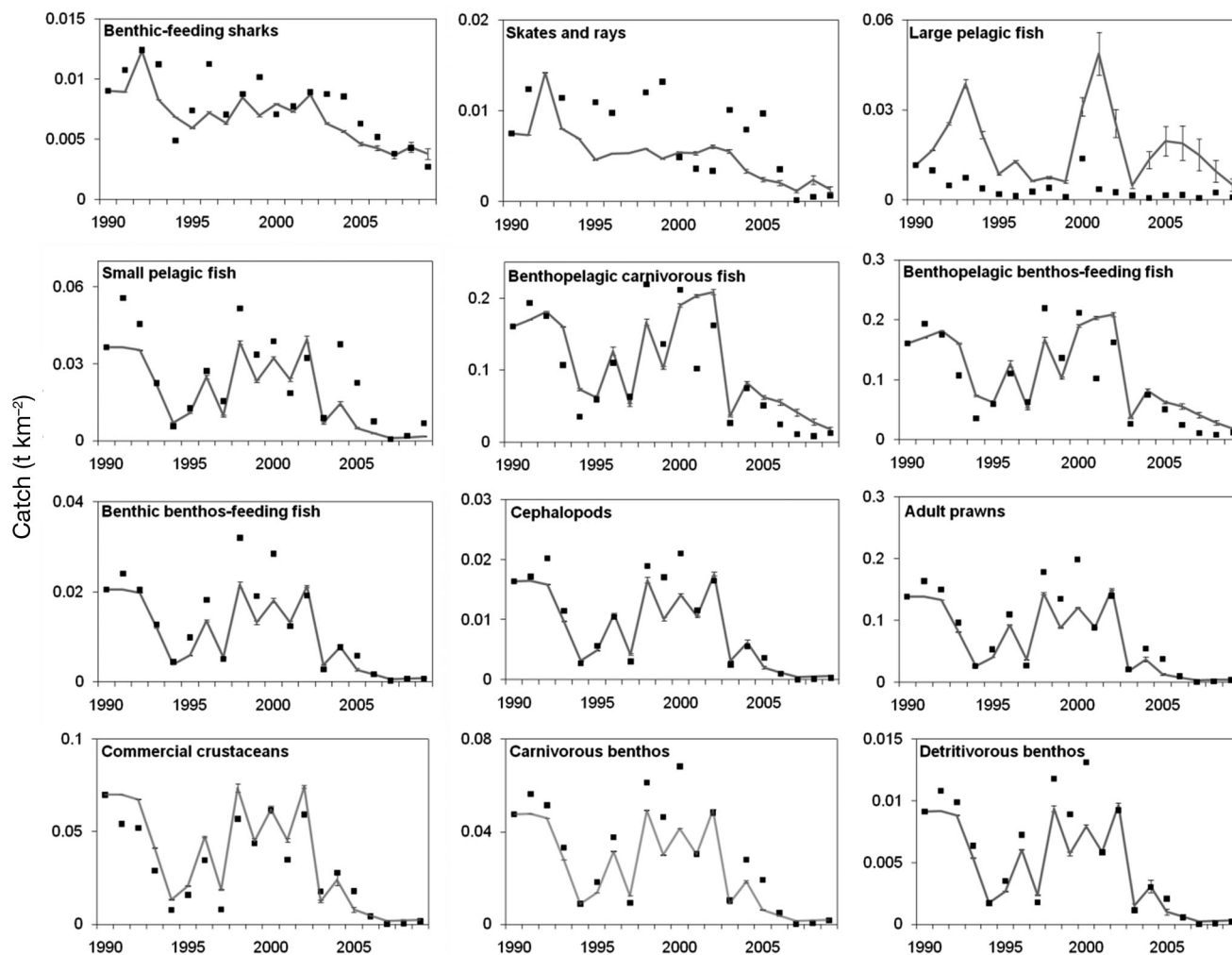


Fig. 4. Fits to catch (t km^{-2}) data averaged over all fitting methods and models ($n = 6$). Lines represent model predictions, squares represent observed catches, and error bars represent ± 1 SD. Note different scales on y-axes

