

# Modelling South African cold-water coral habitats

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## Abstract

Cold-water corals are found globally but little is known about energy flows associated with these habitats. The degree to which the benthic ecosystems containing cold-water corals are linked to the overlying pelagic ecosystems is also poorly understood. Observational studies have indicated that fish abundance is greater in the waters surrounding cold-water coral reefs compared to nearby waters over barren seafloor, implying enhanced productivity in the cold-water coral ecosystems. Support for this hypothesis is tested in this study using a customised Ecopath with Ecosim model. The model is applied to Childs Bank, a region on the west coast of South Africa located in the southern Benguela eastern boundary ecosystem. A previously constructed Ecopath model of the southern Benguela was modified to represent the main groups of organisms found on Childs Bank and additional groups were added to better represent the main groups associated with cold-water coral. In total, including the additional compartments, the model ecosystem consisted of 34 living compartments and three non-living compartments. Three novel living compartments were considered in the model: Cold-water corals, Sponges and Tube-worms. Two additional non-living compartments comprised Coral skeleton and Coral mucus. The Ecopath model was balanced by assuming that the three additional living groups had the same production to biomass ratios as the Macrobenthos group. The production to consumption ratio of Sponges and Cold-water corals were sourced from literature. An unconstrained non-linear minimisation function was used to solve for the biomass of the Sponge and Cold-water coral groups as their production was needed for the Ecopath model to balance; thus a biomass estimate was required for both these groups. The balanced Ecopath model was used in an Ecosim model, which was applied to three scenarios designed to investigate whether trophic links in the cold-water coral ecosystems could account for increased fish abundance: scenario 1, the removal of both cold-water coral and cold-water coral skeleton; scenario 2, changes in fishing pressure on small pelagic fish; scenario 3, the removal of cold-water coral skeleton without damage to the living coral. Scenario 3 is an artificial scenario designed to isolate the effects of cold-water coral skeleton loss from the trophic interactions from the living cold-water corals. None of the scenarios produced results with notable changes in biomasses of groups in the wider ecosystem. It is thus hypothesised that enhanced fish production results from cold-water corals changing the local oceanographic conditions through their physical structure rather than primarily by their trophic interactions.

# Chapter 1

## Introduction to cold-water corals, their associates and a brief look at a few previous studies

### Abstract

Cold-water corals are globally distributed, being most prevalent in the North Atlantic, where research effort has been focused. Not all cold-water coral species are reef builders. *Lophelia pertusa* is a cosmopolitan reef-building cold-water coral species that is found globally, including in South African waters. The ecology of cold-water corals is the focus of this study. It was previously hypothesised that cold-water corals rely on carbon gas seeps for energy but this has since been rejected and it is now hypothesised that vertical migration of zooplankton and lateral imports provide organic carbon to cold-water coral reefs. *Lophelia pertusa* reefs grow at centimetres a year and can get very old; their slow growth rates mean they can't sustain much physical disturbance. Sponges are often found in association with cold-water coral reefs. Part of the diet of these deep-sea sponges consists of mucus that corals produce. The polychaete *Eunice norvegica* is often found living in association with cold-water corals. *Eunice* spp. feed on large zooplankton; the cold-water corals switch to feeding on small zooplankton in their presence. However, this does not affect the total carbon assimilated by the cold-water corals. Coral calcification increases in the presence of *Eunice* spp. The number of papers on cold-water coral related topics has increased in recent years, providing an opportunity to model the energy flows in communities associated with cold-water corals.

## Cold-water Corals

The term “coral” is not a scientific one; by extension, the subset of corals referred to as “cold-water corals” can also be ambiguous (Roberts *et al.*, 2009). All of the taxa grouped under “corals” can be split into two groups, those that have a symbiotic relationship with zooxanthellae and those that do not. On a tropical coral reef, species belonging to both groups might be present, but cold-water coral reefs contain only azooxanthellate species. The term coral is typically associated with shallow (< 50m) tropical reefs. However, 65% of coral species are found at depths greater than 50m (Roberts *et al.*, 2006).

Cold-water corals are globally distributed (Roberts *et al.*, 2006), being most prevalent in the

North Atlantic (Freiwald *et al.*, 2004). The authors of the dataset of global cold-water coral distribution admit that this high density of cold-water coral sites in the North Atlantic is most likely the result of more cold-water coral research taking place in this region (Freiwald *et al.*, 2017). It is worth noting that the most recent version of this dataset (V4, Freiwald *et al.* 2017) shows many more cold-water coral sites in the southern hemisphere than the original version of the map (Freiwald *et al.*, 2004). This supports the idea that the high density of cold-water corals in the North Atlantic is at least in part due to greater sampling effort. The map published in Freiwald *et al.* (2004) only looked at three species of reef-forming cold-water corals, whereas the latest version contained species from subclass Ococorallia, the orders Scleractinia, Antipatharia, Zoanthidae, and Pennatulacea, as well as from the sub-order Fillicifera. Though this difference is significant, it would not account for the vast difference in the number of southern hemisphere coral reef sites between the two versions of the map. The number of new reef sites is indicative of an increase in cold-water coral research.

A number of cold-water coral sites have been identified in South African waters. These sites and, as a whole, the role that these habitats play in South African waters, remain understudied (Sink, 2016). Despite the paucity of local studies regarding the interactions between cold-water corals and other groups of organisms in the ecosystem, nine of the proposed marine protected areas under Operation Phakisa include cold-water coral habitats (Department of Environmental Affairs, 2014).

At depth, the seafloor can be remarkably barren of macroflora and three-dimensional physical features; the presence of three-dimensional reef structures would provide cover to at least some species. Video studies of cold-water coral reef habitats have shown that species richness and abundance are greater on and around the reef compared to the surrounding seafloor (Buhl-Mortensen *et al.*, 2017a; Costello *et al.*, 2005). This indicates that the presence of cold-water coral reefs either benefits multiple other marine species directly or indirectly, or is an indicator of another mutually beneficial factor. A number of studies have shown that the abundances of commercially-important fish species are greater in the waters over cold-water corals than in non-coral habitats; the species include redfish (*Sebastes* spp.), ling (*Molva molva*) and tusk (*Brosme brosme*) (Buhl-Mortensen *et al.*, 1995; Fosså *et al.*, 2002; Husebø *et al.*, 2002; Milligan *et al.*, 2016). Sponges (Calcinaï *et al.*, 2013) and tube worms (Roberts, 2005) are also associated with cold-water corals and, specifically, with cold-water coral reefs. These will be discussed in greater detail in their relevant sections below.

Not all species of cold-water corals are considered to be reef builders. The ecological benefits of cold-water corals are currently thought to be related, at least in part, to the presence of a reef. This, coupled with the fact that the majority of research focuses on cold-water coral reefs and the species that occur there, means that the discussion about cold-water corals in this dissertation will focus on reef-building species. Of the reef-building cold-water coral species,

*Lophelia pertusa* is the most studied and thus best understood. Given the cosmopolitan nature of this species, it is a good species on which to base a discussion.

*Lophelia pertusa* is a cosmopolitan species (Zibrowius, 1980), with recorded reefs ranging from 55°S (Cairns, 1982) to 71°N (Dons, 1944 as cited in Cairns, 1982 and Husebø *et al.*, 2002). The greatest concentration of *L. pertusa* is found in the North East Atlantic (Freiwald *et al.*, 2017; Gass and Roberts, 2006). Reefs are found over a large depth range, as shallow as 39m in Trondheimsfjord (Tautra Reef) (Freiwald *et al.*, 2004; Svensen *et al.*, 1998), where cold water allows for this, and at depths in excess of 3000 m (Squires, 1959). The vast depth range over which cold-water corals and *L. pertusa*, in particular, are found indicates that barometric pressure is not a defining feature of their habitat (Freiwald *et al.*, 2004). Aquaria growth experiments concur with this observation; *L. pertusa* do not require the pressure experienced at depth. They do, however, require stable, cold temperatures between 4°C and 14°C (Brooke and Järnegren, 2013; Roberts *et al.*, 2009). Apart from temperature, salinity is also important for *L. pertusa*, with a range of between 33 and 37 required; salinities greater than 35 are considered optimal (Freiwald, 2002). As a reef-building species, *L. pertusa* requires a hard substratum for attachment. All cold-water corals require hard substrata, but the sizes of these substrata are relative to the size of each species (Roberts *et al.*, 2006).

All cold-water coral species are azooxanthellate and thus have to obtain organic carbon from external sources. Originally, it was hypothesised that gas seeps provided the organic carbon that cold-water coral species required (Hovland *et al.*, 1994). This hypothesis was expanded upon and developed by multiple authors, including Henriot *et al.* (1998) and Hovland and Risk (2003). A study by Cordes *et al.* (2008) found little overlap in the species assemblage between gas seeps and cold-water coral habitats. Furthermore,  $\delta^{13}\text{C}$  signatures of cold-water corals are not consistent with those of organisms known to rely on carbon derived from gas seeps (Levin and Mendoza, 2007). Levin and Mendoza (2007) found the  $\delta^{13}\text{C}$  signatures of cold-water corals to be closer to those of zooxanthellae corals, which lived at depths where light levels are low and carbon derived from photosynthesis must be supplemented with other carbon sources. These two studies, combined with the lack of evidence to support cold-water corals obtaining their carbon from gas seeps, indicate that this hypothesis is unlikely.

