

Modelling the potential impacts of fisheries on ecosystem dynamics using

tropho-dynamic models

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Abstract

Despite many studies of the effects of fisheries on ecosystem dynamics, the consequences of removing food subsidies or predators from marine ecosystem are still unclear. In this thesis, I addressed two key areas in relation to our understanding of how fisheries affect ecosystem processes: (i) food subsidies and (ii) the effects of removal of predators. These two specific areas were selected as they have a potential of modifying ecosystems, and may lead to loss of the essential goods and services ecosystems provide.

There are several threats to marine ecosystems, one of them being overfishing. The impacts of overfishing include changes in biological assemblages and modification of ecosystems. The Ecosystem Based Management (EBM) in fisheries has been widely advocated as it encompasses interactions within the ecosystem; and ecosystem models, which are able to address various scientific questions in ecosystems, have been widely used as a tool for advancing this process. In my thesis, I aimed to understand the effects of discarding and selective overfishing on ecosystem dynamics.

Studies on the effects of discards on ecosystem dynamics have produced variable results, which creates uncertainty in concluding how ecosystems respond to discards, and presents a management challenge. It is still unclear whether discards should have similar impacts on all ecosystem types. To address this problem, in Chapter 2, I performed a global meta-analysis of 23 studies that were manipulated to explore the effects of discards on ecosystem functions (productivity, respiration and consumption). I examined the following variables: predator biomass, predator catch, total catch, total primary production/ total respiration (TPP/TR), system omnivory index (SOI) and primary production required for the catch (PPR catch) from the studies, with 9 explanatory covariates: area, functional groups, stanza groups, publication type, latitude, study duration, discards biomass, ecosystem type and fleet size. I found that presence or absence of life history age-class structured data (stanzas) gave divergent responses. All variables, except predator biomass, showed an increase in the presence of food subsidies. Explanatory covariates that provided the greatest explanatory power in the models were stanza, ecosystem type and publication type. I concluded that inclusion of stanzas could give different model predictions and presence of discards may increase ecosystem functions. In Chapter 3, I describe the methodology for the models used in Chapters 4 to 6.

The issue of discards has drawn global attention in the recent past, so in Chapter 4, I addressed this problem by exploring the consequences of gradually removing and abruptly banning discards using ecosystem models. Fisheries discards are a major source of Predictable Anthropogenic Food

Subsidy (PAFS) in commercial fisheries. PAFS impact ecosystems by modifying ecological processes and food webs. I found that PAFS increase food pathways of opportunistic scavengers. When PAFS were reduced gradually, scavengers were able to switch their prey. From this work, I recommended gradual reduction of PAFS to allow species exploiting PAFS to adjust to reduction of food subsidy.

Predators play a key role in maintaining the structure and function of ecosystems. Removal of predators resulting from overexploitation could have detrimental effects on ecosystems. In Chapter 5, I examined the consequences of simultaneous removal of predators from different trophic levels of a subtropical food web. I explored the effects of removal of top predators, meso-predators and small predators in Moreton Bay where different types of fishing remove different components of the food web. I found that when crabs were fished out, macrobenthos and prawns increased. Removal of pelagic fish resulted in an increase of jellyfish, while removal of sharks resulted in an increase of major groups, with the highest increase in the pelagic fish. When all predators were fished out, the low trophic level species increase in biomass. The findings emphasized the critical role that predators play in maintaining healthy ecosystems.

The increased incidences of jellyfish blooms in many parts of the world have been related to overfishing. Overfishing results in decline of fish that prey on or compete with jellyfish. In chapter 6, I simulated overfishing of jellyfish in Moreton Bay model. As it was anticipated, overfishing of jellyfish impacted negatively on pelagic fish which prey on jellyfish. In summary and conclusion (Chapter 7), discards increase ecosystem functions (productivity, respiration and consumption); but a gradual ban rather than a complete ban on discards is recommended where mega-fauna have become dependent on discards as a food source. It is necessary to regulate overfishing of predators in order to maintain the structure and health of marine ecosystems. Jellyfish blooms related to overfishing may be reduced by fishing jellyfish, but in some cases may have an effect on major top predators, in such cases, fishing jellyfish may not be a desirable management option.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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Publications during candidature

Peer-reviewed papers

Fondo EN, Chaloupka M, Heymans JJ, Skilleter GA (2015) Banning Fisheries Discards Abruptly Has a Negative Impact on the Population Dynamics of Charismatic Marine Megafauna. PLoS ONE 10(12): e0144543. doi:10.1371/journal.pone.0144543

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Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Research Involving Human or Animal Subjects

No animal or human subjects were involved in this research.

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List of Abbreviations

AFS	Anthropogenic food subsidies
В	Biomass
BSE	Bovine Spongiform Encephalopathy
CI	confidence interval
CSIRO	The Commonwealth Scientific and Industrial Research Organisation
CV	Coefficient of Variation
DAFF	Department of Agriculture, Fisheries and Foresty
EAF	Ecosystem Approach to Fisheries
EBM	Ecosystem Based Management
EE	Ecotrophic efficiency
ESREM	European Regional Seas Ecosystem Model
EwE	Ecopath with Ecosim
F	Fishing mortality
FAO	Food and Agriculture Organisation of the United Nations
FCI	Finn's Cycling Index
GLMM	Generalised Linear Mixed Model
IBP	International Biological Program
ICES	International Council for the Exploration of the Sea
LRR	Log Response Ratio
MB	Moreton Bay
MPA	Marine Protected Area
MSE	Management Strategy Evaluation
MSVPA	Multi-Species Virtual Population Analysis
MSY	Maximum Sustainable Yield
NPRSR	Queensland Department of National Parks, Sport and Racing
OSMOSE	Object-oriented Simulator of Marine ecoSystem Exploitation
P/B	Production/Biomass ratio
P/Q	Production/Consumption ratio
PAFS	Predictable Anthropogenic Food Subsidies
PPR harve	est Primary Production Required for harvest of the catch
PRISMA	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
Q/B	Consumption/Biomass ratio
RE	Random Effects

REM	Random Effects Model
SAMS	The Scottish Association for Marine Science
SOI	System Omnivory Index
StrathE2E	Strathclyde end-to-end ecosystem model
TAC	Total Allowable Catch
TL	Trophic level
TPP/TR	Total Primary Production/ Total Respiration
TST	Total System Throughput
UNEP	The United Nations Environment Programme

Chapter 1

General Introduction

In this section, I describe one of the major threats to marine ecosystems, that is, overfishing. Other critical threats to these ecosystems include habitat damage, pollution, invasive species and climate change (Suchanek 1994; Bax et al. 2003; Dulvy et al. 2006; Molnar et al. 2008; Vaquer-Sunyer and Duarte 2008; and Wernberg et al. 2011), but overfishing has been identified as one of particular importance, and so is the focus of this thesis. In this first section, I provide an overview of current knowledge about the effects of different aspects of overfishing.

Overfishing

Over-exploitation of harvested organisms is a major threat to ecosystems and a serious problem in many areas of the world with overfishing identified as of particular importance in aquatic ecosystems. Fish is one of the most traded food item in the world with approximately 86 % (136 million tonnes) of produced fish taken for human consumption (FAO 2014). Currently about 31 % of world fish stocks are overexploited while 58 % are fully fished (FAO 2016). The improved fishing technologies, increased fishing effort, and high demand for marine resources is placing intense pressure on marine ecosystems (Aydin 2004). Overfishing in marine ecosystems is aggravated by destructive fishing (use of explosives, poisons and some fishing gear such as prawn otter trawls and other bottom fishing gear) and capture of non-targeted fish species (by-catch) (Jones 1992; Alverson and Hughes 1996; Mcmanus et al. 1997; Althaus et al. 2009).

Effects and impacts of overfishing

Overfishing can affect provision of goods and services by marine ecosystems because overfishing can cause changes in biological assemblages, leading to loss of biodiversity and disrupt ecosystems' structure and functioning (Lotze et al. 2006, Worm et al. 2006). Many marine fisheries in the world are overfished, resulting in depleted fish stocks and degraded marine habitats (Jackson et al. 2001; Ward et al. 2002).

The detrimental ecosystem effects of excessive fishing can be direct or indirect (Botsford et al. 1997; Scheffer et al. 2005). Direct effects result from intense fishing activities such as excess fishing on target and non-target species. Indirect effects result from changes in species assemblages due to: (i) removal of prey population (ii) reduction of predators (iii) changes in life history traits or size composition of species (FAO/UNEP 2009). The impacts of overfishing on marine species

diversity can manifest by: (i) modification of trophic structure (ii) decreased species richness (iii) risk of local extinction (FAO/UNEP 2009).

Selective overfishing

Various commercial fish stocks have been or are still being overfished (Worm et al 2009; Costello et al 2012). Selective fishing of commercial large sized groups diminishes their population relative to those groups that are not fished (Pauly et al. 1998; Zhou et al. 2015); resulting in an abundance of low value small sized fish (Essington et al. 2006; Richardson et al. 2009; Collette et al. 2011).

Fishing can change trophic interactions when competition for food is reduced for lightly fished species or when predation diminishes heavily fished species, causing heavily fished population to drastically reduce (Zhou et al. 2015). For example, the biomass of dog fish and skates on Georges Bank may have increased when cod and flounders were selectively overfished due to the overlaps in food resources between cod and dogfish, flounders and skates (Zhou et al. 2015). The diminished abundance and distribution of heavily fished species may permit the lightly fished species to take over the ranges initially occupied by heavily fished species (Zhou et al 2015). In addition, the lack of recovery of some overfished stocks (e.g. Atlantic cod, haddock) has been associated with altered life-history parameters and modified interspecific interactions resulting from past fishing pressure (Zhou et al. 2015). Serious overfishing may also cause species' ecological extinction due to lack of interactions between heavily fished species and other species (Jackson et al 2001). In their analysis on the historical trends of overfishing, Jackson et al (2001) confirm that in the past, the major ecological changes to coastal ecosystems were caused by excess fishing of large vertebrate and shellfish while presently, large fish and suspension feeders that were previously abundant are now ecologically extinct. Many local populations of marine fishes have gone extinct as a result of excess fishing (Jackson et al 2001).

Discards

"Discards, or discarded catch, is the portion of the total catch that is thrown away or dumped at sea" (FAO 1996, p.2). This occurs for several reasons: (i) exceeded fishing quota, (ii) unwanted species or immature and undersized organisms (iii) illegal species (iv) species of no commercial value, or (v) offal from fish processing on board the vessels (Sardà 2015). Discards may be dead or alive (Sardà 2015).

Fisheries discards from commercial fisheries are a major global problem and started receiving much attention two decades ago (FAO 1996; Kelleher 2005). However, the long term impacts of fisheries

discards in the ecosystem are not well understood. Discards from fisheries are a major conservation concern globally and there have been calls to reduce greatly or even eliminate discards from commercial fisheries. For example the Common Fisheries Policy plan by the European Commission "to enforce the landing of fishing discards as a measure to encourage their reduction" (Sardà 2015) and the Food and Agriculture Organization of the United Nations (FAO) through the Code of Conduct for Responsible Fisheries (FAO 1995) proposes the reduction of discards. Given the long time periods over which discards have been released into the oceans though, the consequences of reducing or eliminating discards on the short and long-term population dynamics of ecosystems are not known.

Globally, discards are estimated to be about 7.3 million tonnes annually (Kelleher 2005), with current reconstructed data estimating up to 10.3 million tonnes (Pauly and Zeller 2016). Some of the regions of the world with largest discard estimates include the Northeast Atlantic region (1.4 million tonnes), the Northwest Pacific region (1.3 million tonnes) and the Western Central Atlantic (0.8 million tonnes) (Kelleher 2005). The highest discard rate is from tropical prawn fisheries, making up to 27% of the global discards (Kelleher 2005). Some reported estimates of discards in areas where shrimp trawling takes place are: Gulf of Mexico – 480,000 tonnes; Arafura Sea – 230,000 tonnes; South Atlantic – 70,000 tonnes; Australian Northern Prawn Trawl – 80,000 tonnes (Kelleher 2005).

The amount and composition of discarded material varies considerably between fisheries, with only a few fisheries, such as artisanal fisheries, discarding a relatively small proportion of the catch (Britton and Morton 1994). In other cases the discard rate is very high e.g. the North Sea *Nephrops norvegicus* trawl fisheries, about 45% of the total catch weight of under-sized fish is discarded; the discard rates of plaice (*Pleuronectes platessa*) in the North Sea flatfish beam trawl fisheries are about 80% in numbers (Catchpole et al. 2008). Programmes and techniques for reducing non-targeted and juvenile species have been developed (Brewer et al. 1998; Bublitz 1995; Løkkeborg 2003).

Although discarding in fisheries has been on going for centuries, it is only recently that research has been focused on this issue (Bellido et al. 2011). Knowledge on impacts of bycatch and discarding is increasingly necessary in the context of ecosystem based management (Kelleher 2005). With the high global demand for protein and depleting fish stocks, the practice of discarding is not sustainable (Bicknell et al. 2013). Studies have shown that discarding can have direct negative impacts on target and non-target stocks and lead to deleterious ecosystem-level effects (Bicknell et al. 2013).

al 2013). On the other hand, discarded biomass represents energy taken out and shortly put back into the ecosytem (Sardà et al. 2015). Discards represent a major food subsidy for marine scavengers such as seabirds, marine mammals and some fish, and have adversely changed some marine food webs (Bicknell et al 2013).

Approaches to fisheries management

Single species management

Previously single species management was applied to fisheries, where the fishing mortality of a species was assigned (Rothschild et al. 1997), without considering species as part of the ecosystem (Mangel et al. 2000). Abundance of the stock was considered as key in population dynamics and the population details for a single species were enough to manage the stock (Mangel et al. 2000). The models developed from this approach did not take into account species interactions (Rothschild et al. 1997; Mangel et al. 2000), or interactions between the species and the broader ecosystem.

The single species management approach had problems. Changes in trophic structure, habitat destruction and effects on non-target species could not be explained and there was a relative failure with the single species approach to management (Parsons 1992; Sutinen and Soboil 2003). Many fisheries collapses have resulted from overfishing which is a consequence of single species management e.g. the collapse of Icelandic herring (Hamilton et al. 2004) and the Pacific sardine *Sardinops sagax* in the California current (Hargreaves et al. 1994).

The single species approach was identified to be problematic as it did not take into account cumulative impacts of fishing (Vinther et al. 2004). When a species' quota was used up before the end of the season; fishing of that species continued as the quota of other species remained (Vinther et al. 2004). This led to inaccurate measure of the species' fishing mortality or closure of the fishery preventing fishing of other healthy stocks (Vinther et al. 2004). However, single species management is still useful for setting MSY of fish stocks (Hilborn 2011).

Multispecies management

In multispecies fisheries, advice was given based on fleet or fishery instead of stock. Exploitation trends at fleet and stock level were used and advice on effects of fishing at ecosystem level was possible (Vinther et al. 2004). Mixed fisheries forecasting was formulated using projections of

population numbers from catch-at-age analysis and fishing mortality-at-age multiplied by a single overall F (fishing mortality)-multiplier (Vinther et al. 2004). It was then possible to estimate a total allowable catch (TAC) and derive the required F. The assumption here was that a fleet would target one species. However, it becomes complicated if there are many fleets targeting mixed species and requires changes in the fishing mortality and some external input, such as a policy decision, on the different species (Vinther et al. 2004).

Multispecies fisheries management continues to be used although, it has some challenges. Catch limits set for many species may lead to species depletion and loss of yields (Hilborn 2011) e.g. groundfish fishery in the California Current Ecosystem with reduced fishing mortality rates, led to loss of productive stocks (Worm et al 2009). Multispecies fisheries management may be complicated when interactions between species involve prey with several predators or competitors (May et al 1979). In addition, it may be difficult to monitor other non-species related factors such as changes in habitat or environment; identifying correct relationships among species; gear related changes; as well as incorporate socio-economic factors related to the fisheries (Seijo et al 1998; Pascoe 2000; McClanahan and Castilla 2007). The lack of consideration of these other factors in management could lead to stock collapse e.g. as with the northern cod in Newfoundland described in Myers et al (1997). With multi species fisheries management the uncertainties related to forecasting the effects of alternative management are high (Botsford et al 1997) and cannot be used for long-term predictions (Ono et al 2017).

Ecosystem based approach to fisheries management

The deteriorating condition of fisheries and increased utilization of aquatic resources in the 20th Century necessitated management (Garcia et al. 2003). Ecosystem-based management takes into account all the elements (e.g. habitats, food webs, target and non-target species) and interactions in the ecosystem (Christensen et al. 1996). In 2001, the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem proposed inclusion of ecosystem approach to fisheries management (FAO 2003).

An "ecosystem approach to fisheries" (EAF) is an approach that takes into account ecosystem components in fisheries management, with an aim of rebuilding and sustaining biodiversity while providing goods and services (Garcia et al. 2003). The EAF provides a holistic approach that incorporates species interaction, habitats and the physical factors in marine ecosystem, supporting

sustainability and reduces uncertainty (Botsford, et al 1997)). Thus EAF applies all details of the Code of Conduct for Responsible Fisheries (Garcia et al. 2003).

The approach incorporates "lessons from ecological sciences to inform management decisions" (Mangel et al. 2000). This approach takes into account, target, non-target species, predator –prey interactions, effects of fishing on the ecosystem, biotic and abiotic interactions (Jennings and Kaiser 1998; Mangel et al. 2000 Murawski 2000).

The Principles of Ecosystem-Based Management (EBM) as stated by Ward (2002) are: to maintain ecosystem structure and function; objectives are established by human use and values; ecosystems and interactions with human use are dynamic; shared vision and objectives set by stakeholders; management based on scientific knowledge and monitoring.

Despite its limitations, the single species approach is still fundamental to fisheries management and EBM compliments this approach and will not replace it (Christensen 2012). The single or multiple species approach can be used to give advice e.g. on catch or effort of individual species in a fishery (Vinther et al. 2004). The EBM approach would come in for example, when advice is required on the ecosystem effects of fishing activity (Christensen 2012).

Data limitation

To be applied effectively, EBM requires data on different components of the ecosystem over space and time (Plagányi and Butterworth 2004; Batista et al. 2011; Béné et al. 2011), which in many cases are lacking and the complexity and variability of marine ecosystems further complicates this situation (as gathering large amounts of data in the dynamic marine ecosystems may be challenging) (Jennings and Kaiser 1998; Lozano-Montes et al. 2011). The ability to work with such limitations in the data is required to support the implementation of EBM (Plagányi and Butterworth 2004). Numerous ecosystem models have been developed to fulfill this requirement for EBM (Heymans et al 2016).

Data poor situations may include (i) developing small-scale fisheries targeting mixed species; (ii) recently developed large-scale fisheries where fisheries research and management failed to keep pace with exploitation; (iii) large-scale fisheries with poor quality data or variable and unreliable (e.g. due to misreporting and discarding); (iv) lack of information on non-target and non-commercial species; (v) lack of other relevant data such as environmental variables and socio-economics. (Pilling et al. 2008).

Ecosystem models

How they are used in EBM?

Compared with terrestrial ecosystems, our knowledge of marine ecosystems is limited by the difficulty of observation of their dynamic nature. Marine ecosystems are complex, very dynamic and are heavily influenced by human activities (Scheffer et al. 2005). Ecosystem models help us understand how species are influenced by each other, their habitats and by human activities. "Ecosystem modelling" has been widely applied and is a useful tool for investigating a wide range of scientific questions in the world's oceans (Plagányi 2007). In addition, models are increasingly used to help us understand how marine ecosystems function and explain management questions (Walters and Martell 2004; Albouy et al. 2010).

Numerical modelling of ecosystem dynamics is key in EBM because several alternative management scenarios can be investigated prior to taking new management actions, minimizing possible risks of undesirable and unexpected ecosystem effects (Lozano-Montes et al. 2011). Further, models also provide a window to study the potential consequences of decisions that aim to sustain marine ecosystems and fish stocks (Albouy et al. 2010). With the various threats and issues facing marine ecosystems, managers, conservationists and policymakers are looking for aids to understand the ecosystem; therefore, models can be useful tools.

The effects of fishing on ecosystems have been modeled using various fishing scenarios. Some ecosystem models, such as OSMOSE (Shin and Cury 2001), Atlantis (Fulton et al. 2004) and Ecopath with Ecosim (EwE) (Walters et al. 1997; Christensen and Walters 2004a), have been used. Each model having its own assumptions and hypothesis to portray different scenarios (Gasche et al. 2012). For example, Bundy and Pauly (2001) used the mass balance model to show the impacts of fishing and interactions between different functional groups in the ecosystem. They demonstrated that small-scale fisheries have higher impacts on the ecosystem than large-scale fisheries. These models use different measures to inform the user about the ecosystem status and fishing impacts.

Examples of ecosystem models

 Multi-Species Virtual Population Analysis (MSVPA) - are minimal realistic models for fish stock assessment that use catch-at-age and gut content information to evaluate past fishing and predation mortalities (Magnússon 1995) in the: North Sea, Baltic Sea, Georges Bank, Eastern Bering Sea. MSVPA was developed by ICES (International Council for the Exploration of the Sea) multispecies working group (Magnússon 1995).

- 2. Object-oriented Simulator of Marine ecoSystem Exploitation (OSMOSE) is a spatial individual based model that uses predation rules to model trophic interactions with focus on fish schools (Shin and Cury 2001; Shin et al. 2004).
- 3. European Regional Seas Ecosystem Model (ESREM) was developed to simulate certain elements (C, N, P, Si) in pelagic and benthic areas of the North Sea and adapted for other areas such as the Baltic, Mediterranean, Arabian Seas (Baretta et al. 1995; Blackford et al. 2004). The models includes diatoms, dinoflagellates, autotrophic flagellates, heterotrophic nanoflagellates, bacteria, micro- and mesozooplankton and can be linked to models of fish dynamics (Baretta et al. 1995; Blackford et al. 2004).
- 4. Atlantis Atlantis is a spatial model that incorporates several aspects such as energy, fisheries, management, human induced and climatic pressures and can be applied to explain management issues on multiple use of resources (Fulton et al 2004). Some examples are models of: Port Phillip Bay, Australia, SE Australian EEZ, continental shelves and estuaries in Australia, Tasmania, Northern California Current. The ATLANTIS model, developed by Beth Fulton from CSIRO (The Commonwealth Scientific and Industrial Research Organisation) in Australia, is being used extensively in management e.g. the Northeast U.S. (NEUS) Atlantis marine ecosystem model used to hind cast and forecast changes under varying pressures (Olsen et al 2016).
- 5. Strathclyde end-to-end ecosystem model (StrathE2E) represents the time-dependent changes of ecosystem components in a spatial region that is horizontally uniform, but vertically layered (Speirs et al. 2010). The regional setting is defined by fixed qualities (layer thicknesses and sediment porosity), time dependent drivers and boundary conditions. Biological properties are defined by parameters of the various processes (biogeochemical, excretion, mortality et.) (Speirs et al. 2010).

Why Ecopath with Ecosim models

Ecopath with Ecosim models include the full range of organisms in an ecosystem, and can be used for dynamic and spatial simulations (Fulton et al. 2011). Ecopath with Ecosim models have been applied to many ecosystems, making comparisons across different ecosystem types possible (Colléter et al. 2015). EwE is freely available online, relatively easy to use, has training and user

support and allows for the estimation of a number of missing parameters. In addition to making ecosystem analyses possible, the EwE modelling approach requires collection and use of available biological information for species of a given ecosystem (Morissette 2007). Ecopath representation of a natural system helps identify data gaps, serves as a reference point for specific research on ecosystems, allows an understanding of interactions between species groups in an ecosystem (knowing the impact of one group on others is important in management), and the universal format provides a platform for comparing different ecosystem models. EwE models are beneficial in that they incooperate obtained data into an "ecosystem context" (Christensen 1991).

Uses of EwE models

There are hundreds of EwE models developed for terrestrial and aquatic ecosystems to:

- Identify and quantify major energy flows (Wolff et al. 1998; Vega-Cendejas and Arreguin-Sanchez 2001; Bulman 2002; Rybarczyk and Elkaïm 2003; Zetina-Rejón et al. 2003; Morales-Zárate et al. 2004; Wilson et al. 2009)
- Describe ecosystem resources and their interactions (Harvey et al. 2003; Arbach Leloup et al. 2008)
- Evaluate ecosystem effects of fishing (Cox et al. 2002; Bundy 2005; Guénette et al. 2006; Hoover et al. 2013)
- Evaluate effects of environmental change (Trites et al. 1999; Watters et al. 2003; Tam et al. 2008; Hoover et al. 2013)
- Evaluate management strategies and uncertainty in the management process (Buchary et al. 2002; Gribble 2003; Arreguin-Sánchez et al. 2004; Velasco et al. 2007; Arreguin-Sánchez et al. 2008)
- Explore management policy options incorporating economic, social, and ecological considerations (Arreguin-Sánchez et al. 2004; Christensen and Walters 2004b; Zeller and Reinert 2004; Heymans et al. 2009; Jones et al. 2011)
- Evaluate impact and placement of MPAs (Beattie et al. 2002; Albouy et al. 2010; Lozano-Montes et al. 2011; Colléter et al. 2012; Valls et al. 2012)
- Evaluate pollution and predict bioaccumulation of persistent pollutants (Okey et al. 1999; Carrer et al. 2000; Booth and Zeller 2005)

- 9. Evaluate the impacts of invasive species (Feroz Khan and Panikkar 2009; Arias-González et al. 2011)
- 10. Explore conservation strategies (Okey et al. 2004; Jiang et al. 2008)

History of EwE and the foraging arena

Single species assessments are the foundation of fisheries management; they are thus important in how we manage resources on a yearly basis or seasonally. "*Fish eat fish, no fish is an island*" is the famous quote that Villy Christensen uses when referring to management at the ecosystem level, stressing the need to recognise that fish interact with each other and that fish species are affected by environments; and the need to understand what governs the changes occurring in ecosystems; and whether the changes are caused by humans or the environment (Christensen 2012).

Raymond Lindeman, the pioneer of studies on trophic dynamics, showed how food webs can be examined in terms of energy flow (Lindeman 1942). Finn (1976) developed the concept of average path length in ecological flow networks and Ulanowicz (1986) established indices of natural community development based on flow networks. After the large-scale International Biological Program (IBP) ecological and environmental studies (1964 to 1974), Jeffrey Polovina developed a mass-balance model for Hawaii data, which then became the original Ecopath model (Polovina 1984).

An Ecopath model measures the energy in and energy out of each species group and replicates this across the whole ecosystem, resulting in a snapshot of the ecosystem at a given point in time: what was there at that time and how all the different groups interact. Christensen and Pauly (1992) worked with several ecosystems using Polovina's Ecopath model combined with network analysis. The work by EP Odum (1969), which inspired Christensen, provided how an ecosystem could be ranked from immature to mature systems and assigned attributes to all the development stages and showed the importance of Lindeman's thermodynamics work in ecosystems.

The scientists working at the IBP recognised the importance of adding a dynamic dimension to these snapshot models. They used the foraging arena in the model, where it was recognised that prey can be in different behavioural states (Christensen 2012). If prey is split up into prey being available and not available to predation then Lotka-Volterra models can still be used, the models perform and make a big difference. So they used foraging arena theory for different ecosystems and

time series models to incorporate food web effects, fishing pressure and environment changes and be able to make predictions (Christensen 2012).

The foraging arena theory states that "*prey make themselves available to predation through activities such as foraging and dispersal*" (Walters et al. 1997). Thus, there are vulnerable and invulnerable prey in the ecosystem and not all prey are available to their predators at all times. In EwE, each biomass pool consists of a group of prey the is vulnerable and antoher one is safe from predators (Christensen 2012). So predation is limited by both the search efficiency of the predator and the exchange rate between the invulnerable and vulnerable prey (Christensen 2012). In EwE, the vulnerability parameter is set to show the proximity of the group to carrying capacity and type of interaction (top-down or bottom up) (Christensen 2012). Top-down interaction is controlled by predation, and in bottom up interaction prey vulnerability limits the predation rate (Walters et al. 1997).

The new developments in Ecopath led to the dynamic version Ecosim (Walters et al. 1997) and the spatial version Ecospace (Walters et al. 1999). An International Conference to mark 30 years since EwE development was held in 2016 (Villasante et al. 2016). Several scientific and technical plugins are available or being development and include EcoTroph (Gascuel and Pauly 2009); for biodiversity and conservation indices (Coll et al. 2014); the habitat foraging capacity and the spatial-temporal-framework model (Christensen et al. 2014) among many others (Steenbeek et al. 2016). A new version of the software (EwE 6.5) was released in July 2016 (http://ecopath.org/). Figure 1 illustrates the advancement of EwE and the number of publications through the 30 years of its development.



Figure 1: The History of Ecopath with Ecosim since 1984 (adopted from the Ecopath with Ecosim training, SAMS)

Addressing uncertainty in EwE models

There are various sources of uncertainty in models that include among others, abundance estimates, model structure and interactions between species (Seijo et al. 1998; Morissette 2007). Complex ecosystem models may or may not accomplish desired tasks because of many functional interactions that are not known and other ecosystem units that we cannot parameterise (Seijo et al. 1998).

There are various ways to get a balanced model in ecosystem modelling. It is thus important to test how sensitive the model outputs are to changes in construction and balancing (Morissette 2007). Sensitivity analyses are important in addressing uncertainty in EwE models to check if the results are robust or sensitive to changes in model construction or input parameters (Morissette 2007). If sensitivity analyses do not significantly change the results then we can place confidence on the model. If the results change much, this can give different conclusions and there is need to take caution in interpretation of the results (Morissette 2007).

Another way of testing model sensitivity to model structure is through inter-model comparison of validated and tested models e.g. Smith et al. (2011) compared the effects of low trophic level fishing from several locations around the world using three different models, always two models in

the same location; and Johnson et al. (2010) compared EwE vs Atlantis models from the SE Australia. Even in the case of inter-model comparison, there still need of careful interpretation of results.

To address the uncertainty in an Ecopath model, there is the pedigree, a code that measures the uncertainty connected to the input values in Ecopath models and is based on the origin of the data (Christensen and Walters 2004a; Morissette 2007). The pedigree is useful for comparison with other models (Christensen and Walters 2004a), allowing one to compare models with different numbers of trophic components. For the sensitivity analysis, the Ecosim part of the software includes a Monte-Carlo routine to find input parameters that minimise the sum of squares with time series (Morissette 2007). The pedigree is useful in setting the confidence intervals that are applied in the Monte-Carlo simulations (Heymans et al 2016).

Incorporating models to answer management questions

Models are increasingly being used to answer management questions. Some examples of models used to answer questions in fisheries management include: Tremblay-Boyer et al. (2011) used an EcoTroph model to estimate the effects of fishing on the biomass of the world's oceans. In Australia, Atlantis models contributed in the driving force to fundamental change in the fisheries management, where they were used to finalise quantitative analysis of the management strategy evaluation (MSE) (Fulton et al. 2007). Kaplan et al. (2010) used Atlantis to establish management reference points and decision mechanisms for the US West Coast. Many EwE models have been developed in Australia and have been used to "*inform management strategies*" in different ecosystems (Bulman et al. 2014) Intermediate models can give useful advice on species, environment and fleet interactions (Plagányi et al. 2014; Collie et al. 2016). This is because in these models there is a point at which the level of uncertainty is at a minimum (Collie et al. 2016).

Food web models are useful in evaluating fishing and predation mortalities, quantifying prey for key species and assess changes in prey (Plagányi, 2007). Full ecosystem models are useful in answering questions related to species interactions and climate, habitat, or fleet interactions e.g. the Atlantis model developed for Northeast US shelf (Link et al. 2010).

Aims of the thesis

As multiple fish species are increasingly harvested, predator-prey interactions are being impacted leading to changes in food webs (Aydin 2004) that alter ecosystems and may result in loss of the essential life supporting functions. It is essential to focus on the issue of overfishing not only to

conserve biodiversity, but also because fish is a food source for 3 billion people, contributing 50 percent of animal protein for 400 million people (FAO 2016). Fish is the fifth largest food commodity in the world (FAO 2012)

In my thesis, I focused on two challenging issues related to fisheries: selective overfishing and discarding. I aimed to understand how fisheries affect ecosystem processes and the structure and functioning of marine ecosystems in these two key areas by:

- (i) Performing a global meta-analysis of discards removal on production, consumption and respiration (Chapter 2)
- (ii) Exploring the effects of removal of PAFS (predictable anthropogenic food subsidies)from a subtropical ecosystem (Chapter 4)
- (iii) Understand the effects of overfishing of predators at different trophic levels on ecosystem dynamics in a multi-species fisheries through simultanoeus and interactive overfishing in a subtropical ecosystem (Chapter 5)
- (iv) Explore the interactive effects of overfishing jellyfish (Chapter 6)

Thesis expectations

From the results of the work in this thesis, I expect to provide a better understanding on the effects of overfishing and, in particular, identify the effects of discards on ecosystem functions, determine what the consequences of removing food subsidies from the ecosystem are, provide an understanding on the effects of removing in combination predators at different trophic levels on ecosystem functions, and find how overfishing of jellyfish affects an exploited ecosystem.