scenarios (Fig. 6). Biomasses of groups remained relatively stable from 2009 to 2040 under the scenario of low trawling effort and St. Lucia estuary being closed (50% prawn recruitment). The largest changes in relative biomass were a 4% increase in benthic benthos-feeding fish and 4% decrease in benthopelagic carnivorous fish (Fig. 6). However, when both prawn nurseries were lost (5% recruitment), simulations predicted a decrease in prawn biomass of 54% (Fig. 6). Simulations in which all prawn nurseries were available (100% recruitment) predicted a 36% increase in prawn biomass (Fig. 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. 6). Benthopelagic carnivorous and benthopelagic benthos-feeding fish were impacted negatively by a decrease in prawn

recruitment as they both predate on prawns (Fig. 6). 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. 7). Exploitable biomass was highest when St. Lucia was open (100% recruitment) and lowest when both St. Lucia and Richards Bay/Mhlathuze were no longer sources of recruitment (5% recruitment; Fig. 7).

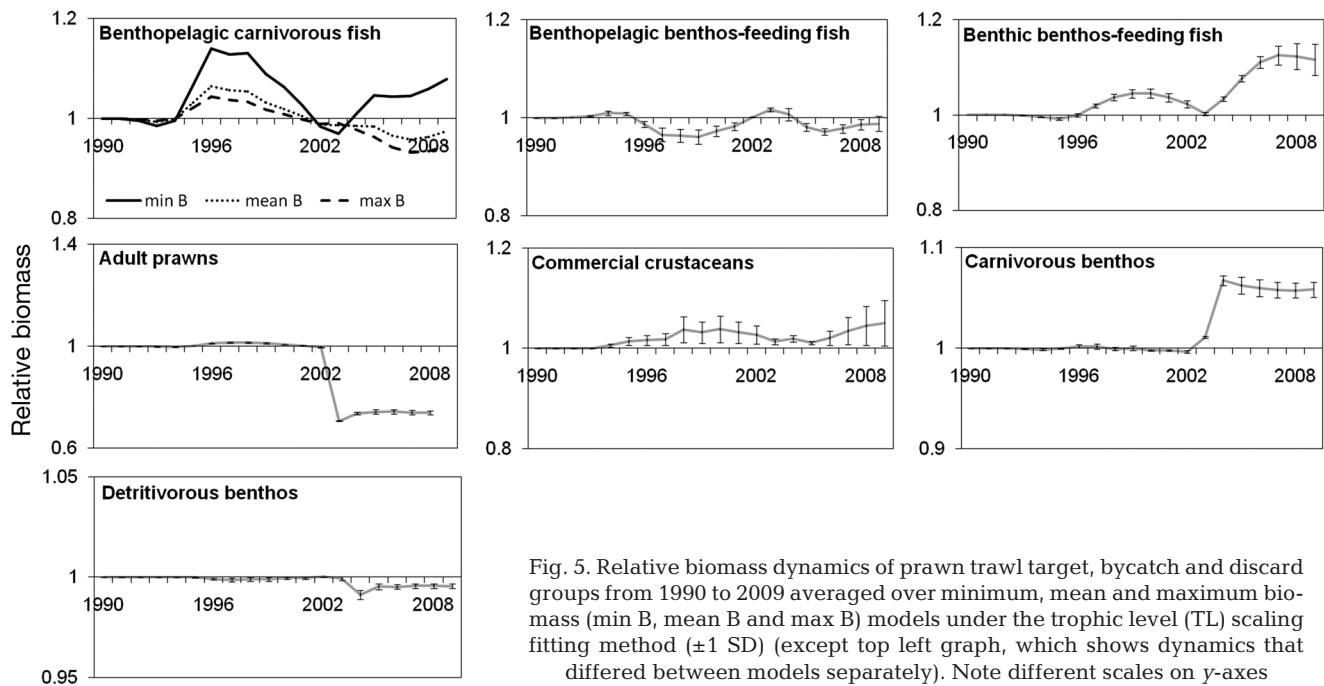


Fig. 5. Relative biomass dynamics of prawn trawl target, bycatch and discard groups from 1990 to 2009 averaged over minimum, mean and maximum biomass (min B, mean B and max B) models under the trophic level (TL) scaling fitting method (± 1 SD) (except top left graph, which shows dynamics that differed between models separately). Note different scales on y-axes