Early studies noted that cold-water corals were associated with regions where currents were sufficient to move food particles into the habitat (Fricke and Hottinger, 1983). Despite these early observations, and potentially because of the shift in research towards a link between cold-water coral habitats and gas seeps, our understanding of how carbon is supplied to cold-water coral habitats is incomplete (Freiwald *et al.*, 2004). At present, evidence strongly suggests that primary production at the surface in part supports the reef (Davies *et al.*, 2009; Duineveld *et al.*, 2004). However, Khripounoff *et al.* (2014) concluded that cold-water corals could not rely solely on surface production as a source of carbon. Cold-water coral reefs tend to be situated in areas

with swift currents and it is hypothesised that these currents play a role in both nutrient supply and waste removal (Mienis *et al.*, 2007). It is thus currently accepted that surface production is supplemented by the lateral import of nutrients and food particles by the strong currents typical of cold-water coral habitats. In addition to currents, internal waves are thought to play a role in importing both resuspended and new nutrients (Mienis *et al.*, 2007). The distribution and morphology of *Lophelia* reefs near Norway support this hypothesis (Buhl-Mortensen *et al.*, 2017a).

It is worth noting that, although the term cold-water coral has been used to discuss the results of many of these previous studies, the species that were studied are primarily reef-building species and, in most cases, the species is *L. pertusa*. The few studies (Gori *et al.*, 2014; Naumann *et al.*, 2011; Wild *et al.*, 2008) that look at other reef-building species suggest that many of these generalisations are valid.

Aquaria experiments have indicated that *L. pertusa* utilises both live and dead food sources (Mueller *et al.*, 2013). Further dietary studies by Mueller *et al.* (2014) suggest that *L. pertusa* is an opportunistic feeder, ingesting a wide range of food (dissolved organic matter, bacteria, algae and zooplankton were used in the study). *Lophelia pertusa* can also utilize food from a substantial size range, with observations of particles of up to 2 cm being ingested in aquaria experiments (Buhl-Mortensen, 2001).

*Lophelia pertusa* creates a coral skeleton and, in order to do so, it must obtain inorganic carbon. This inorganic carbon can be obtained either from the surrounding seawater in the form of dissolved inorganic carbon, or produced metabolically in the form of carbon dioxide. *Lophelia pertusa* primarily relies on external sources of inorganic carbon to drive calcification of coral skeleton (Mueller *et al.*, 2014). The daily rate of metabolic CO<sub>2</sub> incorporation into coral skeletons is between 0.1 and 1.6  $\mu\text{g C day}^{-1} \text{ g}^{-1}$  compared with a mean ( $\pm$  standard deviation) of  $46 \pm 25 \mu\text{g C day}^{-1} \text{ g}^{-1}$  for dissolved inorganic carbon (Mueller *et al.*, 2014). The role that metabolically-derived inorganic carbon plays in calcification rates differs between coral species; there is no increase in respiration for *L. pertusa* when calcification rates increase (Form and Riebesell, 2012; Mueller *et al.*, 2013). In contrast, an increase has been shown for another species, *Desmophyllum dianthus* (Naumann *et al.*, 2011).

## Cold-water coral reefs

Reef-building cold-water coral species have the potential to form massive, complex, three-dimensional structures that can be on the order of kilometres in length and tens of metres in height (Freiwald *et al.*, 2004; Roberts *et al.*, 2008). *Lophelia pertusa* grows at a rate between 5 and 25  $\text{mm y}^{-1}$  (in aquaria: 15-17  $\text{mm y}^{-1}$  (Orejas *et al.*, 2008), in situ: 5  $\text{mm}$  (Järnegren and Kutti, 2008) and  $26 \pm 5 \text{ mm y}^{-1}$  (Gass and Roberts, 2006)). Given these slow growth rates, large reefs are estimated to take thousands of years to form (Buhl-Mortensen *et al.*, 2017a).

## Coral reef damage and recovery

Cold-water coral reefs have been observed in areas and at depths up to 1500m on the continental shelf where bottom trawling can and does take place (Freiwald *et al.*, 2004). In situ observations show that trawling damages cold-water corals (Fosså *et al.*, 2002). Given the slow growth rate of cold-water corals, it is apparent that the rate of coral loss due to trawling damage can be far greater than the capacity for recovery. This is evident in Sørmannsneset, where Fosså *et al.* (2002) found much evidence of trawling and other human activity over the crushed remains of *L. pertusa*. It is worth noting that reef habitat in areas sheltered from the trawling equipment was not damaged, but these sites were few and far between. A further threat to cold-water coral reefs is the presence of mining on the continental shelf. In South Africa, the majority of the west coast shelf is leased out for diamond mining (Sink, 2016). There are at present seven known cold-water coral habitats in South Africa's exclusive economic zone (Department of Environmental Affairs, 2014).

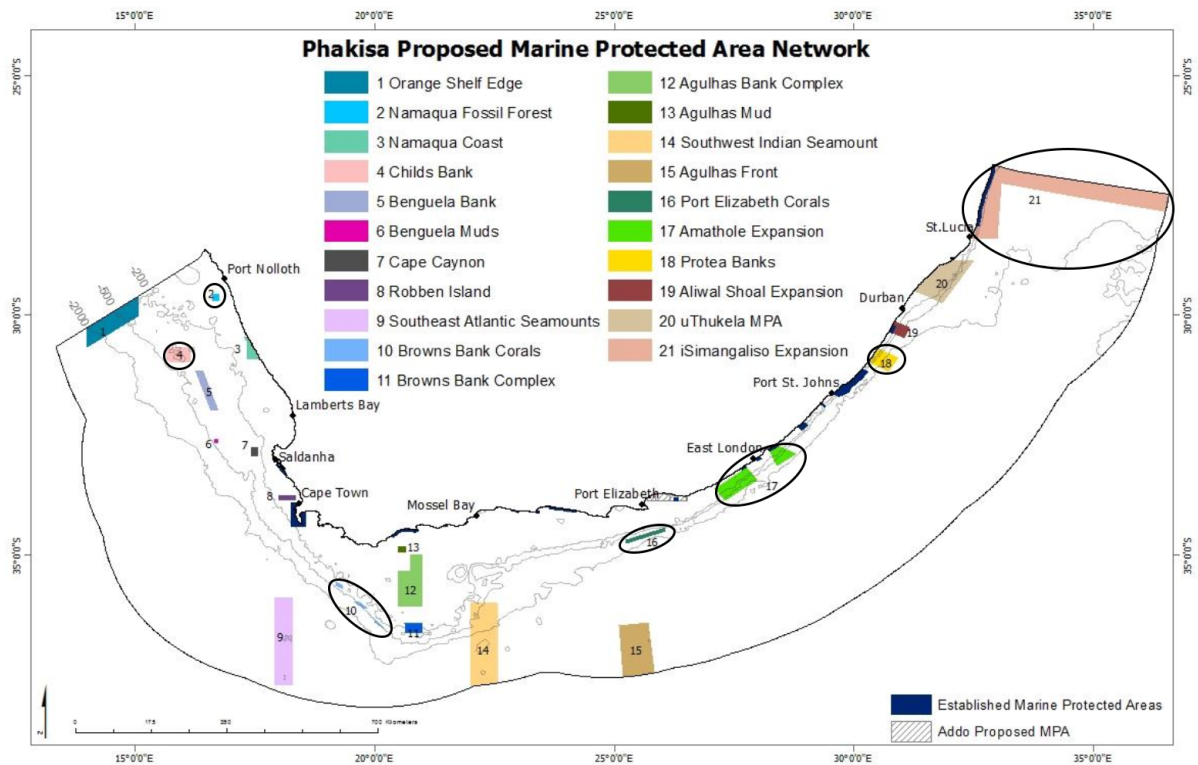


Figure 1.1: Map of marine protected areas under Operation Phakisa as published in Department of Environmental Affairs (2014). Sites that are listed in the report as containing cold-water corals are circled.

Physical disturbance is not the only threat to cold-water corals. In 2010 a massive amount of oil was released into the Gulf of Mexico as a result of the *Deepwater Horizon* blowout (United States District Court for the Eastern District of Louisiana, 2015). The *Deepwater Horizon* oil spill occurred at depth and thus had the potential to impact deep-sea communities. Multiple cold-water coral sites were identified as being negatively affected by the blow out (Fisher *et al.*, 2014). Demopoulos *et al.* (2016) found high variability in meiofaunal and macrofaunal densities,

including cold-water coral communities, nearest to the well-head; according to Schmalhausen's Law, this is indicative that these sites are under stress. These findings agree with those of Fisher *et al.* (2014). The affected cold-water coral sites are still recovering seven years after the oil spill (Girard and Fisher, 2018). This highlights the slow rate at which cold-water coral sites recover from disturbances.

## Sampling of cold-water corals

The location of most cold-water coral sites makes sampling difficult (Naumann *et al.*, 2011; Roberts *et al.*, 2006). A range of different methods has been used to sample cold-water coral sites. For observational studies such as Buhl-Mortensen *et al.* (2017), a remote underwater vehicle (ROV) was used to take videos of the reef. Strong currents can make the use of a ROV challenging (Buhl-Mortensen *et al.*, 2017a). Other video or still photography techniques can also be used to survey these reefs (Buhl-Mortensen *et al.*, 2017b). Sidescan sonar and multibeam surveys can be used to detect suspected reefs by studying the seabed characteristics (Buhl-Mortensen *et al.*, 2017b). Aquaria studies require the collection of live cold-water coral samples. As the corals are not susceptible to trauma, if the location of the reef is well known, the process of removing a live sample is relatively simple. A box core can be used and the corals transferred to cold water storage as soon as they are on deck (Maier *et al.*, 2009). While the process of removing a live sample of cold-water coral can be relatively simple, the complete sampling of the reef is still challenging for the reasons mentioned above and careful planning is required to sample processes and species on the reef.

## Sponges

Sponges, particularly Hexactinellidae (glass sponges) (Freiwald *et al.*, 2004) and Desospongia (Buhl-Mortensen *et al.*, 2017a), are often found in association with cold-water coral reefs. In a cold-water coral reef located off Ghana, Hexactinellidae made up 11% of the reef structure (Buhl-Mortensen *et al.*, 2017a). Due to their association with cold-water coral reefs, this group of organisms is discussed here.

