

NORTH WEST SHELF
JOINT ENVIRONMENTAL
MANAGEMENT STUDY



Benthic habitat dynamics and
models on Australia's
North West Shelf


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NWSJEMS

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- K. Sainsbury

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Final report

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List of technical reports

NWSJEMS Technical Report No. 1

Review of research and data relevant to marine environmental management of Australia's North West Shelf.

A. Heyward, A. Revill and C. Sherwood

NWSJEMS Technical Report No. 2

Bibliography of research and data relevant to marine environmental management of Australia's North West Shelf.

P. Jernakoff, L. Scott, A. Heyward, A. Revill and C. Sherwood

NWSJEMS Technical Report No. 3

Summary of international conventions, Commonwealth and State legislation and other instruments affecting marine resource allocation, use, conservation and environmental protection on the North West Shelf of Australia.

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Management strategy evaluation specification for Australia's North West Shelf.
E. Fulton, K. Sainsbury, D. Hayes, V. Lyne, R. Little, M. Fuller, S. Condie, R. Gray, R. Scott,
H. Webb, B. Hatfield, M. Martin, and D. McDonald

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Management strategy evaluations for multiple use management of Australia's North West Shelf
– Visualisation software and user guide.
B. Hatfield, L. Thomas and R. Scott

NWSJEMS Technical Report No. 18
Background quality for coastal marine waters of the North West Shelf, Western Australia.
K. Wenziker, K. McAlpine, S. Apte, R. Masini

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ACRONYMS

ACOM	Australian Community Ocean Model
AFMA	Australian Fisheries Management Authority
AFZ	Australian Fishing Zone
AGSO	Australian Geological Survey Organisation now Geoscience Australia
AHC	Australian Heritage Commission
AIMS	Australian Institute of Marine Science
AMSA	Australian Maritime Safety Authority
ANCA	Australian Nature Conservation Agency
ANZECC	Australian and New Zealand Environment and Conservation Council
ANZLIC	Australian and New Zealand Land Information Council
APPEA	Australian Petroleum, Production and Exploration Association
AQIA	Australian Quarantine Inspection Service
ARMCANZ	Agricultural Resources Management council of Australia and New Zealand
ASIC	Australian Seafood Industry Council
ASDD	Australian Spatial Data Directory
CAAB	Codes for Australian Aquatic Biota
CAES	Catch and Effort Statistics
CALM	Department of Conservation and Land Management (WA Government)
CAMBA	China Australia Migratory Birds Agreement
CDF	Common data format
CITIES	Convention on International Trade in Endangered Species
CTD	conductivity-temperature-depth
CMAR	CSIRO Marine and Atmospheric Research
CMR	CSIRO Marine Research
COAG	Council of Australian Governments
Connle	Connectivity Interface
CPUE	Catch per unit effort
CSIRO	Commonwealth Science and Industrial Research Organisation
DCA	detrended correspondence analysis
DIC	Dissolved inorganic carbon
DISR	Department of Industry, Science and Resources (Commonwealth)
DEP	Department of Environmental Protection (WA Government)
DOM	Dissolved organic matter
DPIE	Department of Primary Industries and Energy
DRD	Department of Resources Development (WA Government)
EA	Environment Australia
EEZ	Exclusive Economic Zone
EIA	Environmental Impact Assessment
EPA	Environmental Protection Agency
EPP	Environmental Protection Policy
ENSO	El Nino Southern Oscillation
EQC	Environmental Quality Criteria (Western Australia)
EQO	Environmental Quality Objective (Western Australia)
ESD	Ecologically Sustainable Development
FRDC	Fisheries Research and Development Corporation
FRMA	Fish Resources Management Act
GA	Geoscience Australia formerly AGSO
GESAMP	Joint Group of Experts on Scientific Aspects of Environmental Protection
GIS	Geographic Information System
ICESD	Intergovernmental Committee on Ecologically Sustainable Development
ICS	International Chamber of Shipping
IOC	International Oceanographic Commission
IGAE	Intergovernmental Agreement on the Environment
ICOMOS	International Council for Monuments and Sites
IMO	International Maritime Organisation
IPCC	Intergovernmental Panel on Climate Change

IUNC	International Union for Conservation of Nature and Natural Resources
IWC	International Whaling Commission
JAMBA	Japan Australian Migratory Birds Agreement
LNG	Liquified natural gas
MarLIN	Marine Laboratories Information Network
MARPOL	International Convention for the Prevention of Pollution from Ships
MECO	Model of Estuaries and Coastal Oceans
MOU	Memorandum of Understanding
MPAs	Marine Protected Areas
MEMS	Marine Environmental Management Study
MSE	Management Strategy Evaluation
NCEP - NCAR	National Centre for Environmental Prediction – National Centre for Atmospheric Research
NEPC	National Environmental Protection Council
NEPM	National Environment Protection Measures
NGOs	Non government organisations
NRSMPA	National Representative System of Marine Protected Areas
NWQMS	National Water Quality Management Strategy
NWS	North West Shelf
NWSJEMS	North West Shelf Joint Environmental Management Study
NWSMEMS	North West Shelf Marine Environmental Management Study
ICIMF	Oil Company International Marine Forum
OCS	Offshore Constitutional Settlement
PFW	Produced formation water
P(SL)A	Petroleum (Submerged Lands) Act
PSU	Practical salinity units
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SOI	Southern Oscillation Index
SMCWS	Southern Metropolitan Coastal Waters Study (Western Australia)
TBT	Tributyl Tin
UNCED	United Nations Conference on Environment and Development
UNCLOS	United Nations Convention of the Law of the Sea
UNEP	United Nations Environment Program
UNESCO	United Nations Environment, Social and Cultural Organisation
UNFCCC	United Nations Framework Convention on Climate Change
WADEP	Western Australian Department of Environmental Protection
WADME	Western Australian Department of Minerals and Energy
WAEPa	Western Australian Environmental Protection Authority
WALIS	Western Australian Land Information System
WAPC	Western Australian Planning Commission
WHC	World Heritage Commission
WOD	World Ocean Database
www	world wide web

TECHNICAL SUMMARY

As management of marine living resource moves beyond simple single species resource utilisation concerns to ecosystem-based management, consideration of habitat dynamics is becoming an integral part of marine resource management. Previous studies have found that habitat can play a critical role in both single species and community level dynamics of species of commercial concern (Sainsbury, 1987; Sainsbury, 1988; Auster & Malatesta, 1995; Freese et al. 1999; Lindholm et al. 1999; Jackson et al. 2000; Sainsbury et al. 2000). Moreover, benthic habitat is becoming a conservation concern in its own right (Environment Protection and Biodiversity Conservation Act 1999). Useful first steps in understanding local benthic habitat dynamics is to collect observation (preferably through time) of the benthos and then to attempt to create dynamic models that capture the broadscale dynamics of the habitat of interest. Just such an exercise was undertaken for the major benthic habitat types in the North West Shelf of Australia (specifically epibenthic, mainly sponge, habitats, seagrass, macroalgae and mangroves).

Between 1983 and 1997 photographic data on benthic habitats were collected on the North West Shelf of Australia by CSIRO Marine Research. These data were used to calculate proportional coverage of small (≤ 25 cm) and large (> 25 cm) epibenthos on the seabed between depths of 20 and 200 m. These observations and the fisheries effort data for the Taiwanese (1973 to 1981) and domestic fleets (1987 to 1997) were pooled onto a spatial grid of 10 by 10 nautical minutes with a temporal scale of a year. A multivariate analysis of the main factors associated with the distribution of the benthic habitats was undertaken (as a guide for factors to include in the final habitat dynamics model). The observations suggested that there was a strong depth-dependent gradient in the biomass and coverage of benthic habitat, which did not appear to be related to bottom stress, but may have been associated with sediment substrate properties. Given the importance of bottom stress in shaping benthic habitats in many other locations around Australia (Pitcher et al. 2002; Pitcher et al. 2004a; Pitcher et al. 2004b and Phillip England, CSIRO Marine and Atmospheric Research, pers. comm.) it is surprising that the analyses showed it to be a non-significant physical factor in determining proportional coverage on the North West Shelf (NWS).

During the model development phase of the study a dynamic age-structured metapopulation model was created. This habitat model includes depth and substrate dependent recruitment, growth natural mortality and removal rates by fishing and cyclones. The parameters used in this model were either taken from literature or estimated by minimising the sum of squares between the observed and estimated proportional coverage. The model results easily reproduced the observed patterns of strongly depth related recruitment. It also showed that trawl fishing effort (both by Taiwanese and domestic fleets) was probably a significant factor in shaping the current distribution of benthic habitats on the NWS. There were issues with the model's ability to predict recovery rates that match the empirical data – this is almost undoubtedly the result of poorly spatially resolved historical catch time series and a too coarse model resolution. Recasting future analyses and modelling efforts on finer (or more irregular) grids should go a long way to rectifying these issues. Nevertheless, even as is, the model still performs acceptably, particularly within an MSE framework.

The bulk of the data (and subsequent modelling efforts) dealt with epibenthic (mainly sponge) habitats. The same model was also applied (in a more limited extent) to seagrass, macroalgae and mangroves. There was substantially less data available for these groups and the models were parameterised from the literature and expert knowledge. The dynamics predicted for seagrass and macroalgae showed that they are also strongly influenced by depth, substrate, cyclones and fishing; while mangroves are fairly untouched on the North West Shelf.

While the bulk of management relevant modelling work for this NWS study is to be found in Little et al. (2006), it is possible to make a few brief comments on the management implications of the model output. Sparse data availability meant only rudimentary modelling progress could be made for seagrass, macroalgae and mangroves. In contrast, the modelling of benthic habitats showed that there are some large scale management implications that arise from the ecology of these sessile species. Depletion rates are typically very rapid (with most damage occurring within the first five years of an activity such as fishing), while recovery times can be quite slow (20+ years potentially). This means that spatial management may take a long time to produce tangible results, which may lead to division amongst stakeholder groups with regard to the success of the method versus conservation and management goals. On top of which the rapid rate of decline of the habitat, once exposed to an intensive pressure such as trawling, means there is little room for error and that a precautionary approach is vital.

Models may become a crucial part of future spatial management decision processes or support. If they are to be used successfully then they must be used with thought. The habitat dynamics models of the type discussed in this report could be used wisely and well to guide management from within an MSE setting. If direct management tools are called for, however, then regardless of what form of habitat dynamics model was chosen (whether of the form presented here or any other existing form) it would be necessary to go through further rounds of model development and testing before they could be used with confidence in comparison to that bestowed in other management models (e.g. fisheries assessment models).

1. INTRODUCTION

1.1 Study area – North West Shelf of Australia

The North West Shelf (NWS) of Australia (figure 1.1.1) is a 95 000 km² of broad shelf under a tropical hydrographic regime (Wyrтки, 1961; Condie & Andrewartha, 2003; Condie et al. 2003; Condie et al. 2006). The study area is the section of this region north 21°S, west of 119°E and shallower than the 200 m isobath. The area is marked by a sharp break between naturally turbid inshore waters and clearer offshore waters. The seabed of the NWS is primarily calcareous sands and fine muds (Jones, 1973; McLoughlin & Young, 1985) with patchy coverage of reef and sponge beds (CMR and DEP, 2002; Althaus et al. in prep a). Biologically the NWS has reasonably high productivity (Tranter, 1962; Kabanova, 1968; Motoda & Taniguchi, 1978), with a diverse Indo-West Pacific fish fauna (Sainsbury et al. 1997), and productive crustacean populations (Sainsbury, CSIRO Marine and Atmospheric Research, pers. comm.; Bulman and Althaus, in prep). It has also been shown that the biogenic habitats play a large part in structuring the distribution of biological stocks in the area (Sainsbury et al. 1997; Althaus et al. in prep b).

A large number of extractive industries are active on the NWS, including petroleum exploration and extraction, tourism, coastal development, salt production, port operations and fisheries. While fishing is not the biggest of these industries economically it has been found to have significant effects on the biota of the NWS (Sainsbury, 1987, 1988). The area has been exploited by a range of foreign and domestic fishing operations over the last thirty years (figure 1.1.2):

- 1959 to 1963 a Japanese trawl fishery targeted *Lethrinus* between 30 and 120 m from 116°E to 117°30'E (red arrows in figure 1.1.2);
- 1972 to 1989 a Taiwanese pair trawl fishery targeted *Nemipterus*, *Saurida*, *Lutjanus* and *Lethrinus* between 30 and 120 m (light blue region in figure 1.1.2);
- 1984 onwards an Australian trap fishery targets *Lethrinus*, *Lutjanus* and *Epinephelus* down to 80 m (in areas that had seen little trawling) (blue-green region in figure 1.1.2); and
- 1989 onwards an Australian trawl fishery targets *Lutjanus* and *Lethrinus* (also catching *Nemipterus*, *Saurida*) between 30 and 120 m east of 116°45'E (dark blue arrow in figure 1.1.2).

Between 1983 and 1997 there were also research surveys carried out in the area. These have provided information on the composition of the fish community and seabed cover (Sainsbury, 1987; Althaus et al. in prep a and b).

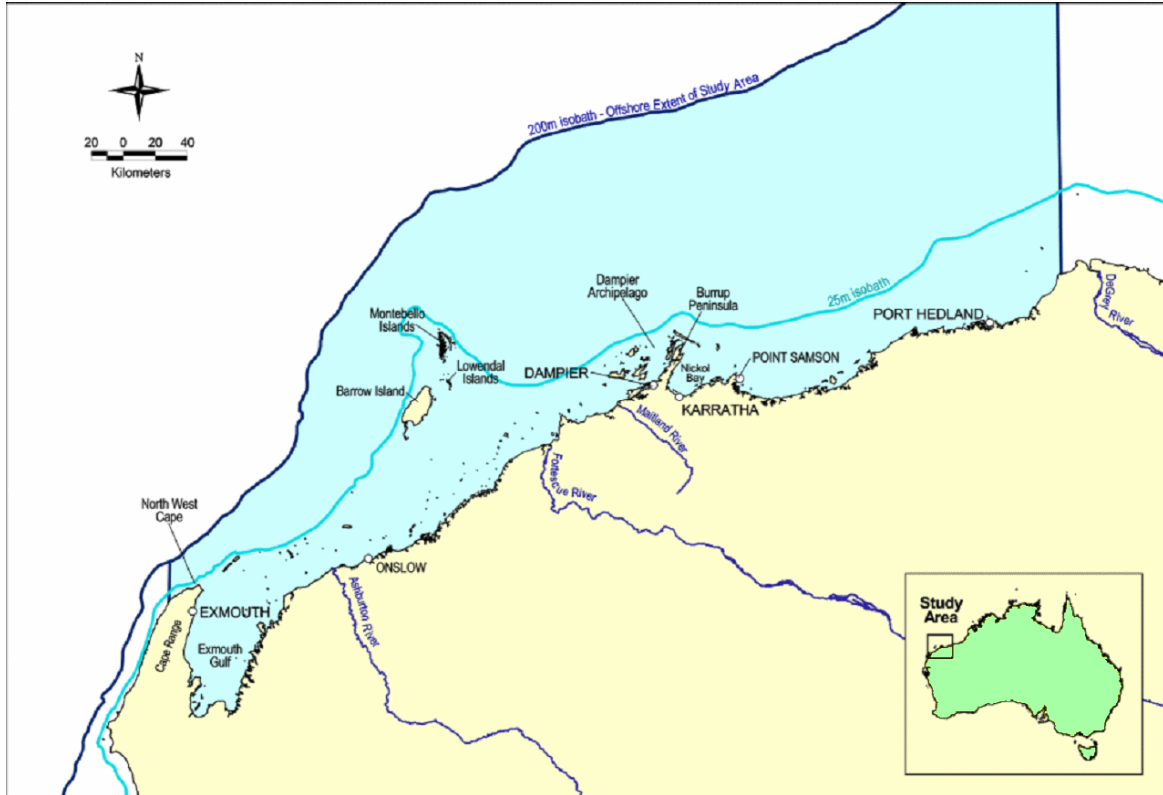


Figure 1.1.1: Map of the North West Shelf of Australia, with study area marked in light blue.

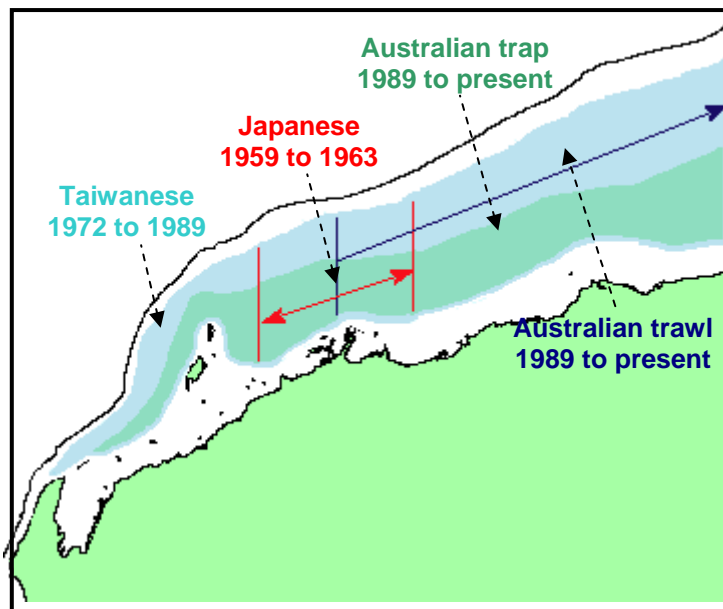


Figure 1.1.2: Map of the distribution of fishing operations on the North West Shelf from 1959. The area of the Japanese fishery lies between the two vertical red lines. The Taiwanese fishery covered the area shaded light blue, including the area lying beneath the area shaded in green (which marks the Australian trap fishery). The Australian trawl fishery is only the area to the west of the vertical black line (situated between the two vertical red lines).

1.2 Benthic habitats

The benthic habitats of primary interest on the NWS are epibenthos, seagrass and mangroves. Macroalgae are also thought to be relatively important as habitat and also as a secondary food sources for large herbivores (e.g. dugong) in the area (Bob Prince, WA Department of Conservation and Land Management – CALM, pers. comm.). All of these habitat types have been found to have significant roles in structuring ecological communities and in supporting local NWS production (Sainsbury, 1991; Loneragan et al. 1994; McCook et al. 1995; Haig, 1997; Duarte & Cebrián, 1996; Sainsbury et al. 1997). Moreover, Sainsbury (1991) and Sainsbury et al. (1997) conclude that benthic habitat structure has a significant influence on the fish community structure on the NWS.

