



Water for a Healthy Country

A comparative analysis of coastal fishery food webs in the Great Barrier Reef region

Peter C. Gehrke

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Executive Summary

The waters of the Great Barrier Reef lagoon have been increasingly subjected to nutrient enrichment and increasing sediment loads from coastal river catchments over the past 150 years, posing a threat to the coral reef ecosystem and the fisheries and tourism industries within the region. Substantial efforts are now being made to change land use practices to reduce contaminant loads to the reef.

Four ecosystem models were developed, for the Wet Tropics, Burdekin, Fitzroy and Burnett-Mary natural resource management regions, as a step toward quantifying the food web processes that support coastal fish production within the GBR, identifying differences in those processes among climatic regions, and assessing ecosystem components that are most sensitive to changes in nutrient delivery.

Fishery catches are dominated by piscivorous species that rely predominantly on pelagic food web pathways, and prawns which rely on benthic pathways, whilst the Burnett-Mary region also provides large catches of detritivorous and herbivorous fish that benefit from primary production by the extensive seagrass beds in this region.

Diagnostic indices for coastal food webs displayed strong positive and negative correlations with catchment indicators related to mean annual rainfall and discharge, seagrass area and land use among regions. Modelled scenarios of nutrient enrichment by 10% over 20 years suggest enhanced energy flow through pelagic food web pathways may support increased biomass of zooplanktivorous, benthivorous and piscivorous fish groups, with an increased risk of seagrass shading leading to a regime shift toward phytoplankton dominance and seagrass depletion. Modelled scenarios of nutrient reduction by 10% over 20 years suggest a reduction in both pelagic and benthic food web pathways leading to reductions in fish biomass. The magnitude of biomass changes under different nutrient scenarios varied according to the magnitude of background variation in nutrient supply and primary production in each region, with predicted changes being smallest in the Fitzroy region where the estimated background variation in primary production was greatest.

These results support the need for alternative strategies, such as wetland habitat protection, rehabilitation, and compensatory habitat construction, to sustain fish resources as improvements in catchment management reduce nutrient loads discharged to the coast. Without alternative strategies, even a modest reduction in nutrient loads discharged into coastal waters may cause a decline in fish stocks available to coastal fisheries.

This study has identified a mis-match between available water quality data and the spatial and temporal resolution of existing information on coastal ecosystems. Data availability on coastal ecosystems in the GBR is patchy in space and time, requiring a number of assumptions when aggregating data to create regional ecosystem models. This mis-match needs to be rectified to improve ability to predict ecosystem responses at higher trophic levels to changes in water quality and catchment management.

Further refinement of the models developed in this study will allow them to support the development of policy to sustain coastal ecosystems and fisheries through changes in catchment management to improve water quality.

Introduction

The effects of changes in land use and water management in coastal catchments on coastal aquatic ecosystems is of increasing concern around the world. The dual effects of modified freshwater flows to the coast, most commonly in the form of reduced flows, and increasing loads of sediments, nutrients and other contaminants discharged from rivers into coastal waters, has caused profound changes in ecosystem processes, economic productivity and amenity of coastal ecosystems (Drinkwater and Frank 1994, Caddy 2000, Gillanders and Kingsford 2002). As noted by Caddy (2000), the ecosystem effects of nutrient enrichment resulting from human activities generally predominate over effects of fishing in semi-enclosed seas, affecting both aquatic biodiversity and fisheries themselves. These effects require coordinated remedial actions within the catchment area, since fisheries management strategies do not provide effective tools for rectifying terrestrial ecosystem impacts.

These concerns are echoed in the Great Barrier Reef (GBR) region of eastern Australia where increasing loads of material entering the sea from coastal catchments are having detrimental impacts on the coral reef ecosystem, especially in the inshore waters of the reef lagoon (State of Queensland and Commonwealth of Australia 2003, Hutchings and Haynes 2005). McKergow et al. (2005a) estimate that nutrient loads to coastal GBR waters have increased 6.1 times for total phosphorus, and 4.3 times for total nitrogen, since 1850. Over the same time period, the amount of sediment discharged to the coast has increased by a factor of 8 (McKergow et al. 2005b). Efforts are now underway to mitigate future impacts and to reduce the amount of material discharged into coastal waters from reef catchments, as well as creating management zones to restrict control access to reef habitats and resources. Based on Caddy's (2000) study, changing nutrient loads to coastal waters tends to alter the size of the fishery resource available for harvest, whereas zoning and other fishery restrictions tend to focus on how the resource is allocated irrespective of its size. Furthermore, Caddy (2000) argued that increasing nutrient loads to coastal waters can actually result in increased fisheries productivity. These effects are compounded in the GBR by the historical loss in agricultural catchments of wetland habitats that serve as important nursery habitats for coastal fish production (Duke et al. 2003, Russell et al. 2000).

Three fundamental questions arise concerning the priority areas for investment to ensure the sustainability of coastal fish resources in the GBR region, and by association, the viability of coastal fisheries. These questions refer to the respective roles of coastal habitats, conservation refuges, and materials discharged from coastal catchments in supporting fish populations and production. The impact of these questions is far from trivial. For example, increased aquatic productivity resulting from elevated nutrient inputs may sustain increased catch rates without the need to create protected areas where fishing is not permitted. In contrast, reducing nutrient inputs may reinforce the need for protected areas to limit fishing mortality on remaining stocks (e.g. Ley et al. 2002). However, if wetlands and other coastal habitats can be rebuilt, they may provide a source of increased recruitment to coastal populations, and allow increased fishery production despite the reduction in nutrient loads.

Long-term, effective answers to these questions are not readily apparent and major stakeholder groups including agricultural industries, fishing industries, tourism and conservation groups hold differing opinions on the desirable outcomes and how to best achieve them.

A number of studies have investigated coastal ecosystem processes in the GBR lagoon. Robertson and Alongi (1992) documented the hydrodynamics, biogeochemistry, microbial and food web processes by which mangroves contribute carbon to coastal and marine food webs in the Burdekin and Wet Tropics regions. Coles et al. (1989), Lee Long et al. (1993) and more recent studies reviewed by Carruthers et al. (2002) and Waycott et al. (2005) examined processes influencing seagrass distribution, productivity and their contribution to food webs along the coast. Coastal wetland vegetation has been mapped by the Queensland Department of Primary Industries and Fisheries (e.g. Danaher 2005,

<http://chrisweb.dpi.qld.gov.au/chris/>). Recent studies (e.g. McKergow et al. 2005a, 2005b, Furnas 2003) have quantified the amount of nutrients and sediments discharged into coastal waters from all coastal catchments in the GBR. Webster et al. (2005, 2006) reported the biogeochemistry and nutrient dynamics of the Fitzroy estuary and Keppel Bay, whilst Connolly et al. (2005) provided the first comprehensive ecological study of the Port Curtis region. Quantitative studies of specific taxonomic groups include dugongs (Marsh et al. 2005), sea turtles (Limpus et al. 1994) crocodiles (Read et al. 2004), fish (Blaber 1980, Robertson and Duke (1990), Halliday and Young (1996), Currie and Connolly (2005), Sheaves et al. (2006) and sea birds (Hulsman et al. 1996). Comprehensive data on commercial fisheries catches since 1988 are also available from the Queensland Department of Primary Industries and Fisheries.

These and other studies provide a comprehensive source of information from which to develop ecosystem models to explore the implications for coastal food webs and fisheries resources of changes in catchment management. This report presents trophic models of coastal fishery ecosystems for four natural resource management regions adjoining the Great Barrier Reef Marine Park, and compares the models to identify information gaps, differences in ecosystem function, and possible responses to changes in catchment management beyond the traditional jurisdiction of fisheries management agencies.

Aquatic food webs are inherently complex (Woodward et al. 2005), with most representations of food web processes and linkages constituting gross simplifications of the real web in terms of biological resolution, spatial and temporal scale (Morris et al. 2005, Link et al. 2005). However, all decision-making processes, whether they concern fishery management, catchment remediation, or economic implications, involve some model of how the “system” works, whether it be an intuitive conceptual model derived from experience, or a quantitative model based on mathematical representations of the various system components (Walters and Martell 2004). This study has adopted a quantitative approach so that, in the process of developing models, inadequacies in the data, and underlying assumptions can be identified and explored, made explicit to provide a sense of the reliability of the models, and to guide future investment in data collection and model refinement.

Ecological modelling is emerging as a powerful tool to explore ecosystem responses to a number of management scenarios, not necessarily to predict outcomes with a high level of certainty, but more importantly, as a way of identifying hypotheses about how ecosystems function and to recognise where existing knowledge is deficient to provide adequate or robust scientific projections. This study describes the construction of simple conceptual and quantitative models of coastal fishery food webs, based on the regional spatial template already established for managing natural resources in the GBR region. Models were confined to coastal ecosystems on the assumption that estuaries and near-shore coastal waters receive higher concentrations of material discharged from coastal catchments compared to offshore waters, and are likely to respond more rapidly to changes in catchment management.

Methods

Study area

The Great Barrier Reef region is divided into six natural resource management regions (Fig. 1) established to help coordinate remedial actions within catchments. Characteristics of each region included in this study are summarised in Table 1. Despite having the smallest catchment area, the Wet Tropics region receives the highest rainfall and contributes the greatest annual discharge to the GRB lagoon. Population density in the Wet Tropics is almost an order of magnitude greater than in the Burdekin-Dry Tropics (hereafter referred to as the Burdekin region) or Fitzroy regions, and double the value for the Burnett-Mary. Whilst grazing is proportionally the largest land use in each region, the Wet Tropics has larger proportional allocations to conservation, forestry and cropping than the other regions.

It is emphasised that models refer to the whole coast line in each region, and not just selected estuaries that bear the name of the region. For example, the Fitzroy region as defined includes Port Curtis and Shoalwater Bay, and does not refer only to the Fitzroy estuary and adjacent coastal habitats.

Table 1. Statistical summary of catchment characteristics of natural resource management regions in the GBR:

	Wet Tropics	Burdekin	Fitzroy	Burnett-Mary
^a Catchment area (km ²)	19,646	128,095	142,949	50,816
^a Population (2001)	214,900	182,100	199,100	251,600
^a Population density (people km ⁻¹)	10.9	1.4	1.4	5.0
^b Mean annual rainfall mm (station)	3559 (Innisfail)	1122 (Townsville)	805 (Rockhampton)	1156 (Maryborough)
Cyclones crossing coast 1988-2003	6	5	0	1
Mean annual discharge (GI y ⁻¹)	23,208	9,466	9,636	6,090
^a Nature conservation and protected areas	30.1%	7.0%	15.3%	26.0%
^a Grazing	36.7%	89.4%	71.6%	51.9%
^a Forestry production	21.5%	1.1%	6.6%	17.2%
^a Cropping	6.8%	0.9%	3.2%	3.6%
^a Urban intensive	0.2%	0.0%	0.1%	0.1%
^a Other	4.7%	1.6%	14.5%	1.2%
Modelled coastal area (km ²)	1131	987	2172	1426
^c Mangroves (km ²) (%)	399 (35%)	265 (27%)	594 (27%)	254 (18%)
^d Seagrass (km ²) (%)	95 (8%)	195 (20%)	88 (4%)	1027 (73%)

^aRegional profiles from Department of Agriculture, Fisheries and Forestry (<http://www.daff.gov.au>).

^bAustralian Natural Resources Atlas http://audit.ea.gov.au/anra/atlas_home.cfm.

^cChrisweb (<http://chrisweb.dpi.qld.gov.au/chris/>).

^dLee Long et al. (1993).

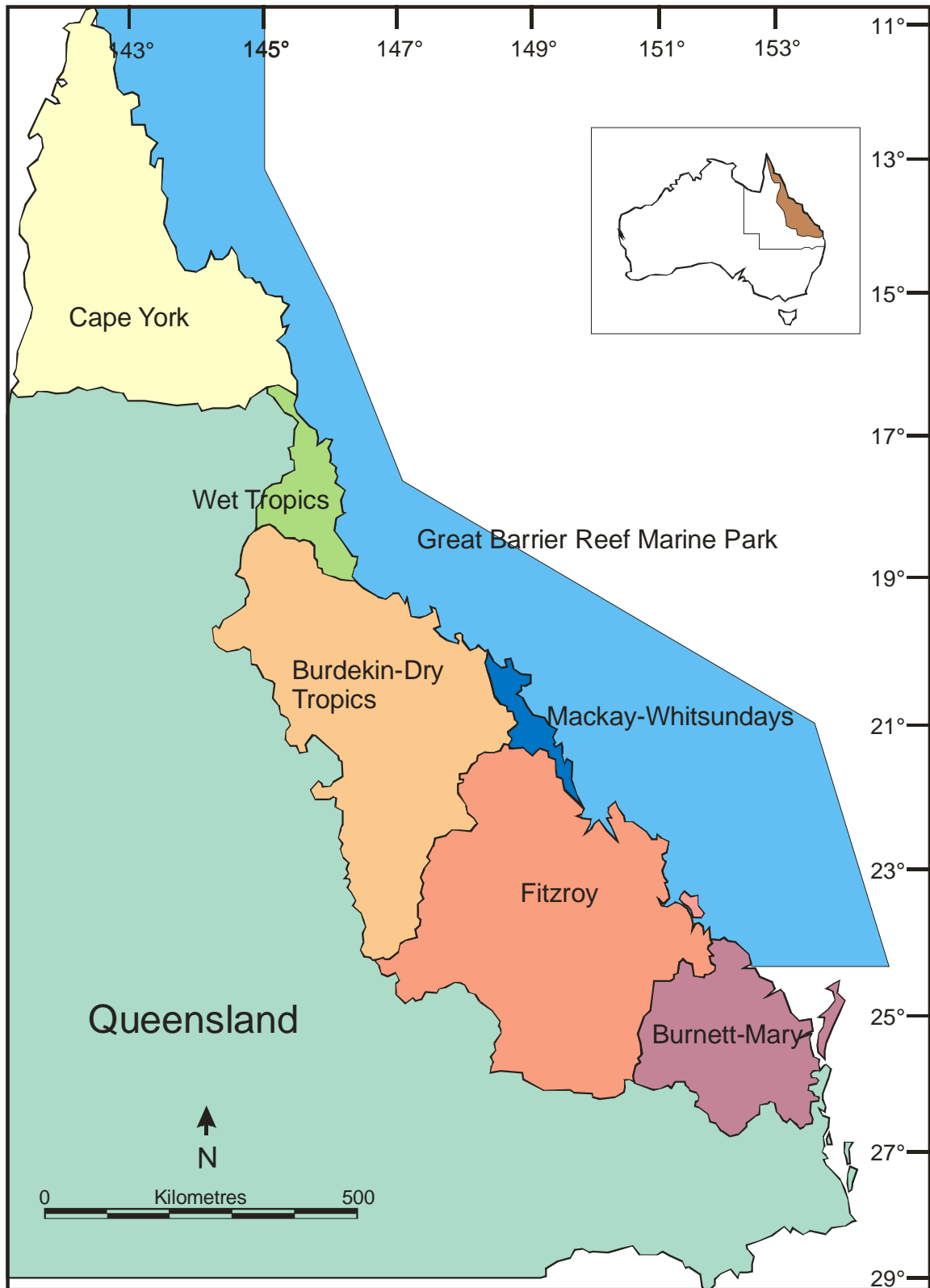


Figure 1. Map of the Great Barrier Reef region showing the six natural resource management regions. Coastal regions covered by this study include the Wet Tropics, Burdekin-Dry Tropics, Fitzroy, and Burnett-Mary regions.

With regard to coastal fish habitats, all regions except the Burdekin have significant coastal channels and island networks that increase the modelled area significantly beyond the linear coastline length. Mangrove development is most extensive in the Fitzroy region, but the proportion of coastal area covered by mangroves is greatest in the Wet Tropics. The Burnett-Mary region contains extensive seagrass beds that account for 73% of the modelled area, compared with the much smaller seagrass areas in other regions. Accordingly, coastal fish habitats in the Wet Tropics are relatively well-flushed by annual wet season runoff from many short rivers, and are dominated by mangrove areas, with seagrasses established in areas less susceptible to frequent cyclone disturbance and high sediment discharge. In contrast, the Burdekin region has similar areas of mangroves and seagrass coupled with lower discharge from predominantly a single large river, resulting in a reduced extent of sedimentation over seagrass areas. The Fitzroy region combines extremes, with the highly turbid, high tidal energy Fitzroy estuary effectively preventing establishment of seagrass (Webster et al. 2006), with estuarine primary production dominated by mangroves and microphytobenthos, whilst the reduced flushing to the south in Port Curtis allows seagrass to become established. The extent of mangrove development is further diminished in the Burnett-Mary region, where the relatively protected waters of Hervey Bay and Great Sandy Strait support extensive seagrass areas. In each of these regions, seagrass area is dynamic and can change dramatically. In the Burnett-Mary, seagrass beds were extensively damaged by a cyclone in 1992, but have since become re-established.