Sponges are suspension feeders (Pile and Young, 2006). They rely on passing relatively large amounts of water through their bodies continuously, both through active pumping and passive flow, in order to provide their cells with nutrients and to remove waste (Gage and Tyler, 1991). Deep water sponges ingest ultrazooplankton ( $< 10\mu m$  (Yahel *et al.*, 2007)) and, when growing in association with cold-water corals, they make use of coral mucus as a nutrient source (Rix *et al.*, 2016). Cold-water corals do not consume ultrazooplankton and thus there is no direct competition for food between sponges and cold-water corals (Pile and Young, 2006).

Rix *et al.* (2016) show that, not only are sponges present in both cold-water and tropical coral reefs, but their use of coral mucus provides a link between the corals and higher trophic

levels via their massive detritus output. Sponges are also consumed by other groups, another potential link between cold-water corals and high trophic levels. The ability of sponges to convert dissolved organic matter, in this case primarily coral mucus, into particulate organic matter (detritus) helps retain this energy in the reef (de Goeij *et al.*, 2013). While de Goeij *et al.*'s (2013) research focused on tropical coral reefs, in which corals are in part primary producers, the sponge loop has been observed on cold-water coral reefs (Rix *et al.*, 2016). Sponges consume dissolved organic matter (DOM) as well as other prey items; the carbon from this consumption is incorporated into the sponge. The detritus production rate of sponges is the result of cell shedding (Alexander *et al.*, 2014). This cell shedding converts part of the consumption of the sponges into detritus, thus converting DOM, produced by the corals, into particulate organic matter (POM), which can be consumed by other groups. Furthermore, sponges have predators; part of the sponge's consumption is thus passed on to its predators. The main predators of sponges in temperate waters are benthic invertebrates, (Wulff, 2006) but they normally do not consume entire adult sponges, and sponges recover quickly from grazing events (Wulff, 2006).

## Tube worms

Tube worms, unlike sponges, live in association with the physical structure of the corals, building their tubes against the coral skeletons (Freiwald *et al.*, 2004; Roberts, 2005). The relationship between tube worms, particularly the polychaete *Eunice norvegica* and *L. pertusa* is complicated, described as non-obligate mutualism by Buhl-Mortensen (2001) but at times seeming more like competition or parasitism.

*Eunice norvegica* lives within the living coral framework and has been observed stealing food from coral polyps, even when food items are being handled by the coral (Buhl-Mortensen, 2001). Multiple studies have found that *E. norvegica* mainly steals large prey items from *L. pertusa* (Buhl-Mortensen, 2001; Mueller *et al.*, 2013). Mueller *et al.* (2013) found that the total carbon and nitrogen uptake of *L. pertusa* was not affected by the presence of *E. norvegica*, but the diet of *L. pertusa* changed to favour more opportunistic feeding.

Calcification by corals is increased in the presence of *E. norvegica* (Mueller *et al.*, 2013). The interaction between *E. norvegica* and *L. pertusa* is not unique to this pair of organisms; other *Eunice* species have been observed in association with *L. pertusa* (Cordes *et al.*, 2008). Likewise, *Eunice* species have been observed interacting with other scleractinian species such as *Madrepora oculata* (Roberts, 2005). In all cases, a tube is produced in the living coral framework by the polychaete and rapidly calcified by the coral (Roberts, 2005). The tubes of the *Eunice* species are built so that there are multiple openings, all of which are near coral polyps (Buhl-Mortensen, 2001). The polychaetes have been observed chasing or attacking other organisms that climb onto the coral, and the polychaetes probably offer the coral some protection from predation.

## Predators of cold-water corals

While it has been hypothesised that *Eunice* spp. protect cold-water corals from predators, predation of any cold-water coral species has only been observed once. The only observation of cold-water coral being consumed was in the Aleutian Islands where sea stars were observed grazing on soft coral *Primnoa* species (Krieger and Wing, 2002). This is also the only observation of predation found in the literature by Freiwald *et al.* (2004).

## Previous models and investigations

Research into cold-water corals has increased in recent years. Web of science searches using the terms “cold water corals” or “*Lophelia pertusa*” or “deep water corals” found 798 records between 1964 and 2018. Alternative search methods found records from much earlier than 1964. The web of science results were analysed to determine the trend in recent research into cold-water corals. The greatest number of publications (88) was in 2014 and linear fitting shows that the trend is increasing as a power function,  $\log(\text{papers} + 1) = 179 \pm 12 \log(\text{year}) - 1360 \pm 90$  (fitted value  $\pm$  standard error). These papers cover a wide range of topics, and thus some of them touch on the topic of modelling. For this introductory discussion, a few of the modelling studies will be discussed, along with several papers investigating the effects of coral on species found nearby.

Using a form of multivariate analysis known as permutational analysis of variance (PERMANOVA), applied to data collected from several separate sites over a range of different habitats in the North East Atlantic, Milligan *et al.* (2016) found that overall species composition significantly differed among the sites. Further analysis suggested that the main driver of this difference was depth (Milligan *et al.*, 2016). This finding agrees with the results of Costello *et al.* (2005). The species assemblages differed significantly between cold-water coral reefs and substrata that did not contain cold-water corals. Milligan *et al.*'s (2016) research is indicative of the difficulty in studying the interactions of cold-water corals with other groups, because the importance of cold-water corals can be species-specific and specific to the location where the corals are found. Likewise, the species assemblage is primarily driven by the location of the site and not by the presence of cold-water corals.

A number of Ecopath models have been published where cold-water corals such as *L. pertusa* are included. In these models, the cold-water corals are often aggregated into the benthic filter feeder group, which, while not incorrect, fails to highlight their exceptionally slow growth rate and lack of predators. Morato *et al.*'s (2009) study, using an aggregated benthic filter feeder group, found that on a seamount the horizontal flux of prey could be sufficient to support the rich communities present. This finding is particularly useful as Khripounoff *et al.* (2014) concluded that surface production could not support the growth seen in cold-water coral communities. These findings not only improve the understanding of how cold-water coral

habitats function, but highlight the importance of models in studying systems that are difficult to sample or observe. Skaret and Pitcher (2016) produced and validated an Ecopath with Ecosim model for the Norwegian and Barents Seas. This model included cold-water corals as an explicit group, referred to simply as corals in the model, but explicitly containing *L. pertusa*. This Ecopath with Ecosim model represents the most similar model found to the one built and used in this dissertation.

The similarity between Skaret and Pitcher's (2016) model and the one that will be presented in chapter 2, means that special attention should be paid to their methods. In their model the cold-water coral group has no predators and consumed a range of groups. Both the lack of predators and the diets of cold-water corals in the model agree with the research previously discussed. This model, however, was not built with the aim of looking at the place of cold-water corals in the greater ecosystem nor the effects of their loss. This means that the value of Skaret and Pitcher's (2016) model, in the context of this study, is as a comparison for the base model and a data source for the base model.

This study aims to better understand cold-water corals in the context of their local ecosystem, primarily looking at their function in benthic-pelagic coupling and the system-wide ramifications of coral loss as a result of anthropogenic activities. Chapter 2 will deal with the creation of a model, based on the Ecopath with Ecosim model, that can be applied to cold-water coral reef systems. Chapter 3 will deal with the application of this model and the results of three scenarios designed to investigate whether trophic links in the cold-water coral ecosystems could account for increased fish abundance in the surrounding waters.

# Chapter 2

## Building a customised Ecopath with Ecosim model including cold-water corals

### Abstract

The Ecopath with Ecosim (EwE) model is a widely used and well documented ecosystem model. This model has been applied to a large number of systems and thus data are available for it. In order to investigate whether trophic links drive the increased fish abundance observed in the waters surrounding cold-water coral reefs, an EwE model was applied. However, in order to account for some of the cold-water coral processes, the EwE model needed to be modified. The model is based on a previous model of the Southern Benguela. Three novel living compartments were considered in addition to those in the original model: Cold-water corals, Sponges and Tube-worms. Two additional non-living compartments were also considered: Coral skeleton and Coral mucus. In total, the model consisted of 34 living compartments and three non-living compartments. The three non-living compartments comprised of the Detritus group from the original model and the Coral Skeleton and Coral mucus groups. The Ecopath model was mass-balanced by assuming that the three additional living compartments were originally aggregated in the Macrobenthos compartment and thus retained the same production to biomass ratios; the production to consumption ratios of the groups were then obtained from literature. As additional links were added to the model, the production of the Cold-water coral and Sponge groups were needed, thus biomass was needed. As the standard Ecopath equations could not solve for the biomass of these groups, unconstrained non-linear minimisation was applied such that the Sponge and Coral mucus compartments had ecotrophic efficiencies (EE) as close to 1 as possible. These EE values indicate that most energy that enters these two compartments is transferred to other compartments. As mucus is not retained in the system, this is logical and the sponges shed a large number of cells, resulting in EE values near 1. The modified EwE model was found to be stable when the mass-balanced input from the modified Ecopath model was applied to the modified Ecosim model equations. The results support the hypothesis that the sponge loop helps retain energy in the reef, although natural mortality represents a far greater contribution to detritus.

# Introduction

There are a number of different modelling approaches that can be used to describe biological systems. One such approach is ecosystem modelling. Ecosystem modelling is a useful tool for ecosystem-based approaches to management (Salomon *et al.*, 2002) and also for understanding systems in the context of the ecosystem in which they exist. Even within this subsection of models that can be applied to biological systems, there is a range of different models, each with its own primary focus, strengths and weaknesses (Fulton, 2010). Model selection is thus based both on the aims of the study and what data are available for the system. The Ecopath with Ecosim (EwE) model is widely used and the basic workings of the model are well documented (Christensen and Walters, 2004; Christensen *et al.*, 2005). As a result of its widespread use, Ecopath data are available for a large number of systems.