Over the last decade a lot of attention has been paid to the impact of anthropogenic activities on benthic habitats (and consequently on associated communities). These have largely been in the areas of coastal pollution, spills, and fishing (Jones, 1992; Kiffney & Clements, 1994; Dayton et al. 1995; Auster et al. 1996; Collie et al. 1997; Thorne & Williams, 1997; Goni, 1998; Jennings & Kaiser, 1998; Dorsey & Pederson, 1998; Kaiser et al. 1998; Engel & Kvitek, 1998; Schwinghamer et al. 1998; Bax et al. 1999; Hall, 1999; Moran & Stephenson, 2000; Jennings et al. 2001; Gesteria et al. 2003). At the scale of the NWS the greatest human impacts on benthic habitats are likely to be from fishing (the other industries are more likely to cause localised impacts). As a result, any predictive model of habitat dynamics on the NWS would have to include the effects of fishing in particular. Inclusion of large scale natural disturbance events, like cyclones, must also be included.

The effects of fishing methods on natural systems are varied. Trawl fisheries (like those operated on the NWS over the last three decades) are known to have a substantial impact on habitat structure and complexity. For example, experimental trawling in the Mediterranean showed that after only five sequential tows cover in seagrass meadows was reduced by up to 10% (Goni, 1998) and studies in the North and Irish seas show fragile reef building habitats are even more heavily impacted (Jennings et al. 2001). These impacts can make the habitats become unsuitable for the associated species and so lead to reduced productivity of fished species and to changes in diversity in marine ecosystems (Sainsbury, 1987 and 1988; Freese et al. 1999; Auster & Malatesta, 1995; Lindholm et al. 1999; Jackson et al. 2000; Lindholm et al. 2001; Sainsbury et al. 2000). Furthermore, a reduction in the overall heterogeneity of benthic communities can affect re-colonisation (Eleftheriou, 2000).

1.3 Benthic habitat models

There are a number of existing habitat models, though more in the realm of forest gap models than in the area of marine habitat dynamics. Only a brief review of the various model types will be given here and interested readers should go to the references given for more complete descriptions and discussions of the various approaches.

Forest gap models were first developed in 1969 as an example of individual-tree based models (Siccama et al. 1969). These models represent larger forests as a composite of many small (internally homogeneous) patches, which can have stands of different age or successional stages, with each patch acting separately (i.e. there are no interactions between patches). These simplifying assumptions have made it possible to consider

mixed-species and mixed-age forests without running into computing constraints. These gap models also feature the influence of environmental and anthropogenic influences on the growth and mortality dynamics of the individual patches (Doyle, 1981; Acevedo et al. 1995). The idea of representing larger habitat types by a mosaic of smaller patches that are internally consistent would seem to hold promise for benthos which can be thought of analogously (though more inter-patch interactions may be desirable, at least with respect to seeding recruitment). Bugmann (2001) provides a comprehensive recent review of these kinds of models.

Another area where there has been extensive consideration of habitat models is within the landscape modelling arena. These models can range from dynamic multispecies population models, through genetic algorithms (Wu & David, 2002) to more traditional statistical and successional models (Cranfield et al. 2004). These models show varying degrees of responsiveness, but have been used to good effect in applications such as ATLSS (Across Trophic Level System Simulations), where they provide an environmental background for higher level trophic levels which may have specific habitat requirements (DeAngelis et al. 2000; Gross & DeAngelis, 2001).

The form of habitat model that has since had the most exploration in a biophysical or ecological context are patch dynamic models (some landscape models fall under this heading too). These models are often also called metapopulation models – as they represent a “population of populations” (Levins, 1969, 1970) where distinct subpopulations occupy spatially separated patches of habitat. This approach emphasises spatial structure and dispersal dynamics – the probabilities of extinction and recolonisation are central to metapopulation theory (Hanski & Simberloff, 1997), and dictate the ultimate viability and distribution of the metapopulation. These models have seen implementation in marine systems because patchy benthic habitats are most likely metapopulations. As these kinds of models have been more widely applied it has been recognised that real populations do not adhere to all the assumptions of the classic metapopulation model developed by Levins (1969) and many variants have been proposed (Johnson et al. 1992; Dunning et al. 1995; Sjogren-Gulve & Ray, 1996; Hanski & Simberloff, 1997; Hanski, 1997; Harrison & Taylor, 1997; Tilman et al. 1997; Wiens, 1997; Cronin, 2003), which better incorporate aspects of landscape heterogeneity (including differing patch sizes, patch clumping, individual movement capacities, local patch dynamics, and explicit patch locations). These kinds of models have largely been used in ecology and conservation (Hanski, 1997; Pulliam et al. 1992; Weins, 1997); a good review of this field of modelling can be found in Hanski and Simberloff (1997).

The final benthic habitat model (another variant patch dynamics model) to be considered here is the one by Sainsbury (1991). Sainsbury used this model to provide a carrying capacity for the finfish groups of interest in one of the original NWS MSE scenarios. It considered the seafloor as a mosaic of 4 m² patches, which had associated fixed natural mortality and recruitment probabilities. In turn this was used (via a large product calculation) to give an estimate of the proportion of patches with larger (or small) epibenthos present in any one year. This model proved to be a reasonable representation of the benthic dynamics, but for the purposes of this study it was decided that expanding the recruitment and mortality probabilities to include more explicit mechanisms was desirable.

While benthic habitat models have been developed previously, such as that by Sainsbury (1991), most existing models are patch dynamics models for seagrass or mangrove forest models (Bearlin et al. 1999; Van Nes et al. 2003). These models gave useful inspiration but were not entirely directly applicable for epibenthos, the group with the most available data on the NWS. It was decided to develop a new model, drawing on past models, which incorporates the major processes and lags thought to be important on the NWS. The formulation of this model is detailed in section 3 below.

2. OBSERVATIONS

2.1 Data collection and processing

The CSIRO Marine Research conducted ten survey cruises in the study area between 1983 and 1997. A total of 1019 transects were trawled, with location selected using a stratified random sampling approach (figure 2.1.1) (Althaus et al. in prep a). Sampling on each transect was carried out using a bottom trawl that had a camera system mounted on the headrope (see Althaus et al. in prep a, for details). This camera took still pictures of the seabed every 24 seconds (producing 75 frames per 30 minute trawl). Only 583 of the 1019 transects produced photographic data usable for our purposes.

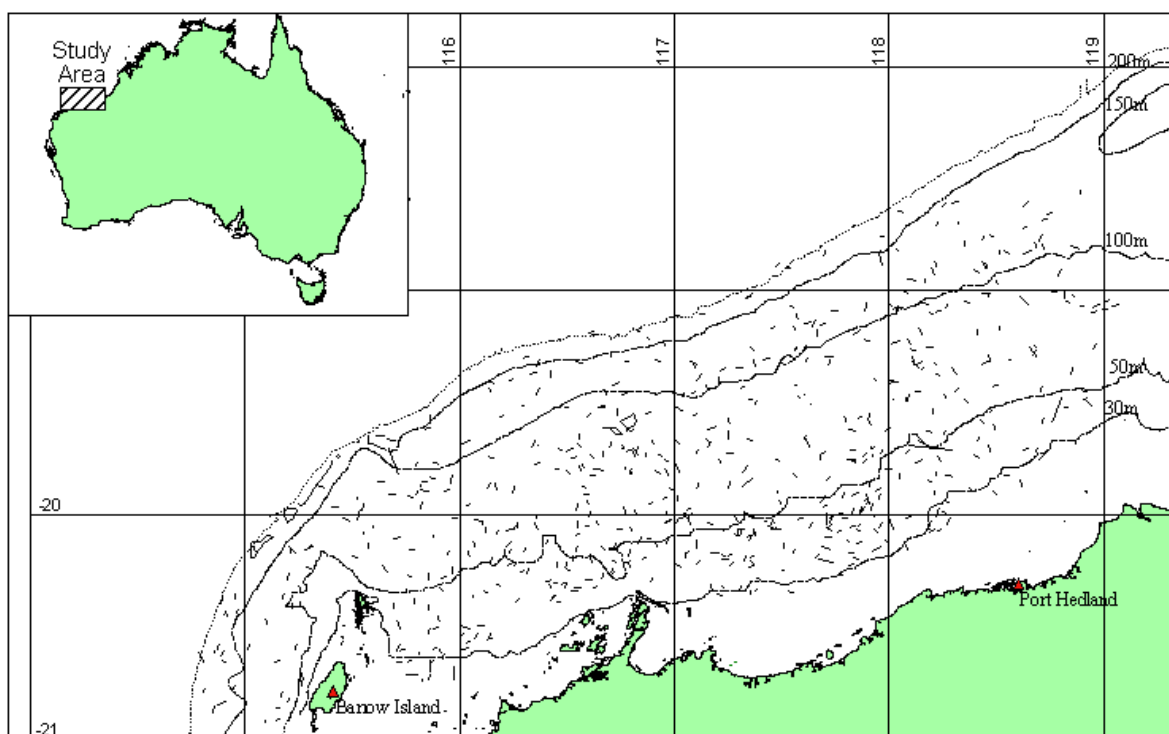


Figure 2.1.1: Map of the North West Shelf of Australia study area showing sampling transects from 1983 to 1997 taken by the CSIRO Marine Research survey cruises. Depth contours of 20, 50, 100, 150, and 200 m, are also shown.

2.1.1 Benthos data and model grids

Benthos data were obtained from the photographs taken on the research cruises. Detailed descriptions on scoring and interpretation of benthos from the photographs can be found in Althaus et al. (in prep). In processing the photographic data the study area was divided into a grid of 218 spatial cells (figure 2.1.2). Each grid has a spatial scale of 10 by 10 minutes, which is approximately 18 by 18 km. This spatial scale was chosen as it is the smallest scale the domestic trawl data can be resolved to.

Within each grid cell the observed proportional coverage of benthos in year t (C_t), was calculated as:

$$C_t = \frac{n_t^b}{N_t} \quad (2.1)$$

where n_t^b is the number of photographic frames with observed benthos in year t ; and N_t is total number of photographic frames taken in year t .

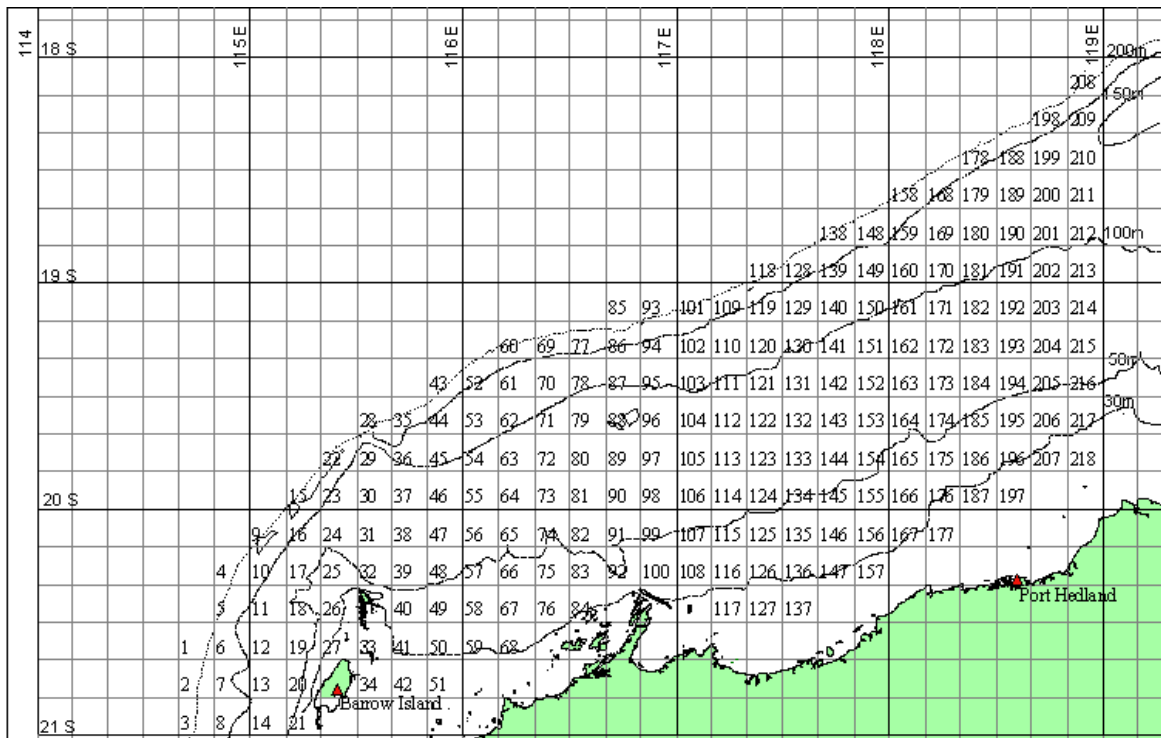


Figure 2.1.2: Map of the North West Shelf of Australia study area showing 218 grids and their numbers used in the models. Depth contours of 20, 50, 100, 150, and 200 m, are also shown.

2.1.2 Fishing effort data

The fisheries effort data included in this modeling study was the Taiwanese pair trawler fishery effort from 1973 to 1989 and the domestic stern trawl fishery effort from 1987 to 1997. These data were drawn from three sources: summarised logbook data from the Taiwanese pair trawler fishery from 1973 to 1981 submitted to the Demersal Fish Research Centre at the National Taiwan University (Anon., 1971-1981); Australian Fishery Management Authority (AFMA) records on the Taiwanese pair trawler fishery from 1982 to 1989; and domestic trawl logbooks and fishery catch and effort statistics data ('CAES') compiled by the Western Australia Fisheries.

For the 1973 to 1981 Taiwanese fishing effort data it was necessary to transform from the number of hauls to number of hours fishing, using the assumption that one haul time is approximately 2.5 hours (Liu, 1976) and to interpolate from the 30 by 30 minute reporting grid to the 10 by 10 minute grid used in this study. The effort was also corrected for the recovery of the logbooks, using recovery values for each year obtained from the annual reports from the Demersal Fish Research Centre at the National Taiwan University.

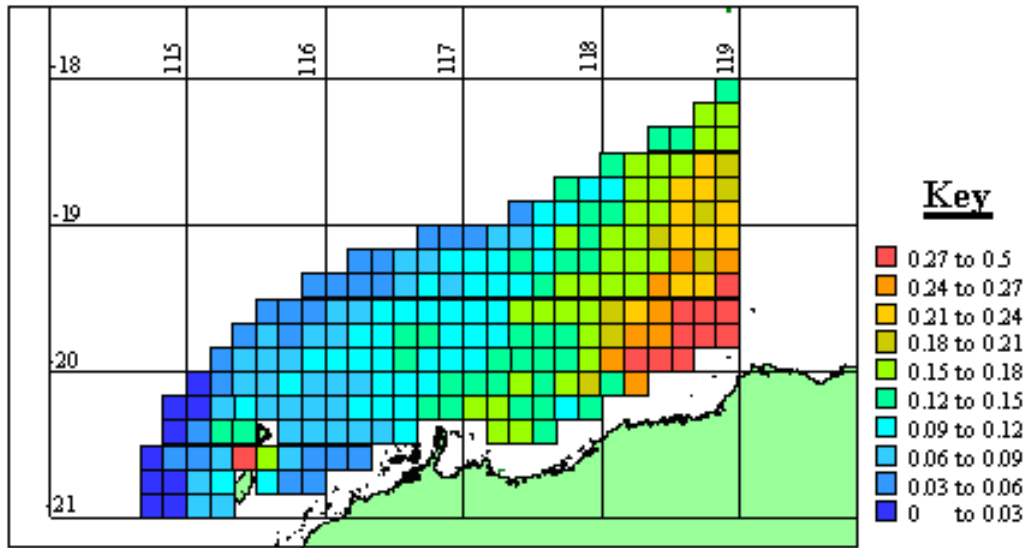
The AFMA data on the foreign, mainly Taiwanese and Chinese, trawling in the study area from 1982 to 1989 was relatively detailed, as it was collected on a trawl by trawl scale. This effort was already recorded as hours of trawling and it was simply a matter of mapping each trawl to the 10 by 10 grid (using the trawl mid-point position).

The CAES data obtained from the Western Australia Fisheries is given in a 1 by 1 degree block, with fishing effort given in number of days fishing. An average of 16 hours fishing per day (Peter Stephenson, pers. comm.) was assumed in order to obtain an estimate of effort in hours for each 1 by 1 degree CAES block. Using the logbook data supplied to Western Australia Fisheries to condition the CAES data, the broader scale data was apportioned to the smaller grid sizes of the logbook data. This was done by calculating the proportion of logbook fishing within each 10 by 10 minute each year, and applying that proportion to the CAES hours of fishing in the larger CAES cells.

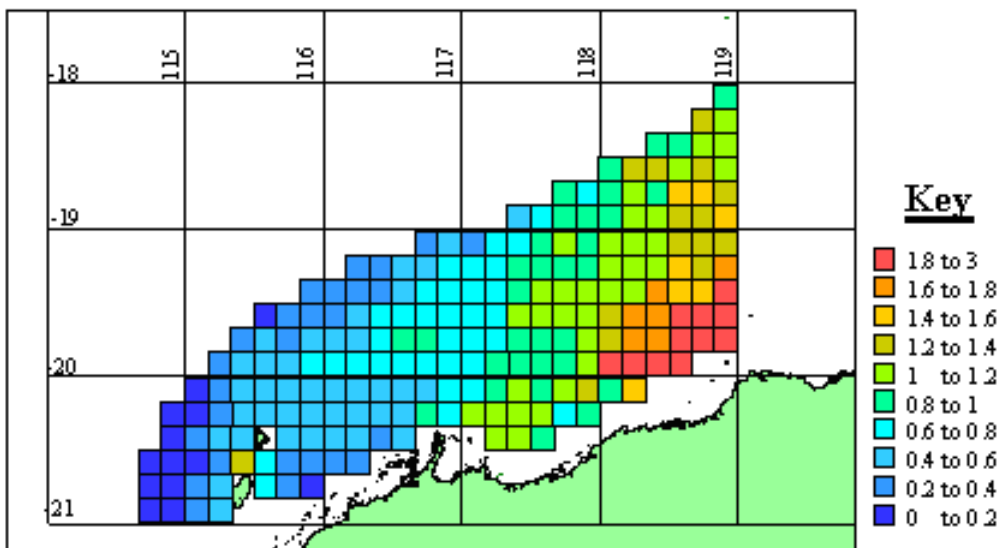
2.1.3 Bottom stress data

Bottom stress has been found to be one of the best predictors of epibenthic fauna composition and biomass in many other areas in Australia (e.g. south-western Australia (Phillip England, CSIRO Marine and Atmospheric Research, pers. comm.); Torres Strait and Great Barrier Reef (Pitcher et al. 2002; Pitcher et al. 2004a; Pitcher et al. 2004b)). Consequently bottom stress in each of the 10 by 10 grid cells was also compiled using physical oceanographic models (Condie et al. 2006). These bottom stress estimates showed a strong east-west trend, with the highest bottom stress occurring east of 118°E from 20 to 50 m (figure 2.1.3). A few grids cells around the Barrow Island also had elevated bottom stress levels.