By restricting the scope of modelling to estuaries and coastal waters up to 2 km offshore, the habitats covered correspond most closely to the High Nutrients Coastal Strip bioregion (NA3) recognised by the Great Barrier Reef Marine Park Authority.

Model development

Assumptions

Available data on coastal aquatic ecosystems is geographically patchy within and among regions, with different sampling methods often meaning that direct comparisons cannot be made. Drawing disparate data sources together requires a number of explicit assumptions. The first assumption is that data drawn from selected studies is representative of the entire region. Secondly, because of the different time periods over which selected studies were conducted, it must be assumed that the times of sampling are actually comparable. Since different methods were used to sample fish in each major study used, it must be assumed that the probability of capture for each species is similar among methods. Representing complex ecosystem structure as a reduced set of biological compartments forces assumptions that the species represented by each compartment are ecologically homogeneous, and that aggregating taxa does not result in a loss of information on critical ecosystem interactions. Finally, where direct data are not available, it must be assumed that data drawn from similar studies outside the study region adequately reflect conditions within the study region. In many cases, these assumptions cannot be accepted blindly. For this reason, the approach adopted here is exploratory, rather than representing an attempt to develop a definitive model. The logic of this approach is embedded in the Ecopath with Ecosim version 5.1 (EwE) software to develop a top-down process for constructing ecosystem models from piecemeal sources of information (Christensen and Walters 2004, Walters and Martell 2004).

Ecopath with Ecosim is based on food web ecology using mass-balance methods that parallel mass-balance methods used to develop material budgets for coastal catchments in the Great Barrier Reef region (e.g. McKergow et al. 2005a, Ford et al. 2005), so that the ecological models developed here may potentially be merged with material transport models in the future in a similar manner to that described by Fulton and Smith (2004). Mass-balance food web models rely on being able to quantify materials such as nutrients, carbon, energy or biomass entering different trophic levels, identifying the trophic pathways through which this material flows, and the fate of material as it is exported, consumed, or metabolised at

successive trophic levels. However, as noted by Walters and Martell (2004), detailed modelling of bottom-up nutrient processes is neither necessary nor sufficient to guarantee meaningful predictions at higher trophic levels, because of the potential influence of ecological interactions that may be included or omitted from the model.

Separate models were developed for coastal waters for each of the designated natural resource management regions considered in this study, viz, Wet Tropics, Burdekin, Fitzroy, and Burnett-Mary (Fig. 1).

The Ecopath approach

Simple food web models were developed using Ecopath with Ecosim 5.1 (EwE) (Christensen et al. 2005). The Ecopath approach is based on a mass-balance model originally derived by Polovina (1984) and includes ecosystem flow analysis tools and ecosystem theory developed from Baird and Ulanowicz (1993) and Christian et al. (2005). The software has been optimised for fisheries-based applications and includes modules for modelling temporal and spatial dynamics. The modelling approach adopted allows quantitative comparison between different ecosystems to develop further insights and hypotheses about how each system functions, and how each may respond to management intervention, rather than merely describing components within a single system.

The Ecopath approach is based on a conceptual model of the biological resources in an ecosystem, represented by biomass “pools” linked by predator – prey interactions (Christensen et al. 2005). Each biomass pool constitutes a trophic group that may represent either single species or ecological guilds of similar species. Trophic groups may be further subdivided into ontogenetic stages to account for differences such as diet, growth rates or mortality at different life history stages. Importantly, Ecopath does not assume a steady state for the modelled ecosystem, rather, it assumes mass-balance during the basic time-step of the model (Christensen and Walters 2004). Fitting the model therefore estimates the biomass required at lower trophic levels to sustain biomass production at progressively higher trophic levels, as well as estimating the efficiency with which biomass is transferred between trophic levels. The Ecopath model is based on two master equations describing production and energy balance in each defined trophic group within the food web. In accord with EwE convention (Christensen et al. 2005), production, P_i , for each group i can be expressed as:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + MO_i \times B_i \quad (1)$$

where for group i , Y_i is the total fishery catch rate, $M2_i$ is the rate of instantaneous mortality due to predation, B_i represents biomass, E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate, and MO_i represents the instantaneous mortality rate from all sources other than predation and fishery mortality. Ecopath establishes one such linear equation for each trophic group defined in the food web model.

To solve Equation (1), Ecopath requires three out of the four requisite input parameters for each group: biomass; production/biomass (P/B) ratio; consumption/biomass (Q/B) ratio; and ecotrophic efficiency (EE), and solves for the remaining parameter. Ecotrophic efficiency represents the proportion of biomass from a given group that is consumed by predators. Other inputs include catch rate, net migration rate, biomass accumulation rate, assimilation rate and diet composition for each group as required. The default time-step used in Ecopath for estimating rates is one year, which corresponds to catch reporting practices in most fisheries, however, shorter time-steps may be used.

Once these equations have been solved to achieve mass-balance between trophic groups, Ecopath determines energy balance within each group according to the equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

The default units for data entry are wet weight biomass expressed as tonnes km⁻², but equivalent measurements expressed as units of carbon, nutrients or energy may be used.

Model development involves an iterative process of adjusting initial input parameters to achieve mass-balance in Ecopath. Each model was fine-tuned by adjusting biomass, P/B, and diet composition where necessary to obtain realistic ecotrophic efficiency values less than 1. Parameter adjustments focussed on those parameters drawn from external sources that involve the greatest assumptions for application in the current models, rather than adjusting empirical values derived from original data within each region.

Once a satisfactory mass-balance has been achieved in Ecopath, simulations of temporal dynamics can be performed using Ecosim. By repeating mass-balance calculations for successive time steps, Ecosim simulates changes in biomass for each trophic group, according to user-specified scenarios of system behaviour such as fishing effort or nutrient loading. Ecosim accounts for the differing vulnerability of prey between refuge habitats, such as among mangrove roots, and open habitats where the risk of predation is high, and allows for prey to switch between habitats for purposes such as feeding. Setting vulnerability for a group to a low value implies the system is controlled by nutrient-mediated bottom-up processes, whilst a high vulnerability value indicates a more top-down, predator-driven control. Each mass-balanced model was optimised for temporal simulations by adjusting vulnerability values within Ecosim to achieve a satisfactory fit against validation time series of fisheries CPUE data.

Each regional model was independently balanced, stabilised, tested and validated against commercial fisheries catch data without reference to the performance of other models to ensure objectivity of model comparisons.

A simple trophic structure with 19 compartments was adopted for initial model development to allow for maximum use of available data and to facilitate comparisons among regions (Figs 2 and 3). Vital components of the ecosystem model were: (i) capacity to reflect detrital inputs generated within the system, and imported from the catchment as DOC or POC (detritus is a required component of the Ecopath model to achieve mass-balance); (ii) a range of primary producers likely to respond to changing nutrient loads, and reflecting microbial, benthic, pelagic, intertidal and riparian production; (iii) secondary consumers representing benthic and pelagic pathways; (iv) specific fish groups representing herbivores, detritivores, zooplanktivores, benthivores or generalist carnivorous species, and piscivores; and (v) other species groups of fishery or conservation importance, such as prawns, crabs, dugong, sea turtles, crocodiles and seabirds.

Sources of information and derivation of input parameter values

The objective of this study was to estimate and quantify ecological linkages between trophic groups to feed into an economic policy model for the Great Barrier Reef region (Smajgl and Gehrke 2006). Whilst the availability of data determines that the models will have relatively coarse resolution, the underlying rationale is to derive best-available estimates that reflect the mass-balance among trophic levels. Accordingly, maximum use has been made of data obtained within each of the regions studied, with data from other regions or outside the GBR used when region-specific data were not available.

Each input value was assigned a data pedigree to indicate whether it was obtained from high resolution quantitative studies within the system of interest, extrapolated from another system, derived from another model, or estimated by the user. These values allow an overall pedigree to be calculated for each model to assess the reliability of outputs, and to help identify future data needs to refine the models. Pedigree values range from 0, for models

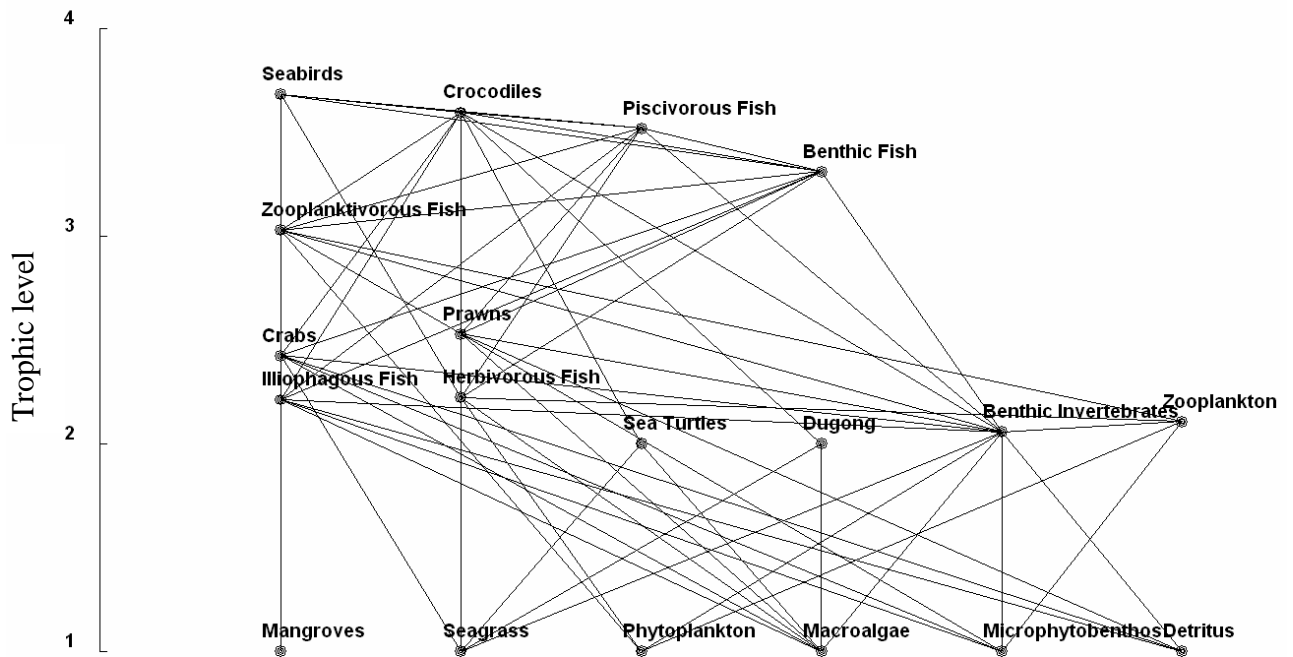


Figure 2. Connectance diagram showing food web pathways and common model structure for coastal Wet Tropics, Burdekin, and Fitzroy regional models. Flows to detritus are not shown.

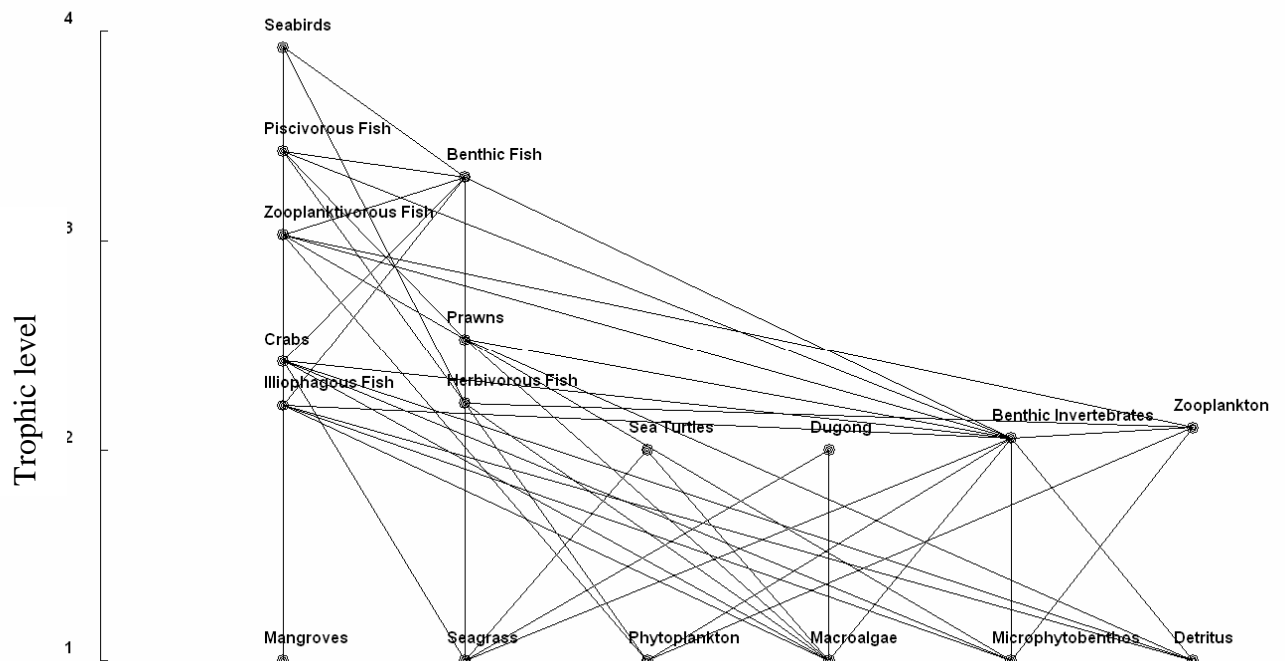


Figure 3. Burnett-Mary connectance diagram, showing the influence of removing crocodiles on food web structure.

Table 2. Information sources for trophic groups, and representative species included in the generic model base for each regional model. B: biomass; P/B: production:biomass ratio; Q/B: consumption:biomass ratio.

Trophic Group	B	P/B	Q/B	Diet	Representative taxa
Seabirds	Hulsman et al. 1996, King 1993 Adult bird weights from http://www.earthlife.net/birds/petrel-ch.html , http://www.faunarescue.org.au/wbirdchartweight.html	Opitz 1996	Opitz 1996	Houston 2006	Sooty tern Common noddy Wedge-tailed shearwater Black noddy Australian pelican Great cormorant
Crocodiles	Read et al. 2004, Webb and Messel 1978	Read et al. 2004, Webb and Messel 1978	Bolton 1989	Taylor 1979	Estuarine crocodile
Piscivorous fish	Blaber 1980, Russell et al. 2000, Coles et al. 1993 Robertson and Duke 1990 Currie and Connolly 2005, Halliday and Young 1996	Opitz 1996	Opitz 1996	Froese and Pauly 2006, Brewer et al. 1991, Salini et al. 1990. Salini et al. 1992. Salini et al. 1998. Morton et al. 1987	Barramundi Carangids Flatheads Threadfins Carcarhinids Wolf herring Lutjanids Belonids Saurids Scombrids Barracudas
Benthic feeding fish	Blaber 1980 Russell et al. 2000, Coles et al. 1993 Robertson and Duke 1990 Currie and Connolly 2005, Halliday and Young 1996	Opitz 1996	Opitz 1996	Froese and Pauly 2006, Brewer et al. 1991, Salini et al. 1990. Salini et al. 1992. Salini et al. 1998. Morton et al. 1987	Pomadasyids Soleids Tetraodontids Gerreids Sparids Sillaginids Teraponids Ariids Ambassids Leiognathids Lutjanids Gobiids
Zooplanktivorous fish	Blaber 1980 Russell et al. 2000, Coles et al. 1993 Robertson and Duke 1990 Currie and Connolly 2005, Halliday and Young 1996	Wolf et al. 2000	Wolf et al. 2000	Froese and Pauly 2006, Brewer et al. 1991, Salini et al. 1990. Salini et al. 1992. Salini et al. 1998. Morton et al. 1987	Ambassids Sygnathids Leiognathids Engraulids Clupeids Atherinids
Detritivorous fish	Blaber 1980 Russell et al. 2000, Coles et al. 1993 Robertson and Duke 1990 Currie and Connolly 2005, Halliday and Young 1996	Lin et al. 1999, Manickhand-Heilman et al. 1998, Zetina-Rejón et al. 2003, Gamito and Erzini 2005, Christian and Luczkovich 1999	Lin et al. 1999, Manickhand-Heilman et al. 1998, Zetina-Rejón et al. 2003, Gamito and Erzini 2005, Christian and Luczkovich 1999	Froese and Pauly 2006, Brewer et al. 1991, Salini et al. 1990. Salini et al. 1992. Salini et al. 1998. Morton et al. 1987	Clupeids Mugilids
Herbivorous fish	Blaber 1980 Russell et al.	Opitz 1996	Zetina-Rejón et al. 2003, Vega-	Froese and Pauly 2006,	Hemiramphids Girellids

	2000, Coles et al. 1993 Robertson and Duke 1990 Currie and Connolly 2005, Halliday and Young 1996		Cedejas et al. 2001,	Tibbetts and Carseldine 2005, Morton et al. 1987	Monacanthids Scatophagids
Sea turtles	Chaloupka 2003, Limpus et al. 1994	Chaloupka 2003	Opitz 1996	Read and Limpus 2002, Brand-Gardner et al. 1999	Green turtles
Dugong	Marsh et al. 2005, Spain and Heinsohn 1975	Okey et al. 2004	Preen 1993	Marsh et al. 1982	Dugong
Crabs	Estimated by Ecopath	Erhardt and Restrepo 1989,	Erhardt and Restrepo 1989,	Hill, 1976	Mud crabs
Prawns	Estimated by Ecopath	Garcia 1985, Gribble 2003	Garcia 1985, Gribble 2003	Robertson 1988	Banana prawns Tiger prawns Endeavour prawns
Benthic invertebrates	Estimated by Ecopath, Daniel and Robertson 1990.	Alongi 1997	Lin et al. 1999, Wolf et al. 2000, Manickhand-Heilman et al. 1998, Zetina-Rejón et al. 2003, Gamito and Erzini 2005, Vega-Cedejas et al. 2001, Christian and Luczkovich 1999	User estimate, based on Gribble 2003.	
Zooplankton	McKinnon and Klump 1998 (Burdekin), other regions estimated by Ecopath	Brey 2001 (Burdekin), Other regions from Lin et al. 1999, Wolf et al. 2000, Manickhand-Heilman et al. 1998, Gamito and Erzini 2005, Vega-Cedejas et al. 2001, Christian and Luczkovich 1999	Lin et al. 1999, Wolf et al. 2000, Manickhand-Heilman et al. 1998, Gamito and Erzini 2005, Vega-Cedejas et al. 2001, Christian and Luczkovich 1999	User estimate	
Mangroves	Clough 1998	Clough 1998			
Seagrass	Coles et al. 1989, Lee Long et al. 1993	Udy et al. 1999			
Phytoplankton	Trott and Alongi 1999	Furnas et al. 2005, Trott and Alongi 1999			
Macroalgae	Estimated by Ecopath	Christian and Luczkovich 1999			
Microphytobenthos	Alongi 1997	Alongi 1997, Alongi et al. 1998			
Detritus	Wolanski et al. 1999	Wolanski et al. 1999			

generated solely from external data, to 1, for models derived from high precision, quantitative local studies (Christensen et al. 2005).