Thesis chapters/ organisation

In the general introduction, I described the causes of overfishing, its impacts on ecosystems and two key fishing practices that can modify ecosystems: discarding and selective overfishing. I discussed approaches that have been used to manage fisheries and evolution of the ecosystem based approach to management and ecosystem models, and how they have been applied in this approach to management. I then described the history of the Ecopath with Ecosim modelling approach which has been widely used in ecosystem based management, and which I have used as a tool for addressing the issues presented in my thesis. I then introduced the aims and expectations of my thesis. In this section, I present the organisation of thesis chapters (Figure 2).



Figure 2: Diagram of thesis organisation

Studies on the effects of discards on ecosystem dynamics have produced variable results and this may pose a challenge to management decisions because of the lack of generality in the predictions and outcomes. In Chapter 2, I examined the results from different studies that examined the effects of fisheries discards to ascertain the effects of food subsidies on specific ecosystem functions, by doing a meta-analysis. The issue of fisheries discards has drawn global attention in the recent past, so in Chapter 4, I addressed this problem by exploring the consequences of gradually removing and abruptly banning discards using ecosystem models. Predators play a key role in maintaining the structure and function of ecosystems. Removal of predators resulting from overexploitation could have detrimental effects on ecosystems. In Chapter 5, I examined the consequences of simultaneously removing predators from the ecosystem, that is, removing predators from different trophic levels of the food web. One of the effects of overfishing is the increased incidences of jelly fish blooms in many parts of the world, as overfishing results in decline of fish that prey on or compete with jelly fish. It has been predicted that global warming will increase the frequency of jellyfish blooms. In Chapter 6, I simulated a management scenario in an exploited ecosystem where

jellyfish abundance is reduced through fishing. Finally in Chapter 7, I gave a systemesis of my research findings, limitations to my research and suggest improvements and future directions.

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Chapter 2

A global meta-analysis of the effects of discards on ecosystem functions

Abstract

Anthropogenic food subsidies (AFS) (food resources not usually accessible to organisms) are geographically widespread and may modify ecosystems. Ecosystems' response to food subsidies is variable, with studies showing either positive, negative or no effects to the presence of AFS, with contrasting or unexpected responses. This variability in results creates uncertainty in concluding how ecosystems respond to AFS and presents a management challenge. A number of variables could contribute to the contrasting ways in which ecosystems respond to AFS. It is still unclear whether AFS should have similar impact on all ecosystem types. To address this problem, I performed a meta-analysis of 23 studies that were manipulated to explore the effects of AFS (fisheries discards) on ecosystem functions (productivity, respiration and consumption). I examined the following variables: predator biomass, predator catch, total catch, total primary production/ total respiration (TPP/TR), system omnivory index (SOI) and primary production required for harvest of the catch (PPR harvest) from the studies, with 9 explanatory covariates: area, functional groups, stanza groups, publication type, latitude, study duration, discards biomass, ecosystem type and fleet size. I hypothesised that the presence of discards will have a positive response (i.e. increase) on predator biomass, predator catch, total primary production/ total respiration and system omnivory index, and a negative response (i.e. decreased) on primary production required for harvest. All variables showed a positive response (increased) to the presence of discards apart from predator biomass. Overall, the covariates or (variables) that explained the most variation in response were ecosystem type (continental shelf vs bay), stanza groups (age classes) and publication type (report vs journal). Results showed that the inclusion of age class structured data in ecosystem models is important in improving the model predictions where discards or by-catch is concerned. The composition of discards may partly explain the unexpected finding that predator biomass decreased in the presence of discards. The ecosystem type may influence the response to discards, with bays tending to show negative responses and thus more vulnerable to modification in the presence of discards.

Introduction

Discards form the main component of food subsidy for many groups of animals in marine ecosystems (Oro et al. 2013). The response of ecosystems to these discards is, however, variable (Oro et al. 2013). Variation in attributes including specific ecosystem, geographical location and composition of discards could contribute to the different ways (positive, negative or no response) that ecosystems have responded to the provision of additional food (Oro et al. 2013; Newsome et al. 2015). Discards may also benefit diverse species differently, offering them different amounts of food and may simultaneously benefit many trophic levels (Oro et al. 2013). Discards include fish and invertebrates returned to the sea and many of these are still alive, but vulnerable to predation after the shock and damage caused by nets and having stayed out of the water for some time (Hill and Wassenberg 1990; Castro et al. 2005).

Different ecosystem models simulating the effects of removing or banning discards have given unexpected or contrasting results (Gribble 2003; Walters et al. 2008; Heath et al. 2014). For example, in the ecosystem model of the North Sea, the landing of discards (as required by legislation) caused bottom-up ecological cascades that had negative effects on seabirds, marine mammals and seabed fauna but provided no benefit to fish stocks. In contrast, where fishing practices limited the capture of unwanted fish, the amount of discards were reduced, resulting in trophic cascades that could benefit seabirds, mammals and most fish stocks (Heath et al. 2014). In the Great Barrier Reef, the ecosystem model for the prawn fishery, indicated that the reduction of discards caused a decrease in the number of species that fed on discards such as seabirds, groupers and sharks, in addition to the targeted commercial prawn species which also fed on the discards (Gribble 2003).

For many ecosystem models, age-class structured data on key species are not available, yet such data may provide different and unexpected results on the effects of discards when included, at least based on simulations using dynamic models. For example, in the Gulf of Mexico, it was anticipated that reduction of by-catch from shrimp trawling would reduce the negative impacts that trawling had on the productivity of menhaden and red snapper (Walters et al. 2008). Surprisingly, results from modelling of the ecosystem that included multi-stanza representation (multiple age-classes) of juvenile groups, showed that reduction of shrimp trawling allowed the recovery of benthic predators (catfishes) of juveniles of menhaden and red snapper, which had been reduced by trawling (Walters et al. 2008). Trawling reduced the abundance of catfish, but reduction in trawling increased their abundance that led to increased predation on juveniles of menhaden and red snapper by catfish (Walters et al. 2008). Such effects would not have been detected without inclusion of the data on

age-classes. Age-class structured data or multi-stanzas groups represent different life stages of species (e.g. juveniles and adults) that have different diets (Christensen and Walters 2004).

While it has been documented that the release of discards may lead to the modification of marine ecosystems (Oro et al. 2013), for many ecosystems, it is not known how discards affect specific ecosystem functions such as production and respiration. Production and respiration are key processes that drive the ecosystem functions (Townsend et al. 2008). They are fundamental to energy flow and reflect ecosystem health (del Giorgio and Duarte 2002; Townsend et al. 2008). In addition, the variability in the effects of discards in different systems creates uncertainty in any broader understanding of how ecosystems respond to discards and, therefore, presents a challenge for decision making in management and policy (Hillebrand 2008). This apparent incoherence in findings may result in differences in the interpretation of results and evaluation of the importance of certain processes such as, nutrient cycling, fluxes of energy and production in ecosystems (Hillebrand 2008). It also makes it difficult to communicate important ecological findings to stakeholders and the general public (Hillebrand 2008). Given that the results of any one study cannot resolve broader issues or necessarily be applied elsewhere (Koricheva and Gurevitch. 2014), a quantitative synthesis that gives a summary of the findings of different studies becomes useful (Hillebrand 2008; Vetter et al. 2013). Here I analyse the findings from multiple studies on the effects of discards from fisheries on specific ecosystem functions (production, respiration and consumption). This is the first study that quantitatively summarises across studies, the effects of discards on these ecosystem functions.

I hypothesised that across a wide range of different systems, the presence of discards would cause positive responses in predator biomass, predator catch, total primary production/ total respiration and system omnivory index, but a negative response on primary production required to support the biomass of the catch (targeted species). This is because:

- (i) predators take advantage of discards enabling them to increase their biomass (Fondo et al. 2015), with a subsequent increase in the catch of those species;
- (ii) in the presence of discards, predators take prey from multiple trophic levels (Oro et al. 2013) so there is an increase in the total number of feeding pathways (Fondo et al. 2015) and this in turn may lead to an increase in the system omnivory index (a measure of the variance of trophic level of consumers' prey in the system Christensen and Pauly 1992);

- (iii) the presence of discards in the system will indirectly lead to an increase in both the total primary production and the ratio of total primary production: total respiration as nutrients are released from the breakdown of discards (Luong et al. 2015);
- (iv) due to predators being able to feed at lower trophic levels (the discards) than when there are no or fewer discards, the primary production required to sustain the harvest of the catch will be reduced (Luong et al. 2015).

The aim of this chapter was to highlight any trends in the effects of discards across different marine ecosystem types (e.g. coastal versus oceanic) and latitudes (tropical versus temperate) and explore the causes of any identified variation in the magnitude of the effects on core ecosystem parameters. I also examined whether inclusion of age-structured (multi-stanza groups; *sensu* Walters et al. 2008) modified the model predictions, making them more robust in relation to our understanding of the effects of by-catch/discards on structure and function of ecosystems.

Methodology

Data

Ecopath with Ecosim (EwE) models from 1984 to 2015 from the EcoBase database were searched to identify studies that met a set of criteria. I used EcoBase (http://ecobase.ecopath.org/) because it is a repository of EwE models (from journal publications, reports and theses), and was constructed to facilitate meta-analyses based on EwE models (Colléter et al. 2013a). In addition, these models have been validated (i.e. they have been reviewed by the 'Model Repository' working group of the Ecopath Research and Development Consortium, and by the models' authors based on metadata, model version, comments and open-access agreement - Colléter et al. 2013a). I also used EwE models because numerous models have been developed (Christensen et al. 2008; Colléter et al. 2015) and provide a good coverage of marine ecosystems of the planet. Since all models used were EwE models, it was possible to compare them, perform a global scale analyses, and quantify important ecological processes.

The PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses http://prismastatement.org/) flow diagram is a standard diagram used in meta-analyses to illustrate the procedure followed in the search and selection of studies (Koricheva and Gurevitch 2014). "*The PRISMA flow diagram is a requirement for publication of meta-analyses studies and is significant in providing transparent reporting of the complete procedure*" (http://prisma-statement.org/). The Prisma flow diagram showing the procedure used for selection of models included in the meta-analysis for this study is given in Figure 3.



Figure 3: PRISMA Flow diagram for the search process and selection of studies used in the meta-analysis

The criteria used for selection of studies were that the studies: 1) had models constructed using the Ecopath with Ecosim software; 2) focused on marine ecosystems and 3) in the models, "Discards" were included as one of the functional groups (as the key question is on discards, it was necessary to have the discards as one of the functional groups). Models without discards as an identified functional group were excluded. From a total of 174 validated models available in EcoBase, only 23 models met these criteria. The reference list of these models is given in Appendix 1.

For each of these 23 models, the functional group "Discards" and the discards data in the fishery, were removed from the original Ecopath models to give the results of the second set of models without discards. The diet matrices were adjusted to supplement for the loss of discards by allocating the differences to the available prey, and the models rebalanced using the ecological thermodynamic rules as detailed in Appendix 2. The detailed changes made to the diet matrices for the each of the models are given in Appendix 3.

The Ecopath models were also transposed (Colléter et al. 2013b) in EcoTroph which uses trophic spectra that give continuous biomass distribution as a function of continuous trophic levels (Gascuel et al 2011) and then simulated where the discards were included or excluded using the EcoTroph R plug-in (Colléter et al. 2013b). The EcoTroph plug-in was used to obtain biomass data instead of the data straight from Ecopath, because in EcoTroph the data are presented in terms of trophic levels as opposed to functional groups (Gascuel and Pauly 2009). In this way, biomass at specific trophic level could be identified. The results of the predator biomass and catch obtained from EcoTroph were then used for the meta-analysis. The detailed references of the publications used were entered in the metadata with references to the encoded EcoBase (Colléter et al. 2015). The models were summarised for the metadata describing: (i) the modelled ecosystems; (ii) the research objectives of the models; and (iii) the structure, scales and units of the models. The detailed metadata are given in Appendix 4.

To quantify the effects of discards on various response variables, I performed a meta-analysis using the R package metafor. I chose the log response ratio as the metric of effect size because it quantifies proportionate changes and gives useful summaries to address the study question. The log response ratio for six response variables were analysed using mixed-effects meta-regression. These variables- predator biomass, predator catch, total catch, total primary production/ total respiration (TPP/TR), system omnivory index (SOI) and primary production required for harvest (PPR harvest) were the ones that showed some differences between the models with and without the discards. In addition, these variables are continuous data that are appropriate to use for meta-analysis (Vetter et al. 2013). Some variables (mean transfer efficiency, primary production required for consumption, Finn's cycling index) were considered for inclusion as potentially informative response variables but were not included for analysis as they had many missing values and gave few data for analysis.

The response variables

Predator biomass – this is the biomass of predators which are at a trophic level equal to or greater than 3.5 (Gasche and Gascuel 2013). The predator biomass is predicted to increase with presence of discards, because they consume the discards or prey that feed on discards, resulting in an increase of their biomass (Oro et al. 2013).

Predator catch – this is the catch of the predators from the fisheries, and this is predicted to increase in the presence of discards; particularly if the predators form part of the discards or if the predators

benefit from the discards. Studies have shown that discards supplement secondary production (Groenewold and Fonds 2000).

Total primary production/total respiration- is a functional index of the system's relative maturity (Odum 1969). Systems with TPP/TR tending towards 1 are mature ecosystems; and this is expected to increase with presence of discards, as discards could be a source of perturbation in the system. Perturbed systems have TPP/TR values of more or less than 1 (Odum 1969).

System Omnivory Index (SOI)- The omnivory index measures the variance of trophic level of prey (Christensen and Pauly 1992). The dimensionless index ranges from 0.0 to 1.0. A value of 0.0 indicates that the consumer is highly specialised, and values approaching 1.0 indicate feeding on many trophic levels (Monaco and Ulanowicz 1997; Rybarczyk et al. 2003). A high SOI indicates the ecosystem has numerous paths in the food web (Christensen and Pauly 1992). Thus, the SOI is expected to be higher in the presence of discards, which benefit several trophic levels (Oro et al. 2013).

Primary production required for harvest of the catch (PPR harvest)– this is the proportion of the net primary production required to sustain the catches (Christensen et al 2008). It is thus an indicator of how well the system can sustain the fisheries (Pauly and Christensen 1995). This variable is expected to increase with the presence of discards as primary production benefits indirectly from the discards through nutrients released from breakdown of detritus (Luong et al. 2015); though it may depend with the depth of the model.

These response variables were categorised according to the following ecosystem functions: production, respiration and consumption as shown in Table 1.

Table 1: A description of the different response variables included in each category ofecosystem function (production, respiration and consumption), and their units.

PPR harvest = Primary Production Required for harvest; SOI = System Omnivory Index

Function category	Functions	Units
Production	Predator biomass	t/km ² /yr
	Predator catch	t/km ² /yr
	PPR harvest	%
Respiration	TPP/TR	
Consumption	SOI	

Meta-analysis statistical modelling approach

The summary or effect size measure for meta-analysis was log response ratio with and without discards for all 23 studies. I used the pedigree index of the study models for weighting of effect sizes and calculated the confidence intervals for each summary or effect size. The data had several continuous and categorised covariates or moderators. I followed the approach outlined in Gilman et al (2016) to identify the covariates to be used in the meta-analysis. The nine covariates or moderators that were considered in the meta-regression analysis were:

Area: Area (size) of the ecosystem studied. This ranged from 0.7 to 484.5 km².

Functional groups: The number of functional groups in the model. These ranged from 18 to 99 groups.

Stanza groups: Whether multi-stanza groups were included in the model or not.

Publication: The type of publication, these were categorised into either report (includes all technical reports and theses) or journal paper (published papers).

Latitude: Latitude location of the ecosystem modelled. The latitude zones were: tropicalsubtropical, temperate, and high latitude as described in Colléter et al (2015)

Study duration: Duration (number of years) covered in the model

Discard biomass: Biomass of discards in t/km²

Ecosystem type: Is the different types of ecosystems. For the purpose of meta-analysis, the ecosystem types were categorised into two: shelf as the continental shelf and includes ocean and reef areas; bay includes bays, estuaries, straits and channels

Fleet size: Number of fleet operating in the ecosystem

A total of 512 models were explored for every combination of the nine moderators. I used mixedeffects meta-regression models as outlined in Gilman et al (2016) to derive the weighted and unweighted response ratios and the results for the 23 studies were displayed in forest plots. Model selection was part of inference and covariates of importance were computed based on 2AICc of all models containing the predictor covariate. The predictor covariate with the largest predictor weight was the most important (Burnham 2015). Based on the models explored, only 2 models met the criterion (models within 2AICc) but 10 models accounted for 95% of evidence weight. Thus the level of significance was set at 80%. To distinguish publication bias from other causes, I performed the contour-enhanced meta-analysis and the results were presented as contour-enhanced funnel plots centred at 0 (Peters et al. 2008). As many meta-analysis studies use unweighted effect measures due to uncertainty resulting from the lack of data, I also performed the unweighted log response ratio to examine any differences in the results.

Results

The world map showing the locations of the studies included this study is given in Figure 4. Most of the studies are located in the northern hemisphere in temperate areas. The ecosystem types were either bay or shelf areas.



🛑 bay 🔵 shelf

longitude

Figure 4: World map showing the locations of the Ecopath studies included in the meta-analysis

Meta-regression models

The inverse-precision weight summary measures (log response ratio) for the 23 studies for predator biomass are summarised in the forest plot shown in Figure 5. The plots for the other response variables are in Appendix 5 a-e. The results of the meta-analysis were summarised and presented in Table 2. For each response variable, I specified the expected response to the presence of discards, i.e. whether the response will be positive, negative or no response in the presence of discards, as derived from the literature, hypothesised, or from the meta-analysis results of the weighted and unweighted approaches. For example, the expected response for predator biomass in the presence of discards is positive from published literature; positive from my prediction, negative for both the weighted and unweighted meta-analysis results (Table 2).

reducer biolinass			
Author(s) and Year		weight	LRR [95% CI]
Okey, 2007 Blanchard et al, 2002 Samb & Mendy, 2004 Fondo et al, 2015 Link et al, 2008a Trites et al, 1999 Galván, 2005 Lees & Mackinson, 2007 Link et al, 2008c Arreguin Sánchez et al, 2002 Pitcher, 2007 Tsagarakis et al, 2010 Field et al, 2006 Link et al, 2009 Okey, 2006 Lassalle et al, 2012 Ainsworth et al, 2002 Araújo et al, 2005 Link et al, 2008b Lobry, 2004 Watson et al, 2013 Bulman et al, 2011		5.13% 2.38% 4.15% 3.37% 4.40% 3.63% 3.30% 3.54% 4.15% 4.259% 4.40% 11.16% 2.74% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.27% 4.40% 3.72% 2.96% 3.16% 4.84%	$\begin{array}{c} -0.62 \left[-2.30 , 1.07 \right] \\ -0.58 \left[-3.05 , 1.90 \right] \\ -0.29 \left[-2.16 , 1.59 \right] \\ -0.15 \left[-2.23 , 1.92 \right] \\ -0.05 \left[-1.87 , 1.77 \right] \\ -0.05 \left[-2.05 , 1.95 \right] \\ -0.05 \left[-2.15 , 2.05 \right] \\ -0.03 \left[-2.06 , 2.00 \right] \\ -0.02 \left[-1.90 , 1.85 \right] \\ -0.02 \left[-2.39 , 2.35 \right] \\ -0.01 \left[-1.83 , 1.81 \right] \\ -0.01 \left[-1.15 , 1.14 \right] \\ -0.01 \left[-2.31 , 2.30 \right] \\ 0.00 \left[-1.85 , 1.84 \right] \\ 0.00 \left[-1.85 , 1.87 \right] \\ 0.00 \left[-1.87 , 1.87 \right] \\ 0.00 \left[-1.82 , 1.82 \right] \\ 0.00 \left[-1.98 , 1.98 \right] \\ 0.00 \left[-2.22 , 2.22 \right] \\ 0.15 \left[-2.00 , 2.30 \right] \\ 0.27 \left[-1.46 , 2.01 \right] \\ \end{array}$
RE Model	+	100.00%	-0.05 [-0.44 , 0.33]
-4.0	00 -1.00 2.0	0	
	Log Ratio of Mear	IS	

Predator biomage

Figure 5: Random-effects forest plot of weighted summary measure of log response ratio (for Predator biomass) with/without discards for the 23 studies (references are in Appendix 1).

LRR = log response ratio; CI - confidence interval; RE - random effects; solid squares represent relative weighting of LRR.

 Table 2: Summarised results of the response variables with predicted and estimated results and the difference between them.

Parameter	Predicted	Му	Estimate	Estimate	Difference
	(literature)	prediction	(weighted)	(unweighted)	
Predator	+/- /0 1,2,3,4	+	-	-	different
biomass					
Predator catch	+ 7	+	+	+	same
PPR harvest	- 5,6,8	-	+	+	different
TPP/TR	+/- 5,?	+	+	+	same
SOI	+/- 5,?	+	+	+	same

+ = positive response, - = negative response, 0 = no response, ? = unknown

1 Heath et al. (2014); 2 Beddington (1984); 3 Hill and Wassenberg (1990); 4 Christensen (1996); 5 Arreguín-Sánchez et al. (2002); 6 Pauly and Christensen (1995); 7 Zhou (2008); 8 Crowder and Murawski (1998)

The responses for weighted analysis

Predator biomass

The average predator biomass response was negative. Thirteen out of the 23 studies showed a negative response, eight studies had no response and only two showed a positive response (Figure 5). Two studies weighted higher than the others these were the studies by Tsagarakis et al. 2010 (11 %) and Lassalle et al, 2012 (10 %) (Figure 5). The ecosystem type, stanza groups and publication type gave a higher contribution to the model fits than the other variables (Figure 6).

Predator catch

Overall, predator catch showed a positive response, i.e. predator catch increased in the presence of food subsidies. Only one study had a negative response and three studies had no response (see forest plot in Appendix 5b). Two studies weighted higher than the others; the studies by Tsagarakis et al. (2010) (12 %) and Lassalle et al. (2012) (11 %) (see weighted forest plot in Appendix 5b). The ecosystem type, functional groups, discards biomass, stanza groups and publication had higher contribution in the model fits than the other variables (see averaged importance terms in Appendix 5b).

Primary Production Required for harvest (PPR harvest)

The PPR harvest showed a positive response in the presence of food subsidies (see forest plots in Appendix 5c). Two studies weighted higher compared with the rest, these are the studies by Tsagarakis et al. (2010) and Lassalle et al. (2012) (see weighted forest plot in Appendix 5c). Generally, the importance of the covariates was not significant (below 80%) but, stanza groups, ecosystem type and publication type contributed the most to the model fits (see averaged importance terms in Appendix 5c).



Model-averaged importance of terms

Figure 6: Covariate contributions to model fitting in the meta-analysis.

Total Primary Production/ Total Respiration (TPP/TR)

For TPP/TR, eleven studies showed a positive response, eight studies had no response while two studies had a negative response (see forest plots in Appendix 5d). On average, TPP/TR increased in the presence of food subsidies. Only three variables showed a greater importance and contributed to the model fit; these were stanza groups, ecosystem type and publication type (see averaged importance terms in Appendix 5d). Only one study weighted higher (13 %) than the others; this is the study by Tsagarakis et al. (2010) (see weighted forest plot in Appendix 5d).

System Omnivory Index (SOI)

The SOI in sixteen studies had a positive response, three had no response and four had negative responses (see forest plots in Appendix 5e). Overall SOI increased in the presence of food subsidies. Two studies weighted higher than the others; studies by Tsagarakis et al (2010) (11 %) and Lassalle et al (2012) (10 %) (see weighted forest plot in Appendix 5e). The stanza groups, ecosystem type and publication gave higher contribution in the REM than the other variables (see averaged importance terms in Appendix 5e).

Unweighted analysis

The unweighted analysis gave similar results to those of the weighted analysis, even though I had to reduce the covariates to four, in the multi-level meta-regression model analysis as the models did not converge due to few data (see Appendix 7 a-e for forest plots). Overall, the explanatory covariates that gave more contribution in most of the response variables were ecosystem type and publication type.

Meta-analysis publication bias

Any publication bias was accounted for by including the publication factor in the models. There was no evidence of publication bias as the various funnel plots for the response variables showed that neither citation author nor citation year was a moderator that contributed to any of the best-fitting models (Figure 7).



Figure 7: Funnel plot analysing for publication bias (PPR harvest)

Meta-analysis examining covariates and interaction terms

Presented in Figures 8 - 10, is an effect display for the unweighted random intercepts fitted to the responses (in this case for PPR harvest) for the different informative covariates. The other displays for the rest of the response variables are given in Appendix 8 a-e. I included a two way interaction term for Area X ecosystem type and ecosystem type X Stanzas effects. Of the nine informative covariates, stanza groups, ecosystem type and publication contributed the most to the GLMM model fit for all of the response variables. There were minimal effects from latitude for all the response variables. Publication effects showed that responses were positive (mean = 0.5) for journals but negative (mean = -0.5) for reports, for PPR harvest and TPP/TR (Fig 6b and Appendix 8d), while the responses were minimal for predator biomass, predator catch and SOI (Appendix 8a, 8b and 8e). Functional group and pedigree effects were minimal for all response variables. Overall, in the two way interaction ecosystem type X stanzas effects, bays had mostly negative responses while shelf areas had positive responses. To find an explanation for this response, I examined the functional groups of the shelf and bay studies. Shelf studies had higher biomass of macrobenthos groups than the bay studies (Tables 3 and 4).



Figure 8: Effect display for random-intercepts fitted to log response ratios (PPR harvest) for informative covariates

Plot (a) area effect and (b) publication. Solid dot = estimated parameter mean, vertical bar = 95% confidence interval around the mean.



Figure 9: Effect display for random-intercepts fitted to log response ratios (PPR harvest) for informative covariates.

Plot (a) functional groups effect and (b) pedigree effect. Shaded polygon = 95% confidence region around line.



Figure 10: Effect display for random-intercepts fitted to log response ratios (PPR harvest) for informative covariates.

Plot (a) area effect, (b) interaction between ecosystem type and stanzas in multipanel display. Solid dot = estimated parameter mean, vertical bar = 95% confidence interval around the mean.

Table 3: Functional groups with the highest biomass in models of shelf studies (References in

Appendix 1)

Citation author	Groups with highest biomass	
Blanchard et al. 2002	Phytoplankton, infauna, epifauna, macrobenthos, zooplankton	
Bulman et al. 2006	Mesopelagic fish, zooplankton	
Field et al. 2006	Phytoplankton, euphausiids, hake, forage fish	
Galván 2005	Phytoplankton, sardines, zooplankton, rays	
Jones et al. 2011	Grass, phytoplankton, benthos, small reef fish, herbivores	
Lassalle et al. 2012	Phytoplankton, zooplankton, demersal fish, horse mackerel	
Lees and Mackinson 2007	Seaweed, mesobenthos, infauna	
Link et al. 2008a	Macrobenthos, phytoplankton	
Link et al. 2008c	Macrobenthos, phytoplankton, small pelagics	
Link et al. 2009	Macrobenthos, small pelagics, copepods	
Link et al. 2008b	Macrobenthos, copepods	
Pitcher 2007	Macro algae, infaunal invertebrates, juvenile reef fish, sessile filter feeders	
Samb and Mendy 2004	Macrobenthos, phytoplankton	
Trites et al. 1999	Herbivorous zooplankton, infauna, pollock	
Tsagarakis et al. 2010	Benthic invertebrates, polychaetes	
Watson et al. 2013	Phytoplankton, zooplankton, macro algae	

 Table 4: Functional groups with the highest biomass in models of bay studies (References in Appendix 1)

Citation author	Groups with highest biomass
Ainsworth et al. 2002	Infauna, phytoplankton, forage fish, euphausiids
Araújo et al. 2005	Primary producers, bivalves, deposit feeders
Arregun Sánchez et al. 2002	Phytoplankton, zooplankton, clupeids
Fondo et al. 2015	Macro algae
Lobry 2004	Macrobenthos, copepods, mysid
Okey 2007	Bivalves, gastropods
Okey 2006	Bivalves, worms

Noteworthy, from the two way interaction ecosystem type X stanzas effects are the contrasting responses. For example, PPR harvest (Fig 6f), the ecosystem type X stanza effects overall showed a negative response (means = - 1.7 for bay and - 0.8 for shelf) in studies with no stanza groups; but the responses were positive (means = 1.2 for bay and 1.0 for shelf) for studies with stanza groups. Predator biomass, also showed some slightly different results, with positive responses for both bay and shelf for the studies with no stanzas; while negative response for bay and positive for shelf for studies with stanza included. This shows the difference multi-stanza groups can make in the results as it was demonstrated in the study by Walters et al. (2008). It has also been pointed out in Heymans et al. (2016) that multi-stanza groups are key when considering the sustainability of fisheries. For this reason, I recommend inclusion of multi-stanzas in the Ecosath with Ecosim models. This will refine the predictions of the models.

Discussion

The results showed that, overall, key ecosystem functions (production, respiration and consumption) increased in the presence of food subsidies. The predator biomass, however, decreased in the presence

of food subsidies, contrary to most theory (Oro et al. 2013, Newsome et al. 2014) and my predictions that predator biomass would increase in the presence of food subsidies as predators benefit from food subsidies. In trying to find an explanation for this, I examined the discards composition from some of the studies: the two extremes, a positive response (for Jones 2011 and Bulman 2006) and a negative response (for Okey 2007 and Blanchard 2002), as well as for two that had no response (Watson et al. 2013 and Link 2009) (see Appendix 6). The positive responses had a wide range of discards, spread out across different trophic levels, while for the negatives, discards are limited to more specific groups at specific trophic levels. The ones with no response were also wide spread but limited to mid trophic levels. Given the widespread of discards over the trophic levels in the positive responses, predators may have a wide range to choose from, leading to their increased biomass. In the limited situation, predators have limited choice and may have to compete for the food subsidies, leading to a decreased biomass. Thus, the results that a decrease in the presence of discards is possible as most of the studies gave negative responses (i.e. decreased in the presence of discards) where predators had limited food supply and increased competition.

Predator catch increased in the presence of food subsidies due to the increased predator biomass, as predators may benefit from discards (Oro et al 2013). These predators may include mostly pelagic fishes which are part of the fisheries; but would exclude top predators such as dolphins and seabirds that form part of incidental catches. Sharks are also excluded as they have been overfished (Worm et al 2013). The PPR harvest increased in the presence of food subsidies as expected from my predictions. This may be because the catch comprises predators that benefit from food subsidies, thus, 1) reducing the primary production required to support their prey and 2) unutilised food subsidies go into the detritus pool which is converted by bacteria into nutrients which are taken up by the primary producers (Crowder and Murawski 1998).

The TPP/TR increase in the presence of food subsidies may be explained as follows: As the primary production increased (due to nutrients from detritus as explained above) and respiration decreased due to removal of living groups through the discards and the catch itself, the TPP/TR increased. However, literature to support these predictions and findings are scarce, as studies on changes in TPP/TR have not been done yet. The SOI increased in the presence of food subsidies as predators consume the discards or prey that benefit from the discards. Discards increase the feeding pathways for predators so

the system becomes more weblike, increasing the SOI (Christensen and Pauly 1992); although this may depend on the number of predators feeding on discards.

The two studies (Tsagarakis et al. 2010 and Lassalle et al., 2012) that weighted higher compared with the others are the ones that had the lowest confidence intervals. These studies with a low CI reflect a better and a tighter possible range than the other studies i.e. these studies have more "power" to detect the intended covariate (Attia, 2005). The 'publication' covariate (report vs journal) was among the ones that contributed most variation in the responses. This may be due to the discard biomass ranges of the two categories. The discards biomass range for journals was higher ($0.006 - 43.5 \text{ t/km}^2$) than for reports ($0 - 10.11 \text{ t/km}^2$) (see Appendix 4).

Overall, the predator biomass decreased in the presence of discards, however, predator biomass increased in the presence of discards mostly in the shelf areas (oceans and reef areas) than in bay areas (channels, straits, embayment, estuaries and lagoons). When predator biomass increases, predation pressure on lower trophic levels may increase and modify other ecosystem functions e.g. consumption (Polis et al. 1996). The effects of discards on the specific ecosystem functions (production, respiration and consumption), which to date have not been quantitatively summarised across studies, showed an overall increase. Thus discards may be important in enhancing ecosystem functions. However, it may be necessary to consider discards composition and their impacts on the different ecosystem compartments, especially for top predators which might be impacted when fishing mortality is higher.