Despite the very useful predictor bottom stress proved in other Australia locations, preliminary statistical models of benthic recruitment in the NWS region showed that bottom stress had an insignificant effect (He, unpublished). In addition, other research in the NWS area has shown that there is no clear connection between current strength and epibenthos cover (Althaus et al. in prep c). As a result bottom stress was dropped from the predictive model formulation stages of this study. It would be an interesting and extremely informative future research exercise to determine what differences between regions such as the NWS and Torres Strait lead to the very different effect of bottom stress on epibenthos in the two areas.



(a)



(b)

Figure 2.1.3: Estimated bottom stress (Nm^{-2}) in 10 by 10 minute grids in the study area. Estimates are (a) mean and (b) maximum bottom stress from physical models.

2.2 Observed trends

The observed percentage cover of small (≤ 25 cm) and large (> 25 cm) benthos are given in figure 2.2.1. There is a clear decrease in observed percentage cover of small and large epibenthos as depth increases (this is even clearer in the scatterplots given in figure 2.2.2). It is also clear from figure 2.2.2 that the variability in the observations is much higher in shallow zones than that in deeper water. This highlights the potential need for depth dependency to be included in any predictive model of benthic habitat dynamics. A multivariate classification used to score the environmental conditions and habitat associations (Althaus, in prep a) has also shown that epibenthic cover is related to grain size and topography. As both of these are strongly correlated with depth on the NWS (Jones, 1973) it may be simpler just to use sediments in the final model. It should be noted here that similar studies elsewhere (e.g. Pitcher et al. 2004b) have also considered the distribution of benthic habitats in relation to nutrient and chlorophyll *a* distributions (which can be considered surrogates for potential prey distribution for the benthic filter feeding organisms that typically form benthic biogenic habitats). This was not attempted here as these measures were not collected during the original cruises and *post hoc* no reliable source for these kinds of information could be found with a temporal or spatial coverage that matched the extent or period of benthic habitat sampling.

Considering the temporal trends in the per cell distributions (figure 2.2.1) and overall average cover (figure 2.2.3), there is the suggestion of a general decreasing trend in the proportional coverage of benthos (again particularly those > 25 cm) from 1983 to 1990 with some recovery after that for large epibenthos (when fishing effort is lower – see figure 2.2.4). The general levels of variability in the plots means that there is no significant difference between the points through time, however. A longer time series or a greater number of data points from cells repeatedly visited through time are required to investigate these trends more closely.

The combined fishing effort plot (figure 2.2.4) shows that there has been a generally steady decline in fishing effort since the time series began in the early 1970s. There were relatively high levels of effort from mid the 1970s to mid 1980s (on the order of 30 000 fishing hours per year or more), mostly due to the Taiwanese fleet. During the period in which the foreign fleets were pulling out of the region and the domestic fleet was only beginning to develop (1986 to 1989) the effort levels were quite low (much less than 10 000 hours a year), relatively speaking. The effort level rose again from 1989 to 1994 as the capacity of the domestic fleet grew to current levels, but never reached the levels of the early fisheries. Since the mid 1990s effort has again dropped off as more stringent management has come into place.

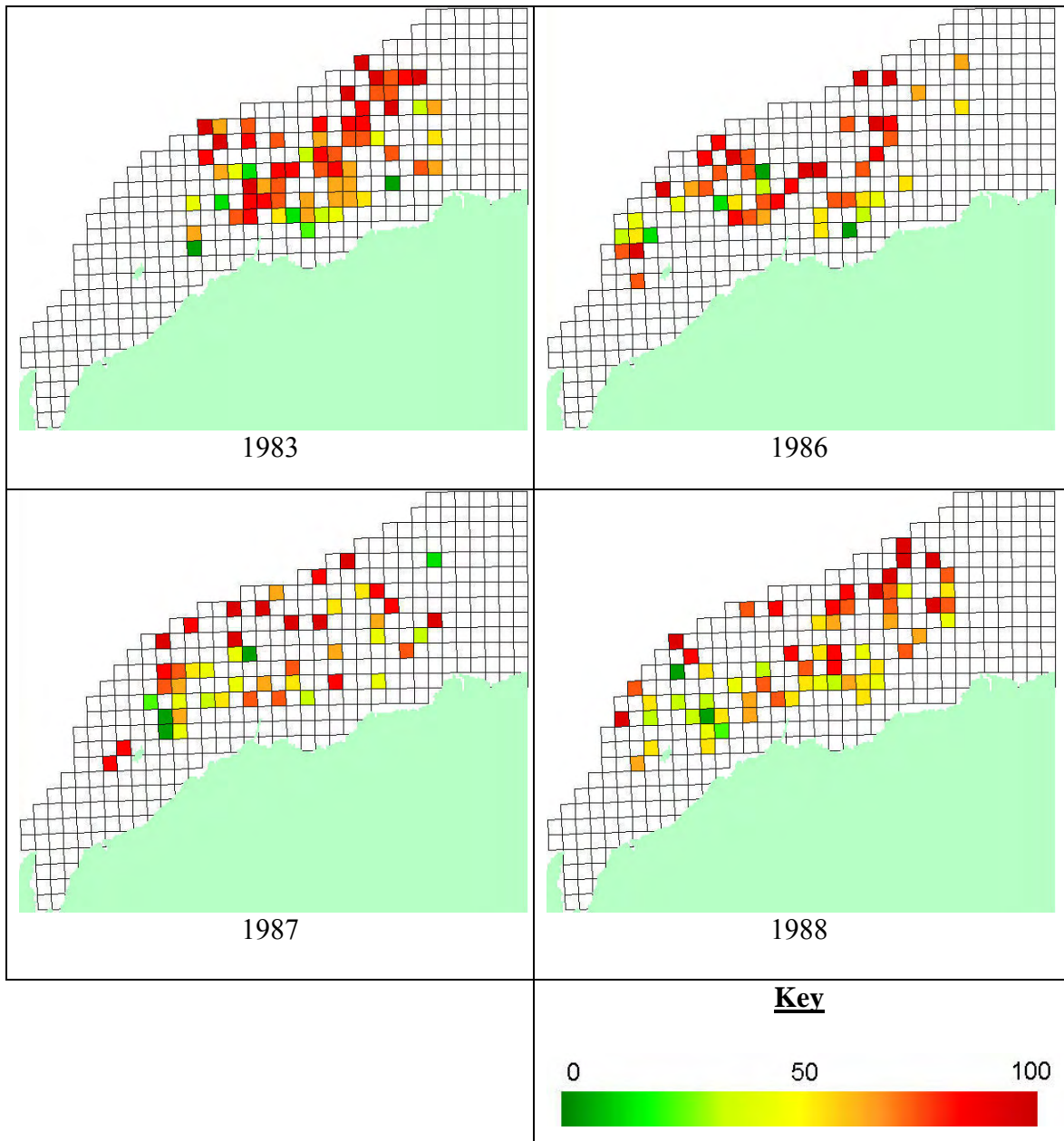


Figure 2.2.1 (a): Observed percentage cover of benthos on the North West Shelf of Australia – small (≤ 25 cm).

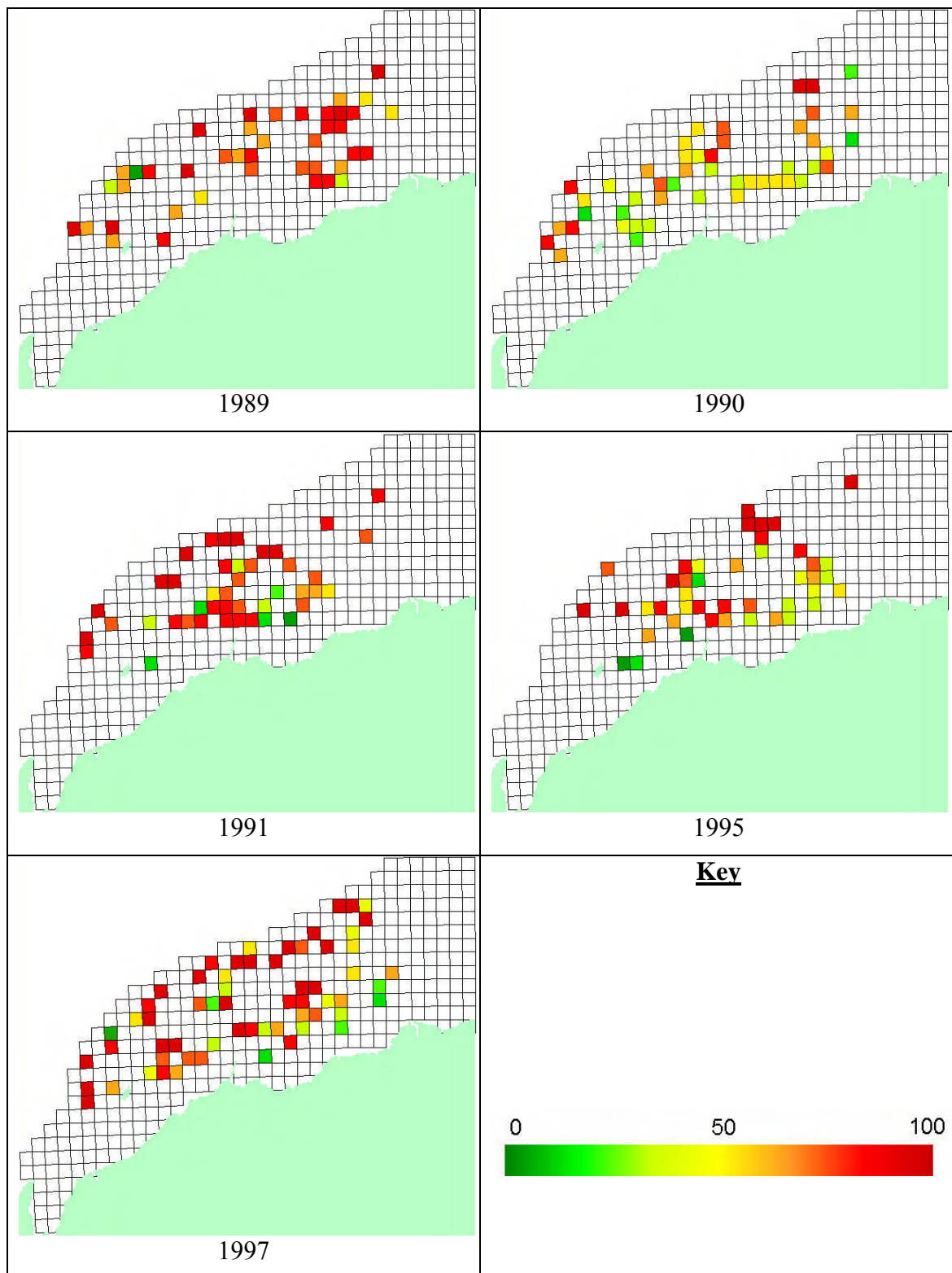


Figure 2.2.1 (a) continued: Observed percentage cover of benthos on the North West Shelf of Australia – small (≤ 25 cm).

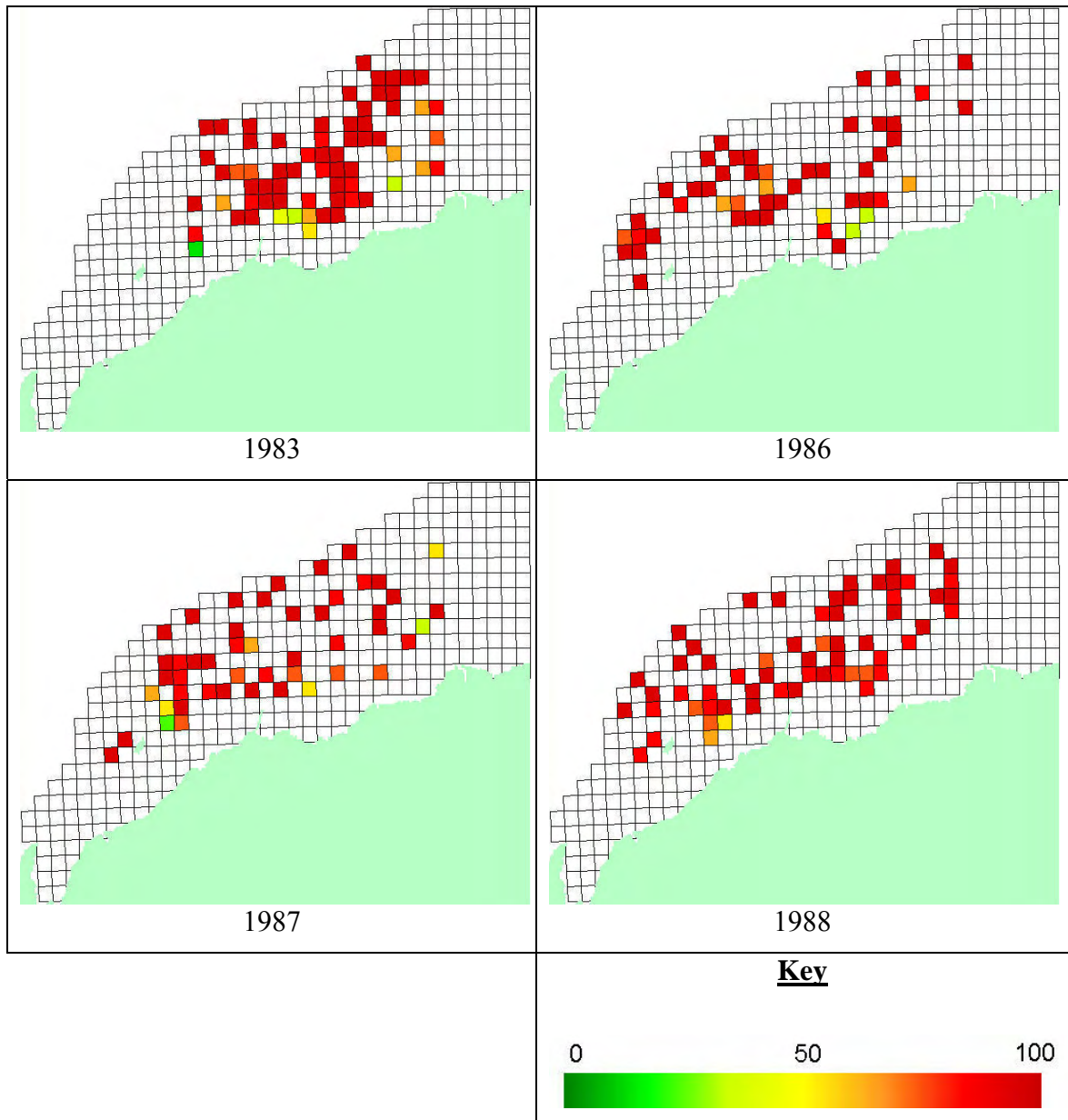


Figure 2.2.1 (b): Observed percentage cover of benthos on the North West Shelf of Australia – large (>25 cm) benthos.