Initial input parameter values were derived from the sources indicated in Table 2. Where multiple data sources were available, variations in parameter estimates were used to define approximate bounds for parameter adjustment during the model balancing process.

Fish were aggregated into five trophic groups according to whether their diet was predominantly plant material (herbivores), detritus and associated material (detritivores = illiophages *sensu* Blaber 1997), zooplankton (zooplanktivores), benthic organisms (benthivores), or fish (piscivores). Where catches were given as relative abundance (Blaber 1980, Wet Tropics model), the mean of reported size ranges was converted into weight estimates using conversion equations for similar species in Fishbase (www.Fishbase.org, Froese and Pauly 2006) and multiplied by catch per unit effort (CPUE) reported by Blaber (1980) to obtain relative biomass estimates. Since the area sampled was not known, an assumption was made that the total biomass of fish in this system fell within the range reported for similar Australian systems (1.3 – 29.0 tonnes km⁻², Halliday and Young 1996, Morton 1990, Robertson and Duke 1990). Within this range, Blaber et al. (1989) reported an average value of 9.1 tonnes km⁻² for the Embley Estuary on the west coast of Cape York Peninsular. Relative biomass estimates for each trophic group were then standardised to sum to an assumed total biomass of 9.1 tonnes km⁻². These values are in broad agreement with values from similar studies. Russell et al. (2000) provide similar values for trophic groups derived from Blaber (1980), but the data and nature of sampling are not quantitative enough to derive absolute biomass estimates. Coles et al. (1993) provide quantitative data for fish from seagrass beds in Cairns Harbour, but the sampling approach largely restricted catches to juvenile fish. Total biomass estimates are likely to fall close to the value used to standardise results from Blaber (1980). Quantitative biomass data were available for other regions modelled.

Commercial catch data were obtained from the QDPIF website (<http://chrisweb.dpi.qld.gov.au/chris/>) for the period 1988 to 2003 to allow validation of model predictions against independent biomass estimates expressed as CPUE. Catch data are reported within 30 min spatial grids that extend well beyond the 2 km coastal band adopted for models in this study. Accordingly, catches were scaled to include only the proportional area of catch grids within the model domain, and restricted to species and fishery sectors operating within that zone (inshore net fishery, some trawl operations, and crab pots). Recreational fishery landings were assumed to equal commercial landings for finfish and crabs (Henry and Lyle 2003).

Crabs were included here as mud crabs (*Scylla serata*) only, an important species in the commercial fishery. Whilst smaller sesarmid and grapsid crabs play an important role in processing mangrove leaf litter (Robertson 1986, Sheaves and Molony 2000), estimates of crab biomass were not available. For this reason, mud crabs were assigned to a single-species crab trophic group, and other crabs were assigned to a generic benthic invertebrate trophic group. Literature sources (see Table 2) were used to estimate P/B and Q/B ratios, whilst allowing Ecopath to estimate biomass values that would balance the model. A similar process was adopted for inshore prawn species.

Remaining consumer trophic groups (benthic invertebrates, zooplankton) were aggregated to minimise the number of assumptions required to balance the models in the absence of quantitative data for each region.

Habitat areas for seagrass were derived from Lee Long et al. (1993), whilst mangrove areas were obtained from the Queensland Department of Primary Industries and Fisheries on-line database (<http://chrisweb.dpi.qld.gov.au/chris/>). Shoreline length (km) for each region was multiplied by 2 km to estimate habitat area including seagrass, with mangrove area added to estimate the total habitat area covered by each model.

The value of comparisons among regional models depends on the amount of region-specific data available for each model. Region-specific data for the Wet Tropics model included fish, mangroves, seagrasses, seabirds, crocodiles, turtles, and dugongs. The Burdekin model used region-specific data for fish, zooplankton and phytoplankton, seabirds, crocodiles, turtles, dugongs, mangroves and seagrasses. The Fitzroy model was developed from local data from fish surveys in Port Curtis (biomass data courtesy of David Currie, unpublished

data), seabirds, crocodiles, turtles, dugongs, mangroves and seagrasses. Local data for the Burnett-Mary model included fish, seabirds, turtles, dugongs, mangroves and seagrasses.

Sensitivity analyses

The user interface for EwE 5.1 provides default estimates for a number of model components that can significantly affect model results if accepted uncritically (Christensen and Walters 2004, Christensen et al. 2005, Plagányi and Butterworth 2004). Once a balanced model was achieved, sensitivity analyses were performed by altering all input parameters by $\pm 10\%$, 20% , 30% , 40% , and 50% to identify input parameters most likely to cause large variations in key outputs.

Scenario evaluation

Ecosim represents nutrient cycling and potential for nutrient limitation of primary production in a simple fashion (Christensen and Walters 2004) that partitions total nutrient concentration between the proportion bound in system biomass, and free nutrients in the environment which are available to primary producers. Changes in total nutrient loading can be simulated by applying a forcing function. The rate of production by primary producer groups is calculated from the free nutrient concentration during each time step of the simulation, assuming Michaelis-Menten uptake relationships. By recalculating-mass balance using the new primary producer biomass, Ecosim simulates the flow-on effects of changes in nutrient loading throughout the food web, subject to the effect of vulnerability settings for each group. In a reverse manner, Ecosim also provides a function to estimate temporal fluctuations in primary production when fitting the model against validation time series, assuming that changes in biomass during the validation time series were actually caused by variations in primary production. Fluctuations in primary production estimated by Ecosim can then be used to estimate changes in relative nutrient loading.

To develop scenarios of changing nutrient loading, the primary production anomaly function was used to estimate underlying trends in free nutrient availability during the 16 year validation period. The relative nutrient availability value for the end-point of the time series was used as a reference value for developing forcing functions that increased or decreased the relative loading of free nutrients by 10% over a 20 year simulation period.

Three scenarios were applied to each model to explore possible responses to future total nutrient changes of $+10\%$, -10% , and no change, applied as simple linear functions over a 20 year period. The scenarios were then applied as nutrient forcing functions to all primary producers except mangroves, since the bulk of mangrove biomass is biologically unavailable. A mediation effect was also applied in the form of a declining sigmoid function to provide capacity for increased shading of seagrass by phytoplankton and suspended fine particulates at increasing nutrient loads. Fishing effort was held constant for the 20 year simulation period.

Results

Input parameter estimates and the final mass-balance solution adopted are shown in Table 3. Diet composition matrices are given in Tables 4 and 5.

The connectance diagram showing all pathways from producers to consumers for the Wet Tropics, Burdekin and Fitzroy coastal food webs (Fig. 2) shows dugong and sea turtles as the only solely herbivorous groups, with a mean trophic level of 2.0. Benthic invertebrates, zooplankton, detritivorous fish and herbivorous fish consume a broader diet which gives them higher mean trophic positions of 2.06, 2.11, 2.21 and 2.22. Crabs (2.42) and prawns (2.53) occupy the roles of scavengers, benthic predators and micrograzers, creating an intermediate trophic level between primary and secondary consumers. Zooplanktivorous fish (3.03) occupy a third trophic level, followed by benthic feeding fish (3.31) and piscivorous fish (3.52). Crocodiles (3.59) consume most other trophic groups along with significant terrestrial imports. Seabirds (3.68) occupy the top levels of this food web as a result of their exclusively piscivorous diet.

The absence of crocodiles from the Burnett-Mary model (Fig. 3) reduces the number of living trophic groups from 18 to 17, and reduces the number of predators in the model, but has little other effect on trophic structure because crocodiles are not consumed by other groups in the models.

The limited separation of trophic levels between zooplanktivorous, benthivorous and piscivorous fish reflects reality in the sense that many fish grouped with the piscivorous species display a degree of omnivory and derive a significant proportion of their energy from other non-fish groups such as prawns and other benthic invertebrates. Similarly, a number of benthic feeding fish also prey on other fish.

All models were less sensitive to changes in biomass and Q/B input parameters than they were to changes in P/B ratio or ecotrophic efficiency (Fig. 4). For example, the largest biomass response to adjusting the input biomass in the Wet Tropics model by +50% was a conservative 37% increase in zooplankton biomass. In contrast, reducing P/B ratio or ecotrophic efficiency by 50% resulted in biomass increases of 100% to 108% for crabs, prawns, benthic invertebrates and zooplankton. Accordingly, errors introduced by setting an assumed value for total fish biomass in the Wet Tropics are likely to be smaller than those associated with estimating P/B and Q/B ratios or ecotrophic efficiency. Errors associated with P/B ratios, Q/B ratios and ecotrophic efficiency are consistent across all models since they were estimated in the same way. Satisfactory fits were obtained for all models (Table 6), despite the relatively coarse specification of model structure. Low pedigree values for all models indicate substantial capacity for model improvement by collecting additional region-specific data. The biomass of fish trophic groups varied dramatically among regions (Fig. 5), with the Burdekin region having the greatest biomass of 28 tonnes km⁻² (wet weight). Total fish biomass in the Wet Tropics (9.1 tonnes km⁻²) reflects assumptions used to convert the original data to biomass per unit area, but biomass values for the Fitzroy and Burnett-Mary are low by comparison, at 2.9 tonnes km⁻² and 3.0 tonnes km⁻², respectively. Whilst these differences in biomass reflect a combination of differences in sampling methods, habitats sampled, and real differences in biomass, the most similar methods were employed in the Burdekin and Burnett-Mary regions, indicating that the magnitude of biomass differences is largely real.

In the Wet Tropics, piscivores accounted for 53% of the fish biomass, followed by detritivores (19%), zooplanktivores (14%), benthivores (13%) and herbivores (1%). Zooplanktivores were the dominant group (40%) in the Burdekin, followed by piscivores (30%), benthivores (14%) and detritivores (13%), with herbivores (3%) again representing the smallest proportion. Biomass distribution in the Fitzroy was very different, with zooplanktivores accounting for 38% of the total, followed by benthivores (36%), piscivores (15%), detritivores (8%) and herbivores (2%). However, larger, fast-swimming piscivores

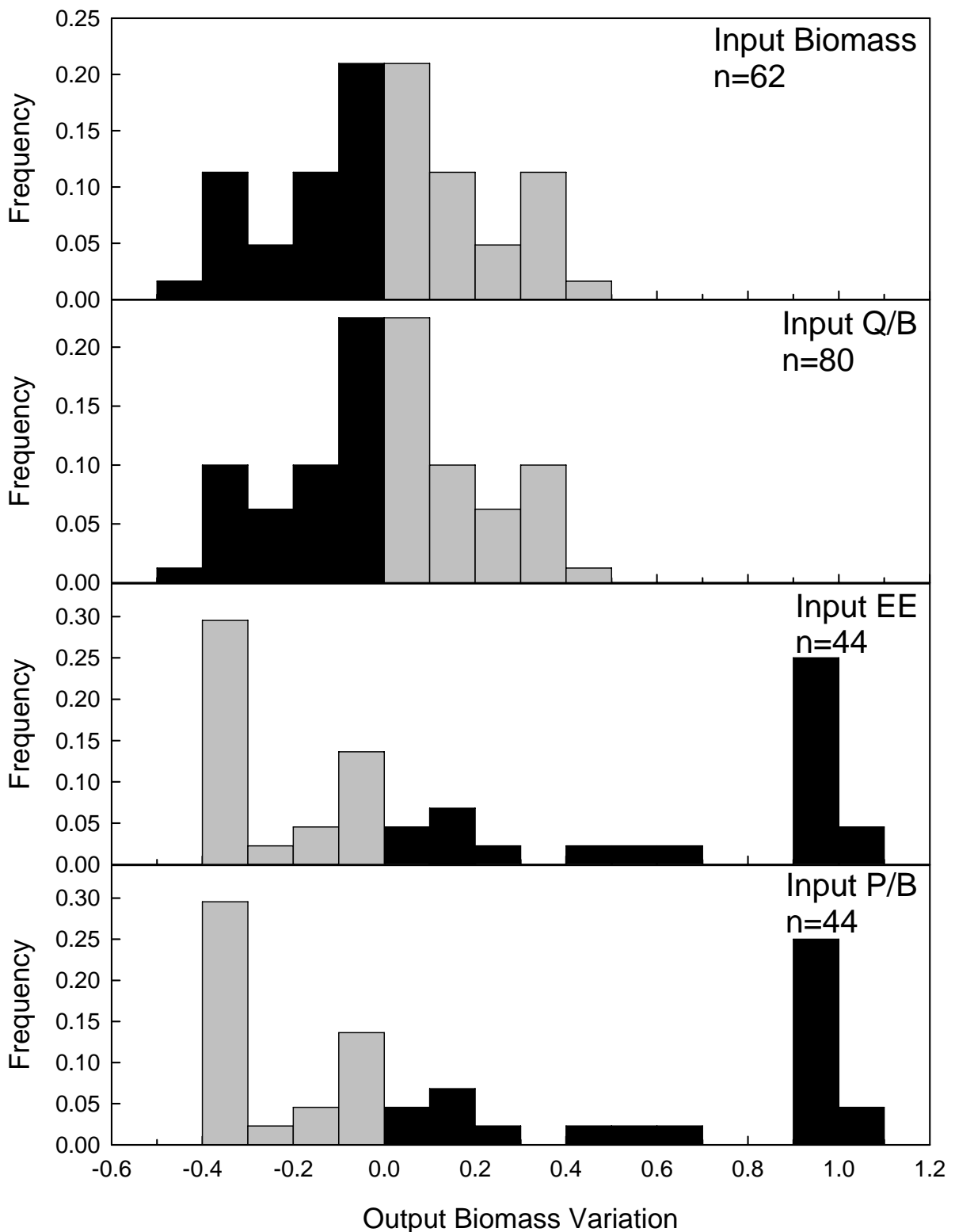


Figure 4. Sensitivity analyses for food web models. Frequency represents the proportion of sensitivity runs returning the indicated variation in output biomass. Input parameters were adjusted by - 50% (black bars) or +50% (grey bars) for runs shown, and resulted in relatively low sensitivity (proportional change <0.50) of estimated biomass to changes in input biomass and Q/B ratio, but relatively high sensitivity (proportional change => 1.0) to changes in P/B and ecotrophic efficiency.

Table 3. Input parameter estimates and Ecopath mass-balance solution for each regional model. Values in normal type were derived from local data or literature sources. Values in bold type were calculated by Ecopath. Italic values for ecotrophic efficiency were estimated by the user to allow Ecopath to estimate the biomass required.