Overall in the two way interaction between ecosystem type and stanzas effects, bays had mostly negative responses on the covariates to models with no stanzas; while shelf areas had positive responses on the covariates to models with no stanzas. Examination of functional groups in the shelf and bay studies showed that shelf studies have greater biomass of macrobenthos groups than the bay studies. Macrobenthos may benefit from discards in two ways: directly by feeding on discards and indirectly by feeding on detritus which may be from unconsumed discards (Groenewold and Fonds 2000). Covariates showing negative responses in the presence of discards in Bays, may indicate that bays are more susceptible to changes and thus more likely to modification in the presence of discards. This is because Bay areas are shallower and smaller in area compared to shelves (see Appendix 4), thus discards in Bay areas may have restricted distribution compared with shelves areas where the distribution may be widespread. Discards form a source of energy that is suddenly put into the

ecosystem (Sarda et al 2015) and can be a source of disturbance, influencing the ecosystem dynamics (Okey et al 2007).

The contrasting results from the two way interaction between ecosystem type and stanzas effects shows the difference multi-stanza groups can make in the results thus supporting the study by Walters et al. (2008). It has also been pointed out in Heymans et al. (2016) that multi-stanza groups are key when considering the sustainability of fisheries. For this reason, I recommend inclusion of multi-stanzas in the Ecopath with Ecosim models. This will refine the predictions of the models.

Limitations

1. The low number of models did not allow a lot of manipulations to test for different combinations of the variables.

2. The analysis was based only on separate univariate models for each response variable, but this could be further combined into a multi-model but I lacked the covariates required to do so.

3. The models could further be run with the Monte Carlo procedure (up to 1000 runs) to sample and get variances which could be then used for the meta-analysis.

4. The analysis was done only for Ecopath models, the dynamic Ecosim models with simulations of removal of discards could have given interesting or different results. The Ecosim models were not reviewed because they are not available in Ecobase and due to time limitation, I could not proceed with the procedure of acquiring the data for simulation from authors.

Gaps

The issue of discards has gained attention lately and policies have been put in place to reduce or eliminate them (for example, in the Common Fisheries Policy of the European Union, Sardà et al. 2015). In many ecosystem models however, discards have not been included as part of the functional group to account for the changes that they may have on the ecosystems. Inclusion of discards is essential to insert in a valid robust ecosystem model.

In Ecopath models, it is important to ascribe a level of uncertainty in the pedigree based on the origin of the data (Christensen and Walters 2004, Morissette 2007). This is required for setting confidence intervals with the data used in the Monte-Carlo procedure (Morissette 2007). The pedigree index for most of the models I used in the meta-analysis, had to be sourced as these were not presented in the original models. The pedigree index was used for weighting the models. Even though pedigree is important in assessing the reliability of the models and can be derived from the EwE software, many models do not enter the required input variables for deriving the pedigree output from the model (Morissette 2005; Colléter et al. 2015). Most of the models usually have low pedigree values because of lack of accurate data (Morissette 2005). This is a gap that has been identified, and future ecosystem modellers are encouraged to ascribe the input variables for deriving the pedigree output from the models. The pedigree index is also useful for comparison of the models, meta-analysis, and statistical analysis. A suite of other recently developed techniques to account for model uncertainty that are also available in the EwE software have been recommended in Heymans et al. 2016.

Conclusions

This study provides supportive evidence for the inclusion of age structured data (stanzas) in ecosystem models and shows that inclusion of this data is important in improving the precision of ecosystem models, particularly where discards or by-catch is concerned. Discards play an important role in modifying ecosystems, but responses are variable and in some cases unexpected, as in the case of predator biomass which showed a negative response to presence of food subsidies contrary to my predictions and to most literature. Overall, the meta-analysis results showed that the ecosystem functions - production, respiration and consumption responded positively to the presence of discards. The ecosystem type may also influence the way in which the ecosystem functions respond in the presence of discards. Given these findings there are implications for management and future research of discards or by-catch and fisheries managers are encouraged to record data on discards (amounts and composition) for effective monitoring of the short, medium and long term effects of discards by researchers.

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Chapter 3

Methodology

Introduction

Ecosystem modelling is used widely as a tool to address management questions. In this thesis, I used Ecopath with Ecosim to explore current global management issues in marine ecosystems i.e. problems of discards, overfishing of predators and jellyfish blooms.

In Chapters 4, 5 and 6, I used Moreton Bay, in SE Queensland (Australia) as my model ecosystem to address these issues. In this chapter, I provide an introduction to the physical setting of Moreton Bay and present the Moreton Bay Ecopath model used as the baseline model in these chapters. The information in the current chapter will be referred to throughout the remainder of the thesis, to avoid unnecessary duplication of information in the individual chapters.

Study area

Moreton Bay is located in south east Queensland, Australia between 27°01'S - 27°50'S and 153°19'E-153°25'E (Figure 11). This wedge-shaped Bay has a surface area of 1,845 km², an average depth of 6.25 m and is bordered by four sand islands Bribie, Moreton, and North and South Stradbroke Islands (Brand-Gardner et al 1999; Eyre and McKee 2002). The Bay has several rivers running into it, including the Brisbane, Pine and Logan Rivers, and saltwater inputs from the Coral Sea (Pollock 1982; Eyre and McKee 2002). Habitats in the Bay include mangroves, extensive seagrass beds, sand and mud banks, and deeper coastal waters (Brand-Gardner et al. 1999; Manson et al. 2003; Skilleter et al. 2007). Coral reefs are found in the Green and Peel Islands, Myora and Flinders Reefs (north of Moreton Island) and Flat and Boat Rock (Chilvers et al. 2005). The wetlands surrounding the Bay are protected under the United Nations Convention on Wetlands of International Importance as Ramsar Site No. 4, and covers 110 000 ha of intertidal mudflats, marshes, sand-flats and mangroves (Chan and Dening 2007). The Moreton Bay Marine Park covering 3400 km², was established in 1993 (NPRSR 2015). In 1997, the initial Marine park zoning was implemented and in 2007 a review resulted in an increase in the no-take zone from 5% to 16% (NPRSR 2015).



Figure 11: Map of Moreton Bay in south east Queensland, Australia (adopted from Ross et al 2015)

Functional groups for use in the Model

"A total of eighteen functional groups were selected to represent the Moreton Bay ecosystem, including: seagrass, macroalgae, phytoplankton, discards, detritus, dugongs, green turtles, zooplankton, jellyfish, prawns, macrobenthos, sand crabs, omnivores, demersal fish, pelagic fish, sharks, dolphins and seabirds (see Appendix 9). The primary producers represented by phytoplankton,

macroalgae and seagrass, form an important part of the trophic structure. Detritus and the discards form the component of excreta and dead biomass. Zooplankton, dugongs and green turtles represent the primary consumers. Dugongs and turtles play a key role in structuring the seagrass and algal abundance and affect the distribution and biomass of benthic macrofauna in Moreton Bay via their feeding (Chaloupka et al. 2004; Skilleter et al. 2007). Jellyfish are included as they can respond to changes in environmental conditions by forming blooms (Pitt and Purcell 2009). The jellyfish in the Bay are represented by Catostylus mosaicus (Carr and Pitt 2008). Macrobenthos represent consumers that are important in bioturbation and feed on the remains of discards and detritus (Brenchley 1982). Prawns, sand crabs and fish form an important component of Bay fisheries (DAFF 2014). Sharks, seabirds and dolphins represent the top predators in the system. The fisheries were represented by commercial catches (landings) through five fleets: beam and otter trawling (targeting prawns), lines (targeting fish), nets (targeting fish) and pots (targeting crabs) (DAFF 2014)" (Fondo et al 2015).

Modelling

"To model the structure and interactions of Moreton Bay ecosystem, I constructed a mass balance model in Ecopath with Ecosim (version 6.4.3). Ecopath trophic models describe the static state of energy flows in a food web and are based upon the model of Polovina (1984). Ecopath with Ecosim models represent complex food web interactions where each functional group of the web may be a species, a group of species or a detritus group (Christensen and Pauly 1992; Walters et al 1997; Christensen and Walters 2004)" (Fondo et al 2015).

"The Ecopath master equation defines the mass-balance between consumption, production, and net system exports over a given time period for each functional group (i) in an ecosystem as follows:

Production = Predation+ Fishery catches + Biomass accumulation + Net migration + other Mortality

 $Bi^*(P/Bi) EE = Yi + \sum Bj (Q/B)j *DCj$

where Bi and B j are biomasses (the latter pertaining to j, the consumers of i); P/Bi is the ratio of production to biomass, equivalent to total mortality; EEi is the ecotrophic efficiency which is the fraction of production that is consumed within, or caught from the system (by definition between 0 and

1); Y i is equal to the fisheries catch (i.e., Y = FB); Q/B j is the food consumption per unit of biomass of j; and DCji C is the contribution of (i) to the diet of (j), and the sum is overall predators (j). Biomass accumulation and migration can also be added to the right hand side of the equation. Each model can deal with an unknown parameter (B or EE; P/B or Q/B) that can be estimated by the model, if no data is available.

The basics of Ecosim consist of biomass dynamics expressed through a series of coupled differential equations. The equations are derived from the Ecopath master equation and is as follows:

 $dBi/dt = gi \sum Qji - \sum Qij + Ii - (M0i + Fi + ei)Bi$

where dBi/dt represents the growth rate during the time interval dt of group (i) in terms of its biomass, Bi, gi is the net growth efficiency (production/consumption ratio), M0i the non-predation ('other') natural mortality rate, Fi is fishing mortality rate, ei is emigration rate, Ii is immigration rate, (and ei·Bi-Ii is the net migration rate). The two summations estimates consumption rates, the first expressing the total consumption by group (i), and the second the predation by all predators on the same group (i). The consumption rates, Qji, are calculated based on the 'foraging arena' concept, where Bi's are divided into vulnerable and invulnerable components." (Christensen et al. 2008)

"The input parameters - Biomass (B), Production to Biomass ratio (P/B), Consumption to Biomass ratio (Q/B) and Ecotrophic Efficiency (EE) (see Table 5), were derived from relevant literature and reports on studies done in Moreton Bay, databases and other Ecopath models of similar ecosystems or estimated by the model. I constructed a diet matrix (Table 6) that gives the proportions of food items for each functional group. The input parameters were entered into the Ecopath software to give the outputs: the trophic structure and interactions between the groups" (Fondo et al 2015). I used the ecological thermodynamics laws to balance the Ecopath model following Darwall et al. (2010) and Heymans et al. (2016) (details in Appendix 2). The balanced model was used in Ecosim where time series data were fitted.

"In the dynamic Ecosim model, I used fisheries catch data from the QFish database available at the Queensland Government, Department of Agriculture and Fisheries (<u>http://qfish.daff.qld.gov.au/</u>) to

drive and calibrate the model (Appendix 12 gives the catch data). I calibrated the model using the baseline model alone and then included fishing, with various vulnerabilities and forcing functions on primary producers (see details in Appendix 11), to select the best fit for the data. I did a sensitivity analysis of the model using the Monte Carlo routine and examined the model results with differing CVs (100 trials each) for the input parameters. The biomass estimates resulting from the Monte Carlo simulations are given in Appendix 14. The resulting biomass ranges were wide with increasing CV for the functional groups but followed the general patterns found in the model" (Fondo et al 2015).

The Ecosim model fitted the 24 years of catch data well for omnivores (Pearsons correlation r=0.049; p>0.05) and sand crabs (r=0.189; p>0.05) (Figure 12) with no significant variation between the observations and the model predictions. However, there were significant differences between the observed landings and the Ecosim model predictions for sharks (r= 0.481; p<0.05), pelagic fish (r=0.650; p<0.05), demersal fish (r=0.498; p<0.05) and prawns (r=0.400; p = 0.05).

Table 5: Basic parameter estimates for Moreton Bay ecosystem model

(Values in italics were estimated by the model) TL= Trophic level; B= Biomass; P/B= Production/Biomass ratio; Q/B= Consumption/Biomass ratio; EE= Ecotrophic efficiency; P/Q= Production/Consumption ratio

	Group name	TL	В	B P/B		EE	P/Q
			(t/km²)	(/year)	(/year)		
1	Seabirds	3.790	0.005	0.050	0.183	0.196	0.274
2	Dolphins	3.960	0.092	0.013	0.045	0.000	0.300
3	Sharks	4.260	0.037	0.225	1.000	0.253	0.225
4	Pelagic fish	3.500	0.430	0.400	1.400	0.343	0.286
5	Demersal fish	3.440	0.390	0.400	1.369	0.955	0.292
6	Omnivores	2.750	0.200	0.350	1.396	0.958	0.251
7	Dugongs	2.000	0.008	0.009	0.030	0.000	0.295
8	Turtles	2.000	0.007	0.020	0.080	0.786	0.250
9	Sand crabs	2.900	0.600	0.700	2.400	0.495	0.292
10	Prawns	2.120	0.700	1.972	7.500	0.368	0.263
11	Jellyfish	3.110	1.075	0.090	0.400	0.697	0.225
12	Macrobenthos	2.450	0.800	1.800	6.000	0.576	0.300
13	Zooplankton	2.110	6.420	8.480	30.000	0.420	0.283
14	Seagrass	1.000	16.000	25.550	0.000	0.001	
15	Macroalgae	1.000	25.910	20.000	0.000	0.001	
16	Phytoplankton	1.000	11.300	28.000	0.000	0.549	
17	Discards	1.000	2.000			0.960	
18	Detritus	1.000	3.836			0.006	

Table 6: Diet matrix for the Moreton Bay model

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1	Seabirds													
2	Dolphins													
3	Sharks													
4	Pelagic fish	0.508	0.630	0.562	0.040		0.002							
5	Demersal fish			0.246	0.121	0.089	0.016							
6	Omnivores	0.300	0.220				0.045							
7	Dugongs													
8	Turtles													
9	Sand crabs			0.080	0.100	0.230								
10	Prawns			0.092		0.381	0.022			0.140				
11	Jellyfish				0.112									
12	Macrobenthos				0.005	0.249	0.338			0.360			0.005	
13	Zooplankton				0.600		0.105			0.200	0.105	1.000	0.400	0.100
14	Seagrass						0.100	0.800	0.427				0.100	
15	Macroalgae				0.015		0.216	0.200	0.373				0.100	
16	Phytoplankton						0.040						0.095	0.900
17	Discards	0.192	0.150	0.020	0.007	0.001				0.018			0.010	
18	Detritus					0.050	0.116			0.282	0.745		0.290	
19	Import								0.200		0.150			
20	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



Figure 12: Ecosim fits of the Moreton Bay ecosystem model to catch data for six functional groups between 1990 and 2013. The solid lines represent the biomasses estimated by the model and the green triangles are the observed catch data.

Limitations

There were some limitations to the Moreton Bay model. Some functional groups e.g. pelagic fish were grouped together because of lack of detailed information, this may have concealed significant species interactions. Changes in diet due to seasons or growth were also not addressed. The data used for parameterization was limited because temporal data on biomass and diet for the study site was lacking. A better parameterization will be necessary in the future as the required data become available. Despite these limitations, EwE is a useful ecosystem modelling method for evaluating the Moreton Bay ecosystem as it can classify data-poor systems and incorporate relevant functional groups and fishing activities.

In future it would be necessary to do the following procedure to improve the current model:

- PREBAL diagnostics on the Ecopath model PREBAL shows where the ecological boundaries
 of the species in the model are (Link 2010). This diagnostic will identify the input parameters
 (biomass, production/biomass ratio and consumption/biomass ratio) that are under- or overestimated; and re-parameterisation may be required for the groups that have been under- or
 over-estimated to improve model predictions (Heymans et al. 2016).
- 2. Fitting of time series data- In Ecosim, the time series data is then fitted to the balanced model with adjusted input parameters. It is expected that the model predictions will improve especially for the groups (sharks, pelagic fish, demersal fish and prawns) that showed significant differences between the observed landings and the Ecosim model predictions.
- 3. Simulation of the scenarios with the best fitted model.
- 4. Monte Carlo routine on the scenarios for sensitivity analysis. The Monte Carlo modelling gives outputs related to the uncertainty around the input data (Heymans et al. 2016). A hundred Monte Carlo runs based on different coefficient of variations (CV) of 0.1, 0.2, 0.3, 04 and 0.5 around the input parameters for biomass, P/B, Q/B and EE is recommended.

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Chapter 4

"Banning fisheries discards abruptly has a negative impact on the population dynamics of charismatic marine megafauna"(Fondo et al. 2015)

Preface

This chapter is taken from a peer reviewed paper by the candidate, Milani Chaloupka, Johanna Greg Skilleter which published in PLoS ONE Heymans and was (http://dx.doi.org/10.1371/journal.pone.0144543). It explores the effects of gradual removal and a ban on food subsidies in marine ecosystems. The study was featured in the media, in the UQ news (https://www.uq.edu.au/news/article/2016/03/sudden-ban-fish-throwbacks-could-harm-ecosystemsresearchers) and in the European Commission's Science for Environment Policy Newsletter (http://ec.europa.eu/environment/integration/research/newsalert/pdf/immediate_ban_fisheries_disca rds destabilise marine ecosystems 449na1 en.pdf).

"Abstract

"Food subsidies (easily accessible and abundant food resources not usually available to organisms) have the potential to modify ecosystems and affect the provision of goods and services. Predictable Anthropogenic Food Subsidies (PAFS) modify ecosystems by altering ecological processes and food webs. The global concern over the effects of PAFS in ecosystems has led to development of environmental policies aimed at curbing the production or ultimately banning of PAFS. However, the effects of reducing or banning PAFS are not known. I explored the consequences of PAFS removal in a marine ecosystem under two scenarios: 1) gradual reduction, or 2) an abrupt ban, using a mass balance model to test these hypotheses – The reduction or loss of PAFS will: i) modify trophic levels and food webs through effects on foraging by opportunistic species, ii) increase the resilience of opportunistic species to food shortages, and iii) modify predator–prey interactions through shifts in prey consumption. I found that PAFS lower the trophic levels of opportunistic scavengers and increase their food pathways. Scavengers are able to switch prey when PAFS are reduced gradually but they decline when PAFS are abruptly banned. PAFS reduction to a certain minimal level causes a drop in the ecosystem's stability. I recommend

gradual reduction of PAFS to a minimal level that would maintain the ecosystem's stability and allow species exploiting PAFS to habituate to the food subsidy reduction" (Fondo et al, 2015).

Introduction

"Food subsidies usually present an easy ("ready-made") and abundant resource that is normally not accessible or available to organisms. Sources of food subsidies in ecosystems are varied and may be from human activities, for example carcasses discarded by game hunters that are fed on by scavengers (Oro et al. 2013, Mateo-Tomás et al. 2015), rubbish dumps that are fed on by various species of predators (dingoes, coyotes and red foxes) (Newsome et al. 2014); or from natural processes, such as allochthonous dissolved and particulate matter that subsidise lake ecosystems and benefit both benthic and pelagic communities (Bartels et al. 2012), marine carrion and detritus washed on shore providing a trophic base for terrestrial consumers (Polis et al. 1997), stranded kelp on beaches provides a food source for invertebrate shredders and juvenile fish (Robertson 1994). Food subsidies in natural ecosystems have the potential to modify ecosystem dynamics (Oro et al. 2013) causing the decline or the loss of essential goods and services, threatening the world's life support system (Oro et al. 2013)"(Fondo et al 2015).

"Predictable Anthropogenic Food Subsidies (PAFS) (Oro et al. 2013) modify ecosystems by altering consumer-resource relationships, simultaneously benefiting several different trophic levels and changing food web structure (Margalida and Colomer 2012, Oro et al. 2013, Newsome et al. 2014, Mateo-Tomás et al. 2015). PAFS have the capacity to influence directly individuals' fitness, population dynamics and community composition and interactions, resulting in substantial ecosystem modification, with effects pervading adjacent ecosystems (Polis et al. 1997, Oro et al. 2013, Newsome et al. 2014). In cases where natural food resources are scarce, PAFS may be necessary to supplement energy requirements of some endangered species such as European vultures (Margalida et al 2011, Margalida et al. 2013). Predictable supply of food subsidies makes it easier to access than natural prey (Bartumeus et al 2010, Cortés-Avizanda et al 2012). Predictability of food supply may influence, for example, a scavenger's foraging behaviour and distribution (in time and space), factors important in the survival of both the predator and prey. In cases of environmental stress, predictability plays an important role in the survival of the scavengers (Oro et al. 2013) and studies have shown the importance of PAFS in improving demographic parameters for the viability of some endangered species (Oro et al. 2008, Margalida et al. 2014). On the other hand, PAFS can have detrimental effects for example, negative densitydependant effects on fecundity of scavenger species (Carrete et al. 2006). In some cases,

scavengers may increase in number and become over-abundant, modifying ecosystems through changes in food webs (Oro et al. 2013). PAFS can also cause an ecological trap, where species face increased predation risk from opportunistic carnivores attracted to the feeding stations (Morris 2005). Finally, PAFS are considered to have potential as a powerful management tool in conservation and social issues (Oro et al. 2013), for example, where food is provided voluntarily to improve survival of endangered species, although there are risks associated with these animals then becoming dependent on these food sources (Votier et al. 2004)"(Fondo et al 2015).

"The potential impacts of PAFS on ecosystems globally has led to the development of new environmental policies aimed at curbing the production or, ultimately, banning of PAFS. However, some policy decisions can influence or even contradict biodiversity management and conservation efforts (Margalida et al. 2014). In Europe, for example, sanitary regulations have drastically reduced carrion available to vultures (Margalida and Colomer 2012). The effects of sanitary policies on the demographic parameters of long-lived species such as some endangered European vulture species, was evident during the outbreak of Bovine Spongiform Encephalopathy (BSE) (Donázar et al. 2009, Margalida et al. 2014). The vulture population declined due to food scarcity, with the situation worsening in Spain when the policy implementation coincided with the deployment of wind farms within the foraging range of the starved vultures (Martínez-Abraín et al. 2012)." (Fondo et al. 2015)

"In marine ecosystems, discards from fisheries represent a major source of PAFS with over 7 million tonnes of catch discarded annually world-wide (Kelleher 2005). The first comprehensive report on by-catch and discards in world fisheries was published in 1983 (Saila 1983). Historically, discards were acknowledged as a component of fisheries before the Common Era (Matthew 1994), but have only been recognized as a management problem since the beginning of the 20th Century (Alverson et al. 1994). Given this long history, the animals in many ecosystems have adapted to this super-abundant source of energy for multiple generations. The sudden removal of such an abundant food source has the potential for marked impacts on a broad range of organisms across the entire food web, including seabirds (Bicknell et al. 2013), dolphins (Chilvers and Corkeron 2001), sharks (Hill and Wassenberg 1990, Hill and Wassenberg 2000), amphipods, isopods, cephalopods, ophiuroids, fish (Bozzano and Sarda 2002, Svane et al. 2008), hermit crab, starfish, whelk and crabs (Wassenberg and Hill 1990, Ramsay 1996). Internationally, environmental policies are moving towards the banning of discards (e.g. the European Union (EU) Common Fisheries Policy proposed ban on discards, (Bicknell et al. 2013, Votier et al. 2013, Sardà et al. 2015) as part of the global push for greater environmental sustainability of fisheries (Bicknell et al. 2015).

2013, Sardà et al. 2015). The implementation of the discard ban in the EU might still lead to perverse incentives and changes in fishing practices that have not been anticipated and there might be some unknown consequences where the fisheries do not recover but scavengers still suffer from food reduction. However, it is not known how a sudden or even gradual reduction in the availability of PAFS would affect food webs that have long been exposed to the ready food sources. Reducing or banning PAFS could do more harm than benefit to an ecosystem through cascading effects in the food web. In the event of a ban, those species that were previously dependent on PAFS may revert to their original diet, causing a population crash in that prey from sudden increases in predation pressure. An understanding of the effects of reductions in PAFS will assist in making informed decisions on the management of PAFS and conservation of PAFS-dependant species and help to move fisheries to a more sustainable basis" (Fondo et al 2015).

"Even though studies on the impacts of PAFS in ecosystems have been done (Polis et al. 1997, Oro et al. 2013, Newsome et al 2015), very few studies have modelled the role of PAFS in marine ecosystems (Tamsett et al. 1999, Furness et al. 2007, Pichegru et al. 2007). Ecosystem modelling provides an approach to studying the effects of PAFS at very large spatial scales that incorporate natural processes like environmental variability and human activities such as fishing, agriculture etc. Through ecosystem modelling, it is possible to examine the effects of PAFS on ecosystem dynamics and improve our understanding of ecological roles of food and food webs in ecosystems" (Fondo et al 2015).

"In this Chapter, I explored the consequences of the removal of PAFS from a marine ecosystem under two scenarios, a gradual removal (over 20 years) compared with an abrupt ban on their release into the system. These two scenarios model real world situations where, first, legislation may be introduced to bring in bans on discards slowly over many years (e.g. green zones as part of Marine Park zonation (Day 2002) versus an immediate ban on the release of discards into a region (e.g. the European Union Common Fisheries Policy (Bicknell et al. 2013, Sardà et al. 2015). The following hypotheses were tested (after (Oro et al. 2013):

1) Reduction or loss of PAFS will modify trophic levels and food webs through effects on foraging by opportunistic species. Opportunistic species directly exploit PAFS and also consume species at lower trophic levels that also scavenge on PAFS.

2) Reduction or loss of PAFS will increase the resilience of opportunistic species to food shortages. In cases of food scarcity, PAFS can provide supplementary energy requirements of opportunistic species, thus making them resilient to food shortages. 3) Reduction or loss of PAFS will modify predator-prey interactions through shifts in prey consumption. Reduction of PAFS is expected to increase consumption of prey as food resources decrease" (Fondo 2015 et al).

Methods

"The study area was Moreton Bay (see Chapter 3). Prawn trawling is one of the fishing activities taking place in the Bay (Masel and Smallwood 2000). The prawn catch was estimated to be about 500 tonnes annually; with an average by-catch of 3000 tonnes, which is discarded (Wassenberg and Hill 1989). (The prawn catch reported over the last two decades is shown in Appendix 13, Fig. 1). The discards from prawn trawling in Moreton Bay comprise mainly crustaceans and fish (Wassenberg and Hill 1989) (Appendix 13, Table 1). Discards such as fish are eaten by seabirds and dolphins close to the surface, while the remainder is fed on by pelagic fish and sharks as it sinks down. The major demersal scavengers are sand crabs (family Portunidae) in addition to benthic invertebrates such as hermit crabs, other crustaceans, gastropods and polychaetes (Wassenberg and Hill 1989). The reduction in trawling effort due to the established marine protected area (MPA) in the Bay has potentially caused a reduction in discards. I took advantage of this large-scale natural experiment to conduct my study and took the opportunity to develop the first trophic mass balance model (in Ecopath with Ecosim) for the area as described in Chapter 3" (Fondo et al 2015).

"To determine the effects of discards on the ecosystem, I used 2 Ecopath models of Moreton Bay: one with and one without discards. The original MB model (MB 1) had discards as a functional group (Chapter 3); and I constructed another MB model (MB 2) that did not have discards as a functional group. I then examined the differences in the food web structure of the two models. The tables of input parameters and the diet matrices for the model without discards (MB 2) are given in Tables 7 and 8"(Fondo et al 2015).

"In Ecopath with Ecosim, the Finn's Cycling Index (FCI) is the fraction of an ecosystem's throughput that is recycled. This index, developed by Finn (1976), is expressed as a percentage, and quantifies one of Odum's 24 properties of system maturity (Odum 1969). The index also strongly correlates with resilience and stability (Vasconcellos et al. 1997). I used Finn's Cycling Index as an indicator of the ecosystem's stability (the ability to maintain structure and integrity). Cycling is considered to be an important indicator of an ecosystem's ability to maintain its structure and integrity through positive feedback (Monaco and Ulanowicz 1997), and is used as an

indicator of stress (Ulanowicz 1986) and systems maturity (Christensen 1995; Vasconcellos et al. 1997). An increase in the FCI would mean the system would recover faster from a perturbation, whereas a system would be expected to take longer to recover from disturbances (lower FCI) when it is in a more degraded state (Monaco and Ulanowicz 1997)"(Fondo et al 2015).

"Table 7: Basic parameter estimates for Moreton Bay ecosystem model without discards (MB 2) (Values in italics were estimated by the model) TL= Trophic level; B= Biomass; P/B= Production/Biomass ratio; Q/B= Consumption/Biomass ratio; EE= Ecotrophic efficiency; P/Q= Production/Consumption ratio" (Fondo et al 2015).

	Group name	TL	В	<i>P/B</i>	<i>Q/B</i>	EE	P/Q	
			(<i>t/km</i> ²)	(/year)	(/year)			
1	Seabirds	4.28	0.0051	0.05	0.183	0	0.274	
2	Dolphins	4.34	0.0918	0.013	0.045	0	0.3	
3	Sharks	4.32	0.0366	0.225	1	0.247	0.225	
4	Pelagic fish	3.51	0.43	0.4	1.4	0.352	0.286	
5	Demersal fish	3.44	0.39	0.4	1.369	0.920	0.292	
6	Omnivores	2.75	0.2	0.35	1.396	0.944	0.251	
7	Dugongs	2	0.00752	0.009	0.030	0	0.295	
8	Turtles	2	0.007	0.02	0.08	0	0.25	
9	Sand crabs	2.91	0.6	0.7	2.4	0.447	0.292	
10	Prawns	2.12	0.7	1.972	7.5	0.368	0.263	
11	Jellyfish	3.11	1.075	0.09	0.4	0.697	0.225	
12	Macrobenthos	2.45	0.8	1.8	6	0.544	0.3	
13	Zooplankton	2.11	6.42	8.48	30	0.42	0.283	
14	Seagrass	1	16	25.55	0	0.001		
15	Macroalgae	1	25.91	20	0	0.001		
16	Phytoplankton	1	11.3	28	0	0.549		
17	Detritus	1	3.836			0.006		

	Prey/	1	2	3	4	5	6	7	8	9	10	11	12	13
	predator													
1	Seabirds													
2	Dolphins													
3	Sharks													
4	Pelagic fish	0.7	0.78	0.582	0.04		0.002							
5	Demersal fish			0.246	0.121	0.089	0.016							
6	Omnivores	0.3	0.22				0.045							
7	Dugongs													
8	Turtles													
9	Sand crabs			0.08	0.1	0.23								
10	Prawns			0.092		0.381	0.022			0.14				
11	Jellyfish				0.112									
12	Macrobenthos				0.012	0.249	0.338			0.364			0.005	
13	Zooplankton				0.6		0.105			0.2	0.105	1	0.4	0.1
14	Seagrass						0.1	0.8	0.427	0.005			0.1	
15	Macroalgae				0.015		0.216	0.2	0.373	0.009			0.1	
16	Phytoplankton						0.04						0.095	0.9
17	Detritus					0.051	0.116			0.282	0.745		0.3	
18	Import								0.2		0.15			
19	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 8: Diet matrix for the Moreton Bay model without discards (MB2) Page 100 (MB2)

"I used the original MB model (MB 1) to explore the consequences of discard reduction and ban on the ecosystem, by simulating two scenarios. The two scenarios in the Ecosim model were: Scenario 1 (key run)- with gradual reduction of discards, which represents the changes that took place in Moreton Bay from 1990 to 2013 (with the changes in discards as shown in Appendix 13); and Scenario 2- ban discards, where the discards were stopped in 1990 by removing discards in the fishery from the model. To compare the changes in biomass of groups between the two scenarios I used the Mann-Whitney U test which is appropriate for non-normal data and robust for small sample sizes. Other hypotheses presented in (Oro et al. 2013)] were not addressed in this study due to limitations of the models and as they require more detailed data on changes in population density, growth rates, and community diversity, information that are mostly lacking for the Moreton Bay system. Another limitation was the absence of catch and effort data to prior 1990 or before the MPA establishment" (Fondo et al. 2015).

Results

Pathways and trophic levels

"In the Ecopath models of Moreton Bay, the number of pathways increased by 6%, 11% and 10% for seabirds, dolphins and sharks respectively, in the presence of discards (MB1) (Appendix 15, Table 1). In addition, the trophic levels of these groups dropped; with the trophic levels reduced by 10% for both seabirds and dolphins, and 1% for sharks" (Fondo et al. 2015).

Relative biomasses

"In dynamic Ecosim model, for both scenarios there was an overall increase in the relative biomass of most functional groups over the study period, except for seabirds and dolphins. Seabirds and dolphins are the first and major beneficiaries of discards (Wassenberg and Hill 1990) as shown in the diet matrix (Chapter 3, Table 6). In scenario 1 (where the discards were reduced gradually over time), the relative biomass of the major opportunistic species (seabirds and dolphins) was maintained, not declining drastically with the reduction of discards as expected. These species responded slowly to the reduction of PAFS (Figure 13). In contrast, their relative biomasses dropped (by 37 % for seabirds and 11 % for dolphins) in scenario 2 where there was an abrupt ban on PAFS (Figure 14). The Mann-Whitney U test showed a statistically significant change in the biomass of dolphins (Z=-3.918; p<0.05) and seabirds (Z= 4.248; p<0.05) between the two scenarios" (Fondo et al 2015).