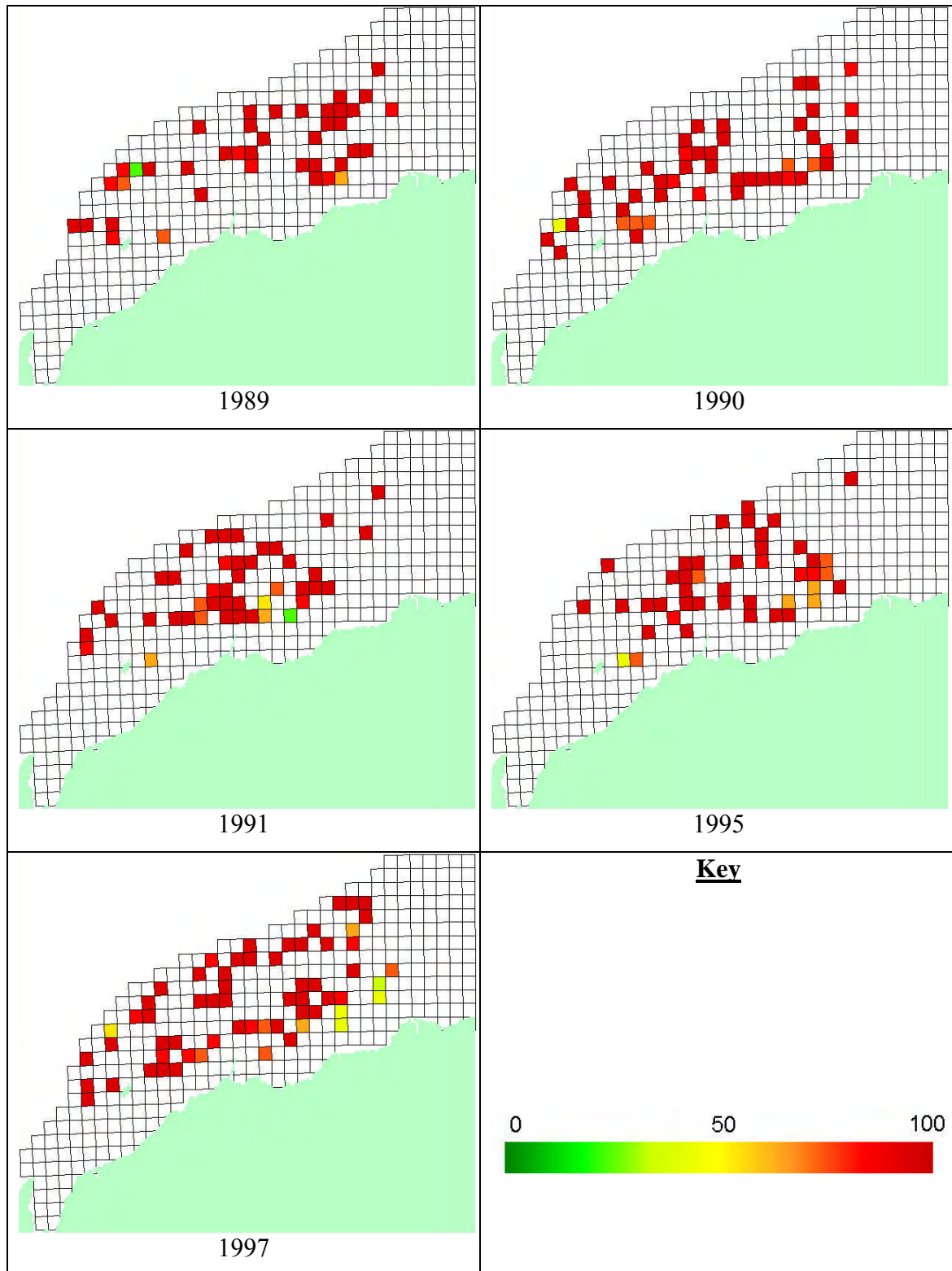
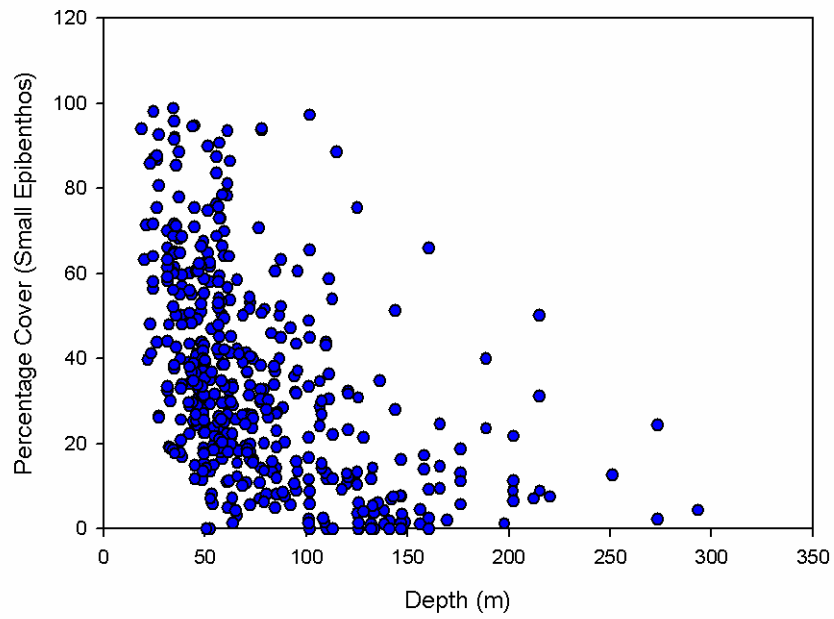
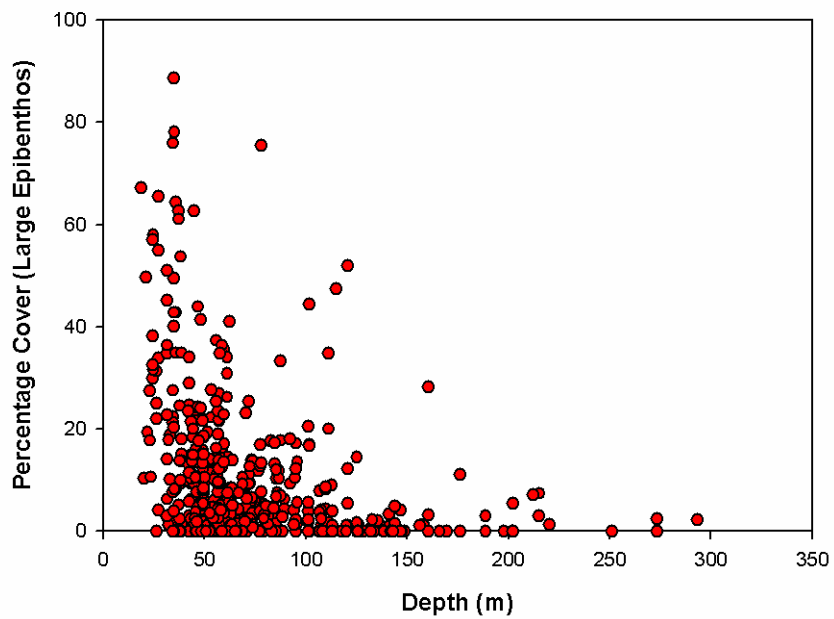


Figure 2.2.1 (b) continued: Observed percentage cover of benthos on the North West Shelf of Australia – large (>25 cm) benthos.



(a)



(b)

Figure 2.2.2: Observed proportions of (a) small and (b) large benthos per depth zone for all grids on the North West Shelf of Australia from 1983 to 1997.

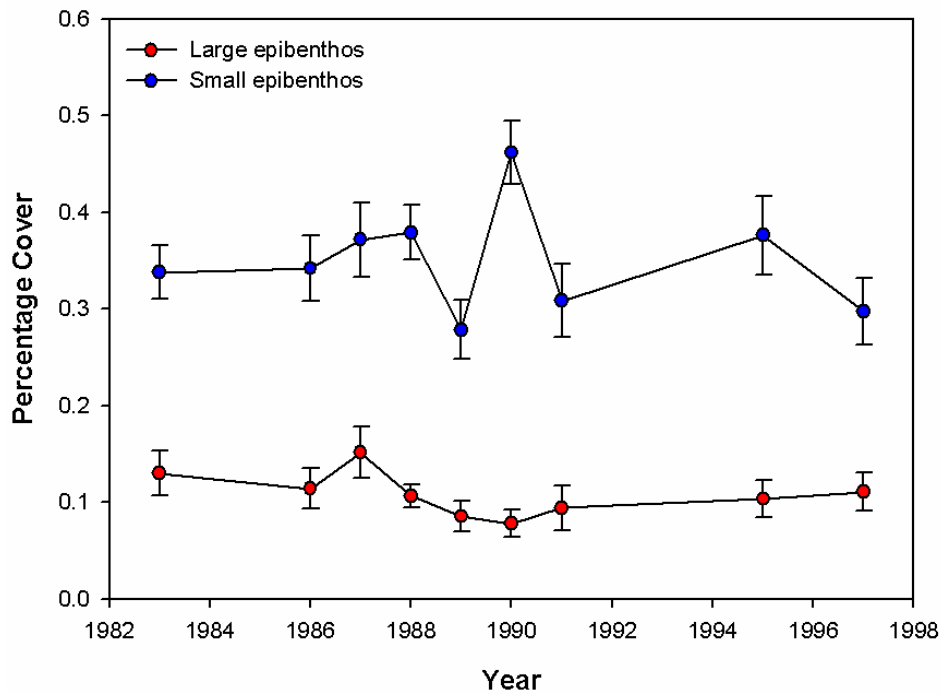


Figure 2.2.3: Observed average proportions of small (≤ 25 cm) and large (> 25 cm) epibenthos on the North West Shelf of Australia versus depth and time from 1983 to 1997. Standard error bars are shown.

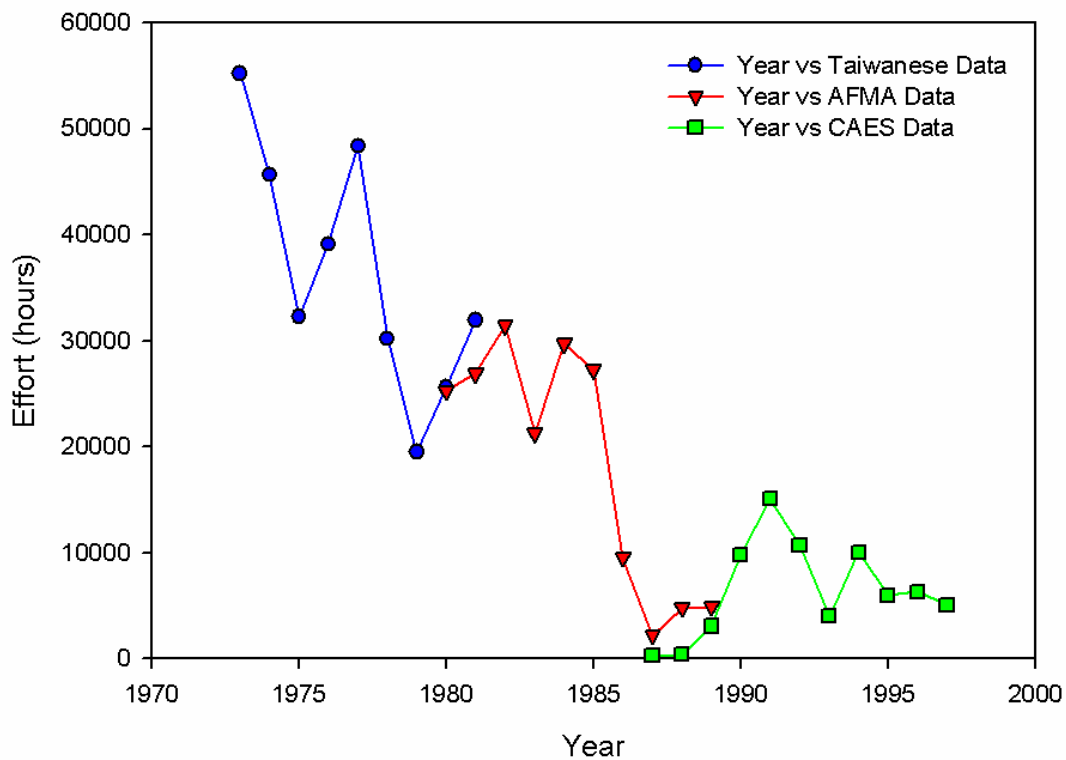


Figure 2.2.4: Total annual trawl fishing effort by foreign and domestic fleets on the North West Shelf of Australia from 1973 to 1997 (as of figure 2 in Althaus et al. 2001).

3. MODEL FORMULATION

During the course of this study a number of statistical and analytical formulations have been used to consider the various forms of benthos on the NWS. The most attention was given to the modelling exercises that were closely tied to the final management strategy evaluation of the NWS ecosystem and its management (NWSJEMS) as discussed in Fulton et al. (2006), Gray et al. (2006), and Little et al. (2006). Consequently, for the purposes of this report only the representations used in the MSE model employed in the NWSJEMS study (i.e. *NWS-InVitro*) will be discussed.

While the data collected was focused on epibenthos such as sponges, the benthic dynamics model developed was written so that it can represent all of the habitat defining groups found on the North West Shelf of Australia. These habitat defining groups – seagrasses, macroalgae, mangroves and epibenthos (corals and sponges) – are represented using a metapopulation model framework that tracks the evolution of percentage cover through time. This approach is adapted from previous habitat and metapopulation modelling work (Levins, 1969; Sainsbury, 1991; Tilman & Kareiva, 1997). Each of the habitat groups (also known as agents) is represented by a series of habitat polygons that cover a specified area. In this case the sets of polygons used are regular grids. The epibenthic habitat grids are based around the grids defined for the observations above. The seagrass, macroalgae and mangrove grids are slightly different (of a size and configuration more appropriate for the depths these groups prefer) – the seagrass and macroalgae grids are 12 by 12 minute and restricted to depths <50 m, and the mangrove grid is 3 by 3 minute and restricted to the coastline. While regional populations are considered for each benthic group in this NWS implementation, the model formulation allows consideration of model areas of a wide range of sizes, from highly restricted (if small scale effects are under consideration) to broadscale (e.g. the entire matrix of epibenthic habitat for the NWS region). Regardless of the spatial scale chosen, within each polygon of a habitat agent the percentage cover, average height and biomass is tracked. These statistics are then used as indices for diversity (empirical observations indicate that there is a direct relationship between diversity and the average height of organisms in biogenic habitats such as sponge beds – Keith Sainsbury, Franzis Althaus and Piers Dunstan, pers comm., CSIRO Marine and Atmospheric Research).

Two formulations are used to represent the different forms of habitat defining groups on the NWS:

1. Mangroves and epibenthic habitat (primarily sponges) are represented using an age/size-structured model, with the percentage cover of small and large organisms tracked separately. Note that patches of these two different size classes may overlap. Therefore, while the percent cover of small benthos is $\leq 100\%$ (similarly for large benthos), the sum of the percent cover of small and large benthos $\leq 200\%$.
2. The seagrass and macroalgae are represented by a model without age-structuring, but with light limitation.

Note that a description of how the model was initialised in each grid is given in section 5.1.

3.1 Small benthos – cover

Small specimens of habitat fauna include the “small” stages of species that grow to a large size as well as those species that always remain small (≤ 25 cm in height for epibenthos and ≤ 100 cm for mangroves).

The basic processes considered for each age/size class of small benthos are:

Change in cover small benthos = horizontal growth + recruitment (smallest class only)
 + ageing (or vertical growth) into the class - natural mortality - catastrophic mortality - ageing (or vertical growth) out of the class

More formally, the proportion of cover of small epibenthos (K_s) per polygon is tracked using the following age/size-structured equations of change, so that delays in habitat recovery can be adequately represented:

$$\frac{dK_s}{dt} = \sum_j \left(\begin{aligned} & \frac{A_j \cdot K_s \cdot (1 - K_s) \cdot \mu_s \cdot U \cdot \Psi}{1 + e^{(-\lambda(j-v))}} + U \cdot \xi \cdot \Psi \cdot (1 - e^{(-rK_T)}) \\ & - A_j \cdot K_s \cdot \left(\frac{\kappa_s}{1 + e^{(\theta(j-\phi))}} + \Phi_j A_j \cdot D_s^t \right) - \frac{A_j \cdot K_s \cdot \omega}{1 + e^{(\phi \cdot (j-\varepsilon))}} \\ & + A_{j-1} \cdot K_s \cdot \omega - A_j \cdot K_s \cdot \omega \end{aligned} \right) \quad (3.1)$$

A_j is the proportion of small habitat in age-size group j at time t . All other symbols are defined in table 4.1 and in the text below. Note that when implemented this is also constrained to remain within the interval $[0,1]$, though checks show that these constraints on extrema are rarely called on in practice.

3.1.1 Horizontal growth

Within each grid cell, horizontal growth of the existing patch(es) is one way the proportional coverage of benthos can increase. This term is non-zero for all age-size classes and both size categories (small and large) and is given by the first term in the sum on the right hand side of equation (3.1). U is light limitation (set to 1.0 for epibenthos, while the mangroves use the same formulation as in equation (3.6) for the seagrass and macroalgae); μ_s is the rate of horizontal growth for small habitat; Ψ is the sediment suitability rating for the habitat polygon (proportional presence of gravel and sand (Jones, 1973; McLoughlin & Young, 1985), scaled so that 1.0 is equal to perfect sediment composition); λ is the index of spread for the logistic growth function; and v is the inflexion point of the logistic growth function.

3.1.2 Recruitment

The second term in the sum is recruitment of new individuals (and initiation of new patches), this is the other way the proportional coverage of benthos can increase.

Where: ξ_j is the rate of recruitment of new small habitat specimens (only non-zero for the smallest class); K_T is the proportion of the NWS region covered with habitat; and r is a recruitment coefficient that scales the contribution of the regional coverage to recruitment (fitting in this case gave $r = 1$). A depth dependency for recruitment (and growth) of small benthos was included in a previous variant of this model, but was

dropped from the formulation discussed here for small benthos as a depth dependency did not appear to be necessary in addition to sediment dependency (which, based on model output, appeared to sufficiently explain observed distribution patterns). Depth dependency was retained for the macrophyte models described below.

3.1.3 Mortality

The third term in the sum is the mortality term. The first part is natural background mortality and the second catastrophic mortality due to fishing and cyclones. In this case κ_s is the natural mortality rate of small habitat; θ is the index of spread for the logistic age-structured natural mortality function; φ is the inflexion point of the age-based natural mortality function; $\Phi_j \sim U(0,1)$, with the sum of Φ_j over j equal to one (this is to avoid the assumption of homogeneous distribution of all age-size classes without necessitating subgrid scale spatial monitoring of patch composition; note these are independently sampled every timestep); and D_s^t is the damage done to small habitat by cyclones, dredging and fishing at time t (a simple percentage overlap of the track of the cyclone or trawl and the polygon is used in a catch equation with vulnerability constants from Hall (1999) to give this damage contribution).

3.1.4 Ageing and vertical growth

The final terms in the sum deal with growth in the vertical plane, that is both growth (and ageing) up through the classes of small benthos and the transition from small to large benthos, where: ω is the vertical growth rate of small habitat (equivalent to ageing); ϕ is the index of spread for the logistic function for the transition to large habitat; and ε is the inflexion point of the transition function. It is worth noting that epibenthos typically do not follow a specific growth curve and so age is a poor predictor of size. In the model, as in reality, size is the main concern for transitioning between classes. Age is not completely removed here as the data available still had aged-based confounding and so the classes had to represent an amalgam of age/size classes rather than simply just size.

3.1.5 Formulation note

Logistic functions were used in this formulation for growth, mortality and transition to large benthos across age classes of small benthos so that age-size dependency was present. Alternative functions (particularly alternative asymptotic functions) could have been used instead. Sensitivity to this formulation assumption has not been considered in depth.