Group name	Trophic level	Habitat area	Biomass in habitat (t/km ²)	Biomass (t/km ²)	P/B (/year)	Q/B (/year)	Ecotrophic efficiency
<i>Wet Tropics</i>							
Seabirds	3.68	1.000	0.0006	0.0006	5.400	80.000	0.972
Crocodiles	3.59	0.350	0.813	0.285	0.100	5.720	0.000
Piscivorous Fish	3.52	1.000	4.889	4.889	0.900	2.100	0.093
Benthivorous Fish	3.31	1.000	1.203	1.203	1.000	2.700	0.472
Zooplanktivorous Fish	3.03	1.000	1.305	1.305	3.900	16.900	0.518
Detritivorous Fish	2.21	1.000	1.697	1.697	3.138	15.156	0.802
Herbivorous Fish	2.22	1.000	0.064	0.064	2.300	6.600	0.181
Sea Turtles	2.00	0.650	1.514	0.984	0.900	3.500	0.018
Dugong	2.00	0.084	0.393	0.033	0.100	48.600	0.986
Crabs	2.42	1.000	1.228	1.228	1.200	11.600	<i>0.950</i>
Prawns	2.53	1.000	3.383	3.383	1.800	19.000	<i>0.970</i>
Benthic Invertebrates	2.06	1.000	8.153	8.153	7.030	23.380	<i>0.950</i>
Zooplankton	2.11	1.000	0.340	0.340	70.800	135.900	<i>0.950</i>
Mangroves	1.00	0.350	39331	13765.850	0.020	-	0.010
Seagrass	1.00	0.084	2640	221.760	5.459	-	0.011
Phytoplankton	1.00	1.000	9.450	9.450	1103.000	-	0.007
Macroalgae	1.00	1.000	4.500	4.500	10.950	-	0.569
Microphytobenthos	1.00	1.000	3.330	3.330	110.000	-	0.384
Detritus	1.00	1.000	65	65	-	-	0.003
<i>Burdekin</i>							
Seabirds	3.68	1.000	0.003	0.003	5.400	80.000	0.047
Crocodiles	3.54	0.270	0.248	0.067	0.100	5.720	0.000
Piscivorous Fish	3.52	1.000	8.390	8.390	0.900	2.100	0.074
Benthivorous Fish	3.31	1.000	3.940	3.940	1.000	2.700	0.240
Zooplanktivorous Fish	3.03	1.000	11.490	11.490	3.900	16.900	0.103
Detritivorous Fish	2.21	1.000	3.700	3.700	3.138	15.156	0.637
Herbivorous Fish	2.22	1.000	0.870	0.870	2.300	6.600	0.020
Sea Turtles	2.00	0.730	1.514	1.105	0.900	3.500	0.004
Dugong	2.00	0.198	0.393	0.078	0.100	48.600	0.098
Crabs	2.42	1.000	2.720	2.720	1.200	11.600	<i>0.950</i>
Prawns	2.53	1.000	15.275	15.275	1.800	19.000	<i>0.970</i>
Benthic Invertebrates	2.06	1.000	42.799	42.799	7.030	23.380	<i>0.950</i>
Zooplankton	2.11	1.000	5.286	5.286	87.276	135.900	0.363
Mangroves	1.00	0.270	39331	10619.370	0.020	-	0.030
Seagrass	1.00	0.198	2640	522.720	5.459	-	0.021
Phytoplankton	1.00	1.000	11.054	11.054	943.000	-	0.069
Macroalgae	1.00	1.000	16.442	16.442	10.950	-	<i>0.700</i>
Microphytobenthos	1.00	1.000	7.500	7.500	110.000	-	0.931
Detritus	1.00	1.000	65	65	-	-	0.011
<i>Fitzroy</i>							
Seabirds	3.68	1.000	0.006	0.006	5.400	80.000	0.014
Crocodiles	3.59	0.274	0.148	0.041	0.100	5.720	0.000
Piscivorous Fish	3.52	1.000	0.443	0.443	0.900	2.100	0.516
Benthivorous Fish	3.31	1.000	1.029	1.029	1.000	2.700	0.119
Zooplanktivorous Fish	3.03	1.000	1.113	1.113	3.900	16.900	0.102
Detritivorous Fish	2.21	1.000	0.241	0.241	3.138	15.156	0.932
Herbivorous Fish	2.22	1.000	0.071	0.071	2.300	6.600	0.034
Sea Turtles	2.00	0.726	1.514	1.099	0.900	3.500	0.002
Dugong	2.00	0.040	0.393	0.016	0.100	48.600	0.292
Crabs	2.42	1.000	0.876	0.876	1.200	11.600	<i>0.950</i>

Table 3 (continued)

Group name	Trophic level	Habitat area	Biomass in habitat (t/km ²)	Biomass (t/km ²)	P/B (/year)	Q/B (/year)	Ecotrophic efficiency
Prawns	2.53	1.000	1.720	1.720	1.800	19.000	0.970
Benthic Invertebrates	2.06	1.000	14.642	14.642	7.030	23.380	0.950
Zooplankton	2.11	1.000	5.268	5.268	87.276	135.900	0.241
Mangroves	1.00	0.274	39331	10776.693	0.020	-	0.010
Seagrass	1.00	0.040	2640	106.392	5.459	-	0.177
Phytoplankton	1.00	1.000	9.450	9.450	1103.000	-	0.086
Macroalgae	1.00	1.000	26.532	26.532	10.950	-	0.700
Microphytobenthos	1.00	1.000	10.453	10.453	110.000	-	0.999
Detritus	1.00	1.000	65	65	-	-	0.017
Burnett-Mary							
Seabirds	3.92	1.000	0.005	0.005	5.400	80.000	0.000
Piscivorous Fish	3.43	1.000	0.810	0.810	0.900	2.100	0.837
Benthivorous Fish	3.30	1.000	1.327	1.327	1.000	2.700	0.728
Zooplanktivorous Fish	3.03	1.000	0.070	0.070	3.900	16.900	0.130
Detritivorous Fish	2.21	1.000	0.532	0.532	3.138	15.156	0.813
Herbivorous Fish	2.22	1.000	0.292	0.292	2.300	6.600	0.795
Sea Turtles	2.00	0.822	1.514	1.245	0.900	3.500	0.000
Dugong	2.00	0.728	0.393	0.286	0.100	48.600	0.000
Crabs	2.42	1.000	1.479	1.479	1.200	11.600	0.950
Prawns	2.53	1.000	1.072	1.072	1.800	19.000	0.970
Benthic Invertebrates	2.06	1.000	13.892	13.892	7.030	23.380	0.950
Zooplankton	2.11	1.000	5.286	5.286	70.800	135.900	0.046
Mangroves	1.00	0.178	39331	7000.918	0.020	-	0.025
Seagrass	1.00	0.728	2640	1921.920	5.459	-	0.003
Phytoplankton	1.00	1.000	9.450	9.450	1103.000	-	0.055
Macroalgae	1.00	1.000	4.500	4.500	10.950	-	0.803
Microphytobenthos	1.00	1.000	3.330	3.330	110.000	-	0.870
Detritus	1.00	1.000	65	65	-	-	0.002

Table 4. Estimates of proportional dietary contribution of each prey group (in rows) for each consumer group (in columns) for the Wet Tropics, Burdekin and Fitzroy models. Diet components obtained from outside the region, such as crocodiles feeding on terrestrial prey, are shown as imports.

Prey Groups	Predator Groups												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Seabirds		0.002											
2 Crocodiles													
3 Piscivorous fish	0.020	0.076											
4 Benthic fish	0.129	0.020	0.050										
5 Zooplanktivorous fish	0.370	0.010	0.250	0.010									
6 Detritivorous fish	0.480	0.030	0.399	0.019									
7 Herbivorous fish	0.001	0.001	0.001	0.001									
8 Sea turtles		0.010											
9 Dugong		0.002											
10 Crabs		0.260		0.270									
11 Prawns			0.200	0.300	0.100								
12 Benthic invertebrates		0.050	0.100	0.400	0.200	0.200				0.400	0.500		0.100
13 Zooplankton					0.600		0.200						0.050
14 Mangroves										0.200			
15 Seagrass							0.500	0.550	0.900	0.050		0.050	
16 Phytoplankton					0.100		0.200					0.200	0.700
17 Macroalgae						0.100	0.100	0.450	0.100	0.100	0.050	0.100	
18 Microphytobenthos						0.600				0.100	0.300	0.500	0.200
19 Detritus						0.100				0.150	0.150	0.100	
Import		0.539											
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 5. Estimates of proportional dietary contribution in the Burnett-Mary region of each prey group (in rows) for each consumer group (in columns), adjusted from other models to account for the absence of crocodiles.

Prey Groups	Predator Groups											
	1	2	3	4	5	6	7	8	9	10	11	12
1 Seabirds												
2 Piscivorous fish	0.060											
3 Benthic fish	0.560	0.150										
4 Zooplanktivorous fish	0.030	0.010	0.001									
5 Detritivorous fish	0.230	0.300	0.001									
6 Herbivorous fish	0.120	0.200	0.028									
7 Sea turtles												
8 Dugong												
9 Crabs			0.270									
10 Prawns		0.200	0.300	0.100								
11 Benthic invertebrates		0.140	0.400	0.200	0.200				0.400	0.500		0.100
12 Zooplankton				0.600		0.200					0.050	
13 Mangroves									0.200			
14 Seagrass						0.500	0.550	0.900	0.050		0.050	
15 Phytoplankton				0.100		0.200					0.200	0.700
16 Macroalgae					0.100	0.100	0.450	0.100	0.100	0.050	0.100	
17 Microphytobenthos					0.600				0.100	0.300	0.500	0.200
18 Detritus					0.100				0.150	0.150	0.100	
Import												
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 6. Ecopath pedigree and sum of squared residuals for Ecosim time series fits against commercial fishery data using CPUE as an index of relative abundance for each regional model.

	Wet Tropics	Burdekin	Fitzroy	Burnett-Mary
No. living groups	18	18	18	17
Pedigree	0.038	0.046	0.037	0.039
Ecopath t*	0.15	0.18	0.15	0.15
Ecosim SSR	5.83	6.70	6.50	13.71

would have been under-represented in the original data derived from beam trawl samples in this region. In the Burnett-Mary region, benthivores (44%) dominated the fish biomass, followed by piscivores (27%), detritivores (18%), herbivores (10%) and zooplanktivores (2%). The shift in trophic composition in the Burnett-Mary reflects the increasing temperate influence of herbivores such as luderick (*Girella tricuspidata*), and abundant benthivores such as yellowfin bream (*Acanthopagrus australis*).

The percentage of primary production required to sustain the coastal fish biomass in each region was estimated to be 11% in the Burdekin, 4% in the Fitzroy, 2% in the Wet Tropics, and less than 1% in the Burnett-Mary (Fig. 6). Although total fish biomass in the Wet Tropics is three times greater than in the Fitzroy, the trophic composition in the Fitzroy requires twice the amount of primary production in the Wet Tropics to sustain the initial biomass.

Network analysis

Diagnostic indices (Table 7) show that total system throughput, net primary production, net system production and total primary production / total biomass are greatest in the Burnett-Mary region, followed by the Burdekin, Wet Tropics and Fitzroy. Whilst the Fitzroy has the largest coastal area, the intensity of ecological productivity and material transfer is greatest in the Burnett-Mary region.

Food chains were universally short, as would be expected for models with a small number of trophic groups, with a mean path length of 2.0 trophic steps. The mean path length estimates the number of times a unit of material is transferred between trophic groups between entering and leaving the system. However, in a practical sense, path length is determined by food web structure and diet constructions, rather than by empirical data for each region, and so no variation occurred among regions because the same structure was adopted for all models.

Mangrove forests consistently contributed the bulk of the primary producer biomass in each region (Fig. 7), ranging from 78% in the Burnett-Mary to 99% in the Fitzroy. Excluding mangroves, which contain a large component of non-photosynthetic biomass, seagrasses represent the largest primary producer biomass, ranging from 85% in the Burdekin to 99% in the Burnett-Mary (Fig. 8).

Mean trophic efficiency across all trophic levels was highest in the Wet Tropics, at 12.8% per trophic level, whilst the Fitzroy food web was the least efficient at 5.6% (Fig. 9). The high availability of seagrass in the Burnett-Mary led to a relatively constant trophic efficiency about the mean value of 10.8% per trophic level, whereas the general trend in other regional models was for trophic efficiency to decline at progressively higher trophic levels.

Ascendancy refers to the level of ecosystem successional maturity (Scharler and Baird 2005), and can be expressed as a percentage of the system's total development capacity. Values for ascendancy were similar across all regions, ranging between 60% and 70%, and corresponded to regional rankings for mangrove area and biomass. Overheads reflect the difference between an ecosystem's existing development (ascendancy) and potential (total) development capacity, and ranged approximately between 30% and 40% among regions.

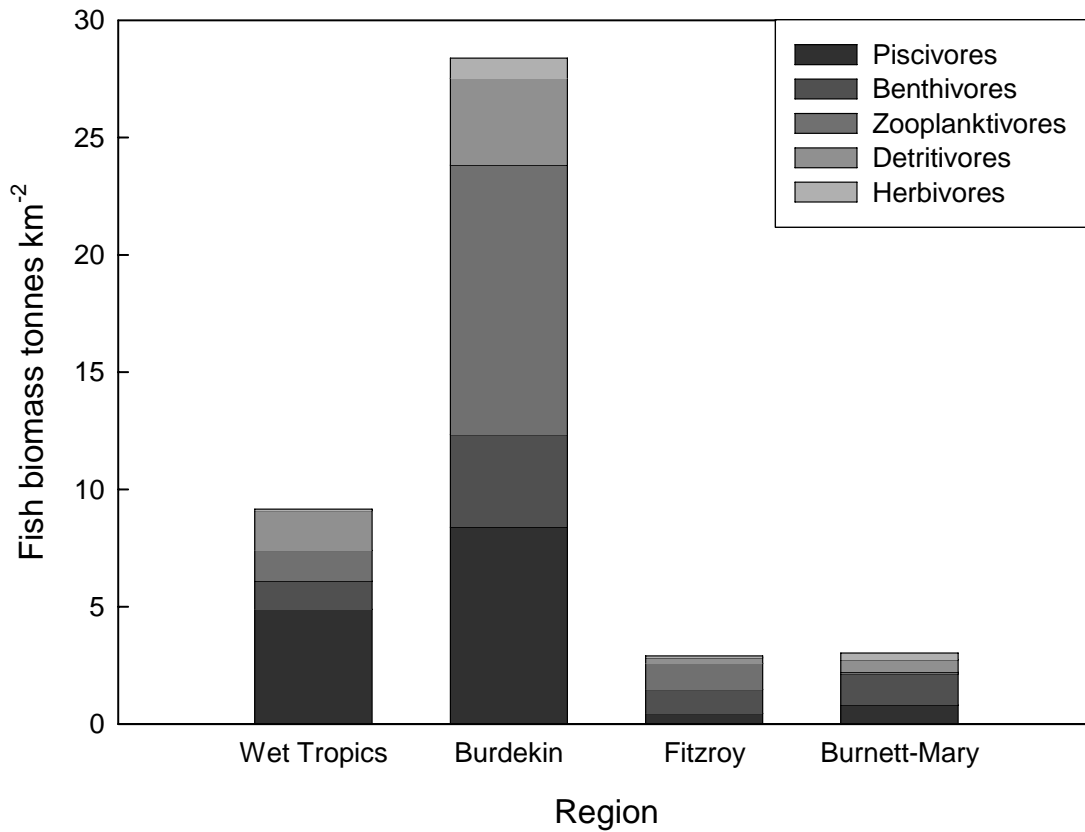


Figure 5. Contribution of fish trophic groups to total fish biomass in each regional model

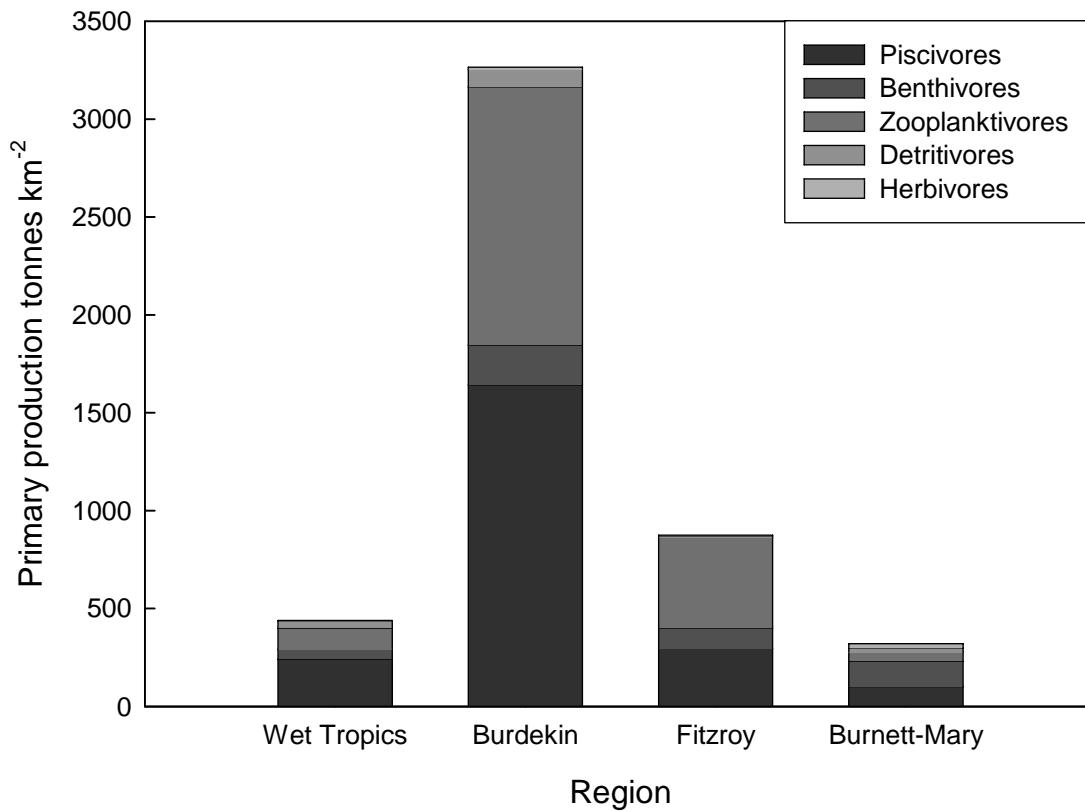


Figure 6. Primary production required to support food consumption by fish across trophic groups in each region.