Figure 13: Changes in relative biomass of some groups in Moreton Bay ecosystem model in Scenario 1 - gradual reduction of PAFS



Figure 14: Changes in relative biomass of some groups in Moreton Bay ecosystem model in Scenario 2ban on PAFS

Prey switching

"The major opportunistic species exhibited prey switching when the discards were gradually reduced (Scenario 1) from consuming discards to mainly eating lower level omnivores; but when PAFS are banned abruptly (Scenario 2), opportunistic species exert greater pressure on their natural prey. For example, seabirds change their diet to increase the proportion of lower level omnivores, with only a slight increase in the major prey pelagic fish in their diet, in response to the deficit resulting from the gradual reduction of discards (Figure 15). Dolphins also show a similar response to gradual reduction of discards (Figure 16). The Mann-Whitney U tests on the proportions of prey in the diets of seabirds and dolphins for the two scenarios were significantly different (Appendix 15, Table 2)" (Fondo et al 2015).



Figure 135: Changes in the proportions of the prey in the diet of seabirds from 1990 to 2013 (Solid lines = Scenario 1; dotted lines = Scenario 2)



Figure 146: Changes in the proportions of the prey in the diet of dolphins from 1990 to 2013 Solid lines – Scenario 1 and dotted lines- Scenario 2

FCI

"In both scenarios, the FCI dropped to zero. In scenario 1, the FCI increased gradually from 1992 to 2009 (to a maximum of 1.6) as the discards were being reduced, and then dropped to zero (Figure 17). In scenario 2, the FCI dropped immediately after the ban, reaching zero in 1992 (Figure 17). The Mann-Whitney U test showed a statistically significant difference between the FCI in the two scenarios (Z=4.237; p<0.05)" (Fondo et al 2015).



Figure 157: Changes in Finn's Cycling Index (FCI) for the two Scenarios from 1990 to 2013

Discussion

"PAFS can affect communities and ecosystems e.g. fisheries discards may influence several ecological processes, trophic levels and adjacent ecosystems (Oro et al. 2013). Discards are exploited by a large number of organisms, from top predators (seabirds, sharks and dolphins) to invertebrates (such as crustaceans) and covering different zones or habitats (e.g. sea surface, pelagic and benthic) (Oro et al. 2013). In the Ecopath models of Moreton Bay, which represent the system's steady state, opportunistic species (seabirds, dolphins, sharks) exhibited an increase in the number of food pathways (the number of all pathways from primary producers or detritus groups leading to the selected consumer via specified prey) and a drop in trophic levels. These results support the findings by Oro et al. (2013) that PAFS alter trophic levels and food webs. The opportunistic species have the potential to exploit PAFS directly, in addition to preying on lower trophic level species that also exploit these PAFS (Oro et al. 2013), resulting in the lowering of their trophic levels. The lowering of the trophic levels may influence the transfer efficiency between the trophic levels; this is of significance especially if the species involved are top predators, as this affects how the energy flows through the ecosystem - and eventually what is produced as "goods" from the ecosystem (production)" (Fondo et al. 2015).

"PAFS may increase the survival, reproduction and alter the social behaviour(s) of predators (Newsome et al. 2014). In harsh conditions, individuals able to access PAFS may successfully reproduce and survive (Martínez-Abraín et al. 2012) e.g. rats dwelling in subsidized habitats grew better than those in non-subsidized habitats when subjected to the same levels of environmental stress (Ruffino et al. 2013). Studies have shown the importance of PAFS in supplementing energy requirements where natural food resources are scarce (Oro et al. 2008, Margalida et al. 2011, Margalida and Colomer 2012, Margalida et al. 2013). In my study, for both scenarios there was an overall increase in the relative biomass of most functional groups over the study period, except for opportunistic species (seabirds and dolphins). In the presence of PAFS, opportunistic species were able to adapt better to the gradual reduction of PAFS than under their sudden removal. These species exhibited prey switching when the discards were gradually reduced (Scenario 1) from consuming discards to mainly eating lower level omnivores; but when PAFS were banned abruptly (Scenario 2), opportunistic species exert greater pressure on their natural prey. For example, seabirds changed their diet to increase the proportion of lower level omnivores and pelagic fish, in response to the deficit resulting from the gradual reduction of discards. This could indicate that these opportunistic species are resilient to changes in food resources and may provide support for the hypothesis that PAFS increase the resilience of opportunistic species when food resources are scarce" (Fondo et al. 2015).

"Predator-prey interactions play a key role in ecosystem structuring (Polis et al. 1997, Hunsicker et al. 2011) and availability of PAFS result in changes in these interactions (Newsome et al. 2014). The results of the dynamic model showed that the major opportunistic species exhibited prey switching when the discards were gradually reduced; but when PAFS are banned abruptly, they exert greater pressure on their natural prey. These results on the changes in proportions of prey in the diets of the major (upper trophic level) opportunistic species show how discards may modify predator-prey interactions and give support to the findings of studies reviewed by Oro et al. (2013). These interactions become important as consumers previously subsidised by PAFS may switch their diet to a focus on specific prey species; if the species subsequently influenced are particularly important in the community, the effects could be far-reaching (Polis et al. 1997). The predatory opportunists (seabirds, dolphins and sharks) may potentially exert notable effects through top-down control over the complexity and structure of trophic interactions (Polis et al. 1997)" (Fondo et al. 2015).

"The FCI dropped to zero in both scenarios (whether discards are removed gradually or banned) and this could indicate that removal of discards may have an indirect effect on FCI. These changes observed in FCI may provide support for the findings of studies reviewed by Oro et al. (2013) that PAFS influence ecological processes such as ecosystem resilience and stability. The trend observed for FCI in Moreton Bay model in scenario 1 suggests that the Moreton Bay ecosystem was initially stressed (between 1990 and 1992) then started to improve, maintaining its structure and slowly maturing as the discards were being reduced. The system reverted back to a stressed condition when the discards were further removed. This suggests that a complete ban on the discards may stress the system and that the presence of a certain quantity of discards in the system might actually be good for the maintenance of the system's structure and maturity, possibly because of the long exposure of the system to discards from fishing" (Fondo et al. 2015).

Conclusions

"Food subsidies have the potential to modify ecosystems. The concern over the effects of PAFS on ecosystem dynamics has led several jurisdictions to reduce or eradicate PAFS. However, these actions may have detrimental effects on some key ecological processes and impact negatively on species or communities that have commercial or conservation value; in some cases a ban or reduction of PAFS may be unnecessary (Zhou 2008)]. The current study has shown that, in general, a gradual removal of PAFS may be beneficial by allowing species to habituate to food scarcity. The rate at which PAFS are removed will depend on the ecosystem in question and requires negotiation with major stakeholders (in case of this study, the fishing industry) and managers. Multiple hypothetical scenarios could be generated to explore different rates of PAFS reduction but here I have used empirical data from a real world scenario and the results could be useful in exploring these hypothetical scenarios" (Fondo et al. 2015).

"An abrupt ban can have a negative impact on the scavenger species especially in ecosystems that have experienced provision of PAFS over a long period of time. As it has been demonstrated, PAFS may modify predator- prey interactions and influence ecosystem stability. When PAFS are removed completely from the system, under either scenario, ecosystem stability drops with the cycling index reaching zero, an indication of a stressed system (a low or zero cycling index is an indication of a 101 stressed system (Ulanowicz 1986, Monaco and Ulanowicz 1997)). Clearly, after so many generations of exposure to the ready food supply of PAFS, a certain minimal level is required to maintain stability. However further studies are required to determine this level in different ecosystems as the effects of providing resource subsidies to higher trophic levels may differ depending on the type of subsidy and the species present (Newsome et al. 2015). Gradual removal of PAFS may be beneficial to allow species exploiting PAFS to switch gradually to alternative prey (and to avoid the predators from drastically reducing the prey populations and driving them to local extinction). Under these circumstances, a gradual reduction of PAFS as opposed to a sudden ban is recommended, and may be a useful approach in the management of PAFS" (Fondo et al. 2015).

"Policy decisions can have important consequences for the management and conservation of natural ecosystems. Both the gradual removal and complete ban on PAFS may affect the ecosystem, decreasing the survival of scavenger species. Managers dealing with PAFS should consider the direct effects of PAFS removal on any endangered species within the system (such as seabirds, dolphins and sharks) that are of regional and global importance. Further studies are needed to determine whether PAFS should be removed completely, reduced or maintained at current levels, for different types of ecosystems, in order to provide guidance to managers and conservation agencies (Donázar et al. 2009, Margalida and Colomer 2012, Margalida et al. 2014)" (Fondo et al. 2015).

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Chapter 5

Fishing down predators at different trophic levels in a coastal embayment

Abstract

Predators play a key role in maintaining the structure and functioning of ecosystems. Global population declines of top-level predators has raised concerns as the loss of predators may impact the provision of goods and services provided by ecosystems. However, not all predators in marine ecosystems are top-level predators. Overfishing in multi-species fisheries, may remove predators at multiple trophic levels, yet the consequences of fishing out predators at different trophic levels are unknown. In this study, I examined the impacts of removal by fishing, of predators at different trophic levels of the food web. I explored the effects of removal of top predators (sharks), meso-predators (pelagic fish) and small predators (resources species like crabs) in a sub-tropical bay ecosystem where different types of fishing remove different components of the food web.

Using Ecopath with Ecosim tropho-dynamic models, I tested seven hypotheses. These were that the rapid removal of: 1) portunid crabs would increase numbers of prawns and other macrobenthos; 2) pelagic fish would increase numbers of lower trophic level species such as crabs and other macrobenthos; 3) pelagic fish and portunid crabs would increase numbers of prawns and other macrobenthos; 4) sharks would result in an increase in pelagic fish; 5) sharks and portunid crabs would increase numbers of fish, prawns and other macrobenthos; 6) sharks and pelagic fish would increase numbers of crabs (and other lower trophic level species); and 7) sharks, pelagic fish and portunid crabs would increase numbers of prawns (and other lower trophic level species).

When crabs were fished out the biomass of sharks, demersal and pelagic fish, seabirds and dolphins all decreased. Removal of pelagic fish however resulted in an increase in the biomass of jellyfish. Removal of sharks resulted in an increase in the biomass of seabirds, pelagic fish and dolphins. When all predators were fished out, there was a negative impact on seabirds and dolphins with an increase in the biomass of jellyfish and demersal fish. The findings emphasize the critical role that predators at all trophic levels play in maintaining healthy ecosystems.
Introduction

Predators play a key role in ecosystems through their regulation of predator–prey interactions and trophic cascades (Myers et al. 2007; Terborgh and Estes 2010). Top predators such as lions, wolves, whales, sharks and otters constrain the populations of other consumers and may indirectly regulate primary production (Heithaus et al. 2012; Atwood et al. 2015). They also influence ecosystem dynamics and stability (Kondoh 2003; Rooney et al. 2006) by controlling population sizes of their meso-consumer prey (Heithaus et al 2008)), and regulate top-down interactions (Terborgh and Estes 2010; Estes et al. 2011; Britten et al. 2014). Excessive removal of predators from a system may trigger instability in the functioning of ecosystems, with the potential for the collapse of the system (Estes et al. 2011).

Globally, reports of population declines of predators in terrestrial (Leopold 1949; Ripple et al. 2001) and marine (Pauly et al 1998; Baum et al. 2003; Myers and Worm 2003; Britten et al. 2014; McCauley et al. 2015) ecosystems have been increasing in frequency. There is evidence to suggest that historical losses of predatory fishes, mammals and reptiles in coastal ecosystems, have triggered noticeable changes in coastal ecosystem structure and function (Bowen 1997; Jackson et al. 2001). The global ocean has lost more than 90% of large predatory fishes (Myers and Worm 2003) raising serious concerns among scientists because:

(1) a loss of predators could lead to trophic cascades passing through food webs, altering the provision of goods and services, and impacting life support systems (McCauley et al. 2015) and;

(2) It poses a challenge to the management of sustainable and healthy ecosystems (Myers and Worm 2003).

Extensive reductions of large predators in the world's oceans are likely to influence smaller-bodied meso-consumers (e.g. smaller predatory fishes, smaller sharks and rays) and, in turn, those species that they consume (resource species or primary consumers such as smaller planktivorous fish, molluscs, crabs and prawns) (Heithaus et al 2008). Meso-consumer communities can respond strongly to the declines in the abundance of top predators, and the effects spread over large areas and long periods (Heithaus et al 2008; Heupel et al 2014). Eliminating predators causes instability in ecosystems, allowing chain reactions that ultimately translate down the food web to the lowest levels (Terborgh and Estes 2010). For example, in southwest Alaska, the decline in the abundance of sea otters due to harvesting for their pelts, resulted in a trophic cascade that led to a the rise of sea urchins in the place of kelp forests, affecting many species (Estes et al. 2009).

Though the impacts of trophic cascades can be widespread, their strengths may differ in species and ecosystems (Estes et al. 2011). For example, the effects of the removal of predators (such as lions) in the Serengeti, Tanzania varied considerably depending on the specific group of herbivores examined. Resident mega-herbivores (elephant, hippopotamus and rhinoceros) were relatively unaffected because these animals were virtually invulnerable to predation (Sinclair et al. 2003); but smaller herbivores (Thompson's gazelle and impala) increased following the disappearance of the predators (Sinclair et al. 2003). Trophic cascades due to loss of predators can also affect other "processes such as the spread of diseases, carbon sequestration, and biogeochemical cycles" (Estes et al. 2011). The effects may remain unnoticed long after the predators have disappeared, making it difficult to restore top-down control (Estes et al. 2011) and reverse any effects (Scheffer et al. 2005). This poses a major challenge to management and conservation efforts.

In a marine ecosystem, when groups of species are organised according to trophic levels, primary producers such as phytoplankton, algae and seagrass represent the lowest trophic level. These are followed by primary consumers or resources species such as planktivorous fish, molluscs, crabs and other invertebrates (Baum and Worm 2009), which may be consumed by meso-predators such as small predatory fish, small sharks and rays, and small mammals (Frederiksen et al. 2006; Terborgh and Estes 2010). Meso-predators are in turn consumed by apex predators (such as sharks, dolphins and seabirds) which occupy the top most level of the trophic structure (Prugh et al. 2009). Human beings can consume species at any level and, through fishing activities, can impact negatively on any or all of these trophic levels.

Globally, overfishing remains one of the major threats to marine ecosystems (Halpern et al. 2007). Overfishing in multi-species fisheries, may result in fishing out of predators at successive levels, causing different effects in the ecosystem. For example, when top predators are removed, meso-predators take over the role of the 'top' predators (Prugh et al. 2009). This causes an increase in the abundance of the meso-predators ('meso-predator release') but has negative effects on the broader marine ecosystem (Heithaus et al. 2008; Baum and Worm 2009; Prugh et al. 2009, Morissette et al. 2012). When the meso-predators are fished out, there is an increase in resource species (Worm and Myers 2003). Many of the studies on marine predator removal have focused on effects at individual trophic levels but, to the best of my knowledge, no study has examined the combined and interactive effects of removing predators at multiple levels, thus the consequences of fishing out predators in this way are still unknown.

In this study, I tested the impacts of removal by fishing of predators at different trophic levels in the food web. I explored the effects of removal of top predators, meso-predators and small predators (resources species) in a marine ecosystem where different types of fishing simultaneously remove different components of the food web. I selected subtropical Moreton Bay, in south-east Queensland, Australia, where a diversity of fishing pressures are exerted by multispecies fisheries using a range of different gear types. It occupies only 3% of the Queensland coastline, but has extensive recreational fisheries and produces 15% of the commercial catch (Chilvers et al. 2005).

The prawn, crab, and finfish fisheries exert pressure on the Moreton Bay ecosystem in different ways. The prawn fisheries use benthic beam trawls and small otter trawls that not only remove prawns but also large quantities of sand crabs and fish (Wassenberg and Hill, 1989; Kienzle et al. 2014; Wang et al. 2015), Moreton Bay bugs (*Thenus orientalis* and *T. indicus*) (DAFF, 2014), squids, mantis shrimp and cuttlefish (Courtney et al. 1995). A crab fishery, using benthic pots and traps, includes both the recreational and commercial sectors targeting portunid species including sand crabs (*Portunus armatus* previously known as *Portunus pelagicus*), mud crabs (*Scylla serrata*) and several other species of *Portunus* and *Thalamita* (Heasman, 1980; Sumpton, 1990; Pillans et al. 2005; Campbell and Sumpton, 2009). An extensive recreational fishery targets numerous species of finfish including snapper (*Pagrus auratus*) (Sumpton and Jackson, 2005; Terres et al. 2015), Spanish mackerel (*Scomberomorus commerson*), bream (*Acanthopagrus spp.*) (Pillans 2006), flathead (*Platycephalus* spp.) (Pillans, 2006), mangrove jack (*Lutjanus argentimaculatus*) and whiting (*Sillago* spp.) (Weng 1986; Krück et al. 2009), all of which are important predators on different components of the system. Sharks in Moreton Bay are caught by commercial gillnetters (Taylor and Bennett 2013; DAFF 2014).

I examined the removal of the different key groups of predators, in isolation and in additive combinations with all the other groups, as the different types of fisheries sometimes overlap in operation, but at other times are operating separately (Courtney et al. 2012; DAFF 2014). I examined these questions using ecosystem modelling, whereby different groups of predators were removed over a period of 23 years. I tested the following hypotheses: That the rapid removal of:

- portunid crabs would increase the abundance of prawns and other macrobenthos, due to reduction in predation pressure from crabs (Williams 1982);
- 2. pelagic fish (e.g. mackerel and tuna) would increase the abundance of demersal fish and lower trophic level species such as crabs, prawns and other macrobenthos, as these form the

primary food source for many species of pelagic fish in Moreton Bay (Brewer et al. 1991; Griffiths et al. 2009; Froese 2015);

- pelagic fish (e.g. mackerel and tuna) <u>and</u> portunid crabs would increase the abundance of demersal fish, prawns and other macrobenthos, as these form the primary food source for pelagic fish and crabs in Moreton Bay (Williams 1982; Brewer et al. 1991; Stephenson 2006; Griffiths et al. 2009; Froese 2015);
- sharks would result in an increase in the abundance of fish, portunid crabs and prawns as these form the primary food source for many species of sharks in Moreton Bay (Taylor 2007; Taylor and Bennett 2013);
- sharks <u>and</u> portunid crabs would increase the abundance of pelagic fish, prawns and other macrobenthos, as these form the primary food source for many species of sharks and crabs in Moreton Bay (Williams 1982; Stephenson 2006; Taylor 2007; Taylor and Bennett 2013);
- sharks <u>and</u> pelagic fish (e.g. mackerel and tuna) will increase the abundance of portunid crabs, prawns and macrobenthos as these form the primary food source for many species of sharks and pelagic fish in Moreton Bay (Morton et al. 1987; Taylor 2007; Taylor and Bennett 2013; Froese 2015);
- sharks + pelagic fish (e.g. mackerel and tuna) <u>and</u> portunid crabs would increase the abundance of prawns and macrobenthos, due to reduction in predation pressure from sharks, pelagic fish and portunid crabs (Williams 1982; Taylor 2007; Taylor and Bennett 2013; Froese 2015).

This work will provide greater understanding of how ecosystem functions are disturbed through simultaneous removal of predators at different trophic levels. It may also serve as a reference for fisheries managers who observe particular changes in the ecosystem that are related to fisheries (e.g. in a multispecies fishery) as to the possible ecosystem responses, if certain trophic levels are being overfished.

Methods

To determine the consequences of simultaneous predator removal at different trophic levels I used the calibrated balanced Moreton Bay model described in Chapter 3, to explore eight scenarios in the Ecosim model as follows:

- 1. Scenario 1- representing the original Moreton Bay ecosystem
- 2. Scenario 2- where sand crabs are fished out
- 3. Scenario 3- where pelagic fish are fished out
- 4. Scenario 4- where pelagic fish and sand crabs are fished out
- 5. Scenario 5- where sharks are fished out
- 6. Scenario 6- where sharks and sand crabs are fished out
- 7. Scenario 7- where sharks and pelagic fish are fished out
- 8. Scenario 8- where sharks, fish and sand crabs are fished out

Table 9 gives a summary of the different levels of predator removal for the scenarios.

Table 9: Summary of the different scenarios representing the fishing out of the three differentpredators (Y= present; N= fished out)

MODEL	sharks	fish	crabs
1	Y	Y	Y
2	Y	Y	N
3	Y	N	Y
4	Y	N	N
5	N	Y	Y
6	N	Y	Ν
7	Ν	Ν	Y
8	Ν	Ν	Ν

The predators were eliminated by using a fishing mortality (F) of 5 (for crabs F was further increased to 10 from 1996). To eliminate the predators from the Moreton Bay ecosystem model, I had to maintain the high F. The Ecosim results from the seven scenarios were compared with the results of the original Moreton Bay model by examining changes in biomass of the groups.

Results

Changes in biomass

Scenario 1: Moreton Bay ecosystem model

In the original Moreton Bay ecosystem model (Figure 18), there was a decrease in the biomass of discards (54%) from 1990 to 2013. There was also a decrease in the biomass of seabirds (19%), dolphins (12%) and turtles (7%), while all the other groups had an increase in biomass. The changes in biomass of the other 7 scenarios were compared with this original Moreton Bay scenario and the results were as follows.

Scenario 2: sand crabs fished out

When crabs were rapidly removed, there was a decrease in the biomasses of sharks (48%), demersal fish (20%), pelagic fish (15%), seabirds (7%) and dolphins (5%) (Figure 18). There was an increase in the biomass of discards (43%), jellyfish (8%), prawns (7%) and macrobenthos (3%).

Scenario 3: pelagic fish fished out

When pelagic fish were rapidly removed, there was a decrease in the biomasses of sharks (87%), seabirds (54%), dolphins (27%), prawns (9%) and macrobenthos (3%) (Figure 18). The biomasses of jellyfish, demersal fish and discards increased by 130%, 116% and 67% respectively.

Scenario 4: pelagic fish and sand crabs fished out

When pelagic fish and crabs were rapidly removed, there was a decrease in the biomasses of sharks (88%), seabirds (54%), dolphins (27%) and prawns (6%) (Figure 18). There were major increases in the biomasses of jellyfish (130%), demersal fish (64%) and discards (49%).

Scenario 5: sharks are fished out

When sharks were rapidly removed, there was a decrease in the biomass of jellyfish (7%) and an increase in the biomasses of discards (58%), seabirds (25%), pelagic fish (17%) and dolphins (11%) (Figure 19). The increase in biomass of portunid crabs and prawns was minimal 0.4% and 0.8% respectively.

Scenario 6: sharks and sand crabs are fished out

When sharks and portunid crabs are rapidly removed, the biomasses of demersal fish and pelagic fish decreased by 22% and 7% respectively (Fig 19). There was an increase in the biomasses of discards (42%), seabirds (5%), prawns (5%), macrobenthos (3%) and dolphins (2%).

Scenario 7: sharks and pelagic fish are fished out

When both sharks and pelagic fish were rapidly removed, there was a decrease in the biomasses of seabirds (52%), dolphins (27%), prawns (9%) and macrobenthos (3%) (Fig 19). There was an increase in the biomasses jellyfish (130%), demersal fish (125%) and discards (68%).

Scenario 8: sharks, fish and sand crabs are fished out

When sharks, pelagic fish and portunid crabs were rapidly removed, there was a decrease in the biomasses of seabirds (54%), dolphins (27%), prawns (6%), and macrobenthos (2%) (Fig 19). There was an increase in the biomasses of jellyfish (130%), demersal fish (69%) and discards (50%). The tables with values on the changes in biomass, and percentage changes for the different scenarios are given in Appendix 17.



Figure 168: The End/Start biomass for the scenarios comparing each scenario with scenario 1 (original Moreton Bay model).

Blue=Moreton Bay; clear= the other scenarios (1) Moreton Bay model (2) sand crabs removed; (3) pelagic fish removed; (4) pelagic fish and sand crabs removed.



Figure 179: The End/Start biomass for the scenarios comparing each scenario with scenario 1 (original Moreton Bay model).

Blue = Moreton Bay; clear = the other scenarios (5) sharks removed; (6) sharks and sand crabs removed; (7) sharks and pelagic fish removed; (8)sharks,fishandsandcrabsremoved.

Discussion

The results from the modelling of the effects of removing of predators simultaneously from different trophic levels on the Moreton Bay ecosystem only partly agreed with my predictions; derived from information in the literature on interactions among different trophic levels. It is possible that mediating effects such as protection or facilitation, could have influenced the outcomes, but these were not considered, as details on mediating effects occurring in the ecosystems were not available. Mediation occurs when other species provide protection for prey, making them unavailable to the predator e.g. juvenile fish may shelter themselves from predators in corals or seagrass; or other species' behaviour may increase the prey's availability to the predator e.g. pelagic fish like tuna may drive smaller fish to the surface, making them easily accessible to birds (Christensen et al 2008).

When portunid crabs were fished out (scenario 2) from the Moreton Bay ecosystem, as predicted, the biomass of macrobenthos and prawns which are their prey (Williams 1982), increased. This increase may be due to release from predation as described by Ritchie and Johnson (2009). These findings are consistent with what was seen in the seas around Alaska in 1960-1980, where fisheries of three major crab species (king, tanner and snow) collapsed and this was followed by a rapid increase in the abundance of shrimps (pink and sidestripe) and prawn (spot prawn) fisheries (Armstrong et al. 1998). Other major changes that resulted from the removal of crabs in Moreton Bay were that sharks, demersal and pelagic fish were negatively impacted by the removal of portunid crabs. Portunid crabs are prey for several Carcharhiniform sharks (such as dusty sharks, scalloped hammerhead sharks and Australian weasel shark - White and Potter 2004, Taylor 2007; Rogers et al. 2012); demersal fish (such as flatheads and breams - Klumpp and Nichols 1983, Bulman et al. 2001) and pelagic fish (such as mackerel and tuna Begg and Hopper 1997, Griffiths et al. 2009). The results also showed that when crabs are removed in Moreton Bay, the biomass of seabirds and dolphins decreased. This decrease may be an indirect effect that resulted from the decreased biomass of pelagic fish, which are their prey (Blaber and Wassenberg 1989; Ansmann 2011). Other studies have found that fisheries for lower trophic level predator species (e.g., anchovies, sardines, crustaceans such as crabs) threaten the future sustainability of upper trophic level predators (e.g. seabirds and mammals) in marine ecosystems (Cury et al. 2011; Smith et al. 2011).

Removal of pelagic fish (scenario 3) from Moreton Bay resulted in an increase of biomasses of jellyfish, demersal fish and discards, but not for prawns and macrobenthos. This only partly agreed

with my prediction that removal of pelagic fish would increase the abundance of demersal fish and lower trophic level species such as crabs, prawns and other macrobenthos. The biomass of demersal fish increased due to reduced predation from pelagic fish such as mackerel and tuna (Griffiths et al. 2009); and the increased biomass of demersal fish may have caused the decrease in prawns and macrobenthos which are their prey (Klumpp and Nichols 1983, Bulman et al. 2001). In Moreton Bay, jellyfish form a minor component of pelagic fish diet (see diet matrix in Table 2, Chapter 3) and therefore the removal of pelagic fish reduced the predation pressure on jellyfish, resulting in the increase in jellyfish biomass. Jellyfish biomass increased also when pelagic fish together with crabs (scenario 4), with sharks (scenario 7) or when all the three predators (scenario 8) were fished out from the Moreton Bay ecosystem. Such incidences of jellyfish blooms are common phenomenon that has been observed in overfished areas (Daskalov 2002). Fishing may favour conditions for jellyfish when their predators and competitors are overfished, allowing great changes in the ecosystem (Purcell et al. 2007).

The removal of pelagic fish from Moreton Bay also impacted negatively on sharks, seabirds and dolphins which prey on pelagic fish (Blaber and Wassenberg 1989; Taylor 2007; Ansmann 2011). The decrease in the biomass of sharks, seabirds and dolphins may have allowed the increase of discards which form part of their diet (Blaber and Wassenberg 1989; Ansmann 2011). A possible explanation for lack of changes in the biomass of prawns and macrobenthos in Moreton Bay could be that they were under predation pressure from the increase in demersal fish. Global pelagic fisheries have dropped drastically in the last 50 years (e.g. Atlantic herring, sardines and anchoveta fisheries) (Beverton 1990). Other studies have shown that when pelagic fish are depleted, top predators are impacted negatively (Kaplan 2013). In the Peruvian upwelling ecosystem, declines in Peruvian anchoveta had negative impacts on seabirds and other top predators (Muck 1989). The collapse of sardine in the Gulf of Guinea in 1973 was followed two years later, by the collapse of its predator the Chub mackerel (Cury et al. 2000). The mackerel took much longer to recover (10 years) after recovery of sardine. In Peru, the collapse of anchoveta was followed by the collapse of bonito, which quickly recovered when anchoveta reappeared in mid-1980's (Cury et al. 2000). In modelling overfishing on small pelagic fish in the southern Benguela, a collapse in anchovy and sardine favoured their competitors, chub mackerel and horse mackerel, which compete for zooplankton prey; but impacted negatively on top predators such as seals, cetaceans and seabirds (Shannon et al. 2000). Other studies have also shown that declines in predatory fish (from fishing) that prey on portunid crabs resulted in an abundance of crabs (de Lestang et al. 2003).

Studies have shown that removal of top predators (e.g. sharks) in marine ecosystems leads to an increase in the abundance of meso-predator and invertebrate predators (Baum and Worm 2009).

Sharks consume on a wide range of prey from small plankton to whales thus controlling the populations of other prey (Wetherbee and Cortés 2004; Heithaus 2012). Therefore, their removal can cause unexpected changes in other species' population; changes which can persist with diminished shark population (Stevens et al. 2000). In my case, removal of top predators (sharks in scenario 5) resulted in an increase in the biomass of the competitors of sharks (seabirds and dolphins). There was also an increase in the biomass of the meso-predators (pelagic fish) reflecting meso-predator release (a concept that has been described by Ritchie and Johnson (2009)). There was also a the loss of top-down control by sharks, supporting the findings by Baum and Worm (2009), implying that shark declines translate through the food web in an intricate way, and supporting findings by Stevens et al. (2000) that shark depletion modifies community structure.

Studies have shown that depletion of sharks may result in changes in species and community composition and high food supply from discards (Parsons 1992, Stevens et al. 2000). Sharks, dolphins and seabirds scavenge on discards (Hill and Wassenberg 1990) and when sharks are depleted, there is greater food supply for the dolphins and seabirds (Stevens et al. 2000), which may result in their increase as shown in my study. Other studies have shown that removal of top predators affected higher trophic levels, but lower trophic levels were unaffected (Nye et al. 2013). Sharks are important in the marine ecosystem because their predatory processes influence ecosystem stability as they prey on top level predators and keep them from drastically consuming the lower trophic levels. Drastic consumption of lower trophic levels can bring imbalances in the ecosystem (Myers et al. 2007; Ferretti et al. 2010; Heupel et al. 2014). Recent findings have actually shown the role of top predators such as sharks in slowing down climate change and that shark removal could accelerate global warming (Atwood et al. 2015).

I predicted that when pelagic fish and crabs were rapidly removed (scenario 4), the abundance of demersal fish, prawns and macrobenthos would increase. From the model results, sharks, seabirds and dolphins were negatively impacted by the removal of pelagic fish and crabs as these are their prey (Blaber and Wassenberg 1989; Taylor 2007; Ansmann 2011). The negative impact on these groups could have led to an increase in the biomass of discards, which form part of their diet (Hill and Wassenberg 1990). The biomass of demersal fish increased due to release from predation (Ritchie and Johnson 2009) by their predators (sharks and pelagic fish) (Taylor 2007; Griffiths et al. 2009) which were reduced. The increase in the biomass of demersal fish impacted negatively on the prawns which are their prey (Bulman et al. 2001).

I predicted that removal of sharks and portunid crabs (scenario 6) would increase the abundance of pelagic fish, prawns and other macrobenthos. From the model results, the removal of sharks and portunid crabs decreased the biomass of demersal fish. This decrease may be due to reduced prey (portunid crabs) (Klumpp and Nichols 1983, Bulman et al. 2001). The biomass of seabirds and dolphins increased due to reduced competition from sharks (Blaber and Wassenberg 1989), and also results in increased predation on pelagic fish (Blaber and Wassenberg 1989; Ansmann 2011) thus reducing their biomass. The decreased biomass of pelagic and demersal fish led to an increase in biomass of their prey (prawns and discards) (Hill and Wassenberg 1990; Begg and Hopper 1997).

When both sharks and pelagic fish were rapidly removed (scenario 7), there was an increase in the biomasses of jellyfish, demersal fish and discards, contrary to my prediction that removal of sharks and pelagic fish would increase the abundance of portunid crabs, prawns and macrobenthos. From the model results, the biomass of seabirds and dolphins decreased as their prey (pelagic fish) (Blaber and Wassenberg 1989) was removed. This also resulted in the increased discards biomass as they form part of the diet for sharks, seabirds, dolphins and pelagic fish (Hill and Wassenberg 1990). The biomass of demersal fish increased due to reduced predation from pelagic fish and sharks (Taylor 2007; Griffiths et al. 2009). The increase in the biomass of demersal fish impacts negatively on their prey (prawns and macrobenthos- Bulman et al. 2001).