3.2 Small benthos – fragmentation

Proportional cover alone is only half the story for habitat. Terrestrial and marine studies have shown that the degree of habitat fragmentation has a big impact both on the long-term health of the habitat patch itself and on its ability to provide ecosystem services to other system components (Sainsbury, 1987; Sainsbury, 1988; Freese et al. 1999; Jackson et al. 2000). For example, larger patches have been found to be more resilient (Eggleston et al. 1999; Hovel & Lipcius, 2001; Roberts & Poore, 2006) and to provide better refuge or nursery habitat for dependent species (Lindholm et al. 1999; Almany, 2004; Dorenbosch et al. 2005). Consequently, it was important to track the degree of fragmentation of the benthos in each grid cell. Nevertheless, while the concept of

fragmentation is easily grasped, there is no universally accepted index of fragmentation. The index used here is a simple measure of number of times coherent patches within the grid cell have been bisected with a measure of recovery (reduction in the index) as the patches grow back over disturbed tracks. Thus the rate of change of fragmentation of small habitat per polygon (B_s) is given by:

$$\frac{dB_s}{dt} = \sum_j \left(\Phi_j \cdot A_j \cdot D_s^{B,t} - \Theta_j \cdot \frac{j^2}{\chi^2} \cdot \left(\frac{A_j \cdot K_s \cdot (1 - K_s) \cdot \mu_s \cdot U \cdot \Psi}{1 + e^{(-\lambda(j-v))}} + U \cdot \xi \cdot \Psi \cdot (1 - e^{(-rK_T)}) \right) \right) \quad (3.2)$$

where Θ_j is the proportion of the edge of unfragmented sections of the habitat of age j in this polygon that have access to fragmented areas; χ is the number of age-size groups of small habitat (set to 10 here); and $D_s^{B,t}$ is the new fragmentation of small habitat in this polygon due to cyclones, dredging and fishing. The quadratic in age was used to approximate the slower recovery dynamics of larger body sizes (which typically have to grow through smaller size classes first).

3.3 Large benthos – cover

Large habitat refers to the large bodied habitat defining species (e.g. some of the largest corals and sponges). In practice, in this implementation, large specimens are considered to be >25 cm tall for epibenthic habitat and >100 cm for mangroves.

The processes considered for large benthos are similar to those for small benthos, specifically:

Change in cover large benthos = horizontal growth - natural mortality – catastrophic mortality + ageing (or vertical growth) into the class

More formally, the rate of change in percentage cover of large habitat (K_L) is handled slightly differently as it is not age structured and is given by:

$$\frac{dK_L}{dt} = \left[K_L \cdot (1 - K_L) \cdot U \cdot \mu_L \cdot e^{\left(-\left(\frac{\sigma \cdot m + \xi}{\Psi}\right)\right)} - (\kappa_L + D_L) \cdot K_L + \sum_j \frac{A_j \cdot K_s \cdot \omega}{1 + e^{(-\phi(j-\varepsilon))}} + A_{\chi-1} \cdot K_s \cdot \omega \right] \quad (3.3)$$

Once again the terms in the model are defined in table 4.1 and discussed in the following text.

3.3.1 Horizontal growth

The first term deals with horizontal growth, where μ_L is the rate of horizontal growth for large habitat; m is the seabed depth in metres; ϖ is the coefficient of the depth effect on horizontal growth of large habitat; and ζ is the coefficient of the sediment effect on the horizontal growth of large habitat.

3.3.2 Mortality

The second term is the mortality term, where: κ_L is the natural mortality rate of large habitat; and D_L^t is the damage done to large habitat by cyclones, dredging and fishing at time t (which is calculated in the same way as for D_s^t).

3.3.3 Ageing and vertical growth

The third and fourth terms in equation (3.3) are the growth of the cover of large benthos due to the vertical growth (and ageing) of small benthos. As stated above, χ is the number of age-size groups of small habitat (set to 10 here); and note that the inflexion point ϕ was chosen based on species age-growth curves so that the size/age transition between the small and large classes occurred at an appropriate point.

3.4 Large benthos – fragmentation

Lastly, the rate of change of fragmentation for large habitat (B_L) is calculated using:

$$\frac{dB_L}{dt} = \left(D_L^{B,t} - \Theta_L \cdot \left(K_L \cdot (1 - K_L) \cdot U \cdot \mu_L \cdot e^{-(\varpi \cdot m + \frac{\zeta}{\psi})} + \sum_j \left(\frac{A_j \cdot K_s \cdot \omega}{1 + e^{(-\phi \cdot (j - \varepsilon))}} \right) + A_{\chi-1} \cdot K_s \cdot \omega \right) \right) \quad (3.4)$$

where Θ_L is the proportion of the edge of unfragmented sections of the large habitat in this polygon that have access to fragmented areas; and $D_L^{B,t}$ is the rate of new fragmentation of large habitat in this polygon due to cyclones, dredging and fishing.

3.5 Macrophyte – cover and fragmentation

The formulation used for seagrass and macroalgae is very similar to that for large benthos (equations (3.3) and (3.4)), with percent cover (K) given by:

$$\frac{dK}{dt} = \left(K^{t-1} \cdot (1 - K^{t-1}) \cdot U \cdot \mu \cdot e^{-(\varpi \cdot m + \frac{\zeta}{\psi})} - (\kappa + D^t) \cdot K^{t-1} \right) \quad (3.5)$$

where

$$U = \min(1.0, I_{top} \cdot \exp(-\gamma \cdot m)) \quad (3.6)$$

and fragmentation (B) given by:

$$\frac{dB}{dt} = \left(D^{B,t} - \Theta \cdot K^{t-1} \cdot (1 - K^{t-1}) \cdot U \cdot \mu \cdot e^{-(\varpi \cdot m + \frac{\zeta}{\psi})} \right) \quad (3.7)$$

where μ is the rate of horizontal growth; m is the seabed depth in metres; ϖ is the coefficient of the depth effect on horizontal growth of large habitat; and ζ is the coefficient of the sediment effect on the horizontal growth of large habitat; κ is the natural mortality rate; D^t is the damage done by cyclones, dredging and fishing at time t ; I_{top} is the level of irradiance at the sea surface; γ is the extinction coefficient (there are different onshore and offshore values for the NWS due to the levels of inshore turbidity); Θ is the proportion of the edge of unfragmented sections that have access to fragmented areas and $D^{B,t}$ is the new fragmentation due to cyclones, dredging and fishing.

4. PARAMETER ESTIMATION

For epibenthic habitat the parameters in the habitat equations (3.1) to (3.4) above were determined by least squares optimisation – simultaneously fitting both small and large K 's in cells with data (fragmentation data was not available and so it was not included in the objective function). Aside from the penalty function used below, all data points were equally weighted. The simplex method (minimising the sum of squares) was used to fit the model to the observations of benthos discussed above. Given the patchy nature of the data, it was necessary to include a penalty function to constrain the parameters to a biologically meaningful range and the final parameter set is given in table 4.1. It was also necessary to fix some of the parameters (these are noted in table 4.1 along with any references used). The relative fit of the model to observations is given in figure 4.1 (for small epibenthic habitat ≤ 25 cm in height) and figure 4.2 (for epibenthic habitat > 25 cm). The discussion of results below refers to the best fit optimisation results.

Consideration of the phase space around this point allowed for the selection of model parameters that gave more optimistic/pessimistic predictions of benthic habitat cover. These were needed as part of an associated Management Strategy Evaluation exercise for the North West Shelf (refer to Little et al. 2006 for further details).

Given the count-like nature of the data being considered, Poisson residuals are the most appropriate means of considering the validity of the methods' assumptions (Vincent & Haworth, 1983; McCullagh & Nelder, 1989). Pooling over time, the quality of the performance is quite good. A plot of the Poisson residuals from the model fitting through time (figure 4.3) shows that while most residuals are fairly tight some of the values for the small benthos can be large. There doesn't appear to be any trend over time in the residuals for large benthos, though there is the suggestion of a slightly decreasing trend in the residuals for the small benthos through time.

When considering the percentage cover per grid cell predicted by the model, 54% of the predictions for epibenthic habitat > 25 cm tall and 40% of the small epibenthic habitat differ from the actual coverage by less than 10% (that is if the observed value is 70% the predicted value was $> 60\%$ and $< 80\%$); and a further 30% of large and small epibenthic habitat predictions differ from the actual value by $< 20\%$. While the tails of these distributions fall away quickly (figure 4.4), they do stretch out and in each case there was at least one prediction that differed from the observation by as much as 90%. Moreover, when considering whether the predicted cover was greater or smaller than the observed cover there is a clear tendency for the model to underestimate the cover of tall epibenthic habitat (the curve in figure 4.4 is shifted to the left). There is no skew in the predictions of epibenthos ≤ 25 cm in height, however – with the curve fairly symmetric about 0. The mismatch that does exist between model and observations is largely due the fact the model cannot resolve habitat patches smaller than the scale of the spatial grid used. Thus, the model predicts aggregate cover that doesn't account for the odd rocky outcrop in areas of sand (or vice versa); such features have a great impact on the observed percentage cover though as epibenthic habitat thrives on such outcrops. Nevertheless the model does give a good indication of overall distributions and general levels of cover.

There was insufficient data to repeat this fitting process for the seagrasses, macroalgae and mangroves. A small amount of data was available on the species present and their overall geographic extent, but on a finer scale (the kinds of scale needed for modelling) it was necessary to rely on expert information on the spatial distributions, presence-absence and general depletion-recovery dynamics of the species in question. As a result the parameters for these habitat forming groups were calibrated via a sensitivity analysis to give the best match to what data was available (the values used are given in tables 4.2, 4.3 and 4.4).

Pessimistic and optimistic variants

As part of an associated Management Strategy Evaluation (MSE) exercise for the North West Shelf (Fulton et al. 2006; Little et al. 2006), optimistic and pessimistic variants of the epibenthic parameter set were chosen by sensitivity analysis. While all epibenthic parameters were varied during initial exploration of the phase space, the final sets settled upon only varied horizontal growth rates and vulnerability to trawling. The results obtained, under variants where other parameters (e.g. natural mortality rates) were varied fell within the bounding set produced by varying the growth rates and vulnerabilities. Consequently, only the growth rates and vulnerabilities were varied, between the final optimistic, intermediate and pessimistic model parameterisations (which are given in table 4.5).

Parameter uncertainty

While no formal confidence intervals are given in the tables of parameters below, the issue of parameter uncertainty was given a good deal of consideration. The optimisation surface was fairly constrained within the biologically plausible parameter space and there is reasonable confidence in the resulting parameter estimates (particularly the growth and recruitment rates). There is slightly less confidence in the mortality rate estimates, due mainly to the degree of sensitivity of the model to the value of these parameters.

The model fitting and sensitivity analyses indicate that the model is most sensitive to the mortality rate and vulnerability parameters (e.g. there is less than 0.0001 between the vulnerability parameter used in the optimistic, intermediate and pessimistic model parameterisations for the epibenthic habitat). The values of these parameters are often quite small so minor differences in value represent substantial changes in relative rates. Future implementations of the model would benefit from attempts to directly measure these parameters for this region – as had been done for north-east Queensland (Pitcher et al. 2004c). Interestingly, while the vulnerability parameters used here are within the range measured for northern Queensland (0.09 versus 0.01 to 0.4), the estimated natural and catastrophic mortality rates are an order of magnitude higher here than for that study (though in both studies the mortality rates for small benthos are much higher than for large benthos). This discrepancy in values is not particularly disturbing however, given that (i) there are a number of other differences observed between the regions (e.g. bottom stress was found to have insignificant effects on recruitment rates on the NWS, while it was a critical factor in north-east Queensland); and (ii) varying the mortality rates lead to results that fell within the optimistic-pessimistic bounding set anyway.

Overall, while questions remain over the mortality parameters in particular, it was felt that between the formal optimisation and the broad ranging and bounding sensitivity analyses carried out for the various forms of benthic flora and fauna, that a good representation of the potential model dynamics was captured. More systematic sensitivity analyses and formal parameter confidence intervals are desirable, but have only been lightly touched upon here due to the complexity and size of these tasks (particularly with regard to systematic gridded multivariate sensitivity analyses of even moderately complex models such as the one discussed here).

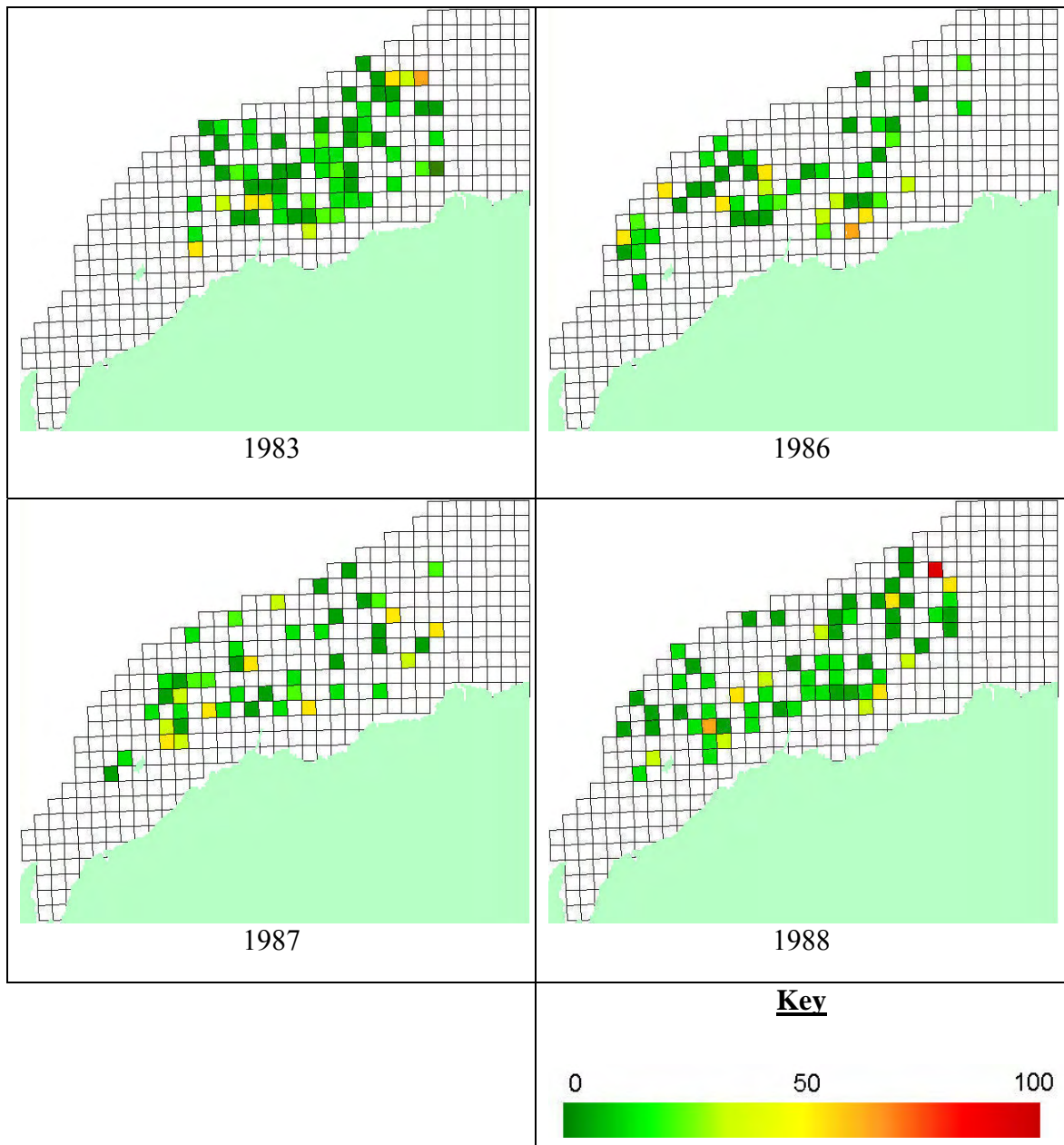


Figure 4.1: Relative fit of model to observations through time for small benthos (≤ 25 cm in height) – this shows the absolute difference in the percent cover observed and that predicted by the model (e.g. 0 means no difference between observed and predicted values of % cover; whereas 50 means that absolute difference between the observed and predicted % cover was 50%, so the observed value may have been 10%, but the predicted was 60%).

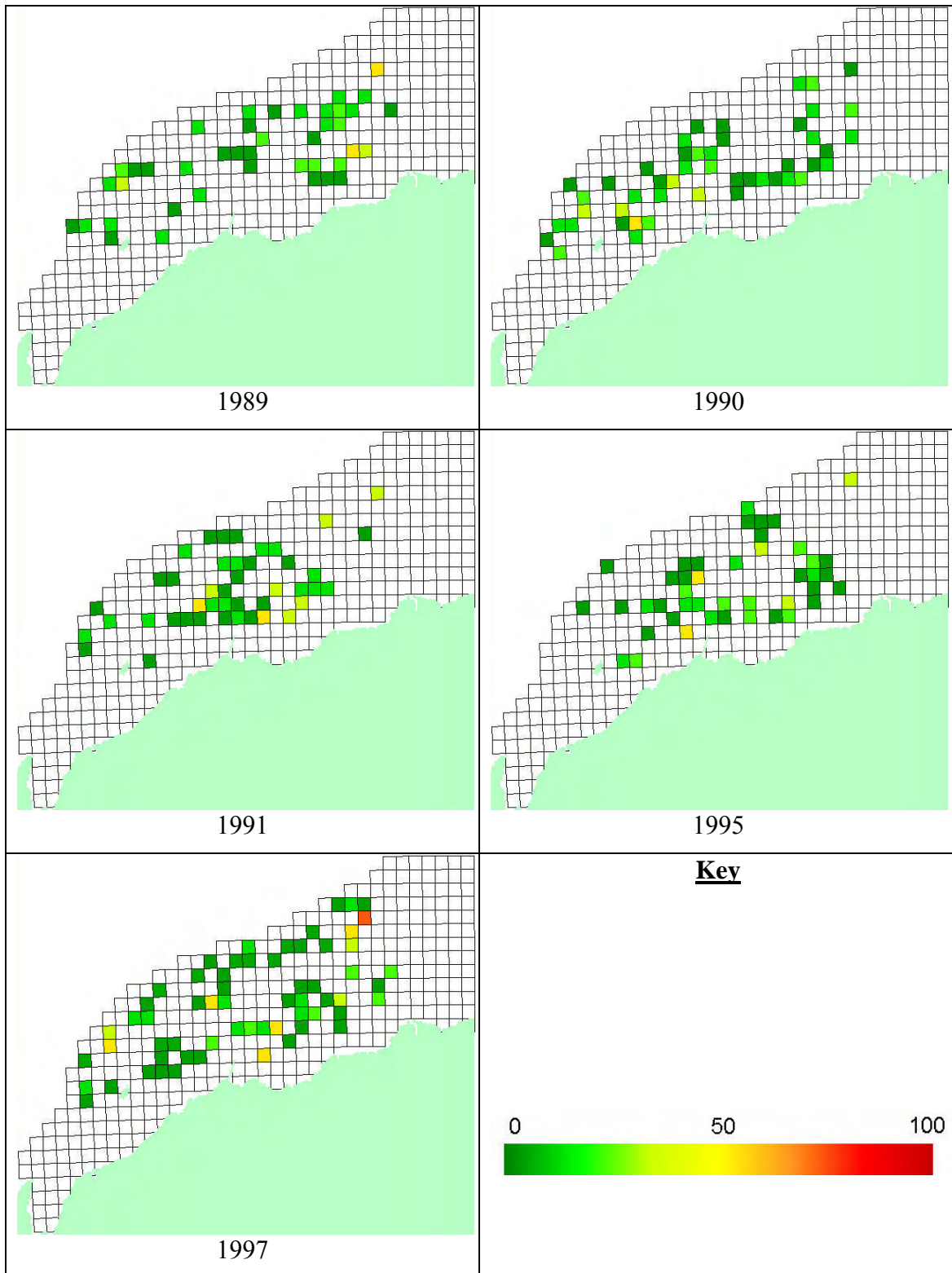


Figure 4.1 continued: Relative fit of model to observations through time for small benthos (≤ 25 cm in height) – this shows the absolute difference in the percent cover observed and that predicted by the model (e.g. 0 means no difference between observed and predicted values of % cover; whereas 50 means that absolute difference between the observed and predicted % cover was 50%, so the observed value may have been 10%, but the predicted was 60%).