An ecosystem model seeks to replicate real world processes in the modelling space (Hall and Day, 1977). Building a model based on both observations and assumptions allows for the testing of those assumptions, by running scenarios and studying the predicted changes. Furthermore, the modelling space can be used to study links that have not yet been directly observed, provided that the model is a fair replication of the real system. These features make ecosystem models very useful for studying groups such as cold-water corals, where observational studies have identified coral-specific processes and the behaviour of the other groups in the ecosystem are relatively well known. However, the interactions between cold-water corals and other modelled groups are not well known. The model space provides a platform for these interactions to be studied in the context of what is known.

The Ecopath model was originally designed by Polovina (1984). This model was then built upon by Christensen and Pauly (1992) and popularised the following year (Christensen and Pauly, 1993). Walters *et al.* (1997) extended the Ecopath model into the dynamic Ecosim model. Since then, the Ecopath with Ecosim (EwE) model has been turned into an open-source software suite (Christensen *et al.*, 2005), which has been applied to numerous ecosystems. At its heart the EwE platform represents trophic interactions and the flow of energy between different model groups. Physical processes, such as current speed and retention, are not explicitly present in the model. Vertical separation of species is dealt with primarily through differences in the diets of groups, as there are no explicit terms for sinking rates.

This study includes benthic-pelagic linkages, although the EwE platform lacks the physical component of benthic-pelagic. The study focuses on the trophic links between groups, and specifically how cold-water corals affect trophic flows. The lack of physical terms reduces the data requirements of the model, thus removing uncertainty where such data need to be estimated for the system. Apart from allowing for modelling without explicit oceanographic data, the lack of physical processes reduces the number of equations. Thus the EwE platform was chosen for this study because of both data availability and the well documented and open

source nature of the model. The latter made it possible to recode and edit relevant processes to include links specific to cold-water corals. This research can be enhanced by following it up with an Ecotran model of the system. Ecotran is based on a transformation of EwE and allows for physical processes to be easily included (Steele, 2009; Steele and Ruzicka, 2011). An Ecotran based study would be especially useful if the results of this study indicate that trophic interactions alone do not account for the increased fish abundance in waters surrounding cold-water coral reefs.

The Benguela is a coastal upwelling system and is one of the four major eastern boundary currents in the world. The current is located off the west coast of southern Africa and can be split into three distinctive subsystems, the Northern Benguela, the Southern Benguela, and the Lüderitz upwelling cell that separates the two. The Southern Benguela ecosystem modelled by Shannon *et al.* (2003) extends from the Orange River (29°S, 19°E) to East London (33°S, 28°E), covering an area of 220 000km<sup>2</sup> off the west and south coast of South Africa (Shannon *et al.*, 2003) (figure 2.2).

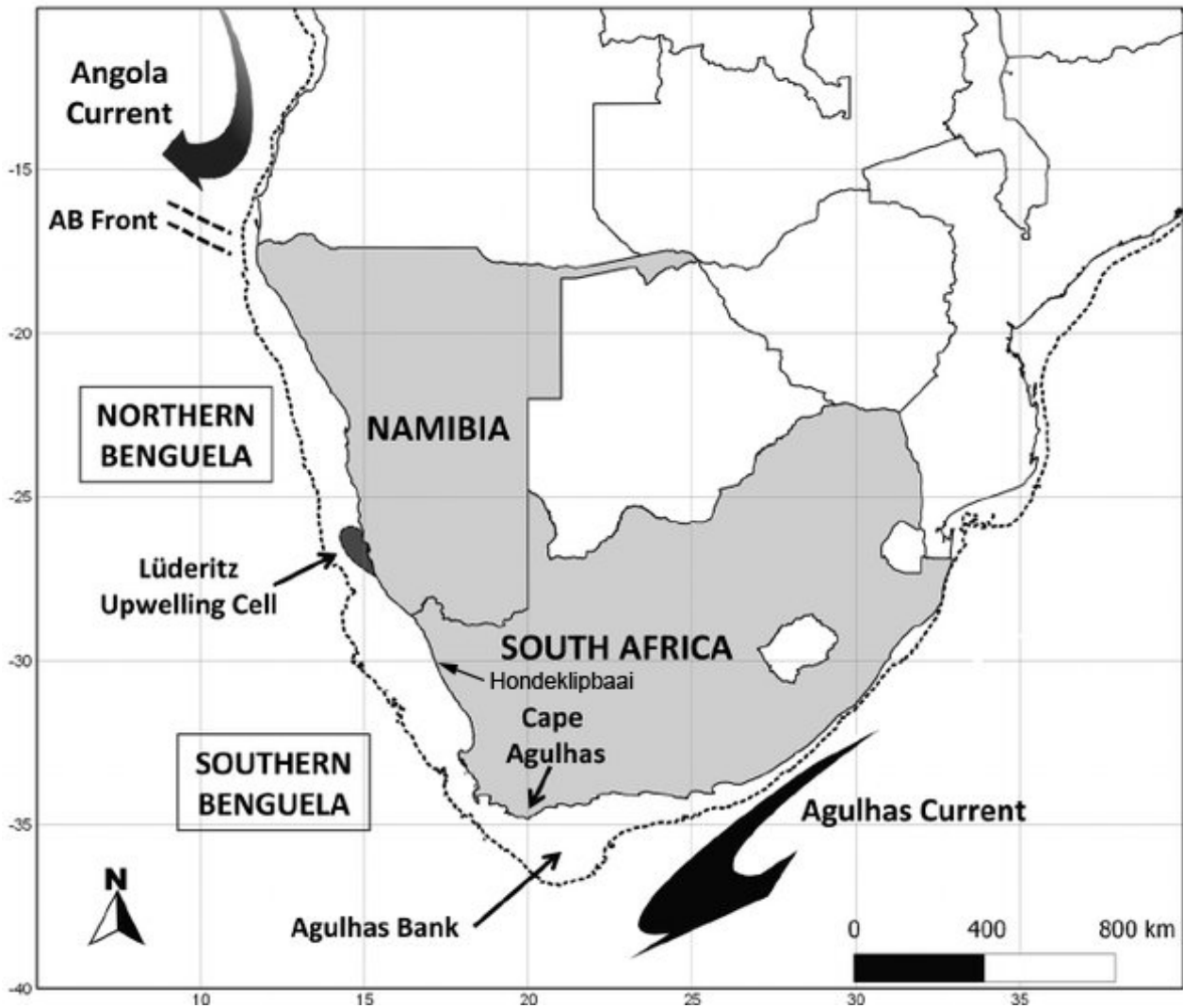


Figure 2.2: Map of the Benguela upwelling region, as published by Roux *et al.* (2013), in relation to southern Africa showing the three distinctive systems in the region. The map has been modified to show the location of Hondeklipbaai (30°S, 17°E).

Within the Southern Benguela system is one of the only known submarine banks in South African waters, Childs Bank, located off Hondeklipbaai (30°S, 17°E) (Sink *et al.*, 2012a; Sink *et al.*, 2012b) (figure 2.2). Cold-water corals are present on Childs Bank (Atkinson, 2009); these are most likely *Lophelia pertusa* (Atkinson *et al.*, 2015). While cold-water corals are present at Childs Bank, no direct observations of a reef are present. This study should thus be interoperated in the context of modelling a potential reef.

This chapter aims to describe the waters above a cold-water coral reef in the Southern Benguela using a customised Ecopath with Ecosim model. In addition to this primary focus, the energy flow between different depth-based habitat groups (pelagic, benthic and groups that live in close proximity to both (intermediate)) will be used to better understand the benthic-pelagic coupling in this system.

# Methods

## Modelling assumptions

All models are based on both observations and logical assumptions. The major assumption of the Ecopath component of EwE is that the ecosystem is mass-balanced over a defined period of time (Christensen *et al.*, 2005). However, given the nature of cold-water coral systems, using a traditional EwE model would have required modelling additional links within the EwE software suite. While such modelling would be possible, customising the model allows for these terms to be added in a more controlled manner and enhances understanding (by the user) of the model. Cold-water corals are, in Ecopath model terms, a consumer group, gaining their organic carbon from other groups by predation. There have been no observed predation events on reef-forming cold-water corals. A single predation event has been recorded on a cold-water soft coral species (Krieger and Wing, 2002) but it cannot be inferred that this occurs also for cold-water corals; this study assumes that *Lophelia* and other reef forming cold-water corals have no known predators. Furthermore a single predator prey interaction is not enough to confirm the existence of a trophic link for modelling purposes. As such, cold-water corals are an apex consumer group. Cold-water corals, like their tropical counterparts, produce carbon-rich mucus. This mucus is utilised by sponges as a source of organic carbon. Sponges have a rapid cellular turnover rate and thus convert much of their ingested carbon into detritus. This conversion of dissolved organic carbon (DOC) to particulate organic carbon (POC) is hypothesised to help retain organic matter on cold-water coral reefs and to support detritivores (Rix *et al.*, 2016). This loop is explicitly contained in the customised version of the EwE model. The model includes consumer, producer and detritus groups, the dynamics of which are modelled using the Ecosim equations. In addition, a second set of links is defined for some groups and applied. Thus, the model is described in two parts. The first part is a description of the EwE model, whereas the second part is a description of the additional links that were added.

## Description of the Ecopath model

The Ecopath model used in this study is based on an Ecopath model of the Southern Benguela (Shannon *et al.*, 2003). The original Ecopath model contained 32 functional groups and one fishery. These 32 groups include two producers (Phytoplankton and Benthic producers), 29 consumers; Microzooplankton, Mesozooplankton, Macrozooplankton, Gelatinous zooplankton, Anchovy, Sardine, Redeye, Other small pelagic fish, Chub mackerel, Juvenile horse mackerel, Adult horse mackerel, Mesopelagic fish, Snoek, Other large pelagic fish, Cephalopods, Small *M. capensis*, Large *M. capensis*, Small *M. paradoxus*, Large *M. paradoxus*, Pelagic-feeding demersal fish, Benthic-feeding demersal fish, Pelagic-feeding chondrichthyans, Benthic-feeding chondrichthyans, Apex predatory chondrichthyans, Seals, Cetaceans, Seabirds, Meiobenthos and Macrobenthos, and one detritus group; Detritus. In this study, the two producer groups were converted into two groups, one representing the primary production imported into the pelagic

system and the other representing lateral import in the benthic system that supplements the diet of cold-water corals; benthic producers are not typically present in cold-water coral reef ecosystems. The diets of functional groups that relied on benthic production were altered by adding this diet component to the single pelagic producer group, as the lateral import group. In practice, the pelagic production group is referred to as “Import” in the model and contains the majority of primary production in the system, primarily the result of phytoplankton growth. The lateral import group is modelled as a producer group but may in practice contain zooplankton, both living and dead, that passes through the system.