When all predators were fished out (scenario 8) from the Moreton Bay ecosystem, there was an increase in the biomass jellyfish and demersal fish; a decrease in the biomass of seabirds and dolphins. This contradicted my prediction that removal of sharks, pelagic fish and crabs would increase the abundance of prawns and macrobenthos. The biomasses of seabirds and dolphins decreased due to reduced prey (pelagic fish- Blaber and Wassenberg 1989; Ansmann 2011). The biomass of demersal fish increased due to release from predation (Ritchie and Johnson 2009) by pelagic fish and sharks- (Taylor 2007; Griffiths et al. 2009). The increased biomass of demersal fish impacts negatively on their prey, prawns and macrobenthos (Bulman et al. 2001).

As studies on consequences of simultaneous removal of predators at different trophic levels from marine ecosystems are lacking, it was not possible to compare my findings for the scenarios 4, 6, 7 and 8 where there were more than one predator involved. In general, it may be difficult to determine the effects of simultaneous removal of predators, as the effects may be variable, cumulative and multiple e.g. reduced predation or increased competition between prey; and cascade to other trophic levels (Schmitz 2007; Douglass et al 2008).

Most studies that have looked at the effects of predator removal have focused on groups at one trophic level (Baum and Worm 2009) and simultaneous removal at different trophic levels have rarely been considered (e.g. where both crabs and fish are fished out). Looking at the patterns from the fishing out of predators from the Moreton Bay ecosystem, it is possible that one group of the predators might have a dominating influence when removed in combination with the other predators. In particular, my results show that in scenarios where the pelagic fish were removed the response was an abundance of jellyfish, accompanied with a decline in seabirds and dolphins. This outcome reflects the importance of these predators in the ecosystem, their removal affecting the ecosystem health and impacting negatively on major charismatic megafauna (seabirds and dolphins).

My model results on the removal of top predators were consistent with other studies (Stevens et al. 2000; Morissette et al. 2012) where declines in top predators resulted in an increase of mesopredators. Declines in predators may cause trophic cascades in marine systems (Estes et al. 2011), where increases of medium-sized predators set off changes in other trophic levels (Pace et al. 1999; Prugh et al. 2009). Predator heterogeneity (due to prey preferences) is evident at higher trophic levels where omnivory and intra-guild predation are common (Polis and Holt 1992; Stachowicz et al. 2007). This heterogeneity in sharks and pelagic fish, which have wide range of prey, may have reduced the effects of single species groups in the food web and diminished trophic cascades (Polis and Holt 1992; Stachowicz et al. 2007). Other studies have shown that variations in predator abundances affect the species composition rather than the total abundance of prey (Duffy 2007; Sieben et al. 2011). However, the cascading effects of removing top-predators on producers strongly depend on resource availability (Siebens et al. 2011). Studies on removal of predators in combination (e.g. depletion of sharks and crabs or pelagic fish) to compare with my results are lacking. More studies on the effects of predator removal from different trophic levels are encouraged. In addition, including other perturbations, which may affect species interactions and ecosystem response such as climate change, changes in habitat and nutrient inputs may give different and interesting outcomes.

Conclusion

Removal of predators results in changes in the biomass of their prey accompanied by trophic cascades and impacts on charismatic megafauna (seabirds and dolphins). Jellyfish blooms are a common feature when meso-predators (pelagic fish) are removed, confirming the speculation that

overfishing could lead to blooms (Purcell et al. 2007) and emphasizing the critical role that predators at all trophic levels play in maintaining healthy ecosystems. The findings from this work may provide insights for fisheries and ecosystem management and a guide to sustaining healthy marine ecosystems.

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Chapter 6

The paradox of reducing jellyfish blooms

Abstract

Increasing frequency of jellyfish blooms have been reported globally. Many explanations have been suggested for the increase such as, overfishing, eutrophication, climate change and artificial structures. Jellyfish blooms are a major concern because they sting swimmers, disrupt fishing and other sea based operations apart from rapidly depleting food resources for fish, causing declines in fisheries. Fishing of jellyfish has been considered as a solution to the problem of jellyfish blooms in some areas like Asia and America. I tested the hypothesis that overfishing of jellyfish will have a negative effect on the abundance of pelagic fish due to a reduction in their prey. Using trophodynamic modelling, I modelled fishing jellyfish in Moreton Bay and simulated overfishing of jellyfish on the different functional groups of the ecosystem. The results show that for both cases top level predators were negatively impacted with a decrease in their biomass. When jellyfish were overfished, there was reduction in species diversity. Thus, jellyfish fishing may not be a desirable solution for Moreton Bay.

Introduction

Overfishing remains one of the major threats to aquatic ecosystems (FAO 2014). The demand for fish has been increasing in the last decade and the improved fishing techniques are putting marine ecosystems under pressure (Aydin 2004). Increased incidences of jellyfish blooms in many parts of the world have been linked with degradation of marine ecosystem from overfishing (Jackson et al. 2001, Purcell 2012). However several other causes for increased populations of jellyfish have been identified, such as climate change, eutrophication, invasions and the ever-increasing number of hard surfaces from construction that form a suitable place for polyps to settle (Purcell et al. 2007).

Even though fishing has been going on for centuries, it was only in the 1950s that jellyfish began to be noticed as a problem (Purcell 2012; Condon et al. 2013). Some fish (such as mackerel, anchovy) are predators of jellyfish thus they are important in regulating jellyfish abundance (Daskalov et al. 2007), while zooplanktivorous fish (such as anchovies, herring and sardines) compete with jellyfish for food (zooplankton) (Purcell and Arai 2001). Overfishing resulting in decline of these fish that

prey on or compete with jellyfish (Daskalov et al. 2007; Mutlu 2009), coupled with poor water quality, favours jellyfish blooms (Purcell 2012).

The increasing populations of jellyfish are of major global concern because of the threats they pose, from interfering with fishing and power production by clogging nets and screens (Daryanabard and Dawson 2008, Nagata et al. 2009, Dong et al. 2010); and the most notable and serious one being stinging of humans (Purcell et al. 2007; Fenner et al. 2010). Other environmental effects of jellies include (1) reduction in fish populations through predation of eggs and larvae (Purcell et al. 2007), (2) reduction in lower trophic level species through predation and competition for food resources (Brodeur et al. 2011) and (3) triggering hypoxia through excess phytoplankton falls that result from depleted zooplankton grazers (fed on by jellyfish) (Møller and Riisgård 2007).

Despite the threats posed by jellyfish blooms, jellyfish abundance is being exploited in Asia (e.g. China, Malaysia and Thailand) for food and medicine, where they have been eaten as a delicacy for centuries (Gibbons et al. 2016; Brotz et al. 2016). These countries have established jellyfish fisheries and have strong market demand for jellyfish (Brotz et al. 2016). Jellyfish fisheries have also been introduced in some countries in the Americas (Brotz et al. 2017). Apart from food and medicinal benefits, jellyfish have other uses such as industrial applications. For example in Russia, jellyfish have been mixed with cement to increase its strength by 50 % (CIESM 2010). It has also been shown that jellyfish can be used as fertilizer (e.g., Fukushi et al. 2004; Kim et al. 2012).

Increased jellyfish populations have been linked with warming caused by climate changes (Attrill et al. 2007; Boero et al. 2016) and nutrient inputs (Pitt et al. 2005). Overfishing of pelagic fish has also been shown to result in increased jellyfish abundance (Purcell et al. 2007) (also demonstrated in Chapter 5 of my thesis). Using causal-loop modelling, I developed a conceptual model (Loiselle et al. 2000; Dambacher et al. 2009) in order to explore the ecosystem dynamics when jellyfish are overfished (Hulot et al. 2000; Chaloupka 2002). Figure 20 shows a causal loop diagram (signed digraph) of the conceptual model where fishing results in a decrease of both pelagic fish and jellyfish (negative effects). Studies have shown that both nutrients and ocean warming due to climate change increase the biomass of jellyfish (Pitt et al. 2005; Purcell et al. 2007; Boero et al. 2016), thus giving a positive response (Figure 20). Ocean warming may increase or decrease pelagic fish depending on other factors such as pollution and habitat changes (Boero et al. 2016); resulting in either positive or negative effects (Figure 20). Following this conceptual model, I predicted that overfishing of jellyfish should have a negative effect on the abundance of pelagic fish due to a reduction in their prey (jellyfish - Daskalov et al. 2007). I tested this hypothesis using tropho-dynamic models for the Moreton Bay ecosystem where jellyfish are abundant and

occurrences of jellyfish blooms have been reported (Matt 2007). Jellyfish fisheries have been considered as one of the solutions to the problem of jellyfish abundance in other areas (Brotz et al 2016). I therefore simulated this solution to the case of Moreton Bay, to include overfishing of jellyfish and test the hypothesis.



Figure 20: Signed digraph of conceptual model used to design the study.

+ = goes in same direction (e.g. when the ocean warms up then jellyfish abundance increases); - = goes in opposite direction (e.g. when fishing increases then abundance of fish decreases); -,+ = either is possible depending on other factors

Methods

I used the calibrated Moreton Bay model presented in Chapter 3 to explore the scenarios of 1) overfishing of pelagic fish and 2) overfishing of jellyfish. Pelagic fish were eliminated by using a fishing mortality (F) of 5 (see Appendix 19 for data used in simulation). I simulated the fishing of jellyfish by using an F of 2. The changes in biomass for these two scenarios were compared with the baseline model. Changes in mean path length, Shannon diversity indices (hereafter referred to as diversity indices) and the total system throughput (TST) between the two scenarios were compared and a single-factor ANOVA was performed to determine any differences. "*The mean path length is calculated as the total number of trophic links divided by the number of pathways*" (Finn 1976). "*The diversity indices measure the diversity of species and are based on the concept of evenness*" (Spellerberg, 2008). "*The TST in the sum of all flows in the system* (*i.e. flows through consumption, exports, respiration and detritus*)" (Christensen et al. 2008).

Results

The changes in the relative biomass of the different groups for the two scenarios (1) overfished pelagic fish and (2) overfished jellyfish compared with the biomass of the baseline Moreton Bay model in Ecosim, are shown in Fig 21 and 22.

Effects of overfishing pelagic fish

When pelagic fish were overfished, there was a decrease in the biomass of sharks (62%), seabirds (53%), dolphins (27%), prawns (9%) and macrobenthos (3%) (Figure 21). The biomasses of jellyfish, demersal fish and discards increased by 130%, 116% and 67% respectively from the baseline biomass (Figure 21).



Figure 21: Percentage change in the end/start biomass for the overfished pelagic fish compared with the baseline model for the different groups



Figure22: Percentage change in the end/start biomass for the overfished jellyfish compared with the baseline model for the different groups

Effects of overfishing jellyfish

Overfishing of jellyfish resulted in a decrease of pelagic fish biomass by 17% (Figure 22), agreeing with my prediction that overfishing of jellyfish would have a negative effect on the biomass of pelagic fish. Other groups impacted negatively were seabirds, sharks and dolphins; whose biomass decreased by 16%, 10% and 7% respectively (Figure 22).

Predation mortality

To investigate the changes in biomass observed when pelagic fish are removed, I examined the predation mortality on affected groups. The predation mortality on demersal fish by pelagic fish decreased when pelagic fish were removed (Figure 23), allowing an increase in the biomass of demersal fish. The increased biomass of demersal fish resulted in an increased predation on macrobenthos and prawns as illustrated by the predation mortality plots (Figure 24), accounting for the reduced biomasses observed. The removal of pelagic fish from Moreton Bay model also resulted in a decrease the biomass of sharks, seabirds and dolphins, which are predators of pelagic

fish. The reduced biomasses of sharks, seabirds and dolphins resulted in a reduced predation on discards (Figure 25), which form part of their diet.



Figure23: Predation mortality on demersal fish by pelagic fish when pelagic fish are removed



Figure24: Predation mortality on macrobenthos and prawns by demersal fish when pelagic fish are removed



Figure25: Predation mortality on discards by seabirds, dolphins and sharks when pelagic fish are removed

Changes in mean path length, diversity indices and TST

The changes in mean path length, diversity indices and TST in the two scenarios are shown in Figure 26. The mean path length and diversity indices were significantly higher (single-factor ANOVA, p<0.05) in the scenario where pelagic fish were overfished than when the jellyfish were overfished. The TST was significantly higher (single-factor ANOVA, p<0.05) when jellyfish were overfished than when pelagic fish were overfished.



Figure26: Changes in the mean path length, Shannon diversity indices and TST in the two scenarios. No J= jellyfish overfished, No F= pelagic fish overfished.

A single-factor ANOVA performed on the mean path length, diversity indices and TST showed that there were significant differences in the mean path length, Shannon diversity indices and TST (single-factor ANOVA p= 1.34×10^{-6} ; 1.03×10^{-5} and 1.03×10^{-18} respectively; p< 0.05) between the two scenarios, overfished pelagic fish and overfished jellyfish.

Limitations

In my model, I included the jellyfish as a single group, which according to Pauly et al (2009) is a poor representation of the diversity and interaction involving jellyfish. Jellyfish also have a complex life cycle with different life-stages (Brotz et al. 2016). Due to lack of data on the different life-stages involved, I did not include the stanzas (representing different life-stages) in the models. Modelling these different life-stages is important in identifying which stages have the greatest

impact e.g. the influence of medusa on top-down control in marine ecosystems has been described in Oguz et al 2001. The different life-stages occupy different zones of the ecosystem; the polyps are benthic while the medusae are pelagic (Duarte et al. 2013). The different life-stages have different diets (Purcell and Mills 1988; Peach and Pitt 2005) which may even change as they grow (Graham and Kroutil, 2001). Thus, when the stages are included in the models, they will provide a better understanding on the role played by jellyfish in food webs and their ecosystem effects. Further, Lynam et al. (2005) and Pauly et al. (2009) have emphasized the need for inclusion of jellyfish life stages in models used for fisheries management. Incorporating seasonal variations in the models is also important as it may give contrasting outcomes, e.g. Ruzicka et al. (2007) found that consumers (pelagic fish and jellyfish) that dominate the Oregon inner shelf ecosystem differed in spring and summer.

Discussion

It is evident from the results that, when pelagic fish were fished out of Moreton Bay model, there was an increase in the biomasses of jellyfish, demersal fish and discards. Jellyfish form part of the diet of pelagic fish and therefore the removal of pelagic fish reduced the predation pressure on jellyfish, resulting in an increase in jellyfish biomass. The biomass of demersal fish increased due to reduced predation from pelagic fish as illustrated in the predation mortality (Figure 23). The increased biomass of demersal fish resulted in the decreased biomass of prawns and macrobenthosas as their predation mortalities increased. The removal of pelagic fish from the Moreton Bay model also resulted in the decreased biomass of their predators, sharks, seabirds and dolphins (Blaber and Wassenberg 1989; Taylor 2007; Ansmann 2011). The decreased biomass of sharks, seabirds and dolphins, in turn, caused the increase in biomass of discards, as predation on discards by these groups decreased (illustrated in the predation mortalities in Fig 25) (Blaber and Wassenberg 1989; Ansmann 2011). Other studies have also associated jellyfish blooms with overfishing (Jackson et al. 2001; Daskalov 2002; Arai 2005). Fishing releases jellyfish from predation and competition by removing their predators and competitors, and modify the ecosystem to suit proliferation of jellyfish (Purcell et al. 2007). It has also been shown that abundance of jellyfish reduces production of fish and marine mammals (Brodeur et al. 2011).

From the results, overfishing of jellyfish caused a decrease in the biomass of pelagic fish. Jellyfish form part of the diet of pelagic fish, thus when jellyfish are removed, pelagic fish biomass decreased. This decrease had an impact on the charismatic megafauna that prey on pelagic fish;

seabirds, sharks and dolphins, which represent the top predators in the Moreton Bay ecosystem. However, these findings are contrary to the findings by Brodeur et al. (2011), that reduction of jellyfish favours fish, seabirds and marine mammals. This contrast in the results may be due to the seasonality changes, which they incorporated in their model. I did not include seasons in my model. I also did not include fish larval stages that have been shown to be negatively impacted through consumption by jellyfish (Brodeur et al. 2002).

Studies on the effects of overfishing jellyfish are lacking. Following from other studies, low jellyfish abundance gives rise to increased fisheries production due to reduced competition for zooplankton prey and reduced predation on fish eggs and larvae by jellyfish (Purcell and Arai 2001; Brodeur 2002; Purcell 2003; Hay 2006). For the case of Moreton Bay model, there was a relatively little change in the zooplankton biomass when either fish or jellyfish were removed (Figs. 2 and 3). Thus, it may be possible that the zooplankton prey is abundant and productivity is high to maintain the zooplankton biomass. It has been shown that pelagic fish will only be negatively impacted when jellyfish biomass is high, if prey is limited (Ruzicka et al. 2007).

There were significant differences in the mean path length, diversity indices and TST between the two scenarios. The mean path length was significantly higher when pelagic fish were overfished than when jellyfish were overfished. Vasconcellos et al (1997) found that mean path length is negatively correlated to recovery time of an ecosystem that is perturbed. Thus, the case where the path length is high, it takes less time for the ecosystem to recover after perturbation. This means that when pelagic fish are removed, the ecosystem will recover faster following perturbation compared to when jellyfish are removed. From the diet matrix (Chapter 3, Table 6), pelagic fish prey on several groups, but removal of jellyfish which impact directly on zooplankton and indirectly on phytoplankton and many more feeding pathways related to these two groups. It is likely that a feedback loop (Jiang et al. 2008) related to these interactions could have caused the observed results on mean path length and diversity index. It also follows that these changes could have an indirect effect on the diversity. When pelagic fish were removed, the diversity is higher, possibly due to increased biomass of prey groups. The low diversity indices resulting from the removal of jellyfish may be because of the more groups that were impacted by removal of jellyfish. The lower TST that resulted from removal of pelagic fish means that there were fewer flows through the system, possibly, as pelagic fish are predators at much higher level than jellyfish, removal of pelagic fish results in less flows through the system (Odum, 1969).

Even though jellyfish blooms have been associated with overfishing (Jackson et al. 2001), there are varied views about how they occur. One view is that there may be different triggers of jellyfish blooms at a local level and broader triggers affect each locale differently (Gibbons et al. 2016). Another view is that globally, jellyfish blooms occur in oscillations of about 20 years and becoming more frequent in recent years (Condon et al. 2013). The increased oscillations in the 1990s reflected an increase in the abundance of jellyfish worldwide (Condon et al. 2013). Eradication of jellyfish has been successful in some places e.g. Hawaii, but in other areas has been less successful e.g. in the Mediterranean Sea (Brotz 2016). To address the problem of jellyfish abundance, jellyfish fisheries has been considered as an option. However, some authors caution that jellyfish fisheries may have unforseen impacts on the ecosystem. This is because of dramatic biomass fluctuations, short fishing seasons and the complex life cycle of jellyfish that makes inclusion of life stages (e.g. the pelagic medusa and the benthic polyps) difficult to model and predict effects of fishing pressure (Omori and Nakano, 2001; Brotz 2016). Other concerns have been raised over jellyfish fisheries, these include that: i) there is the potential for increased mortality on juvenile fish because of bycatch associated with jellyfish fishing. It has been documented that many species of juvenile fishes associate with jellyfish, using medusae as food and shelter from predators. (Kingsford 1993; Purcell and Arai 2001; Hay 2006); ii) turtles may be further threatened by the depletion of a major food source; jellyfish are consumed by turtles (leatherback) and this is an endangered species (Brotz et al. 2016); iii) there is the potential for increased mortality on benthic animals since jelly falls are a source of food for benthic animals (e.g. crustaceans and echinoderms) (Henschke et al. 2013; Sweetman et al. 2014).

Even though incidences of jellyfish blooms are not frequent in Moreton Bay, present factors such as nutrients inputs through rivers, increased development (solid structures), increased shipping activities that could increase alien species, changing climate and fishing pressure; promote suitable conditions for jellyfish proliferation (Pitt et al. 2005, Attrill et al. 2007, Boero et al. 2016). In some areas, jellyfish fisheries have been proposed with the aim of either exploiting the resource sustainably, or to reduce the population size of jellyfish in order to bring the recovery of valuable finfish populations (Gibbons et al. 2016). My results reveal that the effects of overfishing jellyfish in Moreton Bay may have negative impacts on not only pelagic fish but also on other top predators, which are important in structuring the ecosystem. Thus, jellyfish. Other ways may be considered for reducing jellyfish blooms such as (1) reducing eutrophication (through reduction of nutrient inputs), (2) changing design and surface characteristics of artificial structures, which have been linked with increased polyps abundance (such on coastal areas) (Duarte et al. 2013).

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Chapter 7

General Discussion

Outline

Overfishing has been identified as one of the major threats to marine ecosystems. Despite legislation and regional and international collaborations specifically designed to address the problem of overfishing, it continues to be a major challenge to managers and stakeholders. My thesis focused on two key areas related to overfishing: discards and selective overfishing. Using models, I addressed management challenges in these key areas and filled knowledge gaps in the field of ecosystem dynamics. Below I outline highlights of each chapter and then I synthesise the thesis; outline limitations not previously addressed within each chapter and I finally suggest avenues for future research.

Synthesis of findings

From a global analysis of the effects of discards, it was clear that the production of discards increased ecosystem functions (productivity, respiration and consumption) (Chapter 2). Discards impacted on both top-down control (Chapter 2) and bottom-up interactions (Chapter 2 and 4) – two core functions of marine ecosystems. Discards also affected the stability of marine ecosystems (Chapter 4). Selective overfishing impacted on top-down control through predator release with effects cascading through the food web (Chapter 5 and 6). All these effects influenced the ecosystem structure and function, and the consequences manifested on the ecosystem health are likely to affect the goods and services provided by ecosystems. Figure 27 is a diagram of the key concepts emerging from the thesis.

There have been several alternate views about top-down control and bottom up interactions in marine ecosystems. For example, higher trophic levels may be partly controlled by primary production and bottom-up processes (Ryther 1969, Chassot et al. 2007, Chassot et al. 2010, Friedland et al. 2012). Alternatively, top predators may indirectly affect lower trophic levels through trophic cascades (Parsons 1992, Estes et al. 1998, Paine 2002). Different components of the ecosystem may therefore exert either top down or bottom up control depending on their position in the food web (Duffy et al. 2007). Top down and bottom up interactions may occur



Figure 27: Conceptual diagram synthesising the concepts investigated in this thesis.

simultaneously rather than singly, and their relative importance may not be easily discernible (Verheye and Richardson 1998). The findings in Chapters 2 and 4 demonstrate how discards can play a role in influencing these two key processes.

First, discards result in changes in predator prey interactions that benefit top predators, which in turn may exert more top-down control in the trophic interactions (Fondo et al. 2015). Second, the trophic level of charismatic mega-fauna (seabirds, dolphins, and sharks) decreased in the presence of discards (as illustrated in Figure 28) while their number of feeding pathways increased (Fondo et al. 2015). The lowering of trophic levels is particularly important in the lower trophic levels where bottom-up interactions that involve discards, primary production, detritus and nutrient cycling come into play (Dickman et al. 2008). These interactions affect the transfer efficiency and production in the ecosystem (Fondo et al. 2015).



Figure28: Diagram showing the lowering of trophic level for dolphins.

In the absence of discards the trophic level of dolphins is 4.34, they feed on pelagic fish which are a lower trophic level. In the presence of discards, dolphins can feed on discards (Hill and Wassenberg 1990) which are at the lowest trophic level of the food web, in addition to feeding on the pelagic fish which also feed on discards, lowering trophic level (3.96).

		MB 1	MB 2
	Functional group	TL	TL
1	Seabirds	3.79	4.18
2	Dolphins	3.96	4.34
3	Sharks	4.26	4.32
4	Pelagic fish	3.50	3.51

 Table 10: The trophic levels (TL) for the groups in the models with discards (MB 1) and without discards
 (MB 2) from the Ecopath models

Table 10 above shows the number of pathways and trophic levels for the two models: with discards (MB 1) and without discards (MB 2) for the top 4 functional groups, where differences were observed. Here, I focus on the trophic levels to further elaborate on the differences observed from the two models for the top predators in the presence and absence of discards.

The concept of trophic levels was introduced by Lindeman (1942). In Ecopath, the trophic levels are not necessarily integers (1, 2, 3...) as proposed by Lindeman, but can be fractional (e.g., 1.3, 2.7, etc.) as suggested by Odum and Heald (1975). A routine assigns definitional trophic levels (TL) of 1 to producers and detritus and a trophic level of 1 + [the weighted average of the preys' trophic level] to consumers (Christensen et al 2008).

Following this approach, a consumer eating 40% plants (with TL = 1) and 60% herbivores (with TL = 2) will have a trophic level of 1 + [0.4 * 1 + 0.6 * 2] = 2.6. The trophic level is a dimensionless index (Christensen et al 2008).

For the three top predators (seabirds, dolphins and sharks), difference were noticed in the trophic levels in the models with and without discards. For example, in the absence of discards the trophic level of dolphins is 4.34, they feed on pelagic fish, which are at a lower trophic level. In the presence of discards, dolphins can feed on discards (Hill and Wassenberg 1990) which are at the lowest trophic level of the food web (1), in addition to feeding on the pelagic fish, which also feed on discards, lowering trophic level (3.96).

From the diet matrix for MB 2 (without discards) in Chapter 4, Table 8, dolphins consume a proportion of 0.78 pelagic fish at trophic level 3.51 and a proportion of 0.22 omnivores at trophic level 2.75. The trophic level will be:

1 + [0.78*3.51 + 0.22*2.75] = 4.34

From the diet matrix for MB 1 (with discards) in Chapter 3, Table 6, dolphins consume a proportion of 0.63 of pelagic fish at trophic level 3.5; a proportion of 0.22 omnivores at trophic level 2.75 and a proportion of 0.15 of discards at trophic level 1, will have a trophic level of:

1 + [0.63*3.5+0.22*2.75+0.15*1] = 3.96

Trophic level is related to an important ecosystem function, the Food chain efficiency which determines the transfer efficiency and energy flow through the TLs and eventually affects the productivity and ecosystem services (Dickman et al. 2008). Changes at any TL are likely to be translated to other TLs and alter energy transfer through the ecosystem (Dickman et al. 2008). Trophic level is also important in relation to PPR to sustain the catches (Pauly and Christensen, 1995). Pauly and Christensen (1995) demonstrated that commercialised fisheries that operate at higher TLs exhibit high PPR 24.2- 35.3% and such a high PPR will starve top predators many of which are charismatic species. Therefore, such changes in TLs observed in the models are likely to have consequences and exploitation of fishery resources need to be managed.

The role of discards in ecosystems

1. Increase ecosystem functions

These ecosystem functions include consumption, respiration and production (as demonstrated in Chapter 2). Ramsay et al. (1997) demonstrated consumption in the ecosystem increases when discards become available to scavengers and subsidize marine food webs. Discards can then lead to an increase of the consumer population, depending on the amount, temporal variability of discards and the life history of the scavenger species (Ramsay et al. 1997). If the timing of the extra food production matches important periods in the life cycle, or coincides with periods of food shortage, local and/or temporal positive effects on populations of these species are possible (Groenewold and Fonds 2000). Increased consumer populations may lead to top-down changes to occur in the ecosystem (Polis et al. 1996). If consumers include large numbers of top predators, they may suppress the lower trophic level prey species leading to trophic imbalances with far-reaching effects (Polis et al. 1996).

Discards may provide upto 11% of respiratory requirements in an ecosystem (Smith, 1985). Pauly and Christensen (1995) estimated that the PPR catches in tropical shelves and coastal systems (which are ecosystems where intense/commercialised fishing occurs with large amounts of discards) to be about 24.2 - 35.3% and recommended rebuilding the biomasses of groups down the food web to sustain the fisheries.

If production in the ecosystem increases, this means a more productive ecosystem i.e. better provision goods and services by the ecosystem (to some extent). Groenewold & Fonds 2000, demonstrated that discards increased production rates particularly in benthic scavengers. Unutilised discards become organic matter that is transferred back into the food web of the benthic ecosystem; leading to higher ecological efficiency, and therefore, to higher secondary production. Discards can also form resuspended organic matter, which becomes an important food source for demersal filter feeders (Groenewold and Fonds 2000).

2. Alter predator prey interactions, trophic levels and food webs

Discards may alter predator prey interactions and lead to changes in structure of the ecosystem, and trigger trophic cascades (Crowder et al. 1998). Discards consumed at different trophic levels may alter trophic levels this relates to transfer efficiency of the ecosystem, therefore may affect the fisheries and provision of goods and services (Bellido et al. 2011; Fondo et al. 2015). If food webs are altered also results in modification of structure and functions of the ecosystem, affecting sustainability and resilience of the ecosystem (Zhou et al. 2010).

3. Reduction of discards

When removed gradually from the ecosystem, opportunistic species are able to switch prey (Fondo et al. 2015). Removal of discards can have consequences on the opportunistic species they support. Some opportunistic species such as seabirds and mammals have become adapted to discards and a sudden ban can have both direct and indirect effects on these species (Heath et al. 2014; Sardà et al. 2015). However, when removed gradually, opportunistic species are able to switch prey (Fondo et al. 2015). A sudden ban on discards will also lead to loss of biomass ad production in the exploited ecosystem; as discards represent biomass that is removed and immediately returned to the exploited ecosystem (Sardà et al. 2015).; as well as reduction of food supply at various trophic levels (Heath et al. 2014).

Selective overfishing

Selective fishing alters biodiversity, which in turn changes ecosystem functioning and may affect fisheries production, and hinder the achievements of EBM goals (Zhou et al. 2010). Altering ecosystem structure can in turn result in changes to ecosystem function including energy flow, element recycling, species interactions, productivity, and resilience (Coleman and Williams 2002; Zhou et al. 2010). Changes to ecosystem function may then affect sustainability of fisheries (Zhou et al. 2010).

Overfishing of predators has been a major concern in the recent years. In Chapter 5, it was shown that the consequences of overfishing pelagic fish were an increased jellyfish biomass and a negative impact on charismatic megafauna; emphasizing the important role played by pelagic fish in maintaining healthy ecosystems and supporting top predators. Overfishing of predators at lower trophic level (e.g. crabs) had negative impacts on higher trophic level predators, decreasing their biomass. This in turn may affect top-down control. These findings demonstrate that predators at all trophic levels play a key role in ecosystem structure and maintaining healthy ecosystems.

Small reduction in the abundance of common species can cause major losses in individuals and biomass (Gaston and Fuller 2008). These losses (such as demonstrated in Chapter 5) can significantly disrupt ecosystem structure, function and services (Gaston and Fuller 2008). With the threat of climate change, the effects of predator removal on marine ecosystems are likely to worsen, considerably affecting the provision of good and services (Baum and Worm 2009; Atwood et al. 2015). Further, climate change together with other factors such as pollution and coastal development are likely to increase the frequencies of jellyfish blooms thus threatening the health of marine ecosystem (Purcell 2012).

In Chapter 6, when either fish or jellyfish were removed there was relatively little change in the biomass of the zooplankton prey. This lack of change may be related to the primary productivity (phytoplankton) that is able to maintain the zooplankton biomass in Moreton Bay. Several studies have shown that decreased jellyfish abundance promotes fish production due to reduced competition for prey and predation on fish eggs and larvae by jellyfish (Purcell and Arai 2001; Brodeur et al. 2002; Purcell 2003; Hay 2006). Generally, predators of jellyfish are few (about 11 specialist species) and do not have a great impact on jellyfish biomass (Pauly et al. 2009). Thus, jellyfish are prone to have a greater bottom-up control through consumption of zooplankton than top-down control through their predators (Pauly et al. 2009). Since they have few predators, jellyfish robs off production at higher trophic level by consuming zooplankton and become an important energy pathway (Lynam 2005; Ruzicka et al.

2007). Findings by Brodeur et al. (2011) showed that jellyfish have a major impact on lower trophic levels species while translating relatively little production to higher levels in the food web.

Limitations

One major limitation to my research on discards was the lack of data on discards in global fisheries. In many marine ecosystems discards are not recorded or monitored. The last global update of discards (state of discards in the world) was about two decades ago by Kelleher (2005). More recently, estimates on discards have been done using reconstructed data (Pauly and Zeller, 2016) but more monitoring of the discards is required to adequately address research on discards. Due to lack of discard data, many ecosystem models have not included discards as a functional group. This resulted in having very limited number of models to work with in Chapter 2. With this limitation there were few data to work with and this restricted further analysis with different manipulations and combination of variables.

Lack of specific data on species (biomasses and diet changes over time) resulted in poor estimates for input parameters in the models in Chapter 3. Better estimates of crucial data e.g. diet composition of major components is paramount for energy budgets and network analysis (Christensen and Walters 2004) - without this information, flows can only be crudely estimated (most diet studies cover only certain megafauna, probably those of commercial or conservation concern). Inclusion of other less studied species (lower trophic level species, non-target species and non-commercial species) would give a better understanding of the roles played by these species in the ecosystem.