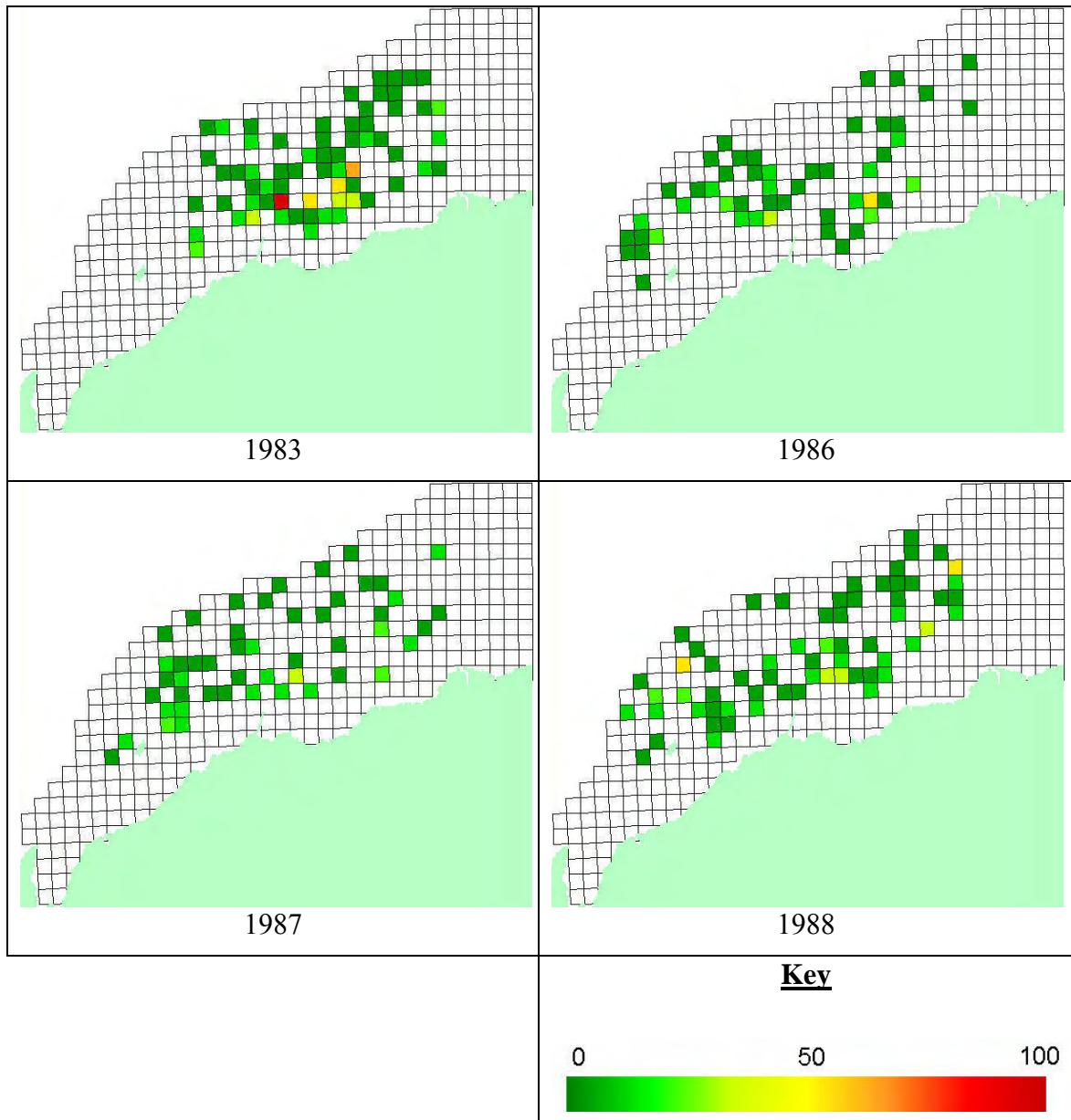


Figure 4.2: Relative fit of model to observations through time for large benthos (≤ 25 cm in height) – this shows the absolute difference in the percent cover observed and that predicted by the model (e.g. 0 means no difference between observed and predicted values of % cover; whereas 50 means that absolute difference between the observed and predicted % cover was 50%, so the observed value may have been 10%, but the predicted was 60%).

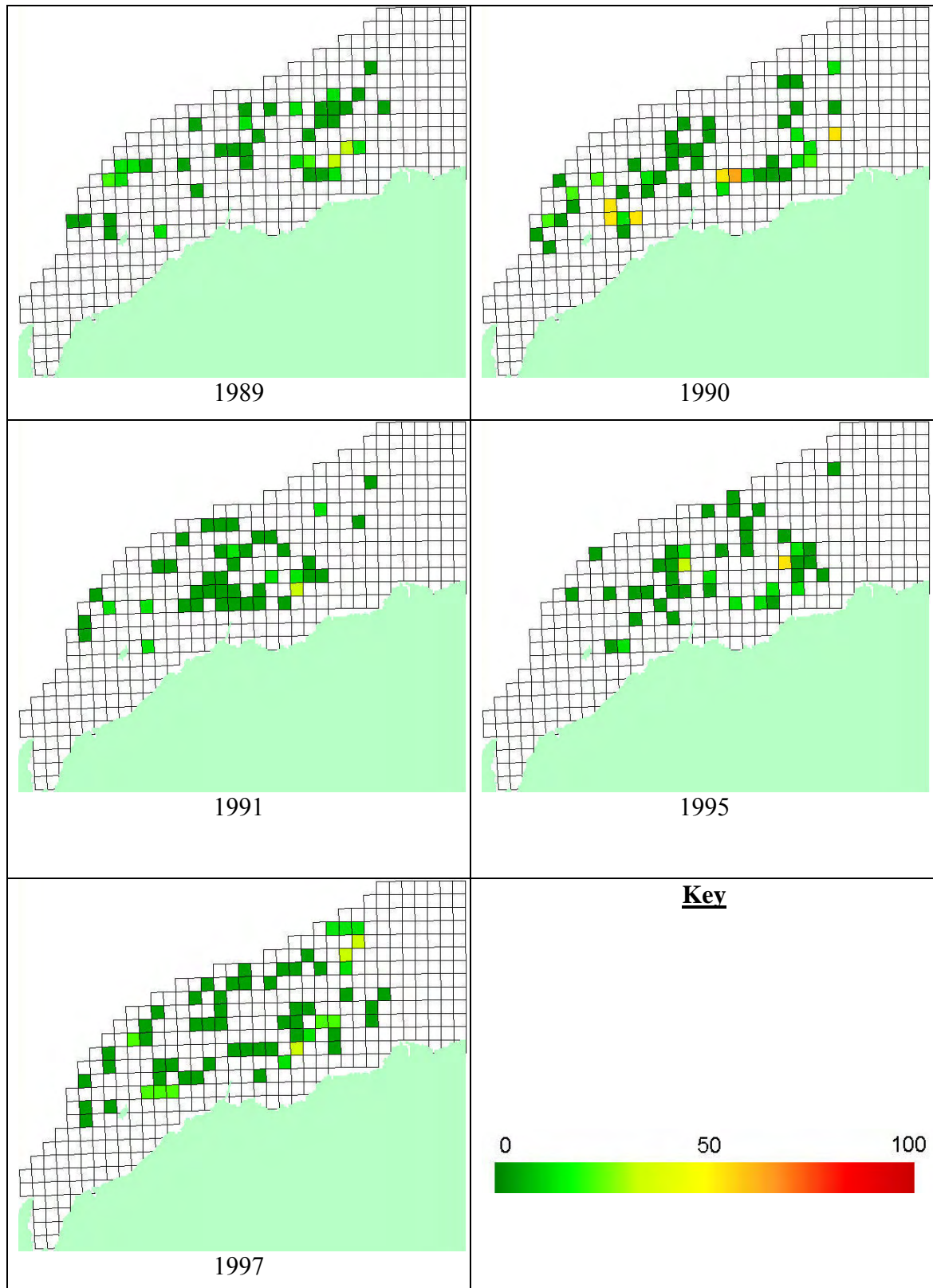


Figure 4.2 continued: Relative fit of model to observations through time for large benthos (≤ 25 cm in height) – this shows the absolute difference in the percent cover observed and that predicted by the model (e.g. 0 means no difference between observed and predicted values of % cover; whereas 50 means that absolute difference between the observed and predicted % cover was 50%, so the observed value may have been 10%, but the predicted was 60%).

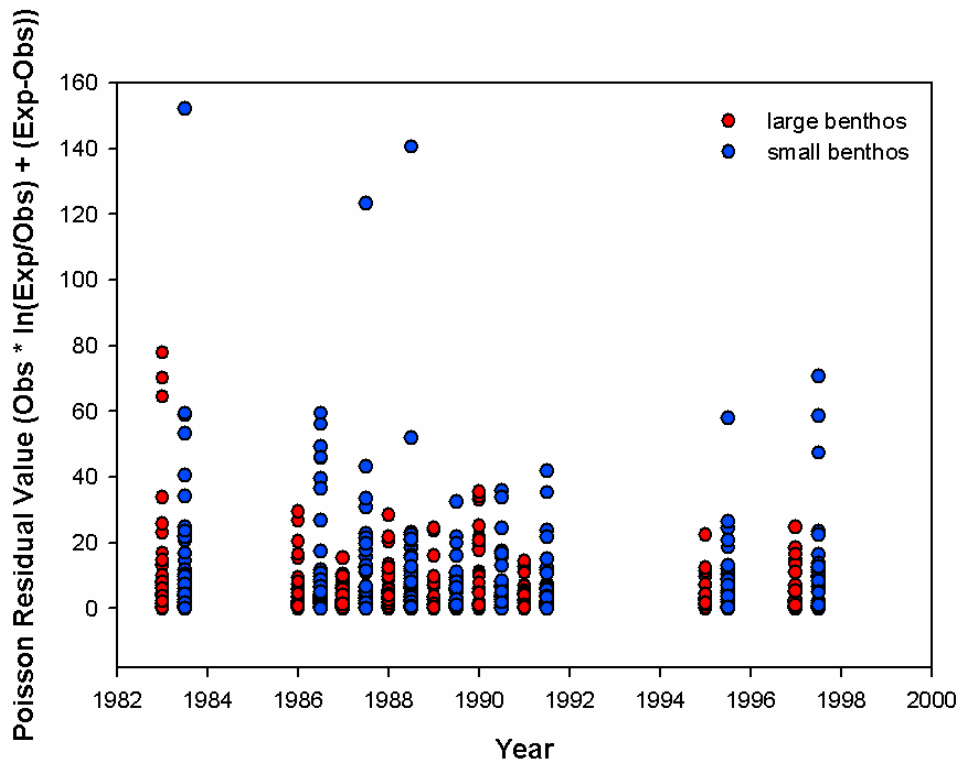


Figure 4.3: The Poisson residual plot from the least squares optimisation fitting the benthic habitat dynamics model to the observed coverage of benthos on the North West Shelf of Australia.

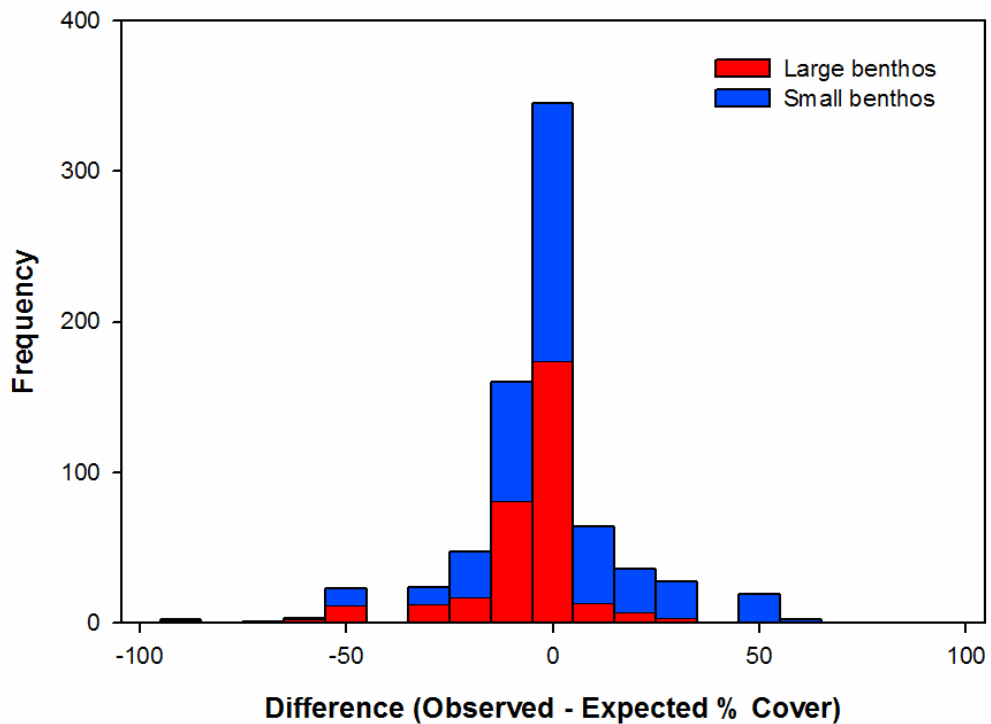


Figure 4.4: The distribution of the differences between observed epibenthic habitat cover on the North West Shelf of Australia and the % cover predicted by the benthic dynamics model.

Table 4.1: Final parameters set for epibenthic habitat in NWS benthic habitat model. Those entries marked with an asterisk are transformed in the calculation dependent on size of habitat patches, activity/event footprint and fragmentation index for that cell of the benthic habitat model. Note p stands for proportion, so p yr⁻¹ stands for proportion of spatial cell per year and pf stands for proportion of the cover in the footprint that is destroyed.

Parameter	Value	Units	Notes
<i>Small epibenthic habitat</i>			
Horizontal growth rate (μ_s)	0.103	p yr ⁻¹	Estimated
Index of spread for growth (λ)	1.0		Fixed (based on expert knowledge)
Inflexion point for growth (ν)	4.0		Fixed (based on expert knowledge)
Recruitment rate (ξ)	0.05	p yr ⁻¹	Estimated
Natural mortality rate (κ_s)	0.012	yr ⁻¹	Estimated
Index of spread for mortality (θ)	1.0		Fixed (based on expert knowledge)
Inflexion point for mortality (ϕ)	11.0		Fixed (based on expert knowledge)
Vulnerability to trawling	0.09	p f	Fixed (based on Hall (1999))
Vulnerability to dredging	1.0	p f	Fixed (based on Roberts et al. (1998) and Newell et al. (2004))
Vulnerability to cyclones	0.4	p f	Fixed (based on Augustin et al. (1997))
Transition (vertical growth) rate (ω)	0.05	p yr ⁻¹	Fixed (based on Harrison & Cowden (1976), Barnes (1987), Garrabou & Zabala (2001) and Bell (2002))
Index of spread for transition (θ)	1.5		Fixed
Inflexion point for transition (ϕ)	9.0		Fixed
Number of age-size classes (χ)	10.0		Fixed (computationally efficient while still capturing the typical span of size and ages for sponges less than 20 cm in height, from information in Barnes (1987))
<i>Large epibenthic habitat</i>			
Horizontal growth rate (μ_L)	0.05	p yr ⁻¹	Estimated
Growth coefficient for depth effect (ϖ)	0.494		Estimated
Growth coefficient for sediment effect (ζ)	0.995		Estimated
Natural mortality rate (κ_s)	0.0048	yr ⁻¹	Estimated
Vulnerability to trawling	0.09	p f	Fixed (based on Hall (1999))
Vulnerability to dredging	1.0	p f	Fixed (based on Roberts et al. (1998) and Newell et al. (2004))
Vulnerability to cyclones	0.5	p f	Fixed (based on Augustin et al. (1997))

Table 4.2: Final parameters set for seagrass habitat in NWS benthic habitat model. Those entries marked with an asterisk are transformed in the calculation dependent on size of habitat patches, activity/event footprint and fragmentation index for that cell of the benthic habitat model. Note p stands for proportion, so p yr^{-1} stands for proportion of spatial cell per year and pf stands for proportion of the cover in the footprint that is destroyed.