Effects of prawn trawling effort (2010–2040 scenarios)

Biomass dynamics predicted by all models were the same under low trawling effort (2009 level) and 0 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. 6). Differences in relative biomass change between low and high trawling effort were greatest for benthic benthos-feeding fish and benthopelagic carnivorous fish (Fig. 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. 7). Lower biomasses were predicted by all models in scenarios with high trawling effort compared to low trawling effort (Fig. 7).

DISCUSSION

Anthropogenic activities occurring within and outside the Thukela Bank affected the biomass of functional groups in the ecosystem. The 3 models of the 1990 Thukela Bank ecosystem based on minimum, maximum and mean biomasses predicted that the system was dominated by benthos groups. This agrees with ecosystem models of the greater KZN Bight (Ayers & Scharler 2011). However, the estimation of biomasses of high and low TL groups with Ecopath was not ideal, as the biomass changes of these groups were not constrained well (Christensen & Walters 2004). By fitting the models to catch data using fishing effort and prawn recruitment time series and calculating feeding interaction values (v) scaled by prey TL between 1 and 5, we were able to reproduce observed catches and expected biomass trends.

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 in response to changes in catch. Similarly, the min B model predicted different relative biomass changes to the mean B and max B models for commercial crabs and benthopelagic carnivorous fish under high trawling effort with 100%