In Chapter 2, I only used the static Ecopath models which gave limited results. It would have been better to have the Ecosim models, as it would have been possible to simulate the effects of discard presence and absence in a dynamic system, which would give more interesting and detailed results for which to include in the meta-analysis. Thus repeating the analysis with the Ecosim models is a potential research topic.

Future research

Findings from Chapter 4 showed that the presence of discards, lowered the trophic levels of opportunistic species, which were top predators, and this finding has implications in the way energy is transferred through the ecosystem and the ultimate goods and services provided (Baird et al. 1991). It has been shown that small changes in trophic level can have marked effects on the flow networks

marine ecosystems (Baird et al. 1991). It is therefore recommended that future research investigate on how food subsidies affect the transfer efficiency of the ecosystem.

Since discarding has been going for centuries, there is a possibility that the composition of discards has been changing over time that could result in shifting regimes of marine ecosystems (Tomczak et al. 2013). In Moreton Bay for example, studies show that in the 1960's, fish (cardinal fish and stripped flathead) dominated the discards (Maclean 1972). In 1990's sand crabs dominated the discards (Wassenberg and Hill, 1990). Such changes in discard composition may be an indication of fishing pressure – *"fishing down the food web"* (Pauly et al. 1998). Thus it would be worth investigating how changes in the composition of discards have affected ecosystems in terms of if the species benefiting from the two eras were different, the changes in ecosystem functions such prey-predator relationships and competition, and if there were regime shifts (such as those described by Tomczak et al. (2013)) resulting from the changes in discards composition.

Differences in the life stages of long-lived late maturing megafauna is important in their population dynamics (Crowder et al. 1994). In addition they are migratory and fisheries can impact on them at various stages of their life cycle. To determine which fisheries and gears are likely to result in the largest negative consequences is important (Wallace et al. 2008). Thus it will be important to model the spatial distribution (in Ecospace – Christensen and Walters 2004) of these groups in the ecosystem in addition to the models developed in Chapters 4-6.

In fishing operations, overfishing of predators occurs simultaneously with discarding (FAO, 2014). Thus incorporating the effects of predator removal in combination with discards reduction or ban would give further predictions of the real world situation where both removal of predators and discarding occur simultaneously. In addition, more studies on the effects of predator removal at different trophic levels incorporating other effects such as climate change, habitat change, nutrient inputs is also recommended. It has been shown that over fishing may affect food-chain length, an attribute that regulates ecosystem services (Dickman et al. 2008). It is therefore important that future studies investigate how overfishing of predators affect the food chain length, transfer efficiency and ecological efficiency, which are crucial for ecosystem services.

Conclusion

- 1. In conclusion, discards promote ecosystem functions (productivity, respiration and consumption);
- 2. Charismatic mega-fauna scavenge and may become dependent on discards thus a gradual reduction rather than a complete ban on discards is recommended where charismatic mega-fauna have become dependent on discards;
- 3. Overfishing of marine predators disrupts the structure and function of marine ecosystems and in some cases resulting in jellyfish blooms. In order to maintain the structure and health of marine ecosystems, it is necessary to regulate overfishing of predators, reduce nutrient inputs, regulate coastal development and regulate anthropogenic activities that promote climate change.
- 4. Fishing jellyfish may have an effect on major top predators, thus fishing jellyfish may not be a desirable management option in some areas.
- 5. The problems addressed in this thesis provide settings linked to the Sustainable Development goals of the Agenda 2030 in particular Goals 2, food security (i.e. sustainable fisheries and providing food); 12, efficient use of natural resources and waste reduction (i.e. well managed fisheries and addressing selective fishing) and 14, conservation and sustainable use of marine resources.

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Appendix 1

List of EcoBase models

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Appendix 2

Ecological thermodynamic rules used for balancing the models

The following rules were used as guidelines (Darwall et al. 2010; Heymans et al 2016) for balancing the models after removing discards from the original models:

1. Ecotrophic Efficiency (EE) is less than 1.0: The EE can never be more than 1 as it is not possible for more biomass to be passed on to the next trophic level than was originally produced—unless the population is in decline. As a guideline an EE close to 1 is expected when the main part of production is consumed by predators or the fishery. A value near to 0 is expected for a group, such as an apex predator, which suffers no predation and is not exploited by a fishery.

2. Gross food conversion efficiency (P/Q) normally has a value of between 0.1 and 0.3 (0.1 < P/Q < 0.3). Values greater than 0.5 are not often found but may be encountered in groups such as bacteria or in specially bred farmed fish. Juveniles have higher P/Q than adults. If P/B change then so should Q/B because P/Q is relatively constant.

3. Net Efficiency is less than P/Q: Net Efficiency is the value for food conversion after accounting for unassimilated food for which the Ecopath default value is 20%. Therefore the Net Efficiency can never exceed P/Q.

4. Respiration/Assimilation (R/A) is less than 1.0: Assimilation = R + P, so the proportion of biomass lost through respiration cannot exceed the biomass of food assimilated. As a guideline k-selected species which are expected to invest a relatively small proportion of energy intake in tissue production are expected to have R/A ratios close to 1.0. reselected species are more likely to invest a greater proportion of energy intake into growth and reproduction resulting in an R/A ratio well below 1.0

5. Production/Respiration (P/R) is less than 1.0: This ratio effectively expresses the fate of assimilated food. Odum (1969) stated that P/R, which is typically less than 1, approaches 1 as the system matures.

6. Respiration/Biomass (R/B): Indicates the "metabolic activity level" of a group. R/B are expected to be within 1–10 per year for fish and may be as high as 50–100 per year for groups with higher turnover such as copepods. The default value for the proportion of unassimilated food (20%) may be changed to better reflect the R/B ratio value expected of the group in question.

7. Diets are modified to ensure mass-balance.

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Appendix 3

Changes made to the diet matrix of Al	batross Bay model (Okey et al, 2007)
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Functional group	Diet	Change
Dolphins	Large teleost benth invert	Increased proportion by
	feeders	0.005 from discards
Octopus	Marine worms	Proportion increased by
		0.005
Octopus	Estuarine meiofauna	Proportion increased by
		0.002 from discards
Banana prawn	Marine bivalves	Proportion increased by
subadults		0.007
Banana prawn	Marine small crustaceans	Proportion increased by
subadults		0.005
Banana prawn	Marine worms	Proportion increased by
subadults		0.005
Banana prawn adult	Stomatopods	Proportion increased by
		0.008 from discards
Banana prawn adult	Marine small crustaceans	Proportion increased by
		0.005 from discards
Banana prawn adult	Marine worms	Proportion increased by
		0.005 from discards
All other commercial	Marine Sediment Detritus	Proportion increased by
prawns		0.003 from discards
Thallasinid prawns	Marine Sediment Detritus	Proportion increased by
(Callianassa)		0.003 from discards
All other nono-	Marine Water - column	Proportion increased by
comercial prawns	detritus	0.001 from discards
All other nono-	Marine Sediment Detritus	Proportion increased by
comercial prawns		0.001 from discards
The mud crab	Marine Sediment Detritus	Proportion increased by
		0.001 from discards
Sand crab	Marine small crustaceans	Proportion increased by
		0.001 from discards

Large gastropods	Estuarine worms	Proportion increased by
		0.009 from discards
Large gastropods	Estuarine small gastropods	Proportion increased by
		0.001 from discards
Echinoids	Estuarine Sediment detritus	Proportion increased by
		0.002 from discards
Echinoids	Marine Sediment Detritus	Proportion increased by
		0.001 from discards
Asteriods	Microphytobenthos	Proportion increased by
		0.02 from discards
Asteriods	Estuarine macroalgae	Proportion increased by
		0.01 from discards
Asteriods	Marine macroalgae	Proportion increased by
		0.01 from discards
Asteriods	Detached Marine	Proportion increased by
	macrophytes	0.01 from discards
Asteriods	Detached Estuarine	Proportion increased by
	macrophytes (estuarine)	0.01 from discards
Asteriods	Estuarine Sediment detritus	Proportion increased by
		0.02 from discards
Asteriods	Marine Sediment Detritus	Proportion increased by
		0.02 from discards
Large gastropods	Import diet	Proportion increased by
		0.002 from discards

Bay of Biscay Model (Lassalle et al, 2012)

Functional group		Diet	Change	
Pursuit	divers	Suprabenthivorous	Increased proportion by 0.02 from	
seabirds		demersal fish	the discards	
Pursuit	divers	Mackerel	Increased proportion by 0.02 from	
seabirds			discards	
Pursuit	divers	Horse mackerel	Increased proportion by 0.02 from	
seabirds			discards	

Pursuit divers	Anchovy	Increased proportion by 0.01 from
seabirds		discards
Pursuit divers	Sprat	Increased proportion by 0.02 from
seabirds		discards
Surface feeders	Horse mackerel	Increased proportion by 0.05 from
seabirds		discards
Surface feeders	Sardine	Increased proportion by 0.14 from
seabirds		discards
Surface feeders	Sprat	Increased proportion by 0.05 from
seabirds		discards
Surface feeders	Macrozooplankton	Increased proportion by 0.05 from
seabirds		discards
Piscivorous and	Sardine	Increased proportion by 0.01 from
benthivorous		discards
demersal fish		
Piscivorous and	Benthic cephalopods	Increased proportion by 0.01 from
benthivorous		discards
demersal fish		
Benthivorous	Piscivorous and	Increased proportion by 0.01 from
demersal fish	benthivorous demersal	discards
	fish	
Carnivorous	Benthic cephalopods	Transferred to Detritus to reduce the
benthic		raised EE of benthic cephalopods
invertebrates		that was causing an imbalance.
Carnivorous	Detritus	Proportion increased by 0.004 from
benthic		benthic cephalopods and 0.01 from
invertebrates		discards.
Necrophagous	Detritus	Increased proportion by 0.02 from
benthic		discards
invertebrates		

Central Gulf of California (Arregun Sánchez et al, 2002)

Functional group Diet Chang	ge
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Sea birds	Carangidae	Increased proportion by 0.01 from discards
Sea birds	Clupaeidae	Increased proportion by 0.1 from discards
Sea birds	Zooplankton	Increased proportion by 0.003 from
		discards
Scombridae	Myctophidae	Increased proportion by 0.03 from discards
Scombridae	Detritus	Increased proportion by 0.01 from discards
Sharks/Rays	Other	Increased proportion by 0.02 from discards
	macrocrus	
Sharks/Rays	Shrimp	Increased proportion by 0.01 from discards
Sharks/Rays	Zooplankton	Increased proportion by 0.002 from
		discards
Carangidae	Phytoplankton	Increased proportion by 0.001 from
		discards
Serranidae	Lutjanidae	Transferred 0.01 of the proportion to
		zooplankton to reduce the high EE of
		Lutjanidae that caused an imbalance
Serranidae	Zooplankton	Increased by 0.01 from Lutjanidae and
		0.0147 from discards
Serranidae	Detritus	Increased proportion by 0.01 from discards
Other fish	Detritus	Increased proportion by 0.0099 from
		discards
Other macrocrus	Detritus	Increased proportion by 0.001 from
		discards
Crabs	Detritus	Increased proportion by 0.001 from
		discards

East Bass Strait (Bulman et al, 2006)

Functional group	Diet	Change
Seal Whiting		Proportion increased by 0.06 from
		discards
Seal	ShSmlnvertFeeder	Proportion increased by 0.0002 from
		discards
Seal	Squid	Proportion increased by 0.05 from
		discards

Seabirds	Macrobenthos	Proportion increased by 0.02 from
		discards
Seabirds	Gelatinous nekton	Proportion increased by 0.032 from
		discards
Demersal sharks	Rays	Proportion increased by 0.005 from
		discards
Demersal sharks	Blue-eye trevalla	Proportion increased by 0.008 from
		discards
Demersal sharks	PelMPredator	Proportion increased by 0.01 from
		discards
Rays	Sm Zooplnkton	Proportion increased by 0.01 from
		discards
ShMedPredator	Macrobenthos	Proportion increased by 0.003 from
		discards

Eastern Bering Sea Model (Trites et al, 1999) - No changes were made, the model did not have any values for discards.

Georges Bank Model (Link et al , 2008)

Functional group	Diet	Change				
Macrobenthos-	Macrobenthos-	Increased	proportion	by	0.002	from
polychaetes	crustacea	discards				
Macrobenthos-	Macrobenthos-	Increased	proportion	by	0.001	from
polychaetes	molluscs	discards				
Macrobenthos-	Macrobenthos-	Increased	proportion	by	0.001	from
polychaetes	other	discards				
Macrobenthos-	Megabenthos-	Increased	proportion	by	0.001	from
polychaetes	filterers	discards				
Macrobenthos-	Megabenthos-	Increased	proportion	by	0.001	from
polychaetes	other	discards				
Macrobenthos-	Phytoplankton-	Increased	proportion	by	0.009	from
crustacea	Primary	discards				
	producers					

Macrobenthos-	Phytoplankton-	Increased proportion by 0.005 from
molluscs	Primary	discards
	producers	
Macrobenthos-	Bacteria	Increased proportion by 0.001 from
molluscs		discards
Macrobenthos-	Phytoplankton-	Increased proportion by 0.01 from discards
other	Primary	
	producers	
Macrobenthos-	Bacteria	Transferred 0.2 of the proportion to detritus
other		to adjust for the high EE of bacteria
Megabenthos-	Bacteria	Increased proportion by 0.02 from discards
other		
Megabenthos-	Macrobenthos-	Increased proportion by 0.0195 from
other	polychaetes	discards
Megabenthos-	Macrobenthos-	Increased proportion by 0.008 from
other	molluscs	discards
Megabenthos-	Demersals-	Increased proportion by 0.0002 from
other	omnivores	discards
Megabenthos-	Demersals-	Increased proportion by 0.0003 from
other	piscivores	discards
Shrimp et al.	Bacteria	Transferred 0.2 of the proportion to detritus
		to adjust for the high EE of bacteria
Shrimp et al.	Detritus- POC	Increased proportion by 0.0616 from
		discards and 0.2 from bacteria
Demersals-	Gelatinous	Increased proportion by 0.005 from
benthivores	Zooplankton	discards
Demersals-	Demersals-	Increased proportion by 0.008 from
benthivores	piscivores	discards
Demersals-	Detritus- POC	Increased proportion by 0.005 from
benthivores		discards
Sea Birds	Large Copepods	Increased proportion by 0.0055 from
		discards
Sea Birds	Micronekton	Increased proportion by 0.061 from
		discards

Sea Birds	Small	Pelagics-	Increased proportion by 0.05 from discards
	anadro	mous	

Gironde Estuary Model (Lobry, 2004)

Functional group	Diet	Change
Suprabenthos	Primary producers	Proportion increased by 0.29
		from discards
Meiobenthos	Primary producers	Proportion increased by 0.335
		from discards
Mullets	Primary producers	Proportion increased by 0.1
		from discards
Mullets	Meiobenthos	Proportion increased by 0.175

Gulf of Carpentaria Model (Okey et al, 2007)

Functional	Diet	Change
group		
Holothurians	Sediment	Transferred 0.2 of the proportion to each group
	Detritus	of other prey
Ophioroids	Zooplnkton	Increased proportion by 0.1 from water
		column detritus to adjust high EE
Ophioroids	Microbial	Increased proportion by .149 from sediment
	heterotrophs	detritus to adjust for high EE of sediement
		detritus
Ophioroids	Phytoplankton	Increased proportion by 0.3 from sediment
		detritus to adjust the high EE of detritus
Ophioroids	Sediment	Transferred proportions to Phytoplankton,
	Detritus	Microbial heterotrophs and Zooplankton
Bivalves	Sediment	Transferred proportions to
	Detritus	Microphytobenthos(.01), Phytoplankton (0.2)
		and Microbial heterotrophs (0.2)
Meiofauna	Sediment	Transferred 0.2 and 0.24 of the proportion to
	Detritus	Microphytobenthos and Microbial
		heterotrophs respectively

Microbial	Water column	Transferred proportion to Microphytobenthos
heterotrophs	detritus	and Phytoplankton to adjust for high EE
Microbial	Sediment	Transferred 0.2 and 0.29 to microphytobenthos
heterotrophs	Detritus	and phytoplankton respectively

Gulf of Maine Model (Link et al, 2009)

Functional group	Diet	Change
Macrobenthos-	Macrobenthos-	Increased proportion by 0.003
polychaetes	molluscs	from discards
Macrobenthos-	Macrobenthos- other	Increased proportion by
polychaetes		0.0029 from discards
Macrobenthos-	Micronekton	Increased proportion by 0.003
crustaceans		from discards
Macrobenthos-	Macrobenthos- other	Increased proportion by 0.002
crustaceans		from discards
Macrobenthos-	Demersals- omnivores	Increased proportion by 0.002
crustaceans		from discards
Macrobenthos- molluscs	Phytoplankton-	Increased proportion by 0.002
	Primary producers	from discards
Macrobenthos- molluscs	Micronekton	Increased proportion by 0.002
		from discards
Macrobenthos- molluscs	Macrobenthos- other	Increased proportion by 0.002
		from discards
Macrobenthos- other	Phytoplankton-	Increased proportion by 0.005
	Primary producers	from discards
Macrobenthos- other	Bacteria	Increased proportion by 0.002
		from discards
Macrobenthos- other	Micronekton	Increased proportion by 0.002
		from discards
Megabenthos- other	Bacteria	Increased proportion by 0.002
		from discards

Megabenthos- other	Megabenthos-	Increased proportion by 0.002
	filterers	from discards
Megabenthos- other	Demersals-	Increased proportion by 0.001
	benthivores	from discards
Megabenthos- other	Demersals- omnivores	Increased proportion by 0.002
		from discards
Megabenthos- other	Detritus- POC	Increased proportion by 0.03
		from discards
Shrimp et al.	Phytoplankton-	Increased proportion by 0.003
	Primary producers	from discards
Shrimp et al.	Micronekton	Increased proportion by 0.003
		from discards
Shrimp et al.	Macrobenthos- other	Increased proportion by 0.02
		from discards
Shrimp et al.	Detritus- POC	Increased proportion by 0.05
		from discards
Demersals- benthivores	Detritus- POC	Increased proportion by 0.012
		from discards
Demersals- omnivores	Detritus- POC	Increased proportion by
		0.0226 from discards
Sea Birds	Small Pelagics- other	Increased proportion by 0.05
		from discards
Sea Birds	Small Pelagics-	Increased proportion by 0.029
	anadromous	from discards

Irish Sea Model (Lees and Mackinson, 2007)

Functional group	Diet	Change
Seabirds	Other Small Gadoids	Increased proportion by 0.05
		from discards
Seabirds	Small Pelagic	Increased proportion by 0.05
	Planktivorous Fish	from discards
Epifaunal Macrobenthos	Infaunal Macrobenthos	Increased proportion by 0.01

		from discards
Epifaunal Macrobenthos	Sessile Epifauna	Increased proportion by 0.01
		from discards
Epifaunal Macrobenthos	Gelatinous	Increased proportion by
	Zooplankton	0.001 from discards
Infaunal Mesobenthos	Carnivorous	Increased proportion by
	Zooplankton	0.001 from discards
Infaunal Mesobenthos	Omnivorous	Increased proportion by
	Zooplankton	0.001 from discards
Infaunal Mesobenthos	Herbivorous	Increased proportion by
	Zooplankton	0.001 from discards
Infaunal Mesobenthos	Phytoplankton	Increased proportion by 0.05
		from discards
Infaunal Mesobenthos	Detritus- Particulate	Increased proportion by 0.05
	Organic matter	from discards

Jalisco and Colima Model (Galván Piña, 2005)

Functional group	Diet	Change
Mamiferos marin	Otros peces	Increased proportion by 0.01
		from discards
Mamiferos marin	Gasterosteidos	Increased proportion by 0.005
		from discards
Mamiferos marin	Peneidos	Increased proportion by 0.01
		from discards
Mamiferos marin	Zooplankton	Increased proportion by 0.01
		from discards
Escombridos	Detritus	Increased proportion by 0.013
		from discards
Tiburones	Ophididos	Increased proportion by 0.01
		from discards
Tiburones	Moluscos	Increased proportion by 0.01
		from discards
Tiburones	Zooplankton	Increased proportion by 0.02
		from discards

Sierra	Otros peces	Increased proportion by 0.003
		from discards
Sierra	Sardinas	Increased proportion by 0.01
		from discards
Sierra	Zooplankton	Increased proportion by 0.02
		from discards
Anguilas y more	Haemulidos	Increased proportion by 0.005
		from discards
Anguilas y more	Tetraodontidos	Increased proportion by 0.01
		from discards
Anguilas y more	Pulpo	Increased proportion by 0.01
		from discards
Anguilas y more	Infauna	Increased proportion by 0.05
		from discards
Anguilas y more	Braquiuros	Increased proportion by 0.05
		from discards
Synodontidos	Haemulidos	Increased proportion by 0.02
		from discards
Synodontidos	Ophididos	Increased proportion by 0.02
		from discards
Synodontidos	Peneidos	Increased proportion by 0.02
		from discards
Synodontidos	Infauna	Increased proportion by 0.008
		from discards
Carangidos	Zooplankton	Increased proportion by 0.01
		from discards
Carangidos	Detritus	Increased proportion by 0.001
		from discards
Aves marinas	Gerreidos	Increased proportion by 0.05
		from discards
Aves marinas	Zooplankton	Increased proportion by 0.05
		from discards
Aves marinas	Infauna	Increased proportion by 0.001
		from discards

Tortugas marina	Otros crustaceo	Increased proportion by 0.001
		from discards
Tortugas marina	Otros macroinve	Increased proportion by 0.001
		from discards
Serranidos	Fitoplancton	Increased proportion by 0.02
		from discards
Serranidos	Detritus	Increased proportion by 0.007
		from discards
Otros peces	Detritus	Increased proportion by 0.005
		from discards
Gasterosteidos	Otros crustaceo	Increased proportion by 0.002
		from discards
Gasterosteidos	Peneidos	Increased proportion by 0.002
		from discards
Gasterosteidos	Infauna	Increased proportion by 0.002
		from discards
Haemulidos	Juveniles Lutja	Increased proportion by 0.003
		from discards
Tetraodontidos	Scianidos	Increased proportion by 0.02
		from discards
Tetraodontidos	Gasterosteidos	Increased proportion by 0.022
		from discards
Tetraodontidos	Estomatopods	Increased proportion by 0.02
		from discards
Ophididos	Estomatopods	Increased proportion by 0.001
		from discards
Ophididos	Moluscos	Increased proportion by 0.001
		from discards
Ophididos	Equinodermos	Increased proportion by 0.002
		from discards
Ophididos	Detritus	Increased proportion by 0.002
		from discards
Rayas	Tetraodontidos	Increased proportion by 0.02
		from discards

Rayas	Detritus	Increased proportion by 0.015 from discards
Pleuronectidos	Moluscos	Increased proportion by 0.007 from discards
Otros crustaceo	Fitoplancton	Increased proportion by 0.011 from discards
Braquiuros	Infauna	Increased proportion by 0.003 from discards
Braquiuros	Detritus	Increased proportion by 0.002 from discards

Low Barent Sea Model (Blanchard et al, 2002)

Functional group	Diet	Change					
Birds	Pelagic	Increased proportion by 0.002 from					
	planktivorous	discards					
	fish						
Lobsters crabs	Other	Increased proportion by 0.05 from discards					
	crustaceans						
Lobsters crabs	Meiofauna	Increased proportion by 0.05 from detritus					
Lobsters crabs	Benthic micro-	Increased proportion by 0.05 from discards					
	organisms						
Lobsters crabs	Benthic	Reduced proportion by half to adjust for					
	Detritus	the high EE that caused imbalance					
Other crustaceans	Infaunal filter	Increased proportion by 0.03 from discards					
	feeders						
Other crustaceans	Meiofauna	Increased proportion by 0.02 from discards					
Prawns and shrimps	Carnivorous	Increased proportion by 0.02 from discards					
	zooplankton						
Prawns and shrimps	Infaunal filter	Increased proportion by 0.01 from discards					
	feeders						
Prawns and shrimps	Herbivorous	Increased proportion by 0.01 from discards					
	zooplankton						
Prawns and shrimps	Phytoplankton	Increased proportion by 0.01 from discards					
Meiofauna	Infaunal filter	Increased proportion by 0.005 from					
		feeders	discards				
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Meiofauna		Planktonic	Increased	proportion	by	0.005	from
		micro-	discards				
		organisms					
Meiofauna		Benthic	Increased	proportion	by	0.005	from
		Detritus	discards				
Benthic	micro-	Water	Increased	proportion	by	0.013	from
organisms		coulumn	discards				
		detritus					
Benthic	micro-	Benthic	Increased	proportion	by	0.002	from
organisms		Detritus	discards				

Mid-Atlantic Bight Model (Link et al, 2008)

Functional group	Diet	Change
Mesopelagics	Phytoplankton-	Increased proportion by
	Primary producers	0.0202 from discards
Mesopelagics	Bacteria	Increased proportion by 0.002
		from discards
Mesopelagics	Microzooplankton	Increased proportion by
		0.0003 from discards
Mesopelagics	Small copepods	Increased proportion by 0.004
		from discards
Macrobenthos-	Macrobenthos-	Increased proportion by 0.001
polychaetes	crustaceans	from discards
Macrobenthos-	Macrobenthos-	Increased proportion by 0.002
polychaetes	molluscs	from discards
Macrobenthos-	Macrobenthos- other	Increased proportion by 0.002
polychaetes		from discards
Macrobenthos-	Megabenthos- filterers	Increased proportion by 0.001
polychaetes		from discards
Macrobenthos-	Macrobenthos-	Increased proportion by 0.002
crustaceans	polychaetes	from discards
Macrobenthos-	Macrobenthos-	Increased proportion by 0.002
crustaceans	molluscs	from discards

Macrobenthos-	Macrobenthos- other	Increased proportion by 0.002
crustaceans		from discards
Macrobenthos-	Megabenthos- filterers	Increased proportion by 0.002
crustaceans		from discards
Macrobenthos- molluscs	Phytoplankton-	Increased proportion by 0.002
	Primary producers	from discards
Macrobenthos- molluscs	Bacteria	Increased proportion by 0.002
		from discards
Macrobenthos- molluscs	Megabenthos- filterers	Increased proportion by 0.002
		from discards
Megabenthos- other	Macrobenthos-	Increased proportion by 0.005
	polychaetes	from discards
Megabenthos- other	Macrobenthos-	Increased proportion by 0.005
	crustaceans	from discards
Megabenthos- other	Megabenthos- filterers	Increased proportion by 0.01
		from discards
Megabenthos- other	Demersals- benthivore	Increased proportion by 0.01
		from discards
Megabenthos- other	Demersals- omnivores	Increased proportion by 0.003
		from discards
Shrimp et al.	Phytoplankton-	Increased proportion by 0.01
	Primary producers	from discards
Shrimp et al.	Bacteria	Increased proportion by 0.01
		from discards
Shrimp et al.	Micronekton	Increased proportion by 0.007
		from discards
Shrimp et al.	Macrobenthos-	Increased proportion by 0.01
	crustaceans	from discards
Demersals- benthivore	Gelatinous	Increased proportion by 0.005
	Zooplankton	from discards
Demersals- benthivore	Micronekton	Increased proportion by 0.002
		from discards
Demersals- benthivore	Macrobenthos-	Increased proportion by 0.003
	polychaetes	from discards

Demersals- benthivore	Detritus	Increased proportion by 0.004
		from discards
Demersals- omnivores	Macrobenthos-	Increased proportion by 0.01
	polychaetes	from discards
Demersals- omnivores	Demersals- benthivore	Increased proportion by 0.01
		from discards
Demersals- omnivores	Demersals- piscivores	Increased proportion by 0.006
		from discards
Sharks- coastal	Gelatinous	Increased proportion by 0.008
	Zooplankton	from discards
Sharks- coastal	Micronekton	Increased proportion by 0.02
		from discards
Sharks- coastal	Macrobenthos-	Increased proportion by 0.02
	crustaceans	from discards
Sea Birds	Small Pelagics-	Increased proportion by 0.05
	commercial	from discards
Sea Birds	Small Pelagics- other	Increased proportion by 0.05
		from discards
Sea Birds	Small Pelagics-	Increased proportion by 0.024
	anadromous	from discards

Moreton Bay refer to Fondo et al., 2015 for the model without discards.