One non-living group was added to the model, Coral mucus. Unconsumed Coral mucus is assumed to not be retained in the system. Three novel living groups were also added to the model namely, Cold-water corals, Sponges and Tube worms. The flows to these groups, as described in the modelling equation section, were accounted for during Ecopath balancing. To balance the Ecopath model, ecotrophic efficiency (EE) of each group must be less than 1; ecotrophic efficiency is the ratio of energy flows out of the group to energy flows into the group. The process by which the Ecopath model was balanced in relation to the additional groups is detailed in the parametrisation of the additional links section later in this chapter.

The modified Ecopath model contains 34 functional groups. These can be presented as 13 aggregated groups to highlight the ways in which the groups are linked. Such a flow diagram (figure 2.3) is useful in presenting the pathways in the full model. The groups were aggregated primarily by diet, combining groups that had similar predators and prey items. Another major consideration while aggregating the groups was whether a group fed primarily in the pelagic or benthic zone. A rather large exception to this is the zooplankton group, which is made up of four zooplankton model groups. However, the four different size categories of zooplankton (micro-, meso-, macro- and Gelatinous zooplankton) have different predators, a prime example of which is that sponges only consume the Microzooplankton group. The actual model groups that were included in each of the aggregated groups are presented the appendix (table A3).

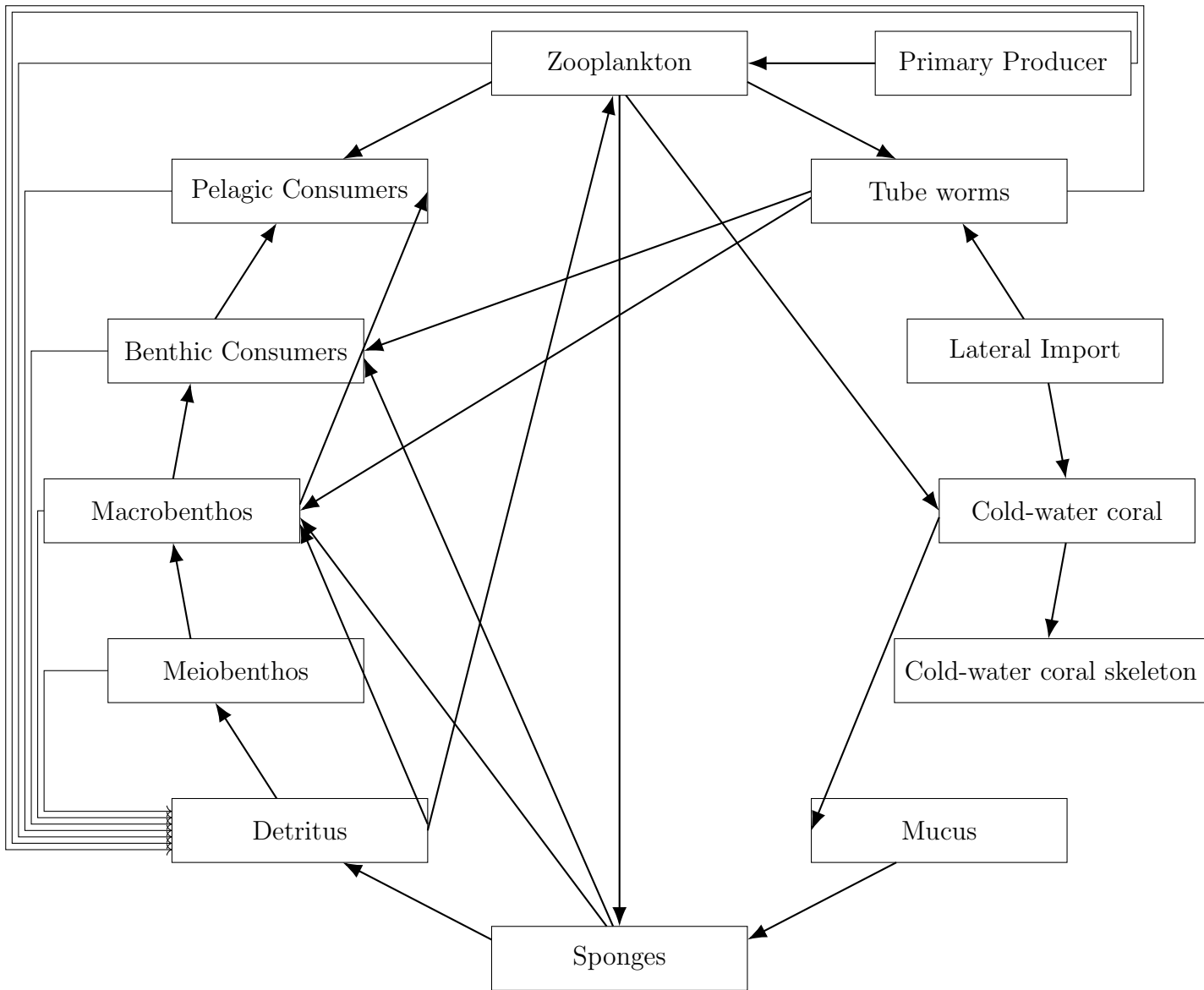


Figure 2.3: A flow diagram showing the pathways among 13 aggregated groups that represent the larger Ecopath model in this study. The links present do not indicate the relative magnitude of each flow.

The model presented in this study seeks to describe the water column above and directly adjacent to a benthic environment containing cold-water corals, based on Childs Bank. The removal of the benthic producers and the fact that the data contained in Shannon *et al.* (2003) were for the full Southern Benguela and not specifically for Childs Bank meant that some adjustments needed to be made to the biomasses of the groups. These adjustments were made based on expert opinion.

## Model equations

### The Ecopath with Ecosim Equations

The Ecopath component of the model is underpinned by two fundamental equations. The first equation balances flows into and out of model groups  $i$ :

$$\text{Consumption}_i = \text{production}_i + \text{respiration}_i + \text{unassimilated food}_i \quad (2.1)$$

The second equation defines the production,  $P$ , of each group as the sum of its losses:

$$P_i = Y_i + M2_i B_i + E_i + B A_i + M0_i B_i \quad (2.2)$$

where  $Y_i$  is the total catch,  $M2_i$  is the predation rate,  $E_i$  is the migration rate (negative representing immigration and positive representing emigration),  $B A_i$  is the biomass accumulation rate,  $M0_i$  represents the mortality rate that is not the result of fishing or predation, in this study referred to as natural mortality but also often referred to as ‘other mortality’, and  $B_i$  is the biomass of the group.

These equations were combined with the diet matrix, which defines the proportion of each consumer’s ( $j$ ) diet that is made up by each other group ( $i$ ), allowing for one unknown to be solved, such that both equations are true and the model is mass-balanced.

The values obtained from this mass-balanced state are applied to the dynamic Ecosim model. The Ecosim model is governed by one fundamental equation that describes the rate of change of biomass ( $\frac{dB}{dt}$ ) for each group:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + E_i - B_i (M0_i + F_i) \quad (2.3)$$

where  $g_i$  is the growth efficiency (how much consumption is incorporated in the group) and is calculated in the Ecopath model,  $Q_{ij}$  is the consumption of  $i$  by  $j$ ,  $E_i$  is the net migration rate, and  $F_i$  is the catch rate.  $M0_i$  and  $F_i$  are calculated during the balancing of the Ecopath model. The catch input into Ecopath ( $Y_i$ ), is divided by biomass of  $i$  to give catch per unit biomass ( $F_i$ ).

The consumption of each group  $i$  by each other group  $j$  is calculated based on the diet matrix and the vulnerabilities of each prey to each predator group.

$$Q_{ji} = \frac{a_{ij} v_{ij} B_i B_j}{2(v_{ij}) + a_{ij} B_j} \quad (2.4)$$

where  $a_{ij}$  is the effective search matrix, representing the rate at which predator groups encounter prey groups based on their consumptions, biomasses and vulnerabilities in the mass-balanced

state. The search matrix used in the Ecosim model differs from the search matrix that is produced in Ecopath results. In the dynamic model the search matrix is calculated using equation 2.5 from the  $v_{ij}$  values of each group. As the search matrix is calculated from mass-balanced state values, it is static over the whole modelling run.

The vulnerabilities ( $v_{ij}$ ) are calculated from the user input value for each vulnerability ( $k_{ij}$ ) by the equation  $v_{ij} = k_{ij} \frac{Q_{ij}}{B_j}$ , where  $\frac{Q_{ij}}{B_j}$  comes from the balanced Ecopath model. The input values for  $k_{ij}$  range from 0 to  $\infty$ , where 0 represents “bottom-up” control, large values represent “top-down” control, and a value of 2 represents mixed control. In this model, similar to older versions of EwE, a scale of 0 to 1 was used for inputs that were then transformed using  $k'_{ij} = \exp(2\exp(k_{ij} - 1))$ . Under this older input style, a value of 0.3 would represent mixed control, and be transformed to a value of  $\approx 2$ .

$$a_{ij} = \frac{2C_{ij}v_{ij}}{v_{ij}B_iB_j - C_{ij}B_j} \quad (2.5)$$

where  $C_{ij}$  is the consumption calculated in the balanced Ecopath model. The  $C_{ij}$  notation is to distinguish it from dynamic consumption ( $Q$ ) calculated by equation 2.4, although at the initial time step the values are equal.  $B_i$  is the biomass of the prey group and  $B_j$  is the biomass of the predator group, both taken from the balanced Ecopath model.