Parameter	Value	Units	Notes
Horizontal growth rate (μ_L)	0.5	p yr^{-1}	Fixed (based on Cambridge et al. (2002) and Campbell (2003))
Growth coefficient for depth effect (ϖ)	0.1		Estimated via a sensitivity analysis
Growth coefficient for sediment effect (ζ)	1.0		Estimated via a sensitivity analysis
Natural mortality rate (κ_s)	0.2	yr^{-1}	Fixed (based on van Tussenbroek (2002) and Biber et al. (2004))
Vulnerability to trawling	0.8	p f	Fixed (based on Hall (1999) and Meyer et al. (1999))
Vulnerability to dredging	1.0	p f	Fixed (based on Cheshire & Miller (1996))
Vulnerability to cyclones	0.4	p f	Fixed (based on Preen et al. (1995))

Table 4.3: Final parameters set for macroalgae in NWS benthic habitat model. Those entries marked with an asterisk are transformed in the calculation dependent on size of habitat patches, activity/event footprint and fragmentation index for that cell of the benthic habitat model. Note p stands for proportion, so p yr^{-1} stands for proportion of spatial cell per year and pf stands for proportion of the cover in the footprint that is destroyed.

Parameter	Value	Units	Notes
Horizontal growth rate (μ_L)	0.1	p yr^{-1}	Fixed (based on Creed et al. (1998))
Growth coefficient for depth effect (ϖ)	0.1		Estimated via a sensitivity analysis
Growth coefficient for sediment effect (ζ)	1.0		Estimated via a sensitivity analysis
Natural mortality rate (κ_s)	0.2	yr^{-1}	Fixed (based on Aberg (1992) and Solidoro et al. (1997))
Vulnerability to trawling	0.7	p f	Fixed (based on Hall (1999))
Vulnerability to dredging	1.0	p f	Fixed (based on Roberts et al. (1998) and Newell et al. (2004))
Vulnerability to cyclones	0.3	p f	Fixed (based on Augustin et al. (1997))

Table 4.4: Final parameters set for mangroves in NWS benthic habitat model. Those entries marked with an asterisk are transformed in the calculation dependent on size of habitat patches, activity/event footprint and fragmentation index for that cell of the benthic habitat model. Note p stands for proportion, so $p\text{ yr}^{-1}$ stands for proportion of spatial cell per year and pf stands for proportion of the cover in the footprint that is destroyed.

Parameter	Value	Units	Notes
<i>Small mangroves</i>			
Horizontal growth rate (μ_s)	0.01	$p\text{ yr}^{-1}$	Fixed (based on Robertson & Alongi (1992))
Index of spread for growth (λ)	0.15		Estimated via a sensitivity analysis
Inflexion point for growth (ν)	1.0		Estimated via a sensitivity analysis
Recruitment rate (ξ)	0.01	$p\text{ yr}^{-1}$	Fixed (based on Robertson & Alongi (1992) and McGuinness (1997))
Natural mortality rate (κ_s)	0.01	yr^{-1}	Fixed (based on Robertson & Alongi (1992))
Index of spread for mortality (θ)	1.0		Estimated via a sensitivity analysis
Inflexion point for mortality (ϕ)	7.0		Estimated via a sensitivity analysis
Vulnerability to clearing	1.0	p f	Fixed (based on Semeniuk (1994), Semeniuk & Semeniuk (1995, 1997))
Vulnerability to cyclones	0.7	p f	Fixed (based on Grove et al. (2000) and Kathiresan & Bingham (2001))
Transition (vertical growth) rate (ω)	0.09	$p\text{ yr}^{-1}$	Fixed (based on Robertson & Alongi (1992))
Index of spread for transition (θ)	0.8		Estimated via a sensitivity analysis
Inflexion point for transition (ϕ)	12.0		Estimated via a sensitivity analysis
Number of age-size classes (χ)	10.0		Fixed (computationally efficient while still capturing the typical span of size and ages for mangroves less than 100 cm in height, from information in Robertson & Alongi (1992))
<i>Large mangroves</i>			
Horizontal growth rate (μ_L)	0.0005	$p\text{ yr}^{-1}$	Fixed (based on Robertson & Alongi (1992))
Growth coefficient for depth effect (ϖ)	1.0		Estimated via a sensitivity analysis
Growth coefficient for sediment effect (ζ)	1.0		Estimated via a sensitivity analysis
Natural mortality rate (κ_L)	0.001	yr^{-1}	Fixed (based on Robertson & Alongi (1992))
Vulnerability to clearing	1.0	p f	Fixed (based on Semeniuk (1994), Semeniuk & Semeniuk (1995, 1997))
Vulnerability to cyclones	0.7	p f	Fixed (based on Grove et al. (2000) and Kathiresan & Bingham (2001))

Table 4.5: Values of parameters varied between the optimistic, intermediate and pessimistic variants for the various forms of benthic habitat (large and small epibenthos, seagrass, macroalgae and mangroves) considered on the NWS.

Parameter	Value in variant		
	Pessimistic	Intermediate	Optimistic
<i>Small benthos</i>			
Horizontal growth rate (μ_s)	0.05	0.103	0.2
Vulnerability to trawling	0.09005	0.09	0.08995
<i>Large benthos</i>			
Horizontal growth rate (μ_L)	0.045	0.05	0.1
Vulnerability to trawling	0.09005	0.09	0.08995

5. MODEL BEHAVIOUR – EPIBENTHIC HABITAT

A brief description of the predicted distribution of epibenthic habitat and the depletion-recovery dynamics predicted by this model for this kind of habitat are given below.

5.1 Distribution of epibenthic habitat

Running the model for 300 years without fishing pressure (using the optimal parameter set) let the model reach a stable state that was assumed to be the pristine distribution (figure 5.1.1). As the *InVitro* model has a total time span horizon of a little over 50 years, to create a century long run in effect the model had to be run for 50 years and then the output from that run was used as the input for another 50 year run. This final unfished distribution was used as the initial conditions for all other runs. It is useful to note that the optimistic and pessimistic parameter sets also reached very similar unfished distributions, though the pessimistic case took a much longer time to achieve it.

The predicted distribution of unfished habitat sees the epibenthic habitat concentrated in the coarser sediments in the mid-shelf and in the Dampier Archipelago (marked in figure 5.1.1 (a)). Offshore deeper waters and finer sediments make the area less suitable for epibenthic habitat (according to the model), while inshore it is fine sediments that make the area less suitable for epibenthos. Seagrass and macroalgae are more prevalent in these inshore areas (predicted initial conditions for these groups are given in figure 5.1.2). The distribution of seagrass, macroalgae and mangroves in these maps does match the qualitative information available from experts in the area (maps of this information were produced under NWSJEMS Task 4.1 – Information inventory from field experts). The low percent cover of small mangroves across much of the NWS is due to the predicted mangrove forest state being largely undisturbed (with lots of mature trees and canopy and few openings for small trees).

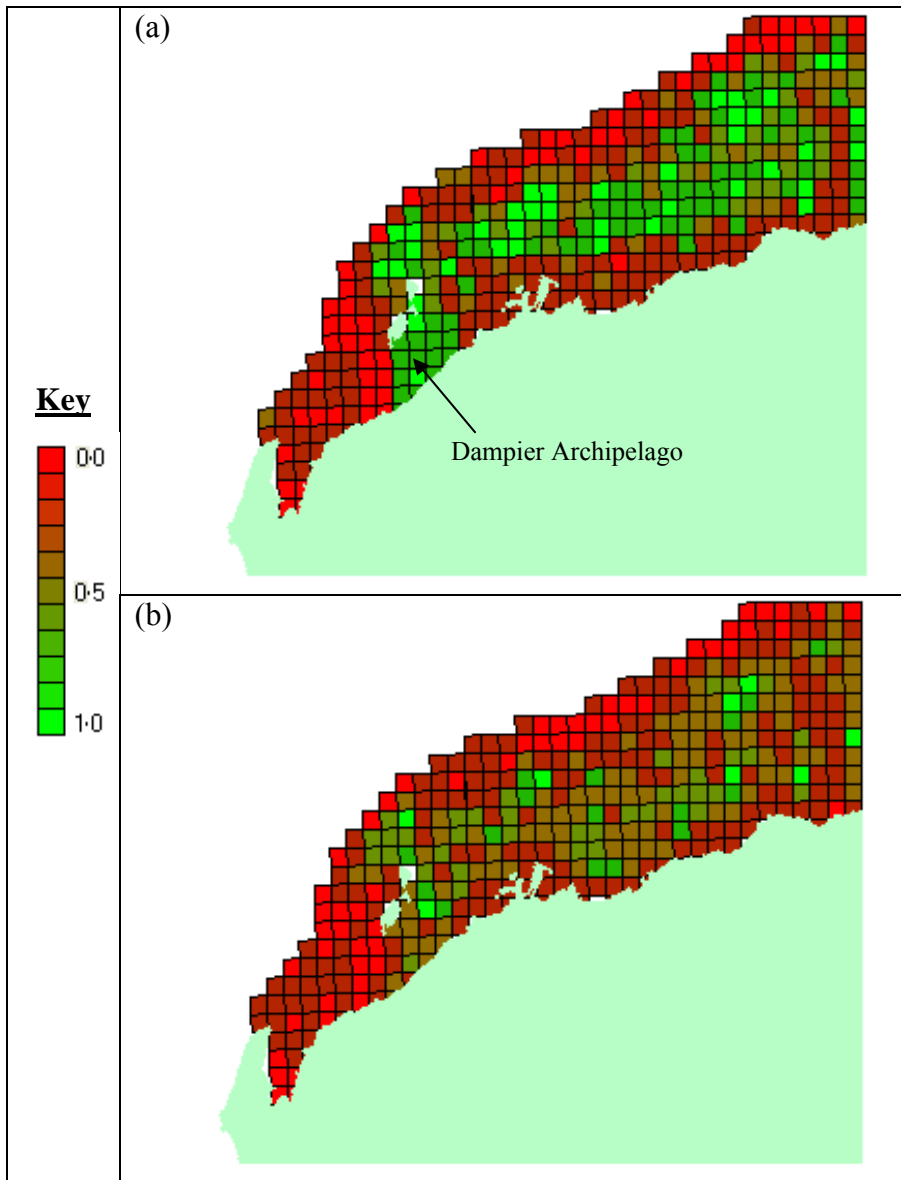


Figure 5.1.1: Predicted unfished distribution of epibenthic habitat on the NWS of Australia; (a) epibenthic habitat ≤ 25 cm, and (b) epibenthic habitat > 25 cm.

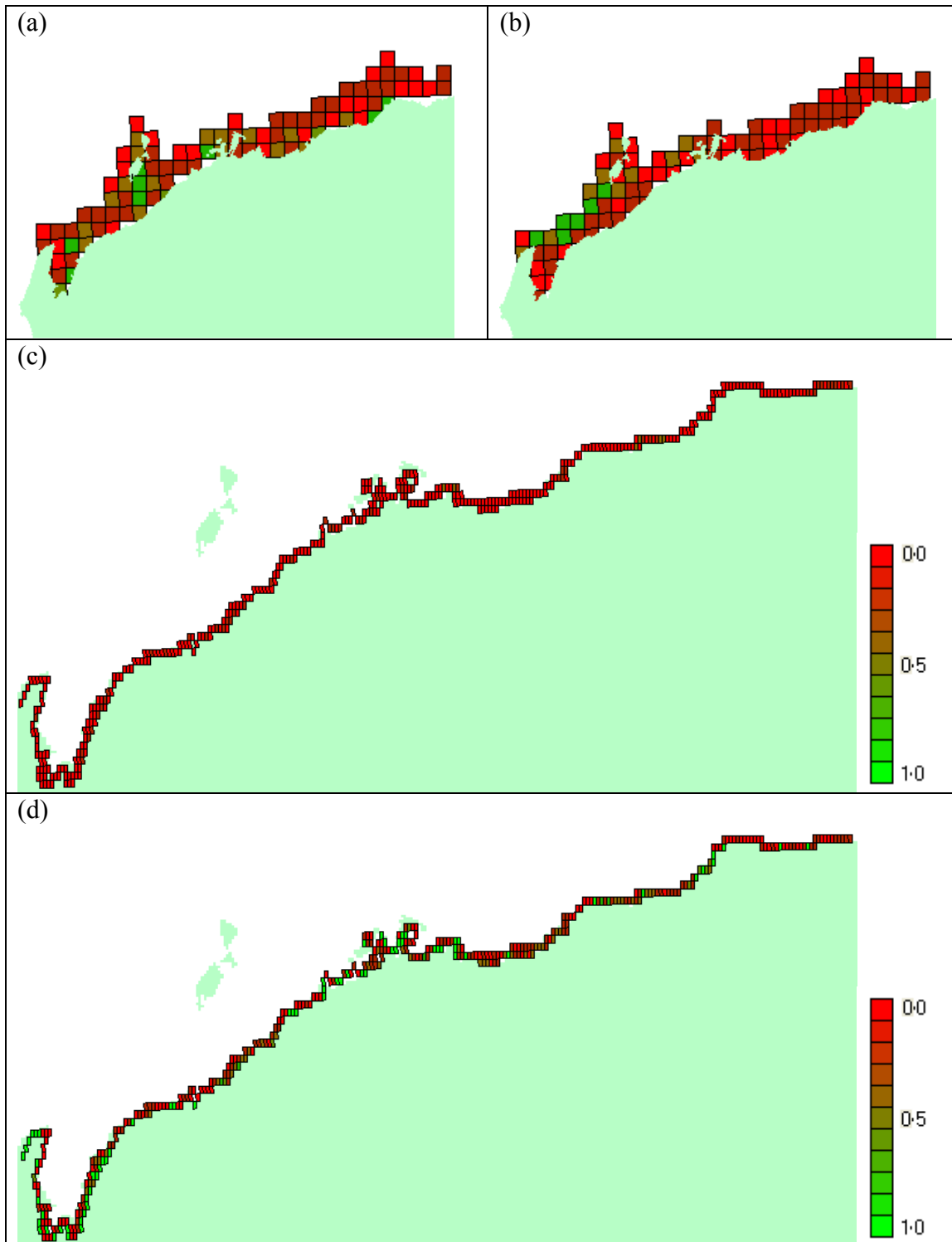


Figure 5.1.2: Predicted unfished distribution of seagrass, macroalgae and mangrove habitat on the NWS shelf of Australia; (a) seagrass; (b) macroalgae; (c) small (≤ 1 m) mangroves; and (d) large (>1 m) mangroves.

5.2 Habitat destruction and recovery

Figures 5.2.1 and 5.2.2 show the depletion-recovery dynamics of the model for small and large epibenthic habitats under the three model parameterisations (optimistic, intermediate, pessimistic). For each parameter specification, the trajectory was created by running the model from 1970 to 2001 with historical foreign and domestic effort imposed and then after 2000 setting fishing effort to zero (to allow for best possible recovery). The same problem with a 50 year time span for *InVitro* runs was encountered here also, so the output of one run (with historical fishing on) was used as the input to a second one (fishing set to zero) to obtain the complete trajectory. Only cells containing sediment and depth conditions conducive for epibenthic growth were included in the calculation of this overall average statistic. If the entire area of the North West Shelf was included the “no growth” result in the cells with only marginal environmental conditions for epibenthos swamped the dynamic responses of the core epibenthic areas.

The impact of fishing on the benthic habitat is rapid, with the bulk of the decline in cover occurring within the first five years of fishing. From that point on the trajectory is dependent on the parameterisation. All of the trajectories show some recovery, but the bulk of the results suggest fairly slow rates of recovery, taking decades to approach starting levels of cover. These overall rates are lower than rates suggested by empirical data (Sainsbury et al. 1997; Pitcher et al. 2004c). Consideration of rates of recovery in individual cells show that they can be much higher than this overall rate (with recovery times in some cells being of the order of 15 to 25 years, which is comparable with the empirical data). In general however, the rates of recovery predicted by the parameter sets determined by estimation are probably too low. This is the result of the relative lack of signal in the data used in the fitting – it is dominated by a decline in cover and so fitting to this has dominated the parameter estimation as there was little if any recovery in the data to condition that aspect of the model fully.

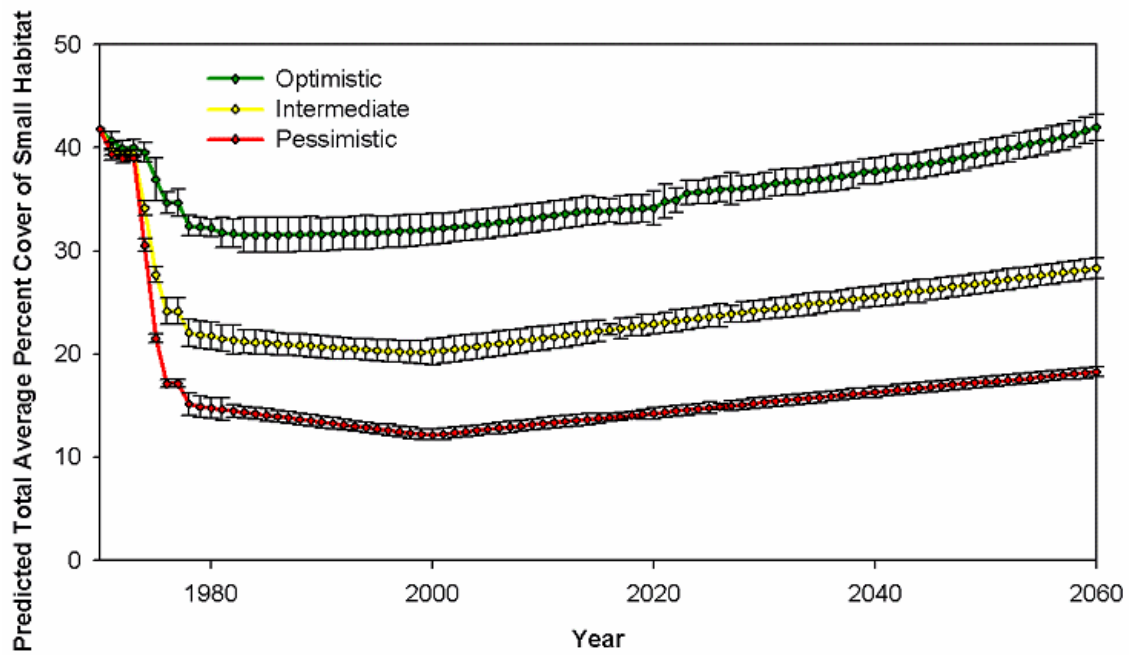


Figure 5.2.1: Depletion and recovery trajectory for small epibenthic habitat component of the NWS benthic habitat dynamics model.