Ningaloo Model (Jones et al 2011)

Functional group	Diet	Change
Foxes	Hatchlings	Increased proportion by 0.002
		from discards
Foxes	Litter	Increased proportion by 0.005
		from discards
Ospreys	Crabs	Increased proportion by 0.01
		from discards
Ospreys	Shells	Increased proportion by 0.01

OspreysZooplanktonIncreased proportion by 0.01 from discardsOspreysLitterIncreased proportion by 0.02 from discardsCoastal seabirdSmall reef fishIncreased proportion by 0.01 from discardsCoastal seabirdKing prawnIncreased proportion by 0.0078 from discardsCoastal seabirdKing prawnIncreased proportion by 0.0078 from discardsCoastal seabirdBanana prawnIncreased proportion by 0.0019 from discardsCoastal seabirdCrabsIncreased proportion by 0.0019 from discardsCoastal seabirdCrabsIncreased proportion by 0.01 from discardsCoastal seabirdBenthosIncreased proportion by 0.02 from discardsCoastal seabirdZooplanktonIncreased proportion by 0.02 from discardsCoastal seabirdLitterIncreased proportion by 0.01 from discardsDolphinsZooplanktonIncreased proportion by 0.01 from discards
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from discards
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from discards
Pelagic sharksDetritusIncreased proportion by 0.001
from discards

North Aegean Model (Tsagarakis et al, 2010)

Functional group	Diet	Change
Suprabenthos	Phytoplankton	Increased proportion by 0.002 from discards
Suprabenthos	Mesozooplankton	Increased proportion by 0.002 from discards

Suprabenthos	Polychaetes	Increased proportion by 0.001
		from discards
Shrimps	Mesozooplankton	Increased proportion by 0.002
		from discards
Shrimps	Macrozooplankton	Increased proportion by 0.002
		from discards
Shrimps	Detritus	Increased proportion by 0.011
		from discards
Crabs	Macrozooplankton	Increased proportion by 0.005
		from discards
Crabs	Benthic invert. (no	Increased proportion by 0.005
	crustacea)	from discards
Other gadiforms	Polychaetes	Increased proportion by 0.005
		from discards
Other gadiforms	DemeFish4	Increased proportion by 0.005
		from discards
Other gadiforms	Detritus	Increased proportion by 0.002
		from discards
Sharks	Shrimps	Increased proportion by 0.001
		from discards
Sharks	Crabs	Increased proportion by 0.002
		from discards
Sharks	Adult anchovy	Increased proportion by 0.002
		from discards
Sharks	Juv sardine	Increased proportion by 0.002
		from discards
Sharks	Adult sardine	Increased proportion by 0.002
		from discards
Rays and Skates	Horse mackerel	Increased proportion by 0.004
		from discards
Rays and Skates	Other Small pelagic	Increased proportion by 0.004
	fishes	from discards
Loggerhead turtle	Jellyfish +	Increased proportion by 0.082
	mnemiopsis	from discards

Loggerhead turtle	Crabs	Increased proportion by 0.1
		from discards
Loggerhead turtle	Benthic invert. (no	Increased proportion by 0.1
	crustacea)	from discards
Sea birds	Benthopelagic	Increased proportion by 0.05
	cephalopods	from discards
Sea birds	Juv sardine	Increased proportion by 0.05
		from discards
Sea birds	Adult sardine	Increased proportion by 0.05
		from discards
Sea birds	Other Small pelagic	Increased proportion by 0.005
	fishes	from discards

Northern British Columbia (Ainsworth et al, 2002)

Functional group	Diet	Change
Odontocetae	Transient salmon	Increased proportion by 0.001
		from discards
Odontocetae	Coho salmon	Increased proportion by 0.002
		from discards
Odontocetae	Juvenile POP	Increased proportion by 0.001
		from discards
Odontocetae	Adult	Increased proportion by 0.001
	planktivorous	from discards
	rockfish	
Odontocetae	Adult halibut	Increased proportion by 0.001
		from discards
Odontocetae	Large crabs	Increased proportion by 0.001
		from discards
Odontocetae	Euphausiids	Increased proportion by 0.001
		from discards
Seabirds	Transient salmon	Increased proportion by 0.001
		from discards
Seabirds	Forage fish	Increased proportion by 0.01
		from discards

Seabirds	Juvenile herring	Increased proportion by 0.01
		from discards
Seabirds	Adult herring	Increased proportion by 0.01
		from discards
Seabirds	Small crabs	Increased proportion by 0.01
		from discards

Northern Californian Current Model (Field et al, 2006)

Functional group	Diet	Change
Dungeness	Juv rock	Increased proportion by 0.005
		from discards
Dungeness	Juv round	Increased proportion by 0.005
		from discards
Dungeness	Juv flat	Increased proportion by 0.005
		from discards
Dungeness	Small flat	Increased proportion by 0.005
		from discards
Sablefish	Infauna	Increased proportion by 0.01
		from discards
Sablefish	Benthic shp	Increased proportion by 0.01
		from discards
Sablefish	Detritus	Increased proportion by 0.01
		from discards
Ssthorny	Infauna	Increased proportion by 0.01
		from discards
Ssthorny	Amphipods	Increased proportion by 0.01
		from discards
Ssthorny	Epibenthic	Increased proportion by 0.01
		from discards
Ssthorny	Carniv-zoops	Increased proportion by 0.002
		from discards
Ssthorny	Benthic shp	Increased proportion by 0.01
		from discards

Gulls	Epibenthic	Increased proportion by 0.02
		from discards
Gulls	Euphausiids	Increased proportion by 0.02
		from discards
Gulls	Carniv-zoops	Increased proportion by 0.02
		from discards
Gulls	Mesopelagics	Increased proportion by 0.01
		from discards
Gulls	Juv rock	Increased proportion by 0.01
		from discards
Gulls	Small flat	Increased proportion by 0.005
		from discards

Raja Ampat Model (Pitcher et al, 2007)

Functional	Diet	Change				
group						
Birds	Mackerel	Increased	proportion	by	0.001	from
		discards				

Senegambia Model (Samb and Mendy, 2004)

Functional group	Diet	Change
Oiseaux marins	Sardinelle rond	Increased proportion by 0.05
		from discards
Oiseaux marins	Sardinelle plat	Increased proportion by 0.05
		from discards
Mammiferes marin	Autres pelagiqu	Increased proportion by 0.05
		from discards
Mammiferes marin	Zooplancton	Increased proportion by 0.05
		from discards
Thonides du lar	Cephalopodes	Increased proportion by 0.05
		from discards
Thonides cotier	Cephalopodes	Increased proportion by 0.025
		from discards

Southern New England Model (Link et al, 2008)

Functional group	Diet	Change
Macrobenthos-	Detritus- POC	Proportion increased by
polychaetes		0.006 from discards
Macrobenthos-	Demersals- benthivores	Proportion increased by
crustaceans		0.007 from discards
Macrobenthos-	Megabenthos- filterers	Proportion increased by
molluscs		0.005 from discards
Macrobenthos- other	Demersals- benthivores	Proportion increased by
		0.005 from discards
Macrobenthos- other	Detritus- POC	Proportion increased by
		0.005
Megabenthos- other	Macrobenthos-	Proportion increased by
	polychaetes	0.05 from discards
Megabenthos- other	Detritus- POC	Proportion increased by
		0.002 from discards
Shrimp et al.	Phytoplankton- Primary	Proportion increased by
	Producers	0.05 from discards
Shrimp et al.	Detritus- POC	Proportion increased by
		0.007 from discards
Demersals- benthivores	Demersals- omnivores	Proportion increased by
		0.01 from discards
Demersals- benthivores	Detritus- POC	Proportion increased by
		0.003 from discards
Demersals- omnivores	Gelatinous Zooplankton	Proportion increased by
		0.015 from discards
Demersals- omnivores	Micronekton	Proportion increased by
		0.01 from discards
Sharks- coastal	Small Pelagics-	Proportion increased by
	commercial	0.02 from discards
Sharks- coastal	Small Pelagics- other	Proportion increased by
		0.02 from discards
Sharks- coastal	Medium Pelagics-	Proportion increased by
	(pisciovres and others)	0.019 from discards

Sea Birds	Small	Pelagics-	Proportion	increased	by
	commercial		0.05 from di	scards	
Sea Birds	Demersals- pisc	ivores	Proportion	increased	by
			0.001 from a	liscards	

Tasmanian Waters (Watson et al, 2013) - no changes made, the proportions of discards in the diets was small that removal caused no changes to the model.

r		
Functional	Diet	Change
1 uneuonui	Diet	Change
group		
group		
Charles	Desfielt	In an and man article by 0.007 from discourds
Snarks	Dogiisn	increased proportion by 0.007 from discards
Sharks	Herring	Increased proportion by 0.005 from discards
Sharks	Mackerel	Increased proportion by 0.004 from discards
Seabirds	Cod iuv	Increased proportion by 0.05 from discards
Scabilus	Cou juv	increased proportion by 0.05 from diseards
Coobinda	Sandaala	Increased properties by 0.04 from discords
Seabilius	Sandeers	increased proportion by 0.04 from discards
~ · · · ·	ã	
Seabirds	Sprat	Increased proportion by 0.005 from discards
	-	
Seabirds	Mackerel	Increased proportion by 0.1 from discards
2 cuentas		increased proportion of our norm discurds

Western Channel Model (Araújo et al, 2005)

Metadata used for the meta-analysis

year	citation.year	citation.author	research.group	publicatio	discard.B	fisheries	aquacultu	environm	structure	pollution	species.o	keystone.
2002	2002	Ainsworth et al	Ainsworth	report	0.07	1	0	0	1	0	0	0
2005	2005	Araújo et al	Araújo	report	0.3	1	0	1	1	0	0	0
2002	2002	Arreguin Sánchez et al	Arreguin Sánchez	journal	0.647	1	0	0	1	0	1	0
2002	2002	Blanchard et al	Blanchard	report	0.02	1	0	0	1	0	1	0
2006	2006	Bulman et al	Bulman	report	0.166	1	0	0	1	0	1	0
2006	2006	Field et al	Field	journal	1.422	1	0	0	1	0	0	0
2015	2015	Fondo et al	Fondo	journal	2	1	0	0	1	0	1	0
2005	2005	Galván	Galván	report	8.62	1	0	0	1	0	0	0
2011	2011	Jones et al	Jones	report	0.278	1	0	0	1	0	0	1
2012	2012	Lassalle et al	Lassalle	journal	43.5	1	0	0	0	0	0	0
2007	2007	Lees & Mackinson	Lees	report	0.192	1	0	0	1	0	0	0
2008	2008a	Link et al	Link	journal	1.263	1	0	0	1	0	1	1
2008	2008c	Link et al	Link	report	0.97	1	0	0	1	0	0	0
2009	2009	Link et al	Link	journal	0.44	1	0	0	1	0	0	0
2008	2008b	Link et al	Link	journal	0.478	1	0	0	1	0	1	1
2004	2004	Lobry	Lobry	report	10.11	0	0	0	1	0	0	0
2007	2007	Okey	Okey	report	1.93	1	0	0	1	0	1	0
2006	2006	Okey	Okey	report	1.93	1	0	0	1	0	1	0
2007	2007	Pitcher	Pitcher	report	0.034	1	0	0	0	0	0	0
2004	2004	Samb & Mendy	Samb	report	0.001	1	0	0	0	0	0	0
1999	1999	Trites et al	Trites	report	0	1	0	0	1	0	1	0
2010	2010	Tsagarakis et al	Tsagarakis	journal	0.49	1	0	0	1	0	0	1
2013	2013	Watson et al	Watson	journal	0.006	1	0	1	1	0	0	0

ecopath	ecosim	ecospace	stanza.gro	number.grou	groups	model.ye	model.ye	duration	duration3	area	area3	depth	depth3
1	0	0	1	53	3	2000	2000	0	1	70	2	200	2
1	1	0	1	52	3	1993	1995	2	1	56.45	2	100	2
1	1	0	0	27	2	1978	1979	1	1	27.9	2	65	1
1	1	0	1	41	2	1990	1990	0	1	1400	3	230	2
1	1	1	0	59	3	1994	1994	0	1	30.26	2	700	3
1	1	0	1	65	3	1960	2004	44	3	70	2	1280	3
1	1	0	0	18	1	1990	2013	23	3	3.5	1	10	1
1	1	0	1	38	2	1995	1996	1	1	0.7	1	90	1
1	1	0	1	53	3	2007	2007	0	1	10.4	2	20	1
1	1	0	0	32	2	1994	2005	11	2	102.58	3	150	2
1	1	0	1	53	3	1973	1973	0	1	58	2	150	2
1	0	0	0	32	2	1996	2000	4	1	59.8	2	300	2
1	0	0	1	33	2	1996	2000	4	1	64.06	2	300	2
1	0	0	1	31	2	1996	2000	4	1	79.12	2	200	2
1	0	0	0	31	2	1996	2000	4	1	43.66	2	200	2
1	0	0	0	18	1	1991	1998	7	2	0.63	1	35	1
1	1	0	1	83	4	1990	1990	0	1	370.2	3	70	1
1	1	1	1	99	4	1986	1992	6	2	5.78	1	40	1
1	1	1	1	98	4	1990	1990	0	1	45	2	200	2
1	0	1	0	18	1	1990	1990	0	1	27.6	2	200	2
1	1	0	0	25	1	1955	1960	5	2	484.5	3	500	3
1	0	0	1	40	2	2003	2006	3	1	8.37	1	300	2
1	1	0	0	47	2	1993	2007	14	2	137	3	300	2

ecosyster	ecosyster	ecosyste	latitude	latitude3	Pred.B	Pred.b	Tot.Y	Tot.y	Pred.Y	Pred.y	TST	tst	T.product	t.producti
bay	marine	benthic	30_58	2	6.35	6.35	2.17	2.07	0.46	0.44	3.85	3.85	3.5	3.5
bay	marine	mixed	30_58	2	2.55	2.55	1.74	1.37	0.34	0.26	3.86	3.85	3.53	3.53
bay	marine	benthic	0_30	1	2.37	2.41	18.35	16.69	0.81	0.27	3.67	3.67	3.36	3.36
shelf	marine	mixed	58_90	3	6.89	12.26	0.32	0.28	0.3	0.27	3.71	3.71	3.28	3.28
shelf	marine	mixed	30_58	2	32.13	27.64	0.76	0.42	0.58	0.31	4.21	4.21	3.9	3.9
shelf	marine	mixed	30_58	2	32.56	32.77	6.12	3.28	3.39	1.77	4.2	4.37	3.88	3.88
bay	marine	benthic	30_58	2	0.48	0.56	0.25	0.17	0.01	0.01	3.41	3.41	3.11	3.11
shelf	marine	mixed	0_30	1	12.54	13.18	22.13	4.87	1.56	1.52	3.9	3.9	3.58	3.58
shelf	marine	benthic	0_30	1	2.15	1.64	0.78	0.22	0.17	0.08	3.83	3.82	3.38	3.38
shelf	marine	mixed	30_58	2	835.34	835.35	85.84	85.84	64.21	64.21	5.87	5.97	5.46	5.61
shelf	marine	mixed	30_58	2	8.28	8.51	2.18	1.8	1.48	1.29	4.39	4.37	3.96	3.96
shelf	marine	mixed	30_58	2	12.97	13.64	7.31	4.79	1.19	0.78	4.21	4.19	3.79	3.79
shelf	marine	mixed	30_58	2	25.48	26.1	4.98	3.04	1.31	0.69	4.25	4.24	3.85	3.85
shelf	marine	mixed	30_58	2	12.37	12.42	2.74	1.85	1.62	1.14	4.12	4.13	3.73	3.92
shelf	marine	mixed	30_58	2	23.51	23.51	2.62	1.66	1.19	0.67	4.21	4.2	3.81	3.81
bay	freshwate	benthic	30_58	2	20.72	20.72	51.35	31.13	9.11	8.32	5.84	5.29	4.84	4.92
bay	marine	mixed	0_30	1	31.97	59.16	0.27	0.01	0.17	0.01	4.52	4.54	3.99	4
bay	marine	mixed	0_30	1	7.34	7.35	4.01	0.16	3.03	0.04	4.31	4.2	3.82	3.82
shelf	marine	mixed	0_30	1	9.81	9.93	3.06	2.99	0.71	0.7	3.93	3.92	3.6	3.6
shelf	marine	mixed	0_30	1	1.02	1.36	16.99	16.99	0.36	0.55	4.43	4.43	4.11	4.11
shelf	marine	mixed	30_58	2	12.53	13.17	2.61	0	0.34	0	3.76	3.76	3.41	3.41
shelf	marine	mixed	30_58	2	2.97	2.99	2.83	1.85	1.06	0.75	3.29	3.25	2.9	2.9
shelf	marine	benthic	30_58	2	3.6	3.6	0.12	0.11	0.02	0.02	3.25	3.25	2.94	2.94

MTLc	mtlc	G.efficien	g.efficien	TPP	tpp	TPP.TR	tpp.tr	SYS.Produ	sys.Produ	TPP.TB	tpp.tb	TB.TST	tb.tst	ТВ
3.297	3.29	0.0007	0.0007	3.44	3.44	2.49	2.49	3.22	3.22	22.15	22.15	0.017	0.017	125.4
2.781	2.712	0.0005	0.0004	3.46	3.46	4.78	3.77	3.36	3.33	15.01	15.01	0.026	0.027	196.33
2.986	2.978	0.0102	0.0098	3.23	3.23	1.38	1.38	2.68	2.68	25.22	25.22	0.014	0.014	68.79
4.111	4.276	0.0002	0.0002	3.04	3.04	1.03	0.99	1.56	0	9.24	9.24	0.022	0.022	118.95
3.936	3.9	0.00	0	3.84	3.84	2.27	2.42	3.59	3.61	28.7	28.7	0.014	0.015	243.61
3.522	3.504	0.0007	0.0004	3.82	3.82	2.71	2.7	3.62	3.62	25.57	25.57	0.016	0.01	258.86
2.556	2.522	0.0002	0.0001	3.09	3.09	11.66	11.66	3.05	3.05	19.43	19.43	0.024	0.024	63.97
2.521	3.076	0.0046	0.0016	3.46	3.46	1.93	1.86	3.14	3.13	12.92	12.05	0.028	0.029	225.02
2.801	2.956	0.0002	0.0001	3.3	3.3	1.07	1.02	2.14	1.65	19.16	19.59	0.015	0.015	106.25
3.753	3.809	0.0006	0	5.28	5.28	0	1.09	0	4.23	34.82	34.82	0.007	0.005	5517.01
3.659	3.715	0.0002	0.0002	3.91	3.91	6.82	4.52	3.84	3.8	34.8	34.8	0.009	0.009	237.79
2.631	2.657	0.0014	0.0011	3.62	3.62	1.27	1.1	2.96	2.59	25.87	25.87	0.01	0.01	164.31
2.902	2.916	0.0008	0.0006	3.68	3.68	1.2	1.06	2.9	2.48	27.23	27.23	0.009	0.01	178.1
3.578	3.58	0.0006	0.000284	3.55	3.81	1	1.67	1.48	3.42	25.54	41	0.01	0.01	141.28
3.187	3.11	0.0005	0.0003	3.63	3.63	1.13	1.01	2.69	1.67	24.81	24.81	0.01	0.01	172.12
3.109	3.142	0.0009	0	4.65	4.65	0	1.01	0	2.89	21.51	21.51	0.003	0.011	2116
3.674	3.776	0.00	0	3.72	3.72	0.84	0.54	0	0	8.08	7.5	0.019	0.02	657.81
3.758	3.393	0.0004	0	3.68	3.68	2.11	1.34	3.4	3.08	22.49	22.49	0.01	0.013	212.99
3.168	3.173	0.0008	0.0008	3.54	3.54	2.82	2.82	3.35	3.35	16.6	16.59	0.024	0.025	212.67
2.771	2.783	0.0014	0.0014	4.06	4.06	2.4	2.4	3.82	3.82	42.14	42.14	0.01	0.01	272.68
3.294	3.294	0.0013	0.0013	3.28	3.28	1.08	1.08	2.18	2.18	7.5	7.5	0.043	0.043	255.95
3.474	3.523	0.0043	0.0034	2.72	2.72	1.98	1.23	2.42	2	16.2	16.2	0.016	0.018	33.04
3.088	3.098	0.0001	0.0001	2.85	2.85	3.09	3.09	2.68	2.68	14.99	14.99	0.026	0.026	47.51

tb	CI	ci	SOI	soi	pedigree	fleet	fleet3	MTE	D.MTE	mte	D.mte	PPR.harve	D.PPRh
125.4	0.167	0.166	0.219	0.217	0.22	19	2	15.6	5 2	15.6	2	2.78	2
196.33	0.169	0.168	0.125	0.12	0.39	9	1	11.7	2	11.6	2	2.66	2
68.79	0.244	0.23	0.326	0.307	0.18	4	1	12.8	8 2	12.5	2	2.51	2
118.95	0.207	0.203	0.228	0.216	0.13	6	1	18.2	2	21.1	2	1.88	1
243.61	0.175	0.173	0.283	0.245	0.28	11	2	NA	0	NA	0	NA	0
258.86	0.185	0.184	0.161	0.153	0.21	7	1	16.1	. 2	15.9	2	3.32	2
63.97	0.218	0.199	0.274	0.23	0.31	5	1	8.1	. 1	7.8	1	0.96	1
241.26	0.278	0.263	0.227	0.208	0.3	3	1	17.4	2	17.2	2	2.24	2
103.89	0.23	0.225	0.227	0.223	0.44	48	2	NA	0	NA	0	NA	0
5517.01	0.213	0.206	0.194	0.187	0.6	1	1	23.8	8 2	12.5	2	4.94	2
237.79	0.222	0.221	0.331	0.313	0.33	9	1	NA	0	20.4	0	NA	0
164.31	0.354	0.342	0.27	0.267	0.41	1	1	15	2	15.1	2	1.54	1
178.1	0.334	0.323	0.302	0.296	0.39	1	1	15.5	2	15.7	2	1.64	1
159.15	0.34	0.329	0.29	0.284	0.4	1	1	15.6	j 2	15.6	2	1.43	1
172.12	0.344	0.334	0.277	0.268	0.41	1	1	13.1	. 2	12.9	2	1.2	1
2116	0.249	0.25	0.124	0.127	0.35	2	1	16	j 2	7.3	2	4.31	2
708.19	0.164	0.159	0.207	0.228	0.457	10	2	NA	0	NA	0	NA	0
212.98	0.14	0.138	0.232	0.231	0.413	8	1	NA	0	NA	0	NA	0
212.67	0.265	0.263	0.431	0.435	0.41	17	2	NA	0	NA	0	NA	0
272.68	0.246	0.23	0.139	0.12	0.39	2	1	e	5 1	6.4	1	3.4	2
255.95	0.296	0.296	0.156	0.156	0.34	1	1	13.5	2	13.5	2	2.64	2
33.04	0.286	0.281	0.175	0.177	0.61	5	1	17.4	2	17.2	2	1.87	1
47.51	0.164	0.163	0.458	0.458	0.25	16	2	11.3	2	11.3	2	1.14	1

ppr.harve	D.pprh	PPR.cons	D.PPRc	ppr.consu	D.pprc
2.74	2	3.78	2	3.78	2
2.61	2	3.64	2	3.64	2
2.44	2	3.46	2	3.46	2
1.96	1	3.79	2	3.87	2
NA	0	NA	0	NA	0
3.17	2	4.17	2	4.17	2
0.88	1	2.42	1	2.43	1
2.04	2	3.76	2	3.8	2
NA	0	NA	0	NA	0
4.71	2	6.13	2	6.14	2
1.87	0	NA	0	3.91	0
1.44	1	4.02	2	4.03	2
1.56	1	4.1	2	4.1	2
1.34	1	4.02	2	4.11	2
0.97	1	3.99	2	4.11	2
4.25	2	5.43	2	5.45	2
NA	0	NA	0	NA	0
NA	0	NA	0	NA	0
NA	0	NA	0	NA	0
3.42	2	4.25	2	4.26	2
2.64	2	3.97	2	3.97	2
1.76	1	3.17	2	3.18	2
1.1	1	2.91	1	2.91	1

Metadata definitions

title	Title of publication
year	The year the study was published
author	Author(s) of the publication
type	Type of publication e.g. a report or a paper
journal	Name of publication type
currency_units	Currency units used in the model (e.g. t/km ² /year)
time_units	Time units used in the model e.g. year or month
discards_in_fishery	Whether discards are included in the fishery
discard.B_t.km2	Biomass of discards in t/km ²
fisheries	Was the study focus on fisheries
aquaculture	Was the study focus on aquaculture
environment	Was the study focus on the environment
	Was the study focus on structure and function of the
structure_function	ecosystem
pollution	Was the study focus on pollution
	Was there a focus on a particular species of importance (icon
species_of_interest	species)
keystone_analysis	Was a keystone analysis done
ecopath	Was Ecopath used in the study
ecosim	Was Ecosim used in the study
ecospace	Was Ecospace used in the study
stanza_groups	Were stanza groups included in the functional groups
number_groups	The number of functional groups in the model
groups	0 1
groups	Group categories
model_year_start	Group categories The start year of the model
model_year_start model_year_end	Group categories The start year of the model The end year of the model
model_year_start model_year_end area	Group categories The start year of the model The end year of the model Area (size) of the ecosystem studied
model_year_start model_year_end area Area	Group categories The start year of the model The end year of the model Area (size) of the ecosystem studied Area category
model_year_start model_year_end area Area depth	Group categories The start year of the model The end year of the model Area (size) of the ecosystem studied Area category Mean depth of the ecosystem study
model_year_start model_year_end area Area depth Depth	Group categories The start year of the model The end year of the model Area (size) of the ecosystem studied Area category Mean depth of the ecosystem study Depth category
model_year_start model_year_end area Area depth Depth ecosystem_type	Group categories The start year of the model The end year of the model Area (size) of the ecosystem studied Area category Mean depth of the ecosystem study Depth category Type of ecosystem

ecosystem_description	If modelled area is pelagic, benthic or mixed
latitude	Latitude location of the ecosystem
Latitude	Latitude category
Pred_B	Predator (TL>2.5) biomass with discards
Pred_b	Predator (TL>2.5) biomass without discards
Tot_Y	Total catch with discards
Tot_y	Total catch without discards
Pred_Y	Predator catch with discards
Pred_y	Predator catch without discards
TST	Total system throughput with discards
tst	Total system throughput without discards
T_production	Total system production with discards
t_production	Total system production without discards
MTLc	Mean trophic level of the catch with discards
mtlc	Mean trophic level of the catch without discards
G_efficiency	Gross efficiency with discards
g_efficiency	Gross efficiency without discards
TPP	Total primary production with discards
tpp	Total primary production without discards
TPP_TR	Total primary production/ Total respiration with discards
tpp_tr	Total primary production/ Total respiration without discards
SYS_Production	System production with discards
sys_Production	System production without discards
TPP_TB	Total primary production/ Total biomass with discards
tpp_tb	Total primary production/ Total biomass without discards
TB_TST	Total biomass/ Total system throughput with discards
tb_tst	Total biomass/ Total system throughput without discards
TB	Total biomass with discards
tb	Total biomass without discards
CI	Connectance index with discards
ci	Connectance index without discards
SOI	System omnivory index with discards
soi	System omnivory index without discards
pedigree	Pedigree index

Pedigree	Category for pedigree index
fleet	Number of fleet operating in the system
Fleet	Category of fleet
MTE	Mean transfer efficiency with discards
D_MTE	Dummie mean transfer efficiency with discards
mte	Mean transfer efficiency without discards
D_mte	Dummie mean transfer efficiency without discards
PPR_harvest	Primary production required for harvest with discards
	Dummie of primary production required for harvest with
D_PPRh	discards
ppr_harvest	Primary production required for harvest without discards
	Dummie of primary production required for harvest without
D_pprh	discards
PPR_consumption	Primary production required for consumption
D-PPRc	Dummie primary production required for consumption
ppr_consumption	Primary production required for consumption
D-pprc	Dummie primary production required for consumption

Unweighted analysis plots

Appendix 5a



(a) Random-effects forest plot of weighted summary measure of log response ratio for predator biomass with/ without discards for all the studies, (b) the corresponding covariate contributions to model fitting in the meta-analysis and (c) funnel plot analysing for publication bias.

Appendix 5b

(a)

(b)





(a) Random-effects forest plot of weighted summary measure of log response ratio for predator catch with/ without discards for all the studies, (b) the corresponding covariate contributions to model fitting in the meta-analysis and (c) funnel plot analysing for publication bias.

Appendix 5c



(a) Random-effects forest plot of weighted summary measure of log response ratio for PPR harvest with/ without discards for all the studies, (b) the corresponding covariate contributions to model fitting in the meta-analysis and (c) funnel plot analysing for publication bias.

Appendix :	5d
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(a) Random-effects forest plot of weighted summary measure of log response ratio for TPP/TR with/ without discards for all the studies, (b) the corresponding covariate contributions to model fitting in the meta-analysis and (c) funnel plot analysing for publication bias.

Appendix 5e



(a) Random-effects forest plot of weighted summary measure of log response ratio for SOI with/ without discards for all the studies, (b) the corresponding covariate contributions to model fitting in the meta-analysis and (c) funnel plot analysing for publication bias.



Graphs showing the composition of discards for two studies each with positive response for predator biomass (Jones, 2011 and Bulman, 2006), negative response (Okey, 2007 and Blanchard, 2002) and no response (Watson, 2013 and Link 2009).

Unweighted analysis plots

-0.80

-0.20

Appendix 7a

(a)

(b)

Predator biomass Author(s) and Year weight LRR [95% CI] -0.62 [-0.62 . -0.62 Okey, 2007 4.35% Blanchard et al, 2002 -0.58 -0.58, -0.58 4.35% Samb & Mendy, 2004 4.35% -0.29 [-0.29 , -0.29 Fondo et al, 2015 4.35% -0.15 [-0.15 , -0.15 Link et al. 2008a 4.35% -0.05 -0.05 -0.05 Trites et al. 1999 -0.05 [-0.05 (-0.05 4.35% Galván, 2005 4.35% -0.05 (-0.05, -0.05 ŧ. Lees & Mackinson, 2007 4.35% -0.03 [-0.03 , -0.03 -0.02 [-0.02 , -0.02 -0.02 [-0.02 , -0.02 Link et al, 2008c 4.35% Arreguin Sánchez et al, 2002 4.35% -0.01 [-0.01 , -0.01 Pitcher, 2007 4.35% Tsagarakis et al, 2010 4.35% -0.01 [-0.01 . -0.01 Field et al, 2006 .35% -0.01 [-0.01 . -0.01 ∎4 Link et al, 2009 0.00 0.00 0.00 4.35% Okey. 2006 4.35% 0.00 0.00 0.00 Lassalle et al. 2012 4.35% 0.00 0.00 0.00 Ainsworth et al, 2002 4.35% 0.00 0.00 0.00 Araújo et al, 2005 4.35% 0.00 0.00 0.00 Link et al. 2008b 4.35% 0.00 0.00, 0.00 Lobry, 2004 4.35% 0.00 0.00 0.00 Watson et al, 2013 4.35% 0.00 0.00, 0.00 Bulman et al, 2006 4.35% 0.15 0.15 0.15 Jones et al, 2011 435% 0.27 0.27 0.27 **RE Model** €00.00% -0.06 [-0.14, 0.01]

0.40





(a) Random-effects forest plot of the unweighted summary measure of log response ratio for predator biomass with/ without discards for all the studies and (b) the corresponding covariate contributions to model fitting in the meta-analysis.

Appendix 7b

(a)

Predator catch

Author(s) and Year	weight LRR [95% CI]			
Samb & Mendy, 2004 Fondo et al, 2015 Lassalle et al, 2012 Watson et al, 2013 Pitcher, 2007	4.55% -0.42 [-0.42 , -0.42] 4.55% 0.00 [0.00 , 0.00] 4.55% 0.00 [0.00 , 0.00] 4.55% 0.00 [0.00 , 0.00] 4.55% 0.01 [0.01 , 0.01] 4.55% 0.01 [0.02 , 0.02]	-		
Ainsworth et al, 2002 Lobry, 2004 Blanchard et al, 2002	 ◆ 4.55% ◆ 0.03 [0.03 , 0.03] ◆ 4.55% ◆ 0.04 [0.04 , 0.04] ◆ 4.55% ◆ 0.09 [0.09 , 0.09] ◆ 4.55% ◆ 0.14 [0.14 , 0.14] 			
Araújo et al, 2005 Tsagarakis et al, 2010 Link et al, 2009 Link et al, 2008a	 4.55% 0.27 [0.27 , 0.27] 4.55% 0.35 [0.35 , 0.35] 4.55% 0.35 [0.35 , 0.35] 4.55% 0.42 [0.42 , 0.42] 			
Link et al, 2008b Bulman et al, 2006 Link et al, 2008c Field et al, 2006	4.55% 0.57 0.57 0.57 4.55% 0.63 0.63 0.63 4.55% 0.64 0.64 0.64 4.55% 0.65 0.65 0.65			
Jones et al, 2011 Arreguin Sánchez et al, 2002 Okey, 2007 Okey, 2006	4.55% 0.75 [0.75 , 0.75] 4.55% 1.10 [1.10 , 1.10] 4.55% 2.83 [2.83 , 2.83] 4.55% 4.33 [4.33 , 4.33]			
Log Ratio of Means				

(b)

Model-averaged importance of terms



(a) Random-effects forest plot of the unweighted summary measure of log response ratio for predator catch with/ without discards for all the studies and (b) the corresponding covariate contributions to model fitting in the meta-analysis.

Appendix 7c

(a)

(b)

PPR catch Author(s) and Year weight LRR [95% CI] Blanchard et al, 2002 5.88% -0.04 [-0.04 , -0.04] • 🔶 Publication Samb & Mendy, 2004 -0.01 [-0.01 , -0.01] 5.88% i 🕪 0.00 [0.00 , 0.00] Trites et al, 1999 5.88% ÷۱. Lobry, 2004 5.88% 0.01 [0.01 , 0.01] Ecosystem.type Ainsworth et al, 2002 5.88% 0.01 [0.01 , 0.01] ٠. Araújo et al, 2005 5.88% 0.02 [0.02 , 0.02] in. Arreguin Sánchez et al, 2002 5.88% 0.03 [0.03 , 0.03] Stanzas Watson et al, 2013 5.88% 0.04 [0.04 , 0.04] -Field et al, 2006 5.88% 0.05 [0.05 , 0.05] Lassalle et al, 2012 5.88% 0.05 [0.05 , 0.05] Functional.groups Link et al, 2008c 5.88% 0.05 [0.05 , 0.05] Tsagarakis et al, 2010 5.88% 0.06 [0.06 , 0.06] -Link et al, 2009 5.88% 0.07 [0.07 , 0.07] . 0.07 [0.07 , 0.07] Link et al, 2008a 5.88% 0.09 [0.09 , 0.09] Fondo et al. 2015 5.88% 0.09 [0.09 , 0.09] Galván, 2005 5.88% Link et al, 2008b 5-88% 0.21 [0.21 , 0.21] --0.05 0.10 0.25 Log Ratio of Means

Model-averaged importance of terms



(a) Random-effects forest plot of the unweighted summary measure of log response ratio for PPR harvest with/ without discards for all the studies and (b) the corresponding covariate contributions to model fitting in the meta-analysis.

Appendix 7d

Author(s) and Year

TPP/TR

(a)

Model-averaged importance of terms LRR [95% CI] weight -0.51 [-0.51 , -0.51] -0.06 [-0.06 , -0.06] 0.00 [0.00 , 0.00] Ecosystem.type 0.00 [0.00 , 0.00]

(b)



(a) Random-effects forest plot of the unweighted summary measure of log response ratio for TPP/TR with/ without discards for all the studies and (b) the corresponding covariate contributions to model fitting in the meta-analysis.

Appendix 7e

(a)

(b)



(a) Random-effects forest plot of the unweighted summary measure of log response ratio for SOI with/ without discards for all the studies and (b) the corresponding covariate contributions to model fitting in the meta-analysis.