Table 7. Summary of diagnostic indices from Ecopath models of each coastal ecosystem.

Parameter	Units	Wet Tropics	Burdekin	Fitzroy	Burnett-Mary
Total system throughput	tonnes km ⁻² y ⁻¹	25,533	31,186	24,826	44,605
Total production	tonnes km ⁻² y ⁻¹	12,426	15,357	12,175	21,951
Calculated net primary production	tonnes km ⁻² y ⁻¹	12,322	14,492	11,601	21,469
Total primary production/total respiration		61.362	14.409	34.929	52.146
Net system production	tonnes km ⁻² y ⁻¹	12,121	13,487	11,269	21,057
Total primary production/total biomass	tonnes km ⁻² y ⁻¹	0.878	1.286	1.062	2.394
Total biomass (excluding detritus)	tonnes km ⁻²	14,028	11,272	10,927	8,966
Total catches	tonnes km ⁻² y ⁻¹	1.121	1.445	0.606	3.274
Mean trophic level of fishery		2.78	2.83	2.71	2.65
System transfer efficiency	%	12.8	8.2	5.6	10.8
Connectance index		0.191	0.191	0.191	0.180
Omnivory index		0.184	0.145	0.132	0.123
Ascendancy	%	68.5	61.4	69.4	61.3
Overheads	%	31.5	38.5	30.5	38.5

Correlation of network diagnostics against regional catchment characteristics (Table 8) revealed the area of seagrass to be associated with diagnostics involving total system throughput, total production and total biomass, as well as total fishery catches. Mangrove area was positively correlated with ascendancy, and negatively correlated with overheads, suggesting the extent of mangrove development as a major feature of ecosystem maturity in these coastal ecosystems. The percentage of catchment area used for grazing was negatively correlated with the total primary production / total respiration ratio, whilst other land uses were positively correlated with this ratio. Total biomass excluding detritus was positively correlated with mean annual discharge. Transfer efficiency within food webs was negatively correlated with catchment area. The level of omnivory within food webs was positively correlated with mean annual rainfall and mean annual discharge, whilst the frequency of cyclones crossing the coast was not correlated with any diagnostic indicator. These results provide correlative support at a large scale to existing evidence that catchment characteristics and land use patterns affect coastal food webs through the transport of contaminants by river flow.

Estimates of total biomass for trophic groups within each regional model are given in Table 9.

Mean annual fishery catches in each region averaged over the period from 1988 to 2003 followed the same pattern as production-based diagnostic indicators, with largest catch rates from the Burnett-Mary (2.7 tonnes km⁻² y⁻¹), followed by the Burdekin (1.4 tonnes km⁻² y⁻¹), Wet Tropics (1.1 tonnes km⁻² y⁻¹), and Fitzroy (0.6 tonnes km⁻² y⁻¹) (Fig. 10). Mean trophic level of the catch was similar across all regions, with values of 2.8 for the Burdekin and Wet Tropics, and 2.7 for the Fitzroy and Burnett-Mary. Catches of finfish were highly selective for piscivores in the Wet Tropics, Burdekin and Fitzroy regions, with the proportion of piscivores in the catch exceeding their relative biomass in the environment. In the Burnett-Mary region, catches were roughly proportional to wild biomass for each group, except for detritivores which were over-represented in the catch. The amount of primary production required to support fishery harvests was greatest in the Burnett-Mary, and declined in more northerly regions.

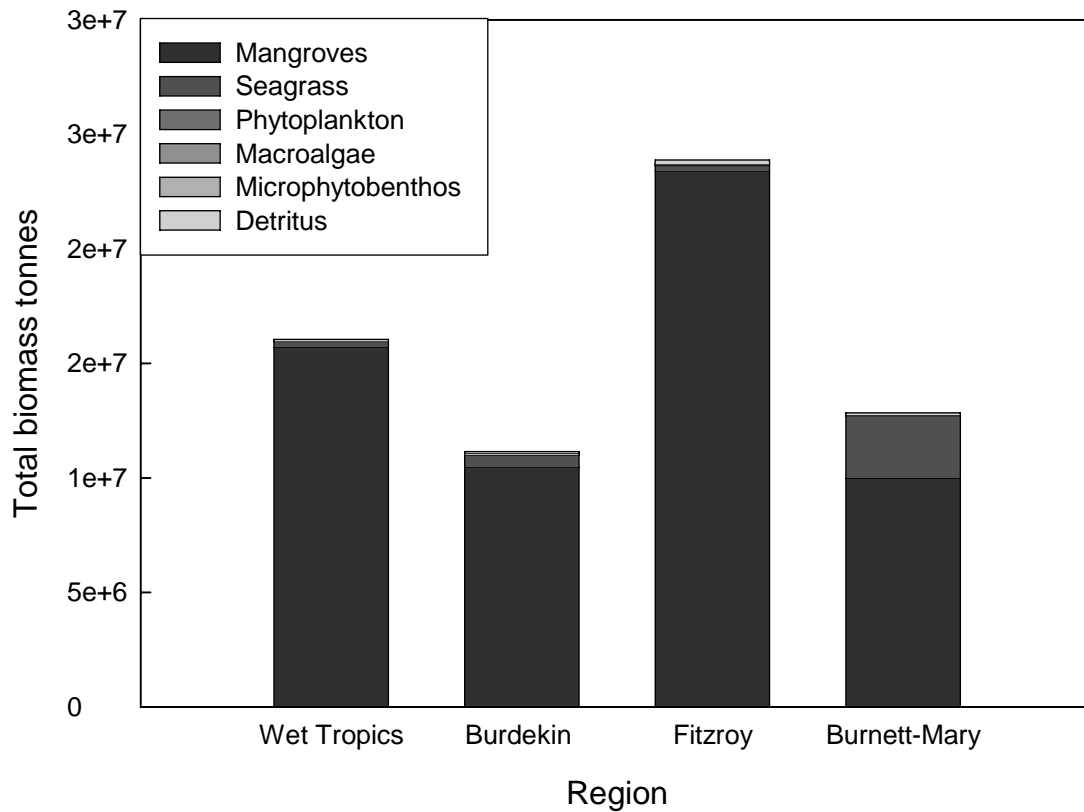


Figure 7. Total biomass of primary producers in each regional ecosystem model.

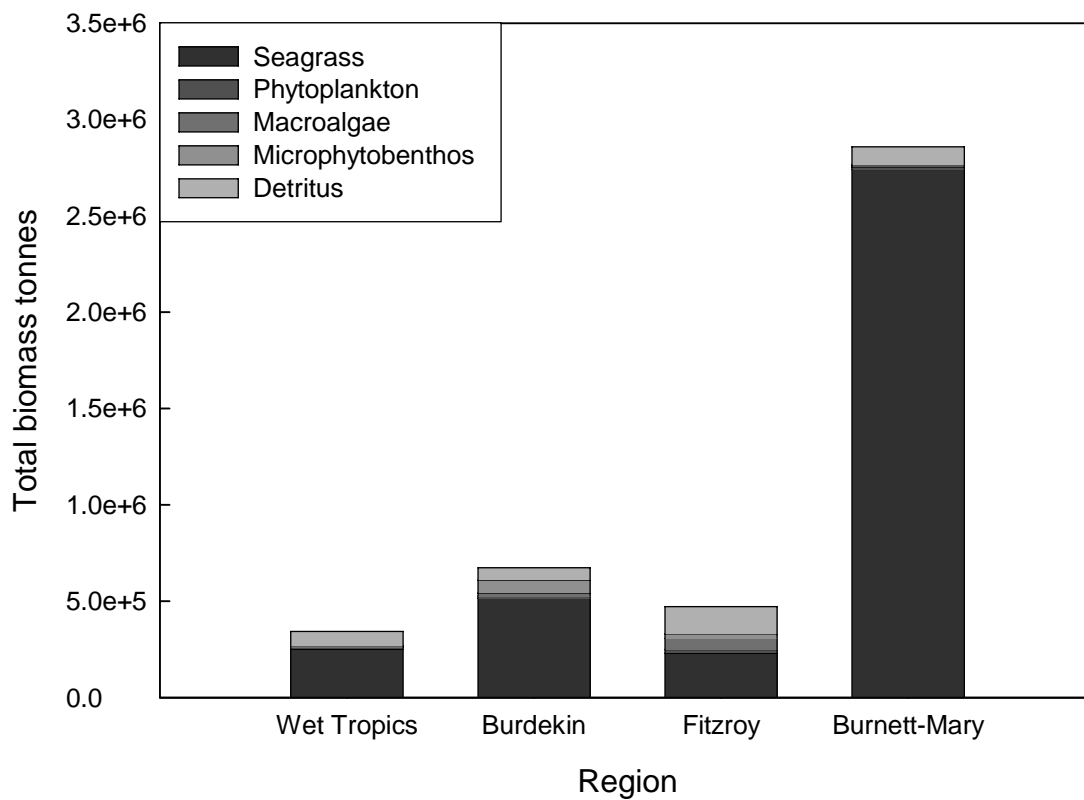


Figure 8. Total biomass of primary producer groups, excluding mangroves, in each regional ecosystem model.

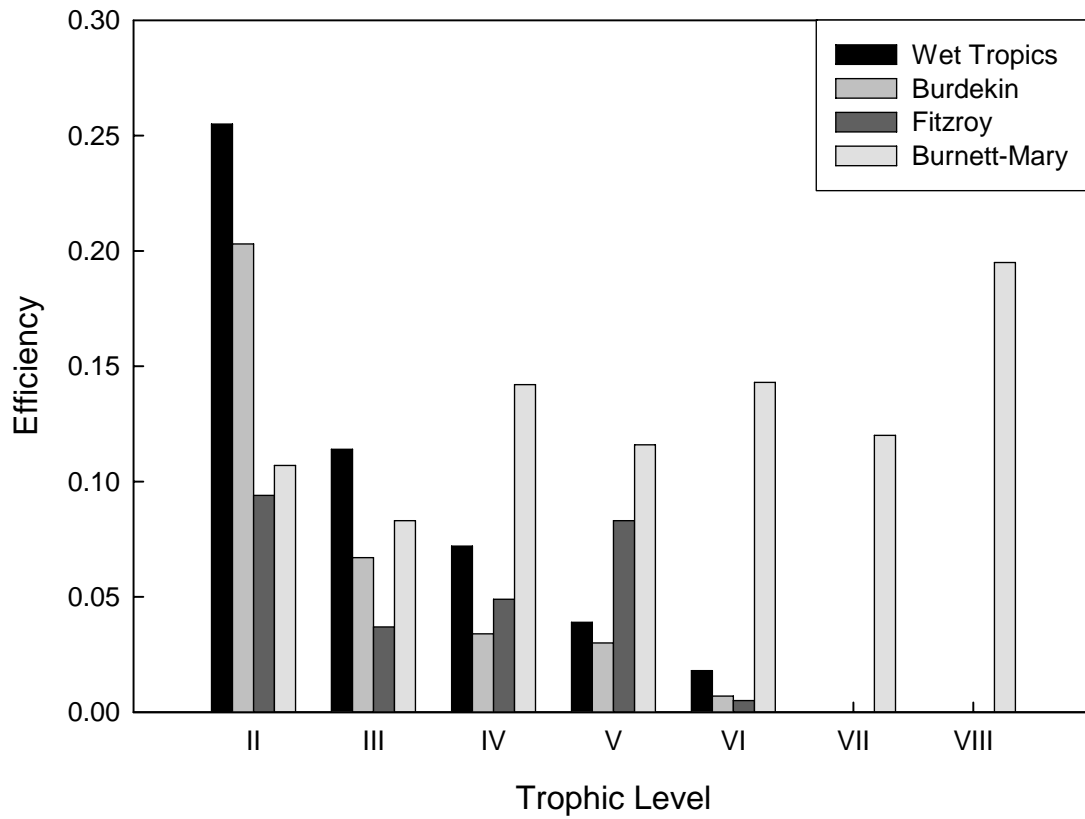


Figure 9. Trophic efficiency at each trophic level within regional coastal ecosystems.

Table 8. Correlation coefficients for network diagnostics against regional characteristics for each model. n=4, *p<0.10; **p<0.05; ***p<0.001

	Catch't area	Mean annual rainfall	Cyclone freq	Mean annual disch.	Nature cons & protect areas	Grazing	Forest'y	Crops	Urban	Mangr. area	Seagr. area
Tot sys throughput	-	-	-	-	-	-	-	-	-	-	0.98**
Tot production	-	-	-	-	-	-	-	-	-	-	0.98**
Calculated net PP	-	-	-	-	-	-	-	-	-	-	0.99**
TPP/tot respiration	-	-	-	-	0.99***	-0.99***	0.98**	0.93*	0.93*	-	-
Net system production	-	-	-	-	-	-	-	-	-	-	0.99***
TPP/ tot biomass	-	-	-	-	-	-	-	-	-	-	0.99**
Tot biomass ex. detritus	-	-	-	0.96**	-	-	-	-	-	-	-
Tot catches	-	-	-	-	-	-	-	-	-	-	0.98**
Mean trophic level of fishery	-	-	-	-	-	-	-	-	-	-	-
Transfer efficiency	-0.97**	-	-	-	-	-	-	-	-	-	-
Omnivory	-	0.94*	-	0.98**	-	-	-	-	-	-	-
Ascendancy	-	-	-	-	-	-	-	-	-	0.90*	-
Overheads	-	-	-	-	-	-	-	-	-	-0.91*	-

Ecosim predictions of fish biomass and CPUE trends for fishery species across regions (Figs 11-14) suggest there has been an increase in biomass and CPUE in the Wet Tropics for the 16 years from 1988 to 2003. Similar general trends are apparent for the Burdekin and Fitzroy regions, but trends in the Burnett-Mary appear to be more stable than in regions further north. Prawns do not show the same increase as most other fishery groups, with decreasing biomass and CPUE most evident in the Fitzroy and Burnett-Mary regions. Zooplanktivore species provide insufficient data points to discern reliable trends, and modelled results should not be used to infer trends for these species.

Tropical cyclones are a major episodic climatic influence on coastal ecosystems in the Great Barrier Reef region. Destructive winds and high river discharges and turbid river plumes are characteristic of cyclone events, and have been linked to fishery recruitment in other systems (e.g. Penn and Caputi (1986) for tiger prawns in Exmouth Gulf, Western Australia), but no consistent cyclone-related patterns are evident in CPUE and modelled biomass trends. In the Wet Tropics, years in which cyclones crossed the coast tend to correspond with suppressed CPUE for prawns, crabs, herbivorous fish and detritivorous fish, especially since 1997. In the Burdekin region, CPUE for prawns and crabs were reduced in 1997 following a cyclone, but not following cyclones at the beginning of the time series. Reduced CPUE in other years indicates that factors other than cyclones have a stronger influence on CPUE. Whilst cyclones passed the Fitzroy region during the modelled period, none crossed the coast. In contrast to other regions, the Burnett-Mary suffered extensive seagrass damage from a cyclone in 1992, a year where catches of prawns and detritivorous fish achieved maximum values within the validation period.

Table 9. Summary of habitat area, biomass density and total biomass for ecosystem components used in regional coastal models.