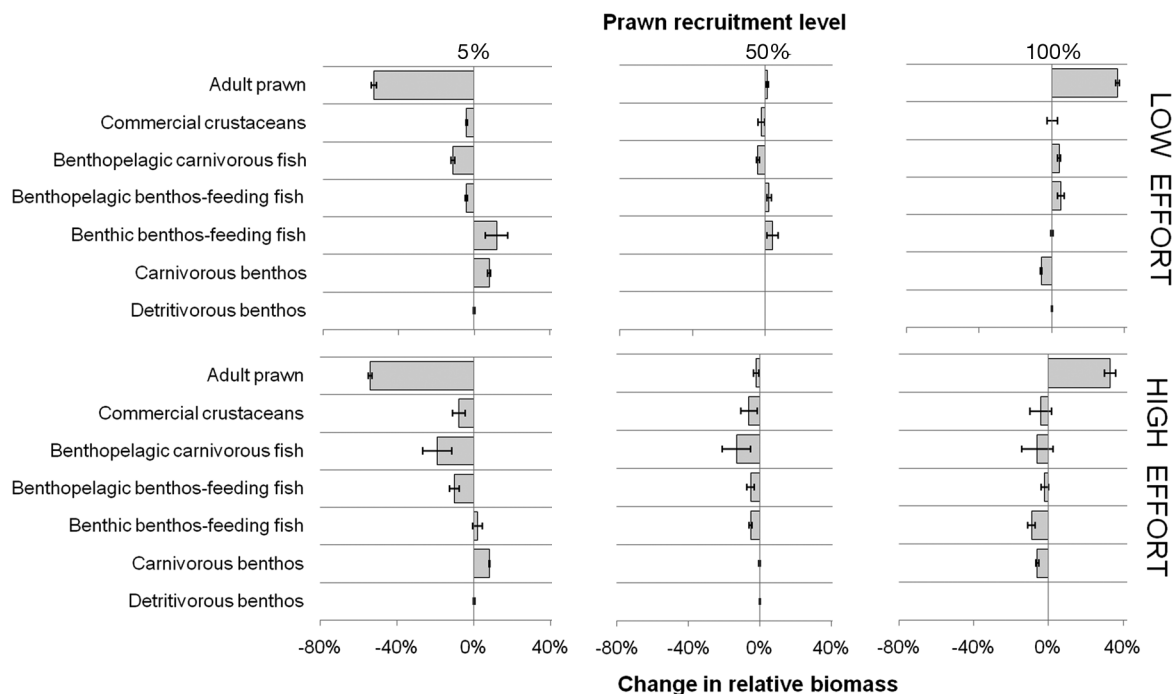


Fig. 6. Biomass in 2040 relative to 2010 of groups caught by prawn trawlers in 6 scenarios of various prawn recruitment and trawling effort levels. Bars represent average over maximum, mean and minimum biomass (max B, mean B and min B models), and error bars represent ± 1 SD

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. These models could incorporate recruitment of fish species to the Thukela Bank from estuaries 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 *Penaeus indicus*, *P. monodon*, and to a lesser extent *Metapenaeus 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 the availability of alternative nurseries while St. Lucia is closed. Vivier & Cyrus (2009) suggested that 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 the 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 the St. Lucia estuary. Therefore, we regard the decrease in prawn recruitment due to the loss of prawn nursery area 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 small populations in smaller neighbouring estuaries such as the Matigulu (Swemmer 2010) and Thukela (DWAF 2004) that may serve as seed populations. In

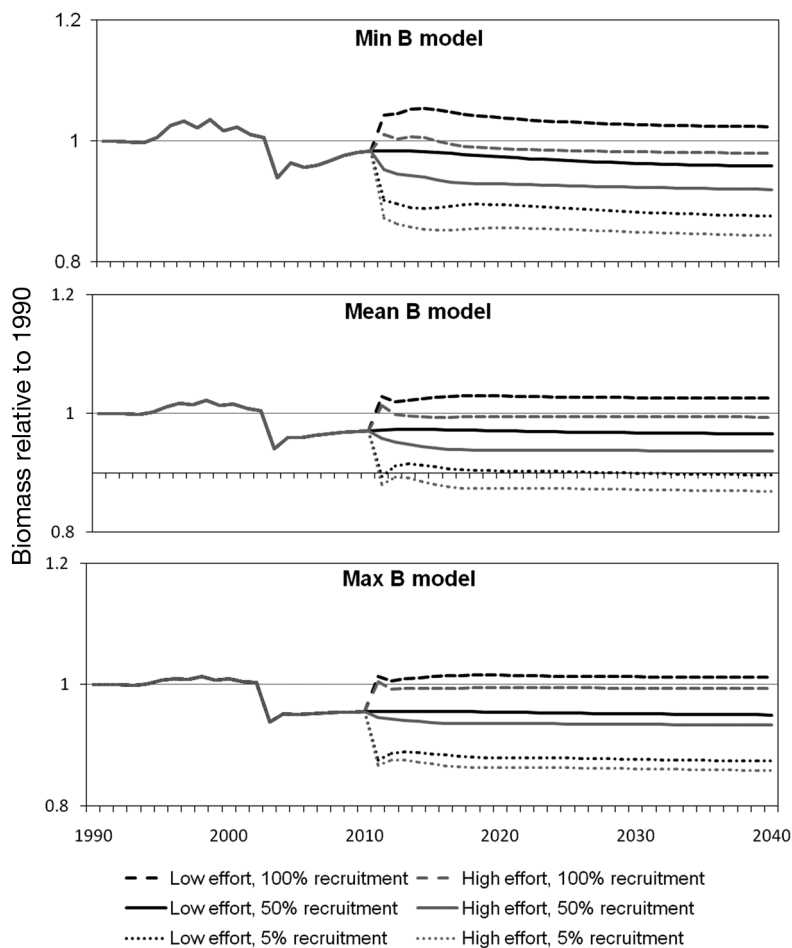


Fig. 7. Change in relative total exploitable biomass (B) between 1990 and 2040 for each model and scenario

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 & 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, we can examine the potential indirect effects of prawn nursery changes on trawl catches on the Thukela Bank. 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 to 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 catches over the past 40 yr (Hamasaki & 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 & 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.

Our models 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. 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.

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