Primary production (PP) is estimated in the model using a simple saturating equation (Walters *et al.*, 1997).

$$PP_i = \frac{r_i B_i}{1 + B_i h_i} \quad (2.6)$$

$B_i$  is the biomass of the producer group,  $r_i$  is a user-defined value that is the maximum  $\frac{P}{B}$  value that the group can have when biomass is low, and  $\frac{r_i}{h_i}$  is the maximum primary production when the biomass of the producer is high and therefore does not limit production. Large  $r$  values result in the biomass of the producer group being more stable, even under high loss conditions. The value of  $h_i$  is calculated from the value of  $r_i$  and the Ecopath parameters for the producer group:

$$h_i = \frac{\frac{r_i}{(\frac{P}{B})_i} - 1}{B_i} \quad (2.7)$$

Both  $r_i$  and  $h_i$  are calculated at the start of the model run, and used in each time step to calculate the primary production.

## The Cold-water Coral Equations

Two main, direct links were added to the model groups. The first link involves the calcification of living coral. Corals lay down calcium-based skeletons as they grow. This is modelled as a function of production (Mueller *et al.*, 2013; Van Oevelen *et al.*, 2018).

$$\text{Cal}_i = \alpha (g_i Q_i) \quad (2.8)$$

where  $Q_i$  is the total consumption of prey by the cold-water coral group,  $g_i$  is the growth efficiency, and  $\alpha$  is the proportion of consumption that is lost to calcification. This calcification rate is subtracted from the Cold-water coral groups at each time step prior to the calculation of the new biomass.

Cold-water corals produce mucus at a rate ( $MU$ ) that is proportional to consumption (Rix *et al.*, 2016).

$$MU_i = \delta (g_i Q_i) \quad (2.9)$$

where  $\delta$  is the proportion of total consumption by the coral group that is secreted as mucus.

The mucus produced by cold-water corals flows to the mucus pool in the model; this pool is modelled as a detritus pool. The mucus production is also subtracted from the change in coral biomass each time step and thus the new change in coral biomass can be expressed as:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - B_i (M0_i + F_i) - \text{Cal}_i - MU_i \quad (2.10)$$

In equation 2.10 the predation loss and both migration terms are left out, because cold-water corals have no predators and are unable to migrate in their adult form.

The Coral skeleton group is not a consumer; it is best described as a detritus pool in the Ecopath model. Change in the biomass of this group is modelled using the following equation:

$$\frac{dB_i}{dt} = \text{Cal}_{i'} + B_{i'} M0_{i'} - L_i \quad (2.11)$$

where  $\text{Cal}_{i'}$  is calcification from the living coral group  $i'$  whose skeleton is described by group  $i$ ,  $B_{i'} M0_{i'}$  is the mortality of the living coral group and  $L_i$  represents the loss of coral skeleton as a result of mechanical disturbance. The subscript  $i'$  is used because the coral skeleton group is linked to a specific corresponding living coral group.

Sponges consume both other groups and Coral mucus. Sponges do not compete for food with cold-water corals, relying on ultra-zooplankton (Pile and Young, 2006), which in this model are included in the microplankton group. Sponges have predators and thus represent the most direct link between the cold-water corals and the rest of the ecosystem. Sponges take up mucus produced by the cold-water coral group. Sponges are the only consumers of the mucus pool and the model is balanced such that, in its mass-balanced state, all of the mucus is taken up by the sponges.

Sponges secrete a large proportion of their total consumption to the detritus pool. This is

modelled as a proportion of their total production:

$$M3_i = \gamma \left( g_i \sum_j Q_{ij} \right) \quad (2.12)$$

where  $M3_i$  is the loss of energy from the sponge group due to cell turnover,  $\gamma$  is the proportion of total assimilated energy that is lost. Ecopath parameters for the sponge, cold-water coral, and mucus groups are set such that the ecotrophic efficiency of the sponge group is 1, thus  $M3_i$  represents the total flow from the sponges to detritus. This decision was made as the values in the literature present cell turnover as a percentage of total consumption rather than of biomass.

As a sessile group, sponges are vulnerable to physical disturbance, as are cold-water corals. As with cold-water corals, there is no migration of sponges. Thus the rate of change in sponge biomass can be expressed as:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} - M3_i - L_i \quad (2.13)$$

The detritus pool receives the natural mortality flows from all the producer and consumer groups, except for lateral import, sponges and corals. An additional term was added to the model to account for the flow to detritus from sponges as a result of cell turnover (equation 2.12). Not all consumption is assimilated; part of the Ecopath data requirement is a value for the proportion of unassimilated ingestion for each predator group. This value represents food that is not assimilated by the predator group and thus flows to a detritus pool. Coral mucus is modelled as a detritus pool because the contents of this pool are DOC and POC, and the pool does not contribute to the main detritus group directly. The loss of cold-water corals by mechanical disturbance does not directly contribute to the detritus pool, as these coral pieces are no longer part of the reef. The disturbance of sponges, however, will contribute to the detritus pool because they die when disturbed and break down into organic carbon. The rate of change in biomass for the detritus pool is expressed as:

$$\frac{dB_i}{dt} = \sum_p \left( UA_p \sum_j Q_{jp} \right) + \sum_p M0_p + \sum_k M3_k + \sum_k Y_k - \sum_i Q_{ij} \quad (2.14)$$

where  $UA_p$  represents the proportion of unassimilated consumption,  $k$  represents the coral groups,  $p$  represents all groups, except for mucus, detritus, and the lateral import group, and  $i$  represents the detritus group.

## Parametrisation of the additional links

The additional links in the model contain several parameters that describe the way in which energy flows from the cold-water coral group to sponges and the larger ecosystem. These parameters were assigned values based on literature sources. The literature sources and methods

used are described in detail in subsections below, for each link. Likewise, as the cold-water coral and sponge groups were not included in the original Ecopath model (Shannon *et al.*, 2003), values for these groups were obtained from literature sources. The balanced Ecopath model, including the additional groups is presented in appendix A Table A1. The diet matrix used is presented in appendix A Table 2A.

### Basic estimates for cold-water coral

The production to biomass value of the cold-water coral group was assumed to be similar to that of the macrobenthos group in the Ecopath model of Shannon *et al.* (2003). The growth efficiency of the cold-water coral group was based on that of *Lophelia pertusa*; this was found to be  $0.08 - 0.17 \mu\text{mol C}_{\text{tracer}} \text{ mmol C}_{\text{coral}}^{-1} \text{ d}^{-1}$  (Van Oevelen *et al.*, 2018). These units were converted to Ecopath input units for growth efficiency ( $\text{y}^{-1}$ ) by converting the mole values of carbon tracer ( $^{13}\text{C}$ ) and coral ( $^{12}\text{C}$ ) to grams. The final values are thus  $0.0316 - 0.0672 \text{ y}^{-1}$ . A value of 0.066 was used in the model.

### Basic estimates for sponges

The growth efficiency of the sponge group is based on Koopmans *et al.* (2010), who found a mean ( $\pm$ standard deviation) growth efficiency of  $0.099 \pm 0.013$  across six specimens of *Haliclona oculata*, which were the only estimates found that were appropriate for use in the model. The mean value of 0.099 was used in this study. As with the cold-water corals, the production to biomass value of the sponge group was assumed to be similar to that of the macrobenthos group.

### Biomass of cold-water corals and sponges

The biomass of both the cold-water coral and sponge groups could not be estimated by the Ecopath model, as the additional links for mucus production and cell shedding require the production of the group to be known at the start of balancing. Thus both  $(\frac{P}{B})_i$  and  $B_i$  are required inputs for these groups. As the mortality of the sponge group is expressed as a function of their production and, in the balanced state all the mucus is consumed by the sponges, the ecotrophic efficiency of these groups would be 1. An unconstrained non-linear minimisation function called “fminsearch”, which comes as a present with Matlab(R2017a), was used to minimise the value of  $|1 - EE|$  for the sponge and mucus groups. The values that were allowed to alter during this minimisation protocol were the biomass of sponges and the biomass of corals respectively. The biomass of coral could be used to alter the  $EE$  of the mucus group as they represent the sole source of flow to the mucus group. The biomass of the sponges was solved first, because the flow out of the mucus was dependent on that value. The Ecopath model was applied using the biomasses obtained from this optimisation and allowed to estimate the  $EE$  values for these groups.

## Calcification

The energy budget was studied in regulated aquaria for the cold-water coral *Desmophyllum dianthus*, which was fed a diet consisting only of zooplankton. The results of these experiments showed that the mean ( $\pm$  standard deviation) calcification rate of fed *D. dianthus* was  $38 \pm 14 \mu\text{mol CaCO}_3 \text{ g}_{\text{skeletal dry mass}}^{-1} \text{ day}^{-1}$  (Naumann *et al.*, 2011). Values for the calcification rate of cold-water corals are rarely presented in literature sources as a proportion of cold-water coral production rates. The best value is presented in Van Oevelen *et al.* (2018), where the carbon budget for *L. pertusa* is presented. This value is 0.023% of their production.

## Mucus production

Several studies have investigated the links between Coral mucus production and the sponge loop. This link is present in both tropical corals and cold-water corals. Wild *et al.* (2008) found that, in aquaria experiments, *L. pertusa* released a mean ( $\pm$  standard deviation)  $47 \pm 19 \text{ mg m}^{-2} \text{ d}^{-1}$  of DOC. The DOC release values for cold-water corals were found to always be positive and relatively stable in contrast with warm-water corals. Warm-water corals lose around 40% of their fixed carbon in the form of mucus production, and the value for cold-water corals is similar (Crossland *et al.*, 1980; Rix *et al.*, 2016; Wild *et al.*, 2008).