Group name	Wet Tropics			Burdekin			Fitzroy			Burnett-Mary		
	Habitat area	Biomass in habitat area (t/km ²)	Total Biomass (tonnes)	Habitat area	Biomass in habitat area (t/km ²)	Total Biomass (tonnes)	Habitat area	Biomass in habitat area (t/km ²)	Total Biomass (tonnes)	Habitat area	Biomass in habitat area (t/km ²)	Total Biomass (tonnes)
Seabirds	1131.4	0.0006	0.7	986.6	0.003	3.0	2172.0	0.006	13.0	1426.0	0.005	7.7
Crocodiles	399.4	0.81	324.7	266.4	0.25	65.6	595.1	0.15	88.1			
Piscivores	1131.4	4.89	5531.4	986.6	8.39	8277.6	2172.0	0.44	962.2	1426.0	0.81	1155.1
Benthivores	1131.4	1.20	1361.1	986.6	3.94	3887.2	2172.0	1.03	2235.0	1426.0	1.33	1892.3
Zooplanktivores	1131.4	1.31	1476.5	986.6	11.49	11336.0	2172.0	1.11	2417.4	1426.0	0.070	99.1
Detritivores	1131.4	1.70	1920.0	986.6	3.70	3650.4	2172.0	0.24	523.5	1426.0	0.53	758.6
Herbivores	1131.4	0.06	72.4	986.6	0.87	858.3	2172.0	0.07	155.1	1426.0	0.29	416.4
Sea Turtles	732.0	1.51	1108.2	720.2	1.51	1090.4	1576.9	1.51	2387.4	1172.2	1.51	1774.7
Dugong	94.7	0.39	37.2	195.3	0.39	76.8	86.9	0.39	34.1	1038.1	0.39	408.0
Crabs	1131.4	1.23	1388.2	986.6	2.72	2683.6	2172.0	0.88	1902.7	1426.0	1.48	2109.1
Prawns	1131.4	3.37	3817.3	986.6	15.28	15070.3	2172.0	1.72	3735.8	1426.0	1.07	1528.7
Benthic Invertebrates	1131.4	8.13	9201.7	986.6	42.80	42225.5	2172.0	14.64	31802.4	1426.0	13.89	19810.0
Zooplankton	1131.4	0.34	383.5	986.6	5.29	5215.2	2172.0	5.27	11442.1	1426.0	5.29	7537.8
Mangroves	399.4	39331	15708801.0	266.4	39331	10477070.0	595.1	39331	23406978.8	253.8	39331	9983309.0
Seagrass	94.7	2640	249981.6	195.3	2640	515715.6	86.9	2640	229363.2	1038.2	2640	2740658.0
Phytoplankton	1131.4	9.45	10691.7	986.6	11.05	10905.9	2172.0	9.45	20525.4	1426.0	9.45	13475.7
Macroalgae	1131.4	4.50	5091.3	986.6	16.44	16221.7	2172.0	26.53	57627.5	1426.0	4.50	6417.0
Microphytobenthos	1131.4	3.33	3767.6	986.6	7.75	66842.2	2172.0	10.45	22703.9	1426.0	3.33	4748.6
Detritus	1131.4	65	73541.0	986.6	65	64129.0	2172.0	65	141180.0	1426.0	65	92690.0
Total			16078498			11185882			23904275			12878796

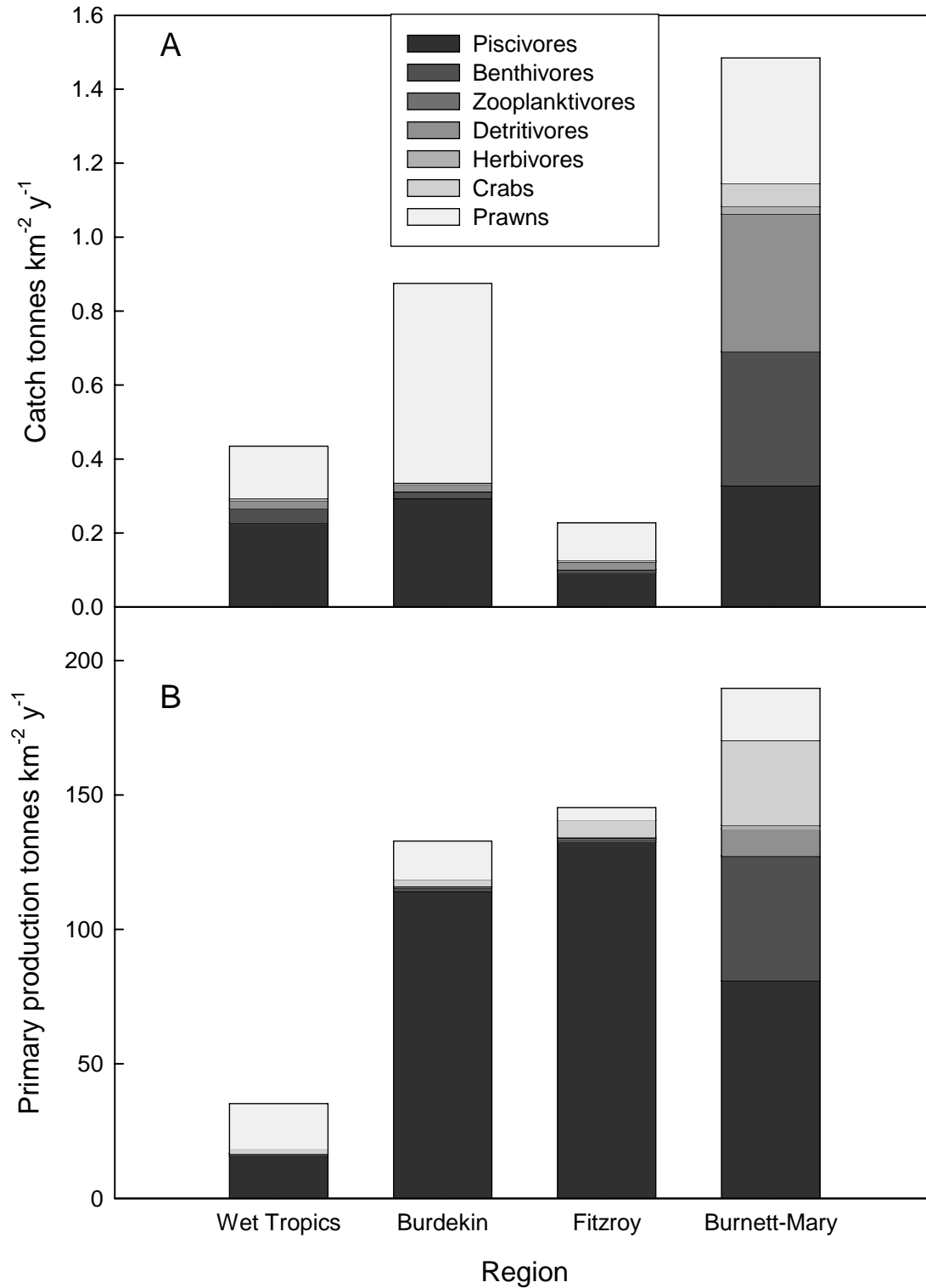


Figure 10. (A) Mean annual fishery landings for harvested groups, and (B) primary production required to sustain harvests of trophic groups in each regional model.

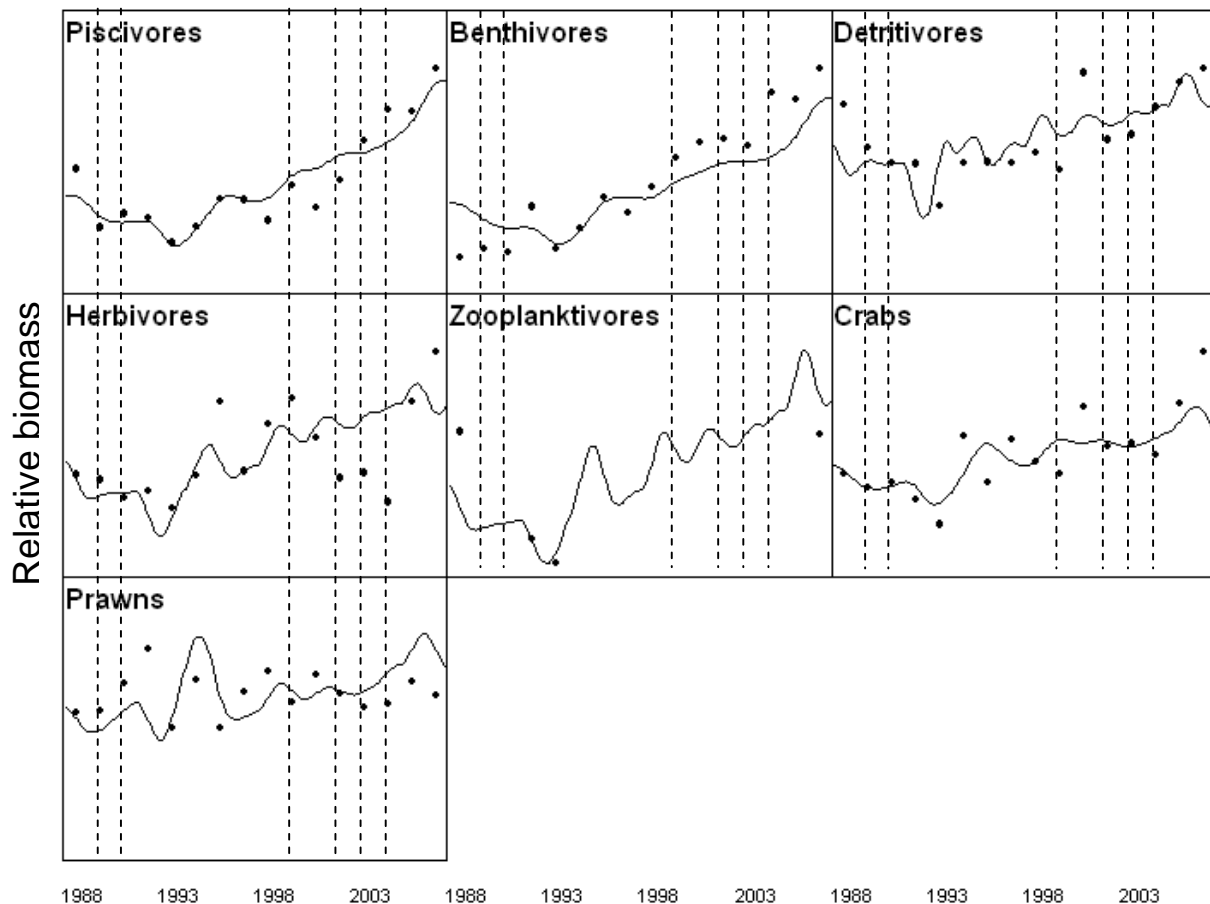


Figure 11. Modelled biomass trends for trophic groups targeted by coastal fisheries in the Wet Tropics region (solid lines), and observed estimates derived from standardised catch per unit effort data (dots). SSR = 5.83. Vertical dotted lines indicate years in which cyclones crossed the coast in this region.

Changing nutrient scenarios

The scenarios presented do not attempt to reproduce the system dynamics responsible for fluctuating biomass and fishery catches during the 16 year validation time series, so that simulated ecosystem behaviour reflects more general trends over time. Under the scenario of constant nutrient supply, all models exhibited stable biomasses within trophic groups, based largely on biomass trajectories of individual groups at the end of the 16 year validation time series, with no unexpected or erratic behaviour (Figs 15-18).

Increasing nutrient supply by 10% over 20 years resulted in increased biomass of trophic groups representing pelagic pathways, such as phytoplankton, zooplankton, zooplanktivorous fish, piscivorous fish, and seabirds. Benthic pathways also demonstrated increased biomass, but to a lesser extent than in pelagic pathways. Prawns in particular showed limited response to increased nutrients. Under the forced mediation effects of phytoplankton shading, seagrass biomass declined in all models, with resultant decreases in dugong, sea turtle and herbivorous fish biomass. Simulated biomass changes mostly occurred gradually, but the Burnett-Mary model demonstrated a rapid trophic regime shift after approximately 8 years of increasing nutrient loads. Although phytoplankton biomass in the Burnett-Mary model increased steadily during the simulation period, seagrass disappeared completely within three to four years after a period of stability.

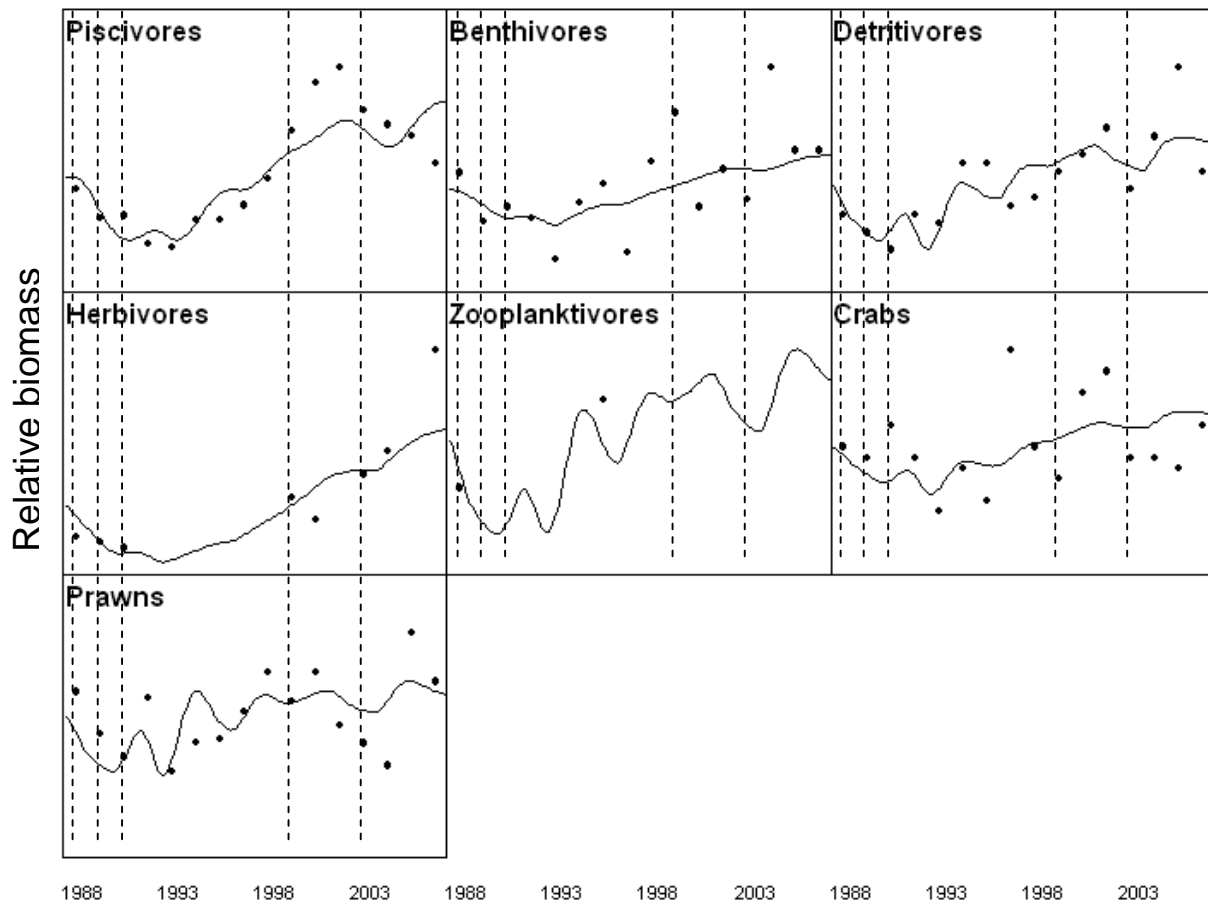


Figure 12. Modelled biomass trends for trophic groups targeted by coastal fisheries in the Burdekin region (solid lines), and observed estimates derived from standardised catch per unit effort data (dots). SSR = 6.70. Vertical dotted lines indicate years in which cyclones crossed the coast in this region.

If shading of seagrass by phytoplankton is disabled within the 10% nutrient increase scenario, seagrass biomass continues to increase with no evidence of regime shifts. In the Burdekin region, however, herbivorous fish biomass increased rapidly, forcing declines in macroalgae through increased grazing, and in sea turtles and zooplanktivores through dietary competition.

Decreasing nutrient supply by 10% over 20 years generally had the reverse effect of increasing nutrients, by reducing the biomass of trophic groups associated with pelagic pathways. However, the biomass of seagrass was also reduced, creating a stronger decline in groups relying on benthic pathways. Responses to decreasing nutrients occurred gradually with no apparent regime shifts.

Responses to the nutrient scenarios presented differed among models according to the magnitude of the 10% change applied in relation to background nutrient availability estimated by the primary production anomaly routine in Ecosim. Background variation was greatest in the Fitzroy model where nutrient changes estimated during the validation period were much larger than the 10% changes simulated, presumably reflecting the extremely episodic nature of flows and nutrient delivery in the Fitzroy. In comparison, background variation in the other regional models was less than or equivalent to the magnitude of the simulated changes.