Effects display

Appendix 8a



Effect display for unweighted meta-regressions (for PPR harvest)





Effect display for unweighted meta-regressions (for predator biomass)





Effect display for unweighted meta-regressions (for SOI)

Appendix 8d



Effect display for unweighted meta-regressions (for TPP/TR)

Appendix 8e



Effect display for unweighted meta-regressions (for predator catch)

Table 1: Functional groups of the Moreton Bay ecosystem model

No.	Functional group	Components
1	Sea birds	Silver gulls, cormorants, crested terns*
2	Dolphins	Indo-Pacific bottlenose dolphins
3	Sharks	Carcharhinus spp
4	Pelagic fish	Trevally, Tuna, Mackerel and Whiting
5	Demersal fish	Rays, Cod, Bream, Snapper, Tailor and Flathead
6	Omnivores	Mullet and Siganus spp
7	Dugongs	Dugong dugon
8	Turtles	Green turtles
9	Sand crabs	Portunus armatus
10	Prawns	Penaeid prawns
11	Jellyfish	Scyphozoa, Catostylus mosaicus
12	Macrobenthos	Other crabs, mantis shrimps, annelids, gastropods, echinoderms
13	Zooplankton	Zooplankton
14	Seagrasses	Seagrasses
15	Macroalgae	Macroalgae
16	Phytoplankton	Phytoplankton
17	Discards	Discards
18	Detritus	Detritus

* (shorebirds (Skilleter pers. comm.) but included here based on the data sources which grouped them as seabirds)
| I able 5. Data sources for the unreferit functional group | arces for the different functional gro | unctional gro | erent func | differe | the | for | sources | Data | ble 3: | Ta |
|--|--|---------------|------------|---------|-----|-----|---------|------|--------|----|
|--|--|---------------|------------|---------|-----|-----|---------|------|--------|----|

- Functional group No. Source Sea birds (Blaber and Wassenberg, 1989); Dunning (2007); Australia Fisheries Management Authority 1 www.afma.gova.au/); (Wassenberg and Hill, 1990) 2 **Dolphins** (Ansmann et al., 2012, Ansmann Ina Christiane, 2011); (Chilvers et al., 2003); Corkeron et al. (1997); (Chilvers and Corkeron, 2001, Chilvers et al., 2005) DAFF; (Stephen, 2007) (Taylor and Bennett, 2013); FishBase; Taylor, (Pierce et al., 2011) 3 Sharks Pelagic fish DAFF; FishBase; (Kruck et al, 2009) 4 Demersal fish 5 DAFF, (Pierce et al., 2011, Kyne and Bennett, 2002); (Morton et al., 1987); FishBase; (Pollock and Williams, 1983); (Pillans, 2006); (Pollock and Williams, 1983, Pollock, 1982a, Pollock, 1982b, Morton et al., 1987 6 Omnivores Gribble 2003; (Edgar and Shaw, 1995); (Capper et al., 2006); (Budarf et al., 2011) 7 Lanyon (Lanyon et al., 2010) (2003); Edgar and Shaw, (1995); Takahashi (2008); (Preen, 1995); (Chilvers et Dugongs al., 2005); (Marsh et al., 1982); (Lanyon et al., 2010); (Perry et al., 1996); (Heinsohn et al., 1977); (Heinsohn et al., 1978); (Sheppard et al., 2006); Burgessa et al 2012; Marsh et al 1999 8 Turtles Gribble 2003; Takahashi (2008); Limpus 2008; (Limpus et al., 1994); (Brand-Gardner et al., 1999); (Arthur et al., 2007); (Kuiper-Linley et al., 2007); (Arthur et al., 2008); (Bjorndal et al., 2000); (Chaloupka et al., 2004); Bjorndal (1997); (Chaloupka, 2001, Chaloupka et al., 2004, Chaloupka and Limpus, 2001) 9 Sand crabs Courtney et al (2009); Criales-Hernandez et al 2006; DAFF; Williams, 1982; (Hill and Wassenberg, 1990):
- Weng 1992; Williams 1981; Wu & Shin 1997; Edgar 1990; (Campbell and Sumpton, 2009)
- 10PrawnsCourtney et al (2009); Courtney et al (1995); Gribble 2003; DAFF; (Barber and Lee, 1975); (Masel and
Smallwood, 2000); (Skilleter et al., 2005); Brey (2001)

11JellyfishWang 2012; Pitt & Kingsford, 2003(Pitt and Lucas, 2014); (Matt, 2007); (West et al., 2009); (Titelman et al.,2006); (Pitt and Kingsford, 2003b, Pitt and Kingsford, 2003a); Pitt et al 2007; (Pitt et al., 2007); (Peach and Pitt, 2005); (Kingsford et al.,2000); (Gershwin et al., 2010)

12 Macrobenthos Edgar & Shaw (1995); Groenewold & Fonds (2000); SeaLifeBase, Brey (2001)

13ZooplanktonGribble 2003; Schlacher et al 2009; (Jacoby and Greenwood, 1989); (Greenwood, 1981); (Carr and Pitt, 2008);(Barber and Lee, 1975); (Greenwood, 1982)

14 Seagrasses EPA 2007; (Young and Kirkman, 1975); (Kirkman, 1978); (Finn et al., 2010); (Boström et al., 2006); Takahashi et al 2008; (McMahon, 2003); (Peterken and Conacher, 1997); (Roelfsema et al., 2009); (Skilleter et al., 2007); (Perry et al., 1996); (Saunders et al., 2013); (Melville and Connolly, 2005)

15 Macroalgae Fulton & Smith 2010; (Watkinson et al., 2005); (Pittman and Pittman, 2005); (Bell and Elmetri, 2007); (Arthur et al., 1991); Quigg et al 2008

16 Phytoplankton Glibert (2006); (Wulff et al., 2011); (Gabric et al., 1998); (James et al., 1998); O'Donohue et al 2000; (Glibert et al., 2006, Glibert and Dennison, 2000); (Schlacher et al., 2008), (Quigg et al., 2010);

17 Discards Gribble 2003; Wassenberg and Hill, 1990; Wassenberg and Hill 1989;

18 Detritus Gribble 2003

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Model Calibration

The Ecosim model was calibrated using the varying vulnerability and forcing functions on primary production repeated for predator and prey/predator interactions as follows: Baseline Baseline and vulnerabilities Baseline and primary production Baseline and vulnerabilities and primary production Fishing Fishing and vulnerabilities Fishing and primary production Fishing and primary production

Name	Sharks	Pelagic fish	Demersa 1 fish	Omnivore s	Sand crabs	Prawns	Beam trawl	Otter trawl	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.0016	0.0108	0.0147	0.0533	0.0022	0.0941	1	1	1	1	1
1991	0.001	0.0118	0.0131	0.0414	0.0023	0.0779	1.251	1.0736	0.5584	1.1738	1.2895
1992	0.0012	0.0124	0.0146	0.0550	0.0017	0.0744	0.739	0.8210	0.2173	1.1170	1.2435
1993	0.0016	0.0153	0.0119	0.0287	0.0020	0.0550	0.4559	0.7876	0.3837	1.3303	1.9511
1994	0.0019	0.0129	0.0130	0.0433	0.0025	0.0575	0.8205	0.6127	0.1707	1.2914	2.4778
1995	0.0018	0.0132	0.0144	0.0543	0.0021	0.0676	0.7176	0.5951	0.1424	1.4930	2.7015
1996	0.0017	0.0154	0.0106	0.0523	0.0022	0.0971	0.4099	0.9573	0.1594	1.6563	2.4507
1997	0.0029	0.0156	0.0136	0.0343	0.0022	0.0661		1.1069	0.5003	2.0542	2.4768
1998	0.0025	0.0125	0.0117	0.0526	0.0025	0.0822		1.192	0.4611	1.6034	2.4541
1999	0.0026	0.0108	0.0131	0.0650	0.0029	0.0971		1.2328	0.5409	1.7484	3.4257
2000	0.0034	0.0163	0.0166	0.038	0.0028	0.0422	0.6456	0.8552	0.23	1.5498	3.5674
2001	0.0028	0.0135	0.0193	0.0736	0.0042	0.0531	1.8930	0.3545	0.1722	1.4349	3.7211
2002	0.0024	0.0084	0.0126	0.0397	0.003	0.0572	1.7667	0.381	0.1870	1.3605	2.8256
2003	0.0033	0.0139	0.0143	0.0479	0.003	0.0436	1.9327	0.31	0.4415	1.7329	3.2071
2004	0.0023	0.0100	0.018	0.0544	0.003	0.0731	1.4833	0.3013	0.3826	1.435	2.2847
2005	0.0024	0.0088	0.0179	0.0453	0.0025	0.0464	1.2356	0.2054	0.5067	1.1615	1.9007
2006	0.0029	0.0087	0.0141	0.0587	0.0024	0.0278	1.4861	0.2231	0.6186	1.1041	1.7981
2007	0.0030	0.0090	0.0174	0.0275	0.0022	2.83E-	1.6593	0.1533	0.5023	0.9929	1.3933
2008	0.0028	0.0077	0 0141	0.0425	0.0021	0.0230	1 1978	0 1034	0 4843	1 1 3 8 4	1 7488
2009	0.0019	0.0071	0.0102	0.0396	0.0029	0.0302	1.204	0.105	0.3795	0.6891	1.6108
2010	0.0012	0.0073	0.0077	0.0345	0.0022	0.0301	0.9408	0.1245	0.2579	0.5279	1.5161
2011	0.002	0.0074	0.0096	0.0311	0.0021	0.0531	0.421	0.1704	0.3191	0.5648	1.5425
2012	0.002	0.009	0.0099	0.0365	0.0025	0.0339	0.3557	0.1291	0.2173	0.631	1.5458
2013	0.002	0.0068	0.0094	0.049	0.0025	0.0507	0.2263	0.1218	0.2627	0.5807	1.7329

Table 1: Catch (t/km²) data inputs for 1990 to 2013 derived from the Qfish database



Fig. 1: Prawn catch, effort and discards from prawn trawling in Moreton Bay.

Data from Qfish database and the discards are estimated from prawn catches as by-catch data was not recorded.

Table 1: Composition of discards from prawn trawling in Moreton Bay (Wassenberg and Hill, 1989)

(weight)

Group	Percentage
Crustaceans	52
Echinoderms	18
Elasmobranchs	15
Teleost fish	8
Cephalopods	3
Others	4

			CV=0.1		CV=0.2		CV=0.3		CV=0.4		CV=0.5	
	Group name	Mean	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
			limit	limit								
1	Seabirds	0.005	0.004	0.006	0.003	0.007	0.002	0.008	0.001	0.009	0.003	0.010
2	Dolphins	0.092	0.073	0.110	0.055	0.129	0.037	0.147	0.018	0.165	0.046	0.184
3	Sharks	0.037	0.029	0.044	0.022	0.051	0.015	0.059	0.007	0.066	0.018	0.073
4	Pelagic fish	0.430	0.344	0.516	0.258	0.602	0.172	0.688	0.086	0.774	0.215	0.860
5	Demersal fish	0.390	0.312	0.468	0.234	0.546	0.156	0.624	0.078	0.702	0.195	0.780
6	Omnivores	0.200	0.160	0.240	0.120	0.280	0.080	0.320	0.040	0.360	0.100	0.400
7	Dugongs	0.008	0.006	0.009	0.005	0.011	0.003	0.012	0.002	0.014	0.004	0.015
8	Turtles	0.007	0.006	0.008	0.004	0.010	0.003	0.011	0.001	0.013	0.004	0.014
9	Sand crabs	0.600	0.480	0.720	0.360	0.840	0.240	0.960	0.120	1.080	0.300	1.200
10	Prawns	0.700	0.560	0.840	0.420	0.980	0.280	1.120	0.140	1.260	0.350	1.400
11	Jellyfish	1.075	0.860	1.290	0.645	1.505	0.430	1.720	0.215	1.935	0.538	2.150
12	Macrobenthos	0.800	0.640	0.960	0.480	1.120	0.320	1.280	0.160	1.440	0.400	1.600
13	Zooplankton	6.420	5.136	7.704	3.852	8.988	2.568	10.27	1.284	11.556	3.210	12.84
14	Seagrass	16.00	12.80	19.20	9.600	22.400	6.400	25.60	3.200	28.800	8.000	32.00
15	Macroalgae	25.91	20.728	31.092	15.546	36.274	10.364	41.456	5.182	46.638	12.96	51.82
16	Phytoplankton	11.30	9.040	13.560	6.780	15.820	4.520	18.080	2.260	20.340	5.650	22.60

Table 1: Biomass estimates from the Monte Carlo routine for CV = 0.1 to 0.5 on 100 trials

Table 1: The number of paths for consumption and trophic levels (TL) for the groups in the models

 with discards (MB 1) and without discards (MB 2) from the Ecopath models

	Functional	MB 1			MB2		
	group						
		No.	of	TL	No.	of	TL
		pathy	vays		pathw	vays	
1	Seabirds	119		3.79	112		4.18
2	Dolphins	119		3.96	107		4.34
3	Sharks	77		4.26	70		4.32
4	Pelagic fish	42		3.5	38		3.51
5	Demersal fish	21		3.44	19		3.44
6	Omnivores	76		2.75	69		2.75
7	Dugongs	2		2	2		2
8	Turtles	2		2	2		2
9	Sand crabs	11		2.9	11		2.91
10	Prawns	2		2.12	2		2.12
11	Jellyfish	1		3.11	1		3.11
12	Macrobenthos	6		2.45	5		2.45
13	Zooplankton	1		2.11	1		2.11

Table 2: Mann-Whitney U tests for the prey biomass of seabirds (A) and dolphins (B) between the two scenarios

Table A: Seabirds

Prey	U-value	Z-score	р
Pelagic fish	0	-5.9282	0*
Omnivores	95	-3.9693	0.00008*
Discards	0	5.9282	0*
* Significant at p=0.05			

Table B: Dolphins

Prey	U-value	Z-score	р
Pelagic fish	0	-5.9282	0*
Omnivores	114	-3.5775	0.00034*
Discards	0	5.9282	0*
*significant at p=0.05			



Changes in the proportions of the prey in the diet of dolphins from 1990 to 2013 Solid lines – Scenario 1 and dotted lines- Scenario 2

groups

Group nar	Sc 1	Sc 2	Sc 3	Sc 4	Sc 5	Sc 6	Sc 7	Sc 8
Seabirds	0.81303	0.756218	0.385058	0.37541	1.016094	0.857226	0.385619	0.375768
Dolphins	0.875448	0.834746	0.637364	0.634734	0.975775	0.892527	0.637522	0.634844
Sharks	1.024249	0.535686	0.39246	0.124022	2.73E-19	2.73E-19	2.73E-19	2.73E-19
Pelagic fis	1.301769	1.095495	2.34E-20	2.34E-20	1.519413	1.210263	2.34E-20	2.34E-20
Demersal	1.384582	1.101525	2.985323	2.273994	1.403807	1.077659	3.116449	2.335899
Omnivore	1.475672	1.487571	1.470492	1.469121	1.481983	1.488546	1.471128	1.468803
Dugongs	0.994439	0.99409	0.994105	0.994101	0.994095	0.99409	0.994106	0.994102
Turtles	0.930606	0.93024	0.930267	0.93026	0.930246	0.93024	0.930268	0.930261
Sand crabs	1.254033	0.164574	1.302726	0.085075	1.2596	0.087712	1.297757	0.084969
Prawns	1.452154	1.51449	1.320841	1.368068	1.463083	1.524145	1.316783	1.364082
Jellyfish	1.051389	1.135256	2.423199	2.422053	0.976281	1.062961	2.423349	2.422217
Macroben	1.464625	1.510503	1.418335	1.441477	1.48244	1.512946	1.414763	1.438767
Zooplankt	1.37872	1.388864	1.396466	1.395862	1.388911	1.388697	1.396545	1.395925
Seagrass	1.469448	1.482009	1.482099	1.482076	1.482035	1.482007	1.482102	1.482079
Macroalga	0.999635	0.999611	0.999701	0.999688	0.999621	0.999608	0.999703	0.999689
Phytoplan	1.264479	1.271542	1.268408	1.268643	1.271552	1.271613	1.268378	1.268618
Discards	0.456139	0.650316	0.763536	0.678929	0.721805	0.647604	0.767771	0.682236
Detritus	1.214215	1.216208	1.21627	1.215968	1.216532	1.216197	1.216269	1.215968

Table 2: Percentage changes for each scenario against scenario 1 (Moreton Bay model)

Percentage change							
Group nar	Sc 2	Sc 3	Sc 4	Sc 5	Sc 6	Sc 7	Sc 8
Seabirds	-6.98764	-52.6392	-53.8258	24.97623	5.435951	-52.5701	-53.7818
Dolphins	-4.64925	-27.1956	-27.4961	11.46008	1.950876	-27.1776	-27.4835
Sharks	-47.6996	-61.6831	-87.8914	-100	-100	-100	-100
Pelagic fis	-15.8457	-100	-100	16.7191	-7.02936	-100	-100
Demersal	-20.4435	115.6119	64.23686	1.388506	-22.1672	125.0823	68.70788
Omnivore	0.806344	-0.35103	-0.44393	0.42767	0.872416	-0.30793	-0.46548
Dugongs	-0.03506	-0.03357	-0.03403	-0.03462	-0.03506	-0.03348	-0.03389
Turtles	-0.03933	-0.03648	-0.03717	-0.03866	-0.03931	-0.03632	-0.03703
Sand crabs	-86.8764	3.882912	-93.2159	0.443928	-93.0056	3.486671	-93.2244
Prawns	4.292658	-9.04264	-5.79043	0.752606	4.957532	-9.32208	-6.06492
Jellyfish	7.976781	130.476	130.367	-7.14374	1.100639	130.4902	130.3826
Macroben	3.132406	-3.16054	-1.58047	1.216352	3.299206	-3.40442	-1.7655
Zooplankt	0.735755	1.287136	1.243327	0.739164	0.723642	1.292866	1.247897
Seagrass	0.854811	0.860936	0.85937	0.85658	0.854675	0.86114	0.859574
Macroalga	-0.00234	0.006632	0.005322	-0.00134	-0.00264	0.006853	0.005482
Phytoplan	0.55857	0.310721	0.329306	0.559361	0.564185	0.308348	0.327328
Discards	42.56984	67.39108	48.84275	58.24253	41.97528	68.31955	49.56773
Detritus	0.164139	0.169245	0.144373	0.190823	0.163233	0.169163	0.144373



All scenarios plots - Relative changes in biomass for scenarios 1 to 8

Time series data (for Chapter 5)

Time series data used for scenario 8, sharks, fish and crabs removed

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.01584	0.1076	0.013126	0.041437	0.0219	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.01584	0.1076	0.014645	0.055018	0.0219	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.01584	0.1076	0.011879	0.028727	0.0219	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.01584	0.1076	0.013032	0.043334	0.0219	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.01584	0.1076	0.014379	0.054303	0.0219	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.01584	0.1076	0.010545	0.052281	0.0219	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.01584	0.1076	0.013593	0.03431	0.0219	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.01584	0.1076	0.011704	0.05261	0.0219	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.01584	0.1076	0.013142	0.065026	0.0219	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.01584	0.1076	0.016575	0.037963	0.0219	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.01584	0.1076	0.019354	0.073612	0.0219	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.01584	0.1076	0.012647	0.039658	0.0219	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.01584	0.1076	0.014341	0.047943	0.0219	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.01584	0.1076	0.017994	0.054413	0.0219	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.01584	0.1076	0.017876	0.045261	0.0219	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.01584	0.1076	0.014148	0.058663	0.0219	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.01584	0.1076	0.017416	0.027491	0.0219	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.01584	0.1076	0.014133	0.042524	0.0219	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.01584	0.1076	0.010202	0.039591	0.0219	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.01584	0.1076	0.007695	0.034525	0.0219	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.01584	0.1076	0.009623	0.031117	0.0219	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.01584	0.1076	0.009925	0.036513	0.0219	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.01584	0.1076	0.00943	0.048963	0.0219	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Time series data used for scenario 7, sharks and fish removed

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.01584	0.1076	0.013126	0.041437	0.002343	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.01584	0.1076	0.014645	0.055018	0.001737	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.01584	0.1076	0.011879	0.028727	0.002028	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.01584	0.1076	0.013032	0.043334	0.0025	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.01584	0.1076	0.014379	0.054303	0.00213	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.01584	0.1076	0.010545	0.052281	0.002229	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.01584	0.1076	0.013593	0.03431	0.002229	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.01584	0.1076	0.011704	0.05261	0.002469	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.01584	0.1076	0.013142	0.065026	0.002911	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.01584	0.1076	0.016575	0.037963	0.002817	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.01584	0.1076	0.019354	0.073612	0.004164	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.01584	0.1076	0.012647	0.039658	0.002962	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.01584	0.1076	0.014341	0.047943	0.002987	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.01584	0.1076	0.017994	0.054413	0.003027	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.01584	0.1076	0.017876	0.045261	0.002529	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.01584	0.1076	0.014148	0.058663	0.002409	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.01584	0.1076	0.017416	0.027491	0.002182	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.01584	0.1076	0.014133	0.042524	0.002099	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.01584	0.1076	0.010202	0.039591	0.002901	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.01584	0.1076	0.007695	0.034525	0.002226	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.01584	0.1076	0.009623	0.031117	0.002087	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.01584	0.1076	0.009925	0.036513	0.002527	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.01584	0.1076	0.00943	0.048963	0.0025	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.01584	0.011795	0.013126	0.041437	0.0219	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.01584	0.012441	0.014645	0.055018	0.0219	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.01584	0.015304	0.011879	0.028727	0.0219	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.01584	0.012854	0.013032	0.043334	0.0219	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.01584	0.013177	0.014379	0.054303	0.0219	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.01584	0.015387	0.010545	0.052281	0.0219	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.01584	0.015638	0.013593	0.03431	0.0219	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.01584	0.012532	0.011704	0.05261	0.0219	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.01584	0.010751	0.013142	0.065026	0.0219	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.01584	0.0163	0.016575	0.037963	0.0219	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.01584	0.013473	0.019354	0.073612	0.0219	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.01584	0.008448	0.012647	0.039658	0.0219	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.01584	0.013935	0.014341	0.047943	0.0219	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.01584	0.010032	0.017994	0.054413	0.0219	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.01584	0.008777	0.017876	0.045261	0.0219	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.01584	0.008653	0.014148	0.058663	0.0219	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.01584	0.009012	0.017416	0.027491	0.0219	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.01584	0.007667	0.014133	0.042524	0.0219	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.01584	0.007087	0.010202	0.039591	0.0219	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.01584	0.007342	0.007695	0.034525	0.0219	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.01584	0.007355	0.009623	0.031117	0.0219	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.01584	0.008968	0.009925	0.036513	0.0219	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.01584	0.00676	0.00943	0.048963	0.0219	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Time series data used for scenario 6, sharks and crabs removed

Time series data used for scenario 5, sharks removed

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.01584	0.011795	0.013126	0.041437	0.002343	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.01584	0.012441	0.014645	0.055018	0.001737	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.01584	0.015304	0.011879	0.028727	0.002028	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.01584	0.012854	0.013032	0.043334	0.0025	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.01584	0.013177	0.014379	0.054303	0.00213	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.01584	0.015387	0.010545	0.052281	0.002229	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.01584	0.015638	0.013593	0.03431	0.002229	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.01584	0.012532	0.011704	0.05261	0.002469	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.01584	0.010751	0.013142	0.065026	0.002911	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.01584	0.0163	0.016575	0.037963	0.002817	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.01584	0.013473	0.019354	0.073612	0.004164	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.01584	0.008448	0.012647	0.039658	0.002962	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.01584	0.013935	0.014341	0.047943	0.002987	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.01584	0.010032	0.017994	0.054413	0.003027	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.01584	0.008777	0.017876	0.045261	0.002529	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.01584	0.008653	0.014148	0.058663	0.002409	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.01584	0.009012	0.017416	0.027491	0.002182	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.01584	0.007667	0.014133	0.042524	0.002099	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.01584	0.007087	0.010202	0.039591	0.002901	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.01584	0.007342	0.007695	0.034525	0.002226	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.01584	0.007355	0.009623	0.031117	0.002087	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.01584	0.008968	0.009925	0.036513	0.002527	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.01584	0.00676	0.00943	0.048963	0.0025	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.000982	0.1076	0.013126	0.041437	0.0219	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.1076	0.014645	0.055018	0.0219	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.1076	0.011879	0.028727	0.0219	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.1076	0.013032	0.043334	0.0219	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.1076	0.014379	0.054303	0.0219	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.1076	0.010545	0.052281	0.0219	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.1076	0.013593	0.03431	0.0219	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.1076	0.011704	0.05261	0.0219	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.1076	0.013142	0.065026	0.0219	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.1076	0.016575	0.037963	0.0219	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.1076	0.019354	0.073612	0.0219	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.1076	0.012647	0.039658	0.0219	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.1076	0.014341	0.047943	0.0219	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.1076	0.017994	0.054413	0.0219	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.1076	0.017876	0.045261	0.0219	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.1076	0.014148	0.058663	0.0219	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.1076	0.017416	0.027491	0.0219	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.1076	0.014133	0.042524	0.0219	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.1076	0.010202	0.039591	0.0219	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.1076	0.007695	0.034525	0.0219	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.1076	0.009623	0.031117	0.0219	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.1076	0.009925	0.036513	0.0219	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.1076	0.00943	0.048963	0.0219	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Time series data used for scenario 3, fish removed

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.000982	0.1076	0.013126	0.041437	0.002343	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.1076	0.014645	0.055018	0.001737	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.1076	0.011879	0.028727	0.002028	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.1076	0.013032	0.043334	0.0025	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.1076	0.014379	0.054303	0.00213	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.1076	0.010545	0.052281	0.002229	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.1076	0.013593	0.03431	0.002229	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.1076	0.011704	0.05261	0.002469	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.1076	0.013142	0.065026	0.002911	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.1076	0.016575	0.037963	0.002817	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.1076	0.019354	0.073612	0.004164	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.1076	0.012647	0.039658	0.002962	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.1076	0.014341	0.047943	0.002987	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.1076	0.017994	0.054413	0.003027	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.1076	0.017876	0.045261	0.002529	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.1076	0.014148	0.058663	0.002409	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.1076	0.017416	0.027491	0.002182	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.1076	0.014133	0.042524	0.002099	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.1076	0.010202	0.039591	0.002901	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.1076	0.007695	0.034525	0.002226	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.1076	0.009623	0.031117	0.002087	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.1076	0.009925	0.036513	0.002527	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.1076	0.00943	0.048963	0.0025	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Time s	eries	data	used for	scenario	2,	crabs	removed	1
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Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.000982	0.011795	0.013126	0.041437	0.0219	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.012441	0.014645	0.055018	0.0219	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.015304	0.011879	0.028727	0.0219	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.012854	0.013032	0.043334	0.0219	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.013177	0.014379	0.054303	0.0219	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.015387	0.010545	0.052281	0.0219	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.015638	0.013593	0.03431	0.0219	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.012532	0.011704	0.05261	0.0219	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.010751	0.013142	0.065026	0.0219	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.0163	0.016575	0.037963	0.0219	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.013473	0.019354	0.073612	0.0219	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.008448	0.012647	0.039658	0.0219	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.013935	0.014341	0.047943	0.0219	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.010032	0.017994	0.054413	0.0219	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.008777	0.017876	0.045261	0.0219	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.008653	0.014148	0.058663	0.0219	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.009012	0.017416	0.027491	0.0219	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.007667	0.014133	0.042524	0.0219	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.007087	0.010202	0.039591	0.0219	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.007342	0.007695	0.034525	0.0219	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.007355	0.009623	0.031117	0.0219	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.008968	0.009925	0.036513	0.0219	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.00676	0.00943	0.048963	0.0219	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

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Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	1	2	3	4	5
Туре	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.000982	0.011795	0.013126	0.041437	0.002343	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.012441	0.014645	0.055018	0.001737	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.015304	0.011879	0.028727	0.002028	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.012854	0.013032	0.043334	0.0025	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.013177	0.014379	0.054303	0.00213	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.015387	0.010545	0.052281	0.002229	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.015638	0.013593	0.03431	0.002229	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.012532	0.011704	0.05261	0.002469	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.010751	0.013142	0.065026	0.002911	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.0163	0.016575	0.037963	0.002817	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.013473	0.019354	0.073612	0.004164	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.008448	0.012647	0.039658	0.002962	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.013935	0.014341	0.047943	0.002987	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.010032	0.017994	0.054413	0.003027	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.008777	0.017876	0.045261	0.002529	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.008653	0.014148	0.058663	0.002409	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.009012	0.017416	0.027491	0.002182	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.007667	0.014133	0.042524	0.002099	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.007087	0.010202	0.039591	0.002901	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.007342	0.007695	0.034525	0.002226	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.007355	0.009623	0.031117	0.002087	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.008968	0.009925	0.036513	0.002527	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.00676	0.00943	0.048963	0.0025	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Time series data used for overfished pelagic fish and jellyfish scenarios (Chapter 5)

Name	Sharks	Pelagic fis	Pelagic fis	Demersal	Omnivore	Sand crabs	Prawns	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	4	5	6	9	10	1	2	3	4	5
Туре	6	6	4	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.025	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1
1991	0.000982	0.1076	5	0.013126	0.041437	0.002343	0.077914	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.1076	5	0.014645	0.055018	0.001737	0.0744	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.1076	5	0.011879	0.028727	0.002028	0.055006	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.1076	5	0.013032	0.043334	0.0025	0.057451	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.1076	5	0.014379	0.054303	0.00213	0.067623	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.1076	5	0.010545	0.052281	0.002229	0.097091	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.1076	5	0.013593	0.03431	0.002229	0.066057		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.1076	5	0.011704	0.05261	0.002469	0.082171		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.1076	5	0.013142	0.065026	0.002911	0.097114		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.1076	5	0.016575	0.037963	0.002817	0.042223	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.1076	5	0.019354	0.073612	0.004164	0.053069	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.1076	5	0.012647	0.039658	0.002962	0.057234	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.1076	5	0.014341	0.047943	0.002987	0.04364	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.1076	5	0.017994	0.054413	0.003027	0.073126	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.1076	5	0.017876	0.045261	0.002529	0.046371	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.1076	5	0.014148	0.058663	0.002409	0.027789	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.1076	5	0.017416	0.027491	0.002182	2.83E-02	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.1076	5	0.014133	0.042524	0.002099	0.023003	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.1076	5	0.010202	0.039591	0.002901	0.030171	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.1076	5	0.007695	0.034525	0.002226	0.030148	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.1076	5	0.009623	0.031117	0.002087	0.053064	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.1076	5	0.009925	0.036513	0.002527	0.033914	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.1076	5	0.00943	0.048963	0.0025	0.050714	0.22627	0.121771	0.262738	0.580676	1.732916

Table 1: Data used for simulation of overfished pelagic fish

Name	Sharks	Pelagic fis	Demersal	Omnivore	Sand crab	Prawns	Jellyfish	Beam trav	Otter traw	Line	Net	Pot
Pool code	3	4	5	6	9	10	11	1	2	3	4	5
Туре	6	6	6	6	6	6	6	3	3	3	3	3
1990	0.001584	0.01076	0.014678	0.053303	0.00219	0.094126	1	1	1	1	1	1
1991	0.000982	0.011795	0.013126	0.041437	0.002343	0.077914	1	1.250984	1.073621	0.558431	1.173841	1.289482
1992	0.001186	0.012441	0.014645	0.055018	0.001737	0.0744	2	0.738986	0.821005	0.217306	1.117008	1.243498
1993	0.001629	0.015304	0.011879	0.028727	0.002028	0.055006	2	0.45593	0.787599	0.383659	1.330252	1.951076
1994	0.001938	0.012854	0.013032	0.043334	0.0025	0.057451	2	0.820549	0.612721	0.17069	1.291379	2.477754
1995	0.001791	0.013177	0.014379	0.054303	0.00213	0.067623	2	0.717615	0.595142	0.14235	1.493047	2.701505
1996	0.001656	0.015387	0.010545	0.052281	0.002229	0.097091	2	0.409923	0.957323	0.159442	1.656284	2.45072
1997	0.002874	0.015638	0.013593	0.03431	0.002229	0.066057	2		1.106852	0.500313	2.054198	2.47682
1998	0.002529	0.012532	0.011704	0.05261	0.002469	0.082171	2		1.19199	0.461142	1.603371	2.454067
1999	0.002628	0.010751	0.013142	0.065026	0.002911	0.097114	2		1.232797	0.540945	1.748355	3.425651
2000	0.003387	0.0163	0.016575	0.037963	0.002817	0.042223	2	0.645551	0.855151	0.219996	1.549841	3.567389
2001	0.002848	0.013473	0.019354	0.073612	0.004164	0.053069	2	1.89302	0.354512	0.172198	1.43488	3.721099
2002	0.002416	0.008448	0.012647	0.039658	0.002962	0.057234	2	1.766669	0.38098	0.187017	1.36049	2.82559
2003	0.003309	0.013935	0.014341	0.047943	0.002987	0.04364	2	1.932731	0.309913	0.441522	1.732865	3.20712
2004	0.002291	0.010032	0.017994	0.054413	0.003027	0.073126	2	1.483269	0.301332	0.382592	1.434955	2.284702
2005	0.002353	0.008777	0.017876	0.045261	0.002529	0.046371	2	1.235628	0.205444	0.506668	1.161494	1.900707
2006	0.002932	0.008653	0.014148	0.058663	0.002409	0.027789	2	1.486065	0.223131	0.618567	1.104054	1.798089
2007	0.003046	0.009012	0.017416	0.027491	0.002182	2.83E-02	2	1.659251	0.153275	0.502331	0.992871	1.393334
2008	0.002845	0.007667	0.014133	0.042524	0.002099	0.023003	2	1.197775	0.103388	0.484288	1.138431	1.748814
2009	0.001866	0.007087	0.010202	0.039591	0.002901	0.030171	2	1.203977	0.104964	0.379531	0.689072	1.610779
2010	0.001173	0.007342	0.007695	0.034525	0.002226	0.030148	2	0.940792	0.124488	0.257937	0.527879	1.516124
2011	0.001596	0.007355	0.009623	0.031117	0.002087	0.053064	2	0.420952	0.170386	0.31907	0.56479	1.542545
2012	0.001966	0.008968	0.009925	0.036513	0.002527	0.033914	2	0.355683	0.129058	0.217306	0.63094	1.545752
2013	0.001757	0.00676	0.00943	0.048963	0.0025	0.050714	2	0.22627	0.121771	0.262738	0.580676	1.732916

 Table 2: Data used for overfished jellyfish