## Mucus consumption and cell turn over

Mucus is consumed by the deep-water sponge *Hymedesmia coriacea* at a mean ( $\pm$ standard deviation) rate of  $1.7 \pm 1.6 \mu\text{mol C}_{\text{mucus}} \text{ mmol C}_{\text{sponge}}^{-1} \text{ d}^{-1}$  (Rix *et al.*, 2016). Sponges turn over a large number of cells, contributing to the detritus pool. The deep-water sponge *H. coriacea* transfers  $40\% \pm 29\%$  (mean $\pm$ standard deviation) of assimilated mucus to detritus (Rix *et al.*, 2016). Rix *et al.* (2016) noted that the standard deviation was high for this experiment. This cell turn-over rate, however represented the only one applicable to this model and thus was included despite the large uncertainty. In this model a value of 40% of the total production of the sponge group was used for cell shedding, thus 40% of the carbon sponges gain from mucus and micro-zooplankton is transferred to detritus. This term replaces the natural mortality term for the sponge group.

## Natural mortality of detritus, and other modified groups

Detritus does not have a natural mortality as it is not a living group. However, it does have a term in place of  $M_0$ , which is the export term. The amount of detritus lost from the system is very important in maintaining a balanced system. The natural mortality of the detritus group and the mucus group, which functions as a detritus group, are calculated during the balancing of the Ecopath model. The other detritus-style group, cold-water coral skeleton, does not have an export term.

Natural mortality or, in this case export, is determined by the EE of the group. As detritus has no production or immigration term, the flows to the detritus act as its ‘production’ while the consumption of detritus represents the amount of ‘production’ that is transferred to other groups. The Ecopath balancing code calculates the EE value of the detritus as the ratio of flows to the detritus to flows from the detritus. This value can be used to work out the amount of detritus that is exported using the equation:

$$MO_i = \frac{1 - EE_i}{\left(\frac{P}{B}\right)_i} \quad (2.15)$$

where the ‘production’ to biomass ratio of the group represents the flows into the detritus pool divided by its biomass.

This same equation is applied to the mucus group. However, the EE value for mucus is set to 1, and there is no export term for the mucus group.

## General flow of energy between pelagic and benthic groups

In order to better understand the general flow of energy in the model, the balanced consumption matrix from the Ecopath model was grouped into four broad classes of model groups, based on each model group’s life history, and the flows between these classes were calculated. The four classes used are: pelagic, benthic, intermediate and detritus. With the exception of the detritus class, which can by definition only contain detrital model groups, all groups can contain a mix of producers and consumers. The intermediate classes contain model groups that are benthic or deep living but move freely: hakes, demersal fish and cephalopods. These groups were put in the intermediate class as they have diets consisting of both benthic and pelagic groups. The lateral import is classed as benthic and the primary producers are classed as pelagic.

## Results

The diagram in figure 2.4 shows the net direction of flow from each class in the balanced Ecopath model. The flow between the benthic and intermediate classes is in the direction of the intermediate class; there is no flow in the opposite direction. The flow between the intermediate and detritus classes is in the direction of detritus; there is no flow in the opposite direction. All the other links have a net direction of flow but there is also some flow in the opposite direction.

The results of this flow analysis indicate that there is net flow out of the pelagic group, which contains the main primary producer group. It also indicates that there is a loop between the detritus, benthic and intermediate groups. There is a net flow into the intermediate class, which contains many of the commercial groups, and thus the net flow into this class is balanced by the removal of organisms from the system. Likewise, there is a net flow into the benthic and detritus classes. The benthic class contains many groups with low growth efficiencies and a

bioaccumulating group in the form of cold-water corals, while the detritus group has an export term; these features account for the net flow to these classes.

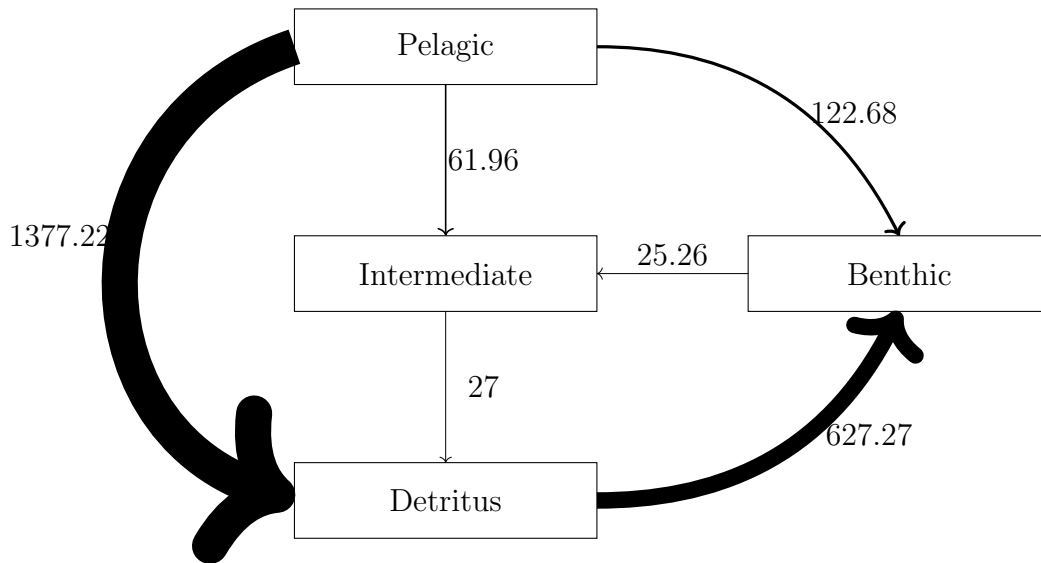


Figure 2.4: Energy flow between different model classes. The values represent the net flow of energy through each link as a result of consumption ( $t C y^{-1}$ ). The widths of the arrows are proportional to the flow.

When the “Ecosim” model is run using the balanced data from the Ecopath model, the relative biomasses of the groups do not change significantly. The exception to this is the cold-water coral skeleton group, which accumulates biomass by design. The cold-water coral skeleton group is not shown in either figure 2.5 or 2.6 as its value for fractional change in biomass ( $\approx 3$ ) over the full model run makes the small changes in the biomass of the other groups impossible to observe. Over the time period, and based on the starting values, the bioaccumulation of the cold-water corals is realistic at an increase of  $50 \text{ kg km}^{-2} \text{ y}^{-1}$ . The presence of a limiting factor to skeleton growth can’t be ruled out. However, any loss from this group would be lost from the system, and thus its absence from the model would only affect the value of this group.

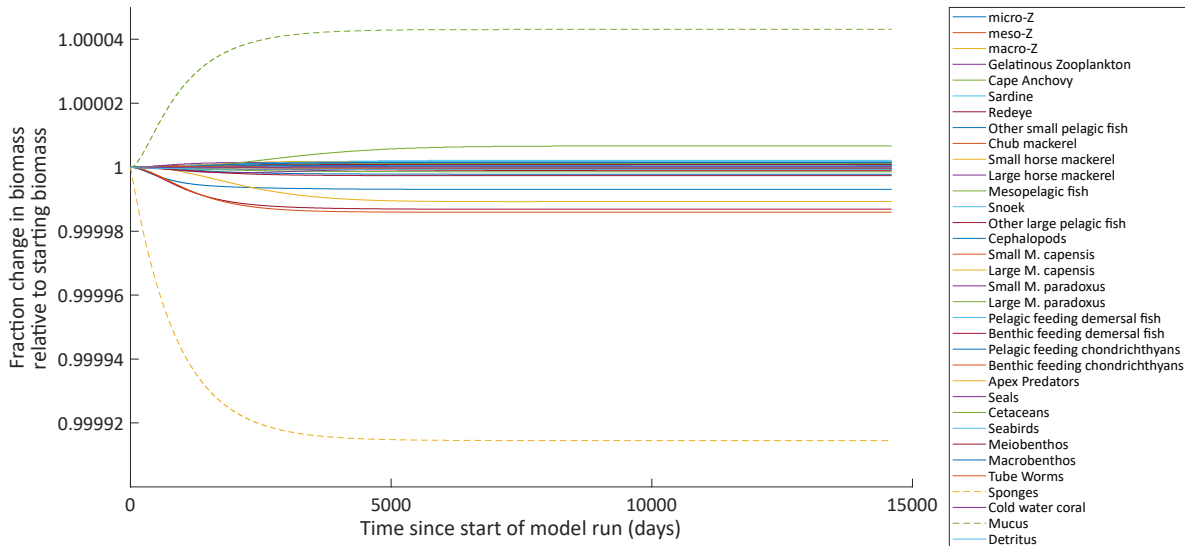


Figure 2.5: The results of running the customised “Ecosim” model using the mass-balanced input data. The fractional change in biomass of all groups, except for the cold-water coral skeleton group, are shown on this graph.

With the exception of Cold-water coral, skeleton which increases at a rate of around  $50 \text{ kg km}^{-2} \text{ y}^{-1}$  throughout the model run, the range of values for fractional change in biomass during the dynamic Ecosim model run (figure 2.5) are on the order of  $10^{-5}$ ; these very small perturbations all stabilize after 7500 days. The groups with the largest perturbations are the additional Sponge and Mucus groups; the original groups exhibit much smaller changes in fractional biomass. After year 20 (day 7300) the model predicts no change in the biomasses of these groups; the biomass of each group changes by less  $4 \times 10^{-7}$  of each group’s biomass at year 20 in the next 20 years (figure 2.6).

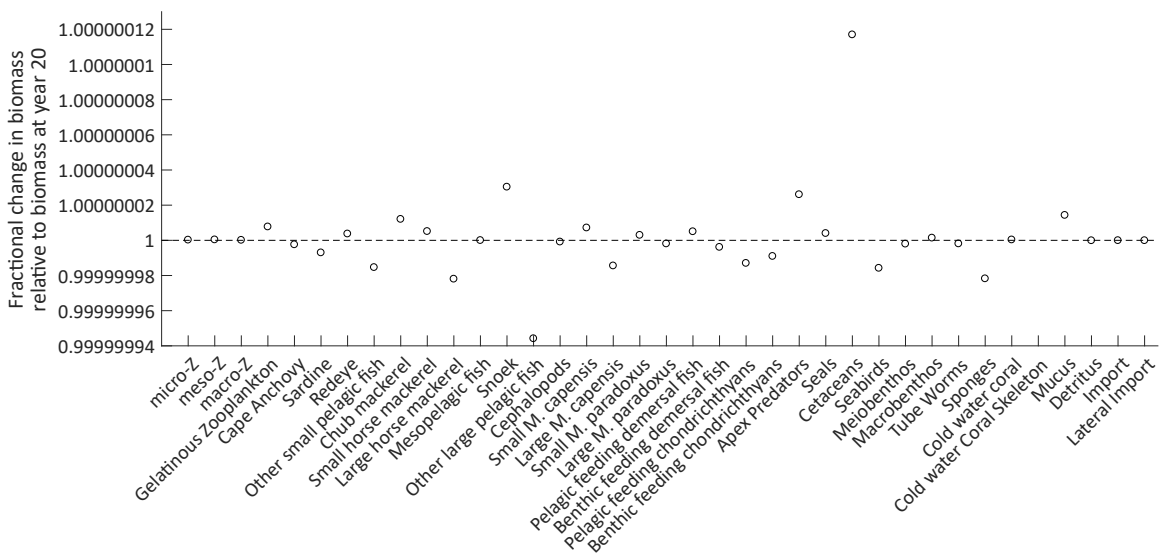


Figure 2.6: The fractional change in biomass at year 40 relative to the biomass at year 20, for the balanced model run forward in time. The value for the cold-water coral skeleton group is not shown on this graph, as it increases at a rate of  $50 \text{ kg km}^{-2} \text{ y}^{-1}$ .

## Discussion

The results from the dynamic model run using the customised Ecosim model are consistent with those expected from a standard EwE modelling run. When no forcing functions are applied to the model the expected output is that the biomass of each group is stable. This consistency indicates that the changes made to the original EwE model equations are valid within the model space. The minor perturbations present at the start of the model run are consistent with the unaltered Ecosim model. When the biomass at year 20 is compared with that at year 40, the results indicate even greater stability. Thus, scenarios run using this model will start at the 20-year mark and the results of such scenarios will be measured 20 years later, unless time is a factor in the scenario.

The EwE model has been modified multiple times by many different authors for a range of purposes. Some of these modifications have been integrated back into the main release in the form of plugins (Steenbeek *et al.*, 2016). The model also has been translated into a range of different programming languages. The alterations done to the model by these authors have rendered many of their customised EwE models so different from the original that the results cannot be compared to each other. Many of the plugins included in the current release of EwE(V6.5) started off as independently developed programs; features as common as the flow diagram were developed external to the main model.

The summary statistics for the customised EwE model differ from those of Shannon *et al.* (2003). Specifically, the total consumption in the customised EwE model is higher than in the EwE model on which it is based. This makes logical sense as there are additional consumption links in the customised model and thus there is higher consumption. The flow to the detritus is greater in the customised model for the same reason. These differences in summary statistics represent the effect of the additional links, and changes in the mass-balanced biomasses of some groups as a result. This is expected as the models, while created from the same dataset, represent different parts of the Southern Benguela. During the balancing processes the additional links and parameters for the cold-water coral groups caused the model presented here to have different estimates for many of the parameters compared with the model from which it was created.

The results of this model can also be compared to those of Skaret and Pitcher's (2016) model of the Norwegian Sea and Barents Sea, as their model also contained an explicit cold-water coral group. Major differences between the two models include the aims, and the biomass of cold-water coral in the model. The differences in biomass are tied into the differences in aims, as Skaret and Pitcher (2016) were describing two entire seas whereas the model presented here aims to describe the waters directly surrounding a cold-water coral reef, and thus has a greater density of coral.

The biomass of the cold-water coral skeleton group increases over the model run. As the natural mortality of the cold-water coral group is considered to be lost from the system, the sole contribution to this terminal group is the calcification rate. The bioaccumulation observed in this group over the total model run (2 tonnes at a constant rate of  $50 \text{ kg km}^{-2} \text{ y}^{-1}$ ) is consistent with the slow growth rates of cold-water corals,  $26 \text{ mm y}^{-1}$  (Gass and Roberts, 2006). Note that Gass and Roberts (2006) rate has no area component.

The results of the balanced Ecopath model indicate that no energy is recycled back to the pelagic group, which is a result of the pelagic class containing the primary producer group. There is some cycling between the detritus, benthic and intermediate groups. This supports the hypothesis that the sponge loop helps retain energy in the reef (de Goeij *et al.*, 2013; Rix *et al.*, 2016) as the net flow of energy to the benthic group from detritus is positive and thus indicates that energy lost by the sponges (a benthic group) is passed back up to the other benthic groups along with the other detrital flows. These energy flows also suggest that the benthic organisms in this model retain detritus in the system. The detritus is primarily produced by the natural mortality of the pelagic group, and cycled through the benthic groups to the intermediate groups. The cold-water corals feed on lateral import, which would pass through the system otherwise, thus while the contribution of Coral mucus via the sponge loop is small compared to natural mortality, it provides an otherwise unusable source of carbon to the system.

## Conclusion

The customised EwE model produces results that are consistent with those of an unmodified EwE model, indicating that the model complies with the assumptions of the unmodified EwE model. The finding that energy is not recycled to the modelling groups that are classed as solely pelagic indicates that such direct coupling may be primarily driven by physical factors, rather than trophic interactions. An extension of this model that includes physical processes such as mixing of the water column may provide greater insight into this potential link. Such an extension would most likely be built using the Ecotran model, with modification added as necessary to account for the cold-water coral specific pathways.

# Chapter 3

## Applying a customized Ecosim model to cold-water coral habitats

### Abstract

The majority of known coral species are found at depths greater than 50m. *Lophelia pertusa* is a cosmopolitan reef-forming cold-water coral species, and is the focus of this modelling study. In the North Atlantic fishers report good fish catches in the waters surrounding cold-water coral reefs. In South Africa and globally, cold-water coral reefs are under threat from trawling damage, seafloor mining and ocean acidification. A customised EwE model was applied to four scenarios, designed to investigate whether trophic links in the cold-water coral ecosystems could account for increased fish abundance: scenario 1, the removal of both cold-water coral and cold-water coral skeleton (a. no mediation effects b. mediation effects are present), scenario 2, changes (a. increase b. decrease) in fishing pressure on small pelagic fishes, scenario 3, the removal of cold-water coral skeleton without damage to the living coral. Scenario 3 is an artificial scenario designed to isolate the effects of cold-water coral skeleton loss from the trophic interactions from the living cold-water corals. The results from all the scenarios indicate that trophic interactions do not account for the increased abundance of fishes observed on cold-water coral reefs. It is thus hypothesised that the driver of this increased abundance is the result of the physical structure of cold-water coral reefs rather than directly through their trophic interactions. It is therefore suggested that further modelling studies should be conducted using the Ecotran model, which is better able to include physical terms.

### Introduction

Deep-dwelling corals make up the bulk of the known coral species; 65% of all documented coral species are found at depths greater than 50m (Roberts *et al.*, 2006). These organisms are distributed globally (Roberts *et al.*, 2006), with the greatest density of reefs in the North Atlantic. This is likely due to unequal sampling efforts compared with other oceans, specifically with the oceans of the southern hemisphere (Freiwald *et al.*, 2017). This study focuses on the cosmopolitan, reef building, species *Lophelia pertusa* (Zibrowius, 1980).

Fishers in Norway and Nova Scotia consider the waters surrounding cold-water coral reefs

to be good fishing grounds, and in Norway they claim that catches have decreased around damaged reefs (Breeze *et al.*, 1997; Fosså *et al.*, 2002). These claims are supported by video studies showing that both species abundance and richness are greater on reefs compared with the surrounding seafloor (Buhl-Mortensen *et al.*, 2017a; Costello *et al.*, 2005). There is little doubt that cold-water coral reefs either benefit multiple other marine species or are indicative of a mutually beneficial factor. There are a number of hypotheses about what benefit cold-water coral reefs have on the species that live on them. The mere presence of a three dimensional structure on an otherwise barren seafloor provides cover to some species, and hunting grounds to others (Costello *et al.*, 2005; Roberts *et al.*, 2006). In the EwE model, protection from predation, or increased vulnerability to predation, is applied to the consumption equation for the predator-prey interaction. The value that is added to the consumption equation is referred to as the mediation effect. This is calculated by the mediation equation and represents the effect of a third group's biomass on an interaction.

Certain species might use cold-water coral reefs as a nursery ground (Costello *et al.*, 2005; D'Onghia *et al.*, 2010; Freiwald *et al.*, 2004; Husebø *et al.*, 2002). Fish can aggregate on reefs and feeding can be enhanced for lower trophic levels around the reef. Carbon is retained on cold-water coral reefs by the sponge loop (Rix *et al.*, 2016) and the retention of this carbon might contribute to sustaining the local reef community.

Laboratory experiments and in situ observations have shown that cold-water corals grow very slowly. Globally, cold-water corals are under threat from trawling, with some of the documented damaged reefs being in excess of 2000 years old (>4000 years old (Hall-Spencer *et al.*, 2002)). Trawling occurs on approximately 33% of Childs Bank, with the trawling footprint evident around the sides of the bank and not over it (Sink *et al.*, 2012b). Other cold-water coral sites in South Africa include Browns Bank, which is extensively trawled (Department of Environmental Affairs, 2