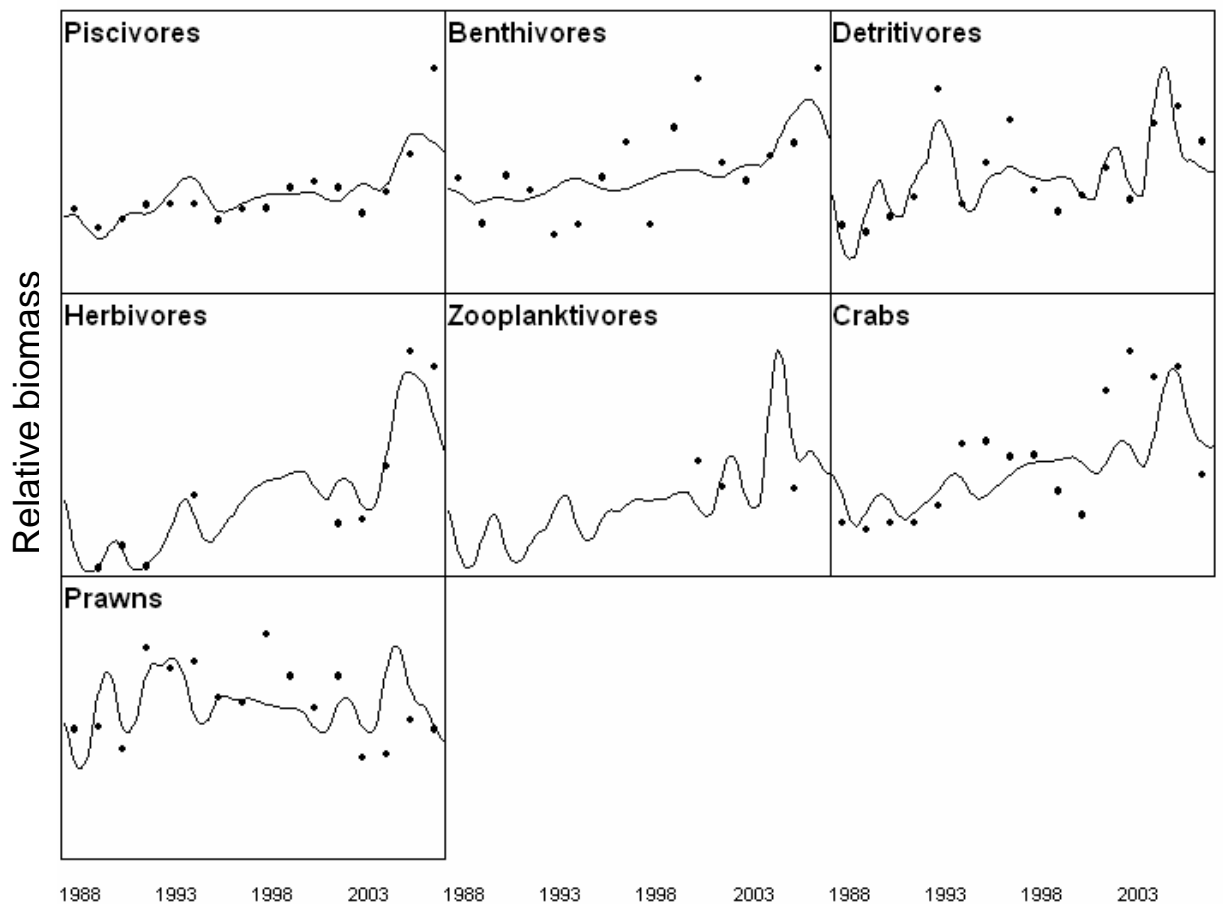


Figure 13. Modelled biomass trends for trophic groups targeted by coastal fisheries in the Fitzroy region (solid lines), and observed estimates derived from fishery catch per unit effort data (dots). SSR = 6.50. No cyclones crossed the coast of the Fitzroy region during the model validation period.

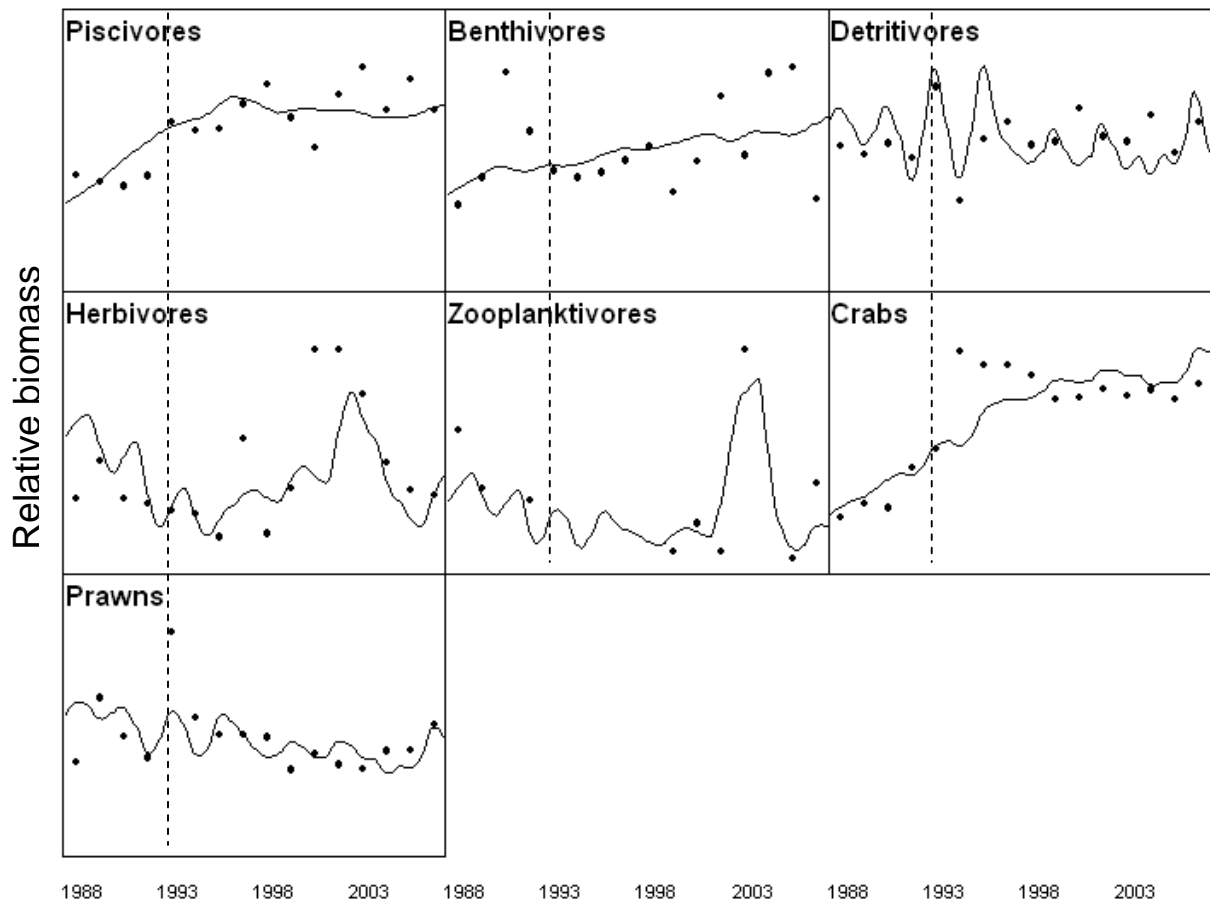


Figure 14. Modelled biomass trends for trophic groups targeted by coastal fisheries in the Burnett-Mary region (solid lines), and observed estimates derived from fishery catch per unit effort data (dots). SSR = 13.71. Vertical dotted lines indicate years in which cyclones crossed the coast in this region.

Discussion

Model limitations

The value of trophic models for understanding differences in coastal food webs within the Great Barrier Reef region lies in the assumptions required in assembling disparate data sets and in building the models themselves. As the data used in this study was drawn from multiple sites at different times, refinement of the existing models by collecting regionally representative data across different coastal habitats and trophic groups with standardised sampling methods is an important future requirement. Standardised data collection will strengthen the ability to draw comparisons among models, however, sensitivity analyses suggest that the existing models are relatively robust with respect to the biomass estimates supplied. In contrast, the models are most sensitive to estimates of P/B ratios and ecotrophic efficiency. Greater improvements in model reliability are likely to be achieved through obtaining local values for these parameters, as well as through improving the representativeness of biomass estimates within each region. Primary producer and benthic invertebrate trophic groups in particular are likely to benefit from these improvements.

The models presented here have been developed around a simple, common trophic structure that aggregates species into functional trophic groups. Some level of aggregation is necessary for all trophic models, so that information on individual species of interest becomes buried within larger functional groups (Morris et al. 2005). However, specifying a larger number of trophic groups increases the number of assumptions concerning parameter estimates, and can make the model unwieldy. This study adopts the approach that models should be no more complex than required to achieve their objective. Constraining regional models to a common structure has the disadvantage of losing the ability to discriminate differences in trophic structure among regional models. However, current data availability dictates that any apparent differences in trophic structure are more likely to reflect the quantity of input data rather than real differences. In the case of the Burnett-Mary model, the absence of crocodiles as a top predator had little effect on model performance or comparability with other models.

Retaining a simple structure also required the assumption that net migration to and from the model domain was zero. Whilst this constraint is unrealistic, most migration occurs at the species level rather than as whole trophic groups (e.g. McCulloch et al. 2005, Sheaves 1995). Where migratory information is available, a more practical approach is to assign those species as separate trophic groups, thereby increasing structural complexity of the model.

The lack of data for the Mackay-Whitsundays natural resource management region prevented development of a model specifically for this region. However, the similarities in responses of the other regional models to scenarios of constant, increasing, or decreasing nutrients suggest that the Mackay-Whitsundays region may behave similarly. This hypothesis remains to be tested with a region-specific model.

No attempt was made in the current models to disaggregate distinct life-history phases where juveniles and adults demonstrate ontogenetic dietary shifts from e.g. zooplankton to fish or plants, or use different habitats. Ecopath with Ecosim has the capacity to represent multiple life-history stanzas for such species, but for the present purposes it was assumed that trophic groups maintained constant composition through time.

Other models such as Atlantis, an expansion of the BM2 model originally developed for Port Phillip Bay in Australia (Fulton and Smith 2004), now have capacity to represent age-structured data for each trophic group and to link trophic interactions to biogeochemical inputs. However, for higher trophic levels such as fish, interpretations from these more elaborate models are no better than those derived from relatively simple models such as EwE which invoke fewer assumptions, and have less demanding data requirements (Walters and Martell 2004).

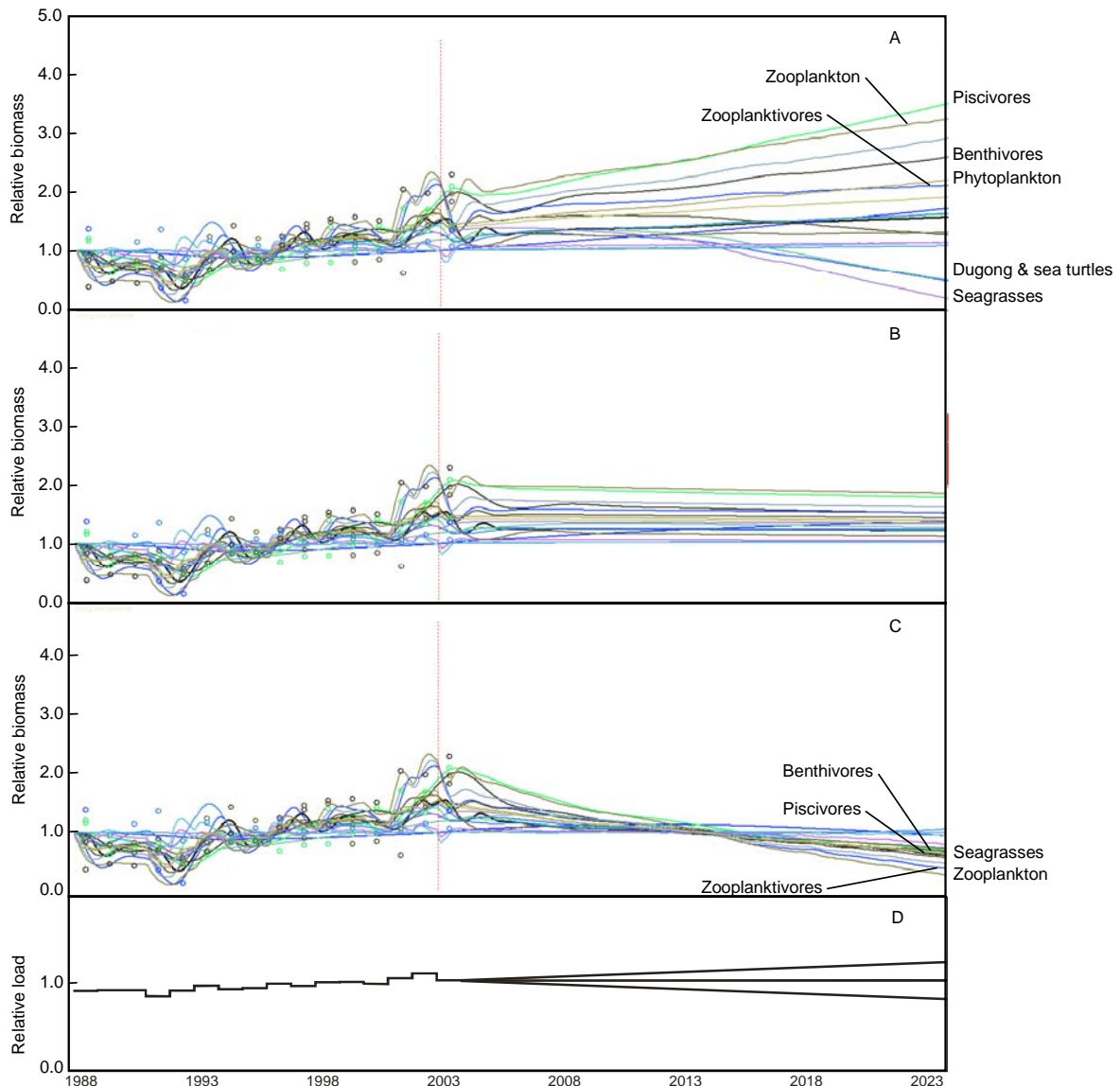


Figure 15. Predicted ecosystem responses to nutrient scenarios in the Wet Tropics region. Open circles represent fishery catches. (A) 10% nutrient increase over 20 years; (B) constant nutrient input over 20 years; (C) 10% nutrient decrease over 20 years; (D) Relative nutrient loads estimated by Ecosim 1988-2003, followed by simulated scenarios.

Comparison of regional models

Estuarine fish biomass estimates vary widely among studies from eastern Australia, with values ranging from 1.3 tonnes km⁻² for Tin Can Bay in the Burnett-Mary region (Halliday and Young 1996), to 29.0 tonnes km⁻² in Alligator Creek in the Burdekin region (Robertson and Duke 1990). For Port Curtis in the Fitzroy region, Currie and Connolly (2005) recorded 0.3 tonnes km⁻², which by estimating beam trawl efficiency as 10% (Wennhage et al. 1997) provides the value of 2.9 tonnes km⁻² applied in this study. In the Embley Estuary in the Gulf of Carpentaria, Blaber et al. (1989) estimated fish biomass as 7.1 tonnes km⁻² to 16.1 tonnes km⁻² in open water, 5.0 tonnes km⁻² on sandy beaches, 8.2 tonnes km⁻² in mangrove creeks, 70.6 tonnes km⁻² for intertidal mudflats near mangroves, and from 0.5 to 1.8 tonnes km⁻² for seagrass beds.