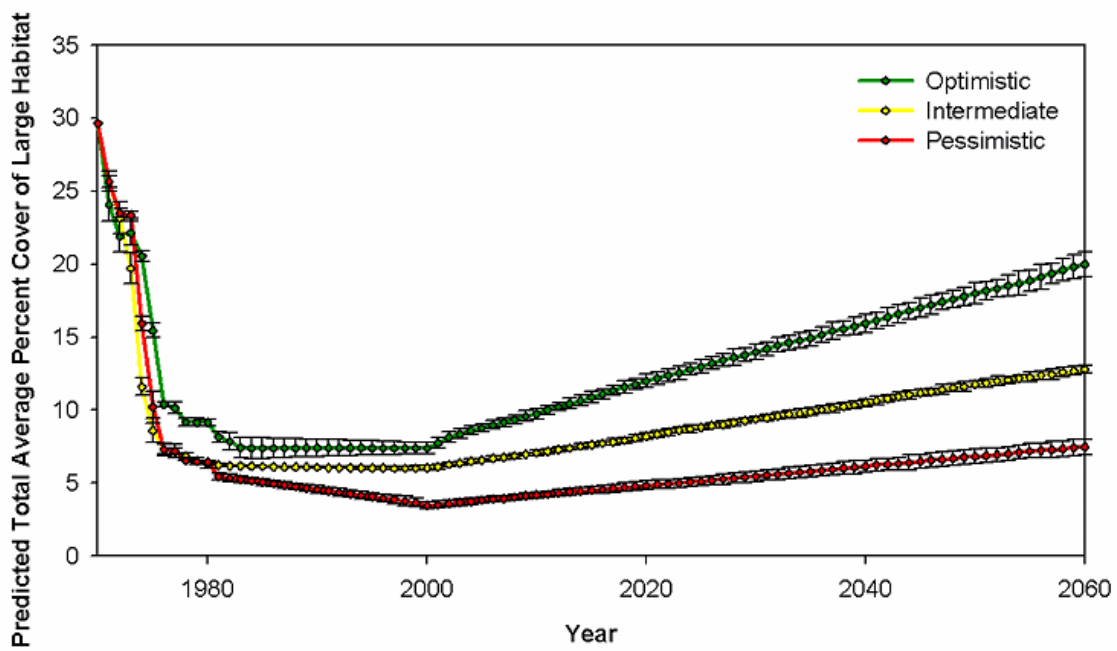


Figure 5.2.2: Depletion and recovery trajectory for large epibenthic habitat component of the NWS benthic habitat dynamics model.

6. DISCUSSION

6.1 Observations and model behaviour

Habitat correlates

The observational data gave good insights into the pressures structuring the epibenthic community distribution. The substrate dependency and the resulting depth correlations for the growth of epibenthic groups is not particularly surprising, with similar patterns found in other studies (Barthel & Tendal, 1993; Pineda & Caswell, 1997; Dahl & Dahl, 2002). In contrast, it is surprising that bottom stress was found to have so little influence (and wasn't even carried through to the modelling stage of the study). Bottom stress is related to current strength (and roughness) and has been found to be very important in studies elsewhere. This importance is due to its role in food supply, clearing attachment sites (by exposing underlying hard substrata) and facilitating respiration for these sessile organisms (Barnes, 1987; Pitcher et al. 2004b; Pitcher et al. 2004c). There are many potential reasons why bottom stress was found to be fairly insignificant as a direct correlate for benthic habitat on the NWS. The most likely (or at least the most obvious) is that the potential importance of bottom stress is being displaced by other factors. The most likely of these are: cross shelf sediment sorting (which seems to lie perpendicularly to the long-shore stress contours evident in figure 2.1.3); inshore turbidity (the shallow inshore waters of the NWS are incredibly turbid out to about 50 m, conditions that are not typically conducive to extensive benthic habitat growth); and fishing pressure (much of the area under observation had already been subject to fishing pressure and disturbance).

Recovery dynamics

The coverage of the observational data is quite good given the logistical constraints associated with an exercise of this spatial and temporal magnitude in such a remote location. The only real weakness in the data was to do with elucidation of recovery dynamics. One fifth of the grid cells sampled over the entire study were sampled half, or more, of the sampling years. In some cases subsequent trawls were in locations very close to earlier samples (consider figure 2.1.1), unfortunately this is not true of the bulk of the trawls and natural small scale spatial variation largely swamps any temporal signal that may be present in data from repeatedly sampled cells. For instance, if we plot the percentage cover of large epibenthos through time in those cells that are sampled in six or more years of the study (figure 6.1.1) it may be possible to identify general trends in some grid cells (e.g. 80), but for others there is no clear pattern (e.g. 146). Similar observations hold true for small epibenthos too and for both size classes the variability of percentage coverage is high, especially in shallow waters. In turn this lack of clear signal meant that the fitting procedure was dominated by the overall depletion through time (which is fit to very well). Unfortunately, in turn, this has meant that the parameters produced by the fitting procedure do not produce recovery forecasts for the entire shelf, in the absence of fishing, that are as high as those suggested by empirical data (Sainsbury et al. 1997).

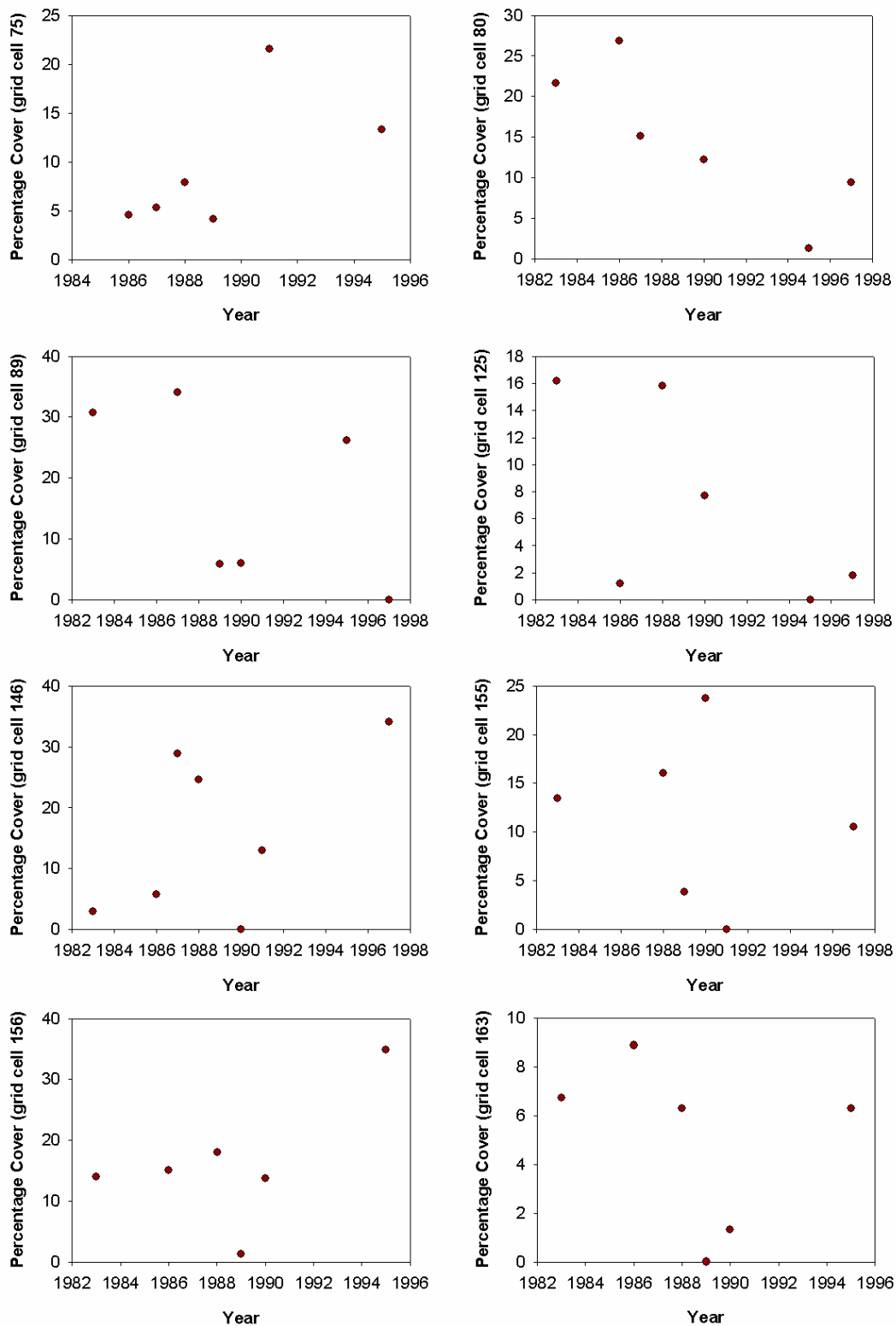


Figure 6.1.1: Percentage cover of large (>25 cm) epibenthos in grid cells sampled in six or more years of the study.

One possible explanation for this mismatch between observed and predicted recovery times is that different scales are being considered. Sainsbury et al. (1997) (and other similar work by Pitcher et al. 2004c) is considering recovery within benthic habitat patches – and when considered at this scale (i.e. within boxes) these rates could be seen in the model predictions. However, the regional scale recovery that was the main focus of the work reported here will not necessarily match these within-patch rates. Regional large scale recovery includes colonisation of empty cells, which can be a much slower process than the increase in cover within an existing patch (e.g. see Pitcher et al. 2004c for observed rates of recruitment versus horizontal growth rates at the same location). Sessile invertebrates often have short dispersal phase larvae or a tendency to rely more heavily on vegetative reproduction. Consequently, patch (re-)growth is typically faster than regional recovery of a denuded seabed. The implications of this is that the model predictions regarding long-term regional scale recovery may not actually be off the mark, but rather a warning about how long these processes may take in reality.

Alternatively, it may well be that the unidirectional signal in the data did lead to recovery rates that were too slow, even at a regional scale. With this in mind a calibration of the model using expert knowledge was undertaken and this alleviated the (potential) problem to some degree. Nevertheless, if this really is a mis-specification (and not a warning about real long-term regional dynamics) than in many respects the simpler benthic dynamics model of Sainsbury (1988) produced superior results in the area of recovery dynamics. This may be a case (much like that observed in Ludwig and Walters (1985) and Fulton et al. (2003)) where simpler models can be a more effective means of considering resource dynamics given available data and associated uncertainties. This would be a fruitful topic of future research. However, whether future refinements of the model see a return to simpler formulations or not, consideration of other components of the NWS ecosystem (Little et al. 2006) show that maintaining a spatial context to the model is imperative.

The potential shortfalls in recovery dynamics and the small percentage of cells where model fits were poor in one year or another are likely to be due to two main issues. The first is that the forcing data was not always optimally suited to driving the model at the resolution chosen – the spatial resolution of fishing effort data, especially the Taiwanese fleet data in early years, is on a much larger aggregated scale which creates anomalies or mis-matches when allocated on the finer grids. Potentially more important for the utility of the model in the future, analysis of spatial distribution and associations of benthos in the study area has indicated highly patchy distribution with high degrees of association of benthos of all sizes (Althaus et al. in prep a). This suggests that some of the problems with the model may be alleviated by moving to a smaller (or irregular) cell size that is better able to capture the very patchy nature of these species. Alternatively, what are known as sub-grid scale processes (implicit representation of processes on a finer scale than the explicit grid, often represented by functional response curves or statistical models) may need to be added; although this would involve adding even more parameters in an already potential data sparse system. Interestingly, it has been observed more generally that dispersal rates are a critical feature in metapopulation models (such as the one discussed here), but that despite the recognised importance of this process, dispersal patterns and dynamics for most species remain poorly known (Wiens, 1997) and studies of dispersal processes are generally not attempted (Kareiva, 1990; Gustafson & Gardner, 1996; Cronin, 2003). While this observation does not relieve us from our own dispersal rate (i.e. recruitment and recovery rates in this case)

problems it does show that it is not a problem unique to this study. One simple solution to these problems is to take guidance from the formulation of Sainsbury (1988) and include a constant recruitment term (which is a likely contributor to that model's higher recovery rates, given it progresses more quickly than a logistic at low population levels). This idea has been implemented as an option in the *NWS-InVitro* model with some success (Gray et al. 2006).

6.2 Model utility

The results of the parameter estimation and model fitting stage of the study show that spatially the model does an acceptable job of representing the distribution and cover of epibenthos. As mentioned above the model does have its flaws at all-of-shelf scales, but it does still do a good job of capturing gross distribution patterns and levels of cover within individual cells. Moreover, within individual cells with environmental conditions conducive for epibenthic growth it does display recovery times comparable with data. As such it provides a sound basis for consideration of the effects of anthropogenic activities (primarily fishing and management interventions) on the marine habitats on the NWS within an MSE context.

6.3 Seagrass, mangroves and macroalgae

The discussion above applied only to the epibenthic implementations of the model, not the primary producer groups. The issues highlighted by the application of the model for the epibenthos suggest that there are undoubtedly problems with the predicted model distributions of these other groups. Unfortunately, data for these groups (particularly data with any degree of perturbation or signal in it) is rare for the NWS and it has been necessary to fall back almost exclusively on expert knowledge of these groups. There is some mangrove (Semeniuk, 1994; Semeniuk & Semeniuk, 1995; Carr & Livesey, 1996; Paling, 1996; Semeniuk & Semeniuk, 1997; Bridgewater & Cresswell, 1999) and seagrass (Walker & Prince, 1987; Australian State of the Environment Committee 2001, and by assuming association of dugongs with seagrass in Prince, 2001) information available from the widely available and grey literature on the area, but it did not provide much of the kind of information needed to fit this kind of model. As a result, it was necessary to consider the model an acceptable component of the MSE biophysical model so long as it reproduced gross location matches with available data (which it did).

While the work discussed here only put cursory attention on seagrass, macrophyte and mangroves future work there is a huge potential for high impact modelling work in this area into the future. To date there are few models dealing with the spatial population dynamics of these groups (and those that do exist deal almost exclusively with mangrove forests). In the last decade there have been very few papers published that directly consider spatial habitat dynamics of marine photosynthetic primary producers. Marine primary producers are increasingly incorporated into biomass dynamics models such as *Ecopath* with *Ecosim*, but dedicated habitat patch dynamics models are still rare. Rarer still are those that explicitly consider patch dynamics and associated processes at the scale dealt with here.

For macroalgae the bulk of the work has been in temperate forests and has focused on water quality impacts rather than a more balanced approach to patch dynamics (Coffaro & Bocci, 1997; Coffaro & Sfriso, 1997; Duarte & Ferreira, 1997; Solidoro et al. 1997; Giusti & Marsili-Libelli, 2005; Trancoso et al. 2005). No papers dealing with tropical macroalgae patch dynamics could be found by the authors of this report during the literature phase of the model scoping for this study. The situation is only a little brighter for seagrass. Seagrass is often present in tropical models as a habitat, but is not often given dynamic consideration. The most notable modelling efforts to date (which could serve as a springboard for a more sophisticated consideration of seagrass habitat dynamics in future studies) are: the patch expansion models of Duarte (1995) and Kendrick et al. (1999); the consideration of seagrass clonal growth by Sintès et al. (2006); the model of patch topography development by Kendrick et al. (2005); the eelgrass disturbance model of Neckles et al. (2005); and the primary productivity model comparison of Pastres et al. (2004).

The group that has seen the most attention is the mangroves. Forest gap models first came into existence in 1969 as a special case of individual-based tree models (Siccama et al. 1969). Since then they have been one of the most successful means of modelling forest dynamics (in temperate and tropical climates; Bossel & Krieger, 1991). Within the last decade their use has expanded from fully terrestrial forests to mangroves (e.g. Chen & Twilley, 1998; Twilley et al. 1999). Given the excellent review of forest models that already exist (in particular Bugmann (2001) and Busing & Mailly (2004)) future consideration of mangrove patches in places such as the NWS should probably focus on the adaptation of these well tested methods. Such an exercise was not attempted here as it is non-trivial and potentially very intensive; and as such should really be the focus of a dedicated study, at least in the first instance. Once a working model is developed (or adapted from existing models such as FORMOSAIC (Liu & Ashton, 1998) or FORMAN (Chen & Twilley, 1998)) it could be readily included in wider ecosystem or habitat focused modelling exercises, such as those that form the core of this study or the much larger NWS MSE study.

6.4 Model implications for management

The lack of any information showing non-negligible or non-local impacts of human activities on groups other than the benthic habitat means that it is hard to say anything about the seagrass, macroalgae and mangroves. Comments are left to the NWS MSE study (Little et al. 2006) and future more targeted work.

In contrast, there is scope to speak to the management implications of the model predictions for the small and large benthic habitat groups. Future development will see how much is gained from further model refinement, but even with that to the side there are strong implications for the sensitivity of the system versus potential recovery times – five years to destroy it, a couple of decades (at least) to recover (even locally). Moreover, such recovery could be very sensitive to the form of recruitment (or any impediments to recruitment), as evidenced by the strong differences in recovery rates at low population levels between Sainsbury's model (with constant recruitment) and the logistic model presented here.

These potentially very slow rates of recovery have quite significant implications for conservation management. If patches of benthic habitat in “good condition” are required components of ecosystem-based fisheries management, or as a conservation and biodiversity target in their own right, then rates of recovery of the order seen here suggest, that even if patches are protected now, it may be decades before these management goals will really be met. This can cause division amongst stakeholders regarding the utility of such zoning if it is not clearly understood from the outset that this is not a goal that will be achieved rapidly.

The speed with which patches are depleted is also a management concern, as it means there is little buffer for error – with impacts reaching potential trigger levels faster than the infrastructure may be able to detect or respond to. In combination with the subsequent potential for slow recovery this makes the management of benthic habitat a difficult, but critical, problem to tackle successfully. It also means that a lot of careful thought must be given to what habitat associated management goals are, how they will be implemented, and what safety margins are being included. In such a situation transparency is paramount and any future management exercise will have to make use of reliable tools. The habitat dynamics models presented here have potential in that role. In their current form they could be used wisely and well within an MSE setting to give an understanding of the broadscale implications of alternative management strategies and scenarios of environmental change. Alternatively, if direct management tools are called for, then habitat dynamics models of this (or any other form currently available) would require a good deal more consideration and sophistication before they could be considered with the same confidence as other management models (such as fisheries assessment models).

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