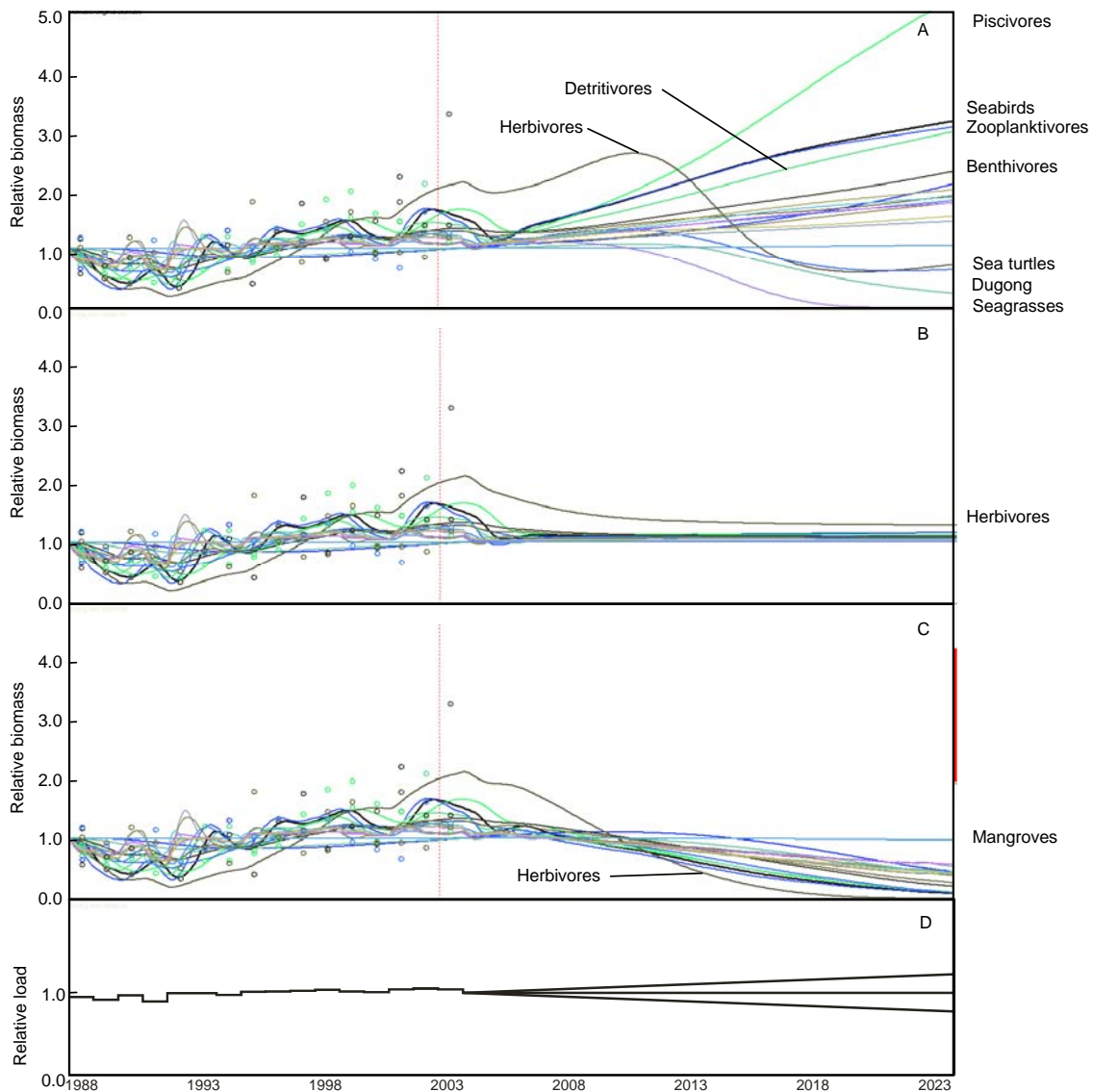


Figure 16. Predicted ecosystem responses to nutrient scenarios in the Burdekin region. Open circles represent fishery catches. (A) 10% nutrient increase over 20 years; (B) constant nutrient input over 20 years; (C) 10% nutrient decrease over 20 years; (D) Relative nutrient loads estimated by Ecosim 1988-2003, followed by simulated scenarios.

Absolute biomass estimates from different systems need to be compared with care because of the substantial variation among habitats within any given system, within and among geographic regions (e.g. Robertson and Duke 1990, Sheaves 1998), temporal variation at seasonal and longer time-scales, and variations in efficiency of different sampling methods. For this reason, differences in absolute biomass presented here for different regions should be considered indicative based on available data, rather than as definitively characteristic of each region. It is therefore more instructive at this stage to compare the trophic structure of food webs, and how they might respond to changes in environmental management.

Scharler and Baird (2005) found transfer efficiency among three South African estuaries increased with increasing freshwater inflows. Similarly, this study found transfer efficiency within the GBR increased with increasing rainfall and catchment vegetation cover, suggesting a link between catchment condition, and the efficiency with which aquatic food

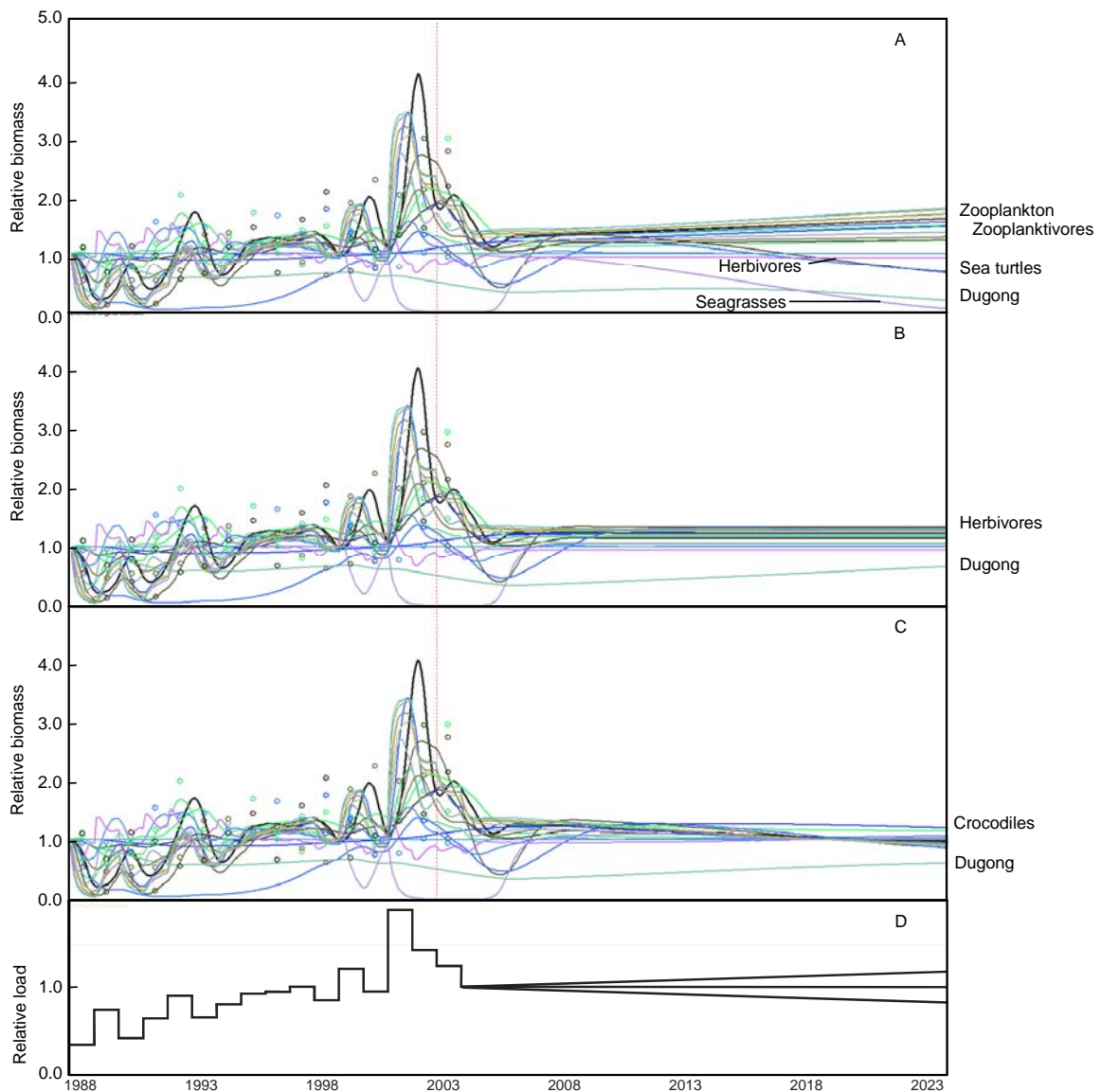


Figure 17. Predicted ecosystem responses to nutrient scenarios in the Fitzroy region. Open circles represent fishery catches. (A) 10% nutrient increase over 20 years; (B) constant nutrient input over 20 years; (C) 10% nutrient decrease over 20 years; (D) Relative nutrient loads estimated by Ecosim 1988-2003, followed by simulated scenarios.

webs assimilate carbon. Diet plasticity, indicated by high levels of omnivory associated with high rainfall and river discharge in the GBR, allows predators to assimilate energy across a wide range of trophic levels, reducing energy losses while feeding on lower trophic levels. High biodiversity in the Wet Tropics (Pusey et al. 2004, Kroon 2004) offers predators a wider choice of prey, whilst the flushing regime influences the proportional consumption of detritus, microbenthic and macrophytic primary producers by higher trophic levels (Sheaves et al. 2006, Webster et al. 2006).

Diagnostic indicators such as ascendancy, overheads and development capacity are related to the concept of ecosystem carrying capacity, which fluctuates widely according to the magnitude of variation in the natural environment. Making equilibrium-based assumptions about ecosystem development capacity, when most hierarchical systems display dynamic,

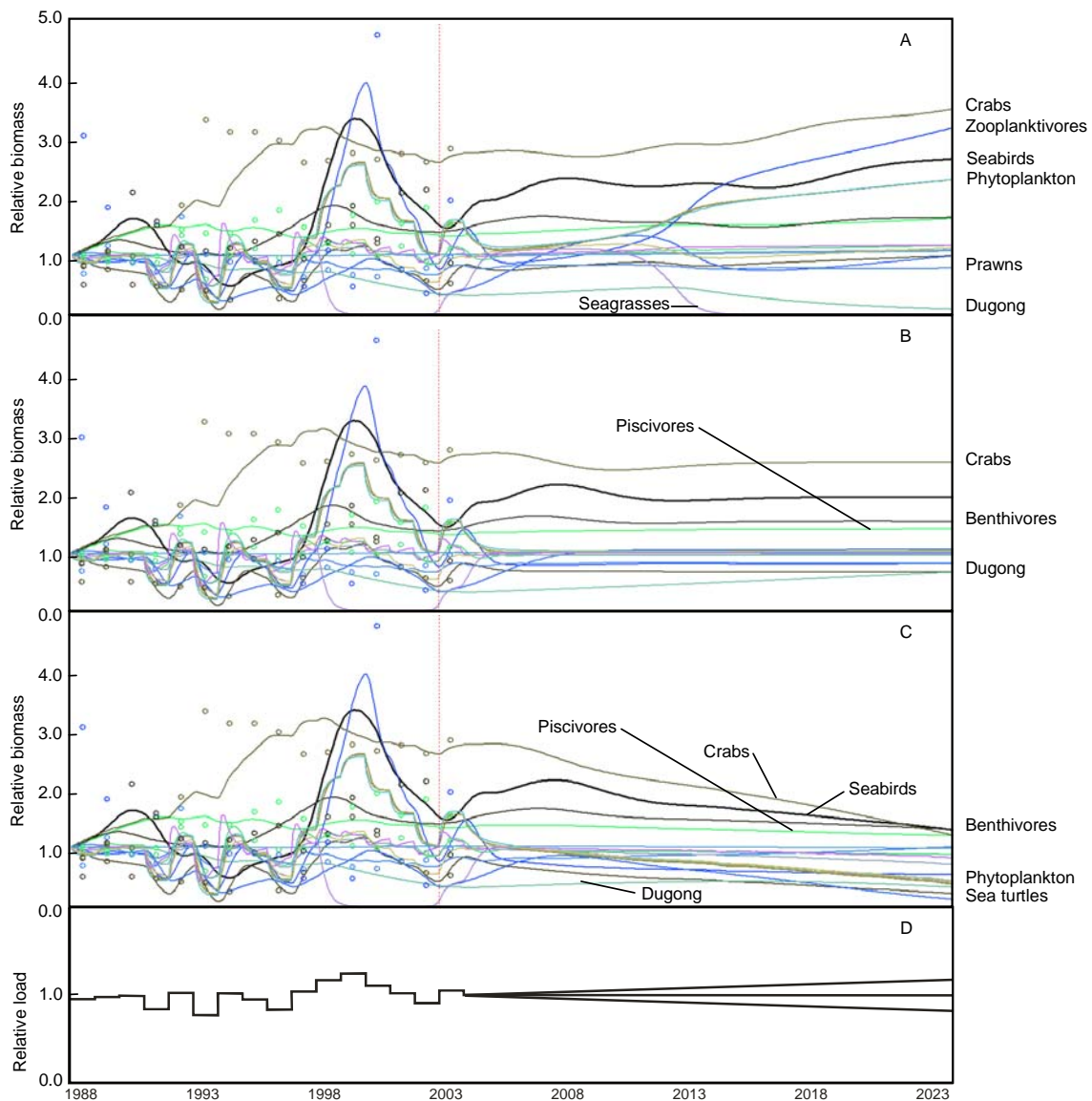


Figure 18. Predicted ecosystem responses to nutrient scenarios in the Burnett-Mary region. Open circles represent fishery catches. (A) 10% nutrient increase over 20 years; (B) constant nutrient input over 20 years; (C) 10% nutrient decrease over 20 years; (D) Relative nutrient loads estimated by Ecosim 1988-2003, followed by simulated scenarios.

and often stochastic behaviour about a quasi-equilibrium (Wu and Loucks 1995, Thorpe et al. 2006), may lead to gross misinterpretation of system behaviour. However, the risk of misinterpretation is minimised when comparing system capacity in a relative, rather than absolute, context. The positive correlation between mangrove area and ascendancy is consistent with previous studies of the role of mangroves in supporting ecological production in coastal ecosystems (e.g. Odum and Heald 1975, Robertson and Alongi 1992, Sheaves and Molony 2000).

Validation of models against commercial fishery data identified increasing biomass trends for trophic groups such as piscivorous fish, benthivorous fish, detritivorous fish and herbivorous fish in the Wet Tropics, Burdekin and Fitzroy regions. These trends are consistent with the progressive increase in nutrient loads discharged from coastal rivers (E.g. Mitchell et al.

2001, McKergow et al. 2005a). Underlying primary production estimated by Ecosim also suggests increasing nutrient loads to coastal ecosystems. Whilst the models presented here are simple in structure, they appear to be sufficiently sensitive to changes in nutrient input to be useful in understanding how coastal fisheries resources and the food webs on which they depend may change in response to changes in catchment management upstream.

Caddy (2000) identified inputs of material from coastal catchments as having a larger impact on semi-enclosed coastal ecosystems than the more obvious effects commonly ascribed to fishing activities. This study supports evidence of catchment impacts on coastal fish resources through identifying correlations between catchment characteristics and multiple diagnostic indicators of coastal food web condition. The models developed in this study provide a further basis for assessing possible effects of changes in nutrient transport on coastal fisheries.

The scenarios presented in this study suggest that increasing nutrient inputs to coastal waters may allow increased production of some pelagic species, with the associated risk of sudden regime shifts to phytoplankton-dominated systems with a rapid loss of benthic producers such as seagrasses. Light-related stress of seagrasses associated with shading by phytoplankton has been identified as a threat to seagrass beds in the GBR region (Carruthers et al. 2002), however available data suggests that seagrasses themselves respond positively to increased nutrient availability where shading does not occur (Waycott et al. 2005). In contrast, successful intervention to reduce nutrient inputs to the GBR may result in a reduction in biomass of trophic groups such as piscivores, benthivores, detritivores and herbivores, as well as crabs, which constitute an economically important component of the coastal fishery.

The magnitude of ecosystem responses to simulated increases and decreases in nutrient supply was influenced by the level of background variation in nutrient availability and primary production. This finding suggests that ecosystem responses to successful catchment intervention may be more difficult to detect in dry tropical regions such as the Fitzroy that are characterised by high interannual variability in rainfall and episodic streamflow (Webster et al. 2005). Because of the long timeframe over which improvements in water quality are likely to be achieved, changes in climate variability and regional hydrology, as well as the magnitude of water quality improvements achieved, are likely to affect the ability to detect ecosystem responses.

In view of the initiatives in place to reduce inputs of sediments and nutrients to the GBR, and the potential for reduced biological production of species harvested by commercial and recreational fisheries, there is a clear need for improved capacity to predict ecological responses to improvements in catchment management in addition to existing investments in predicting changes in water quality. Improved ecological models of nutrient reduction scenarios will support the development of strategies to offset lost fishery production, such as through increased habitat protection, rehabilitation of degraded coastal habitats, and construction of new habitats to compensate for historical losses (Duke et al. 2003).

One of the main causes of change in coastal ecosystems in the GBR region is the loss of mangrove and other wetlands that support valuable inshore fisheries (Robertson and Duke 1990, Blaber 1997) through reclamation for development (Duke et al. 2003, Schaffelke et al. 2005). It is likely that the effects of this habitat loss on coastal fishery production have been masked by nutrient enrichment over the same time period. Refinement of the models presented here is required to further understand potential changes in ecosystem processes and fisheries resources arising from improved water quality, and the capacity to offset these changes through effective habitat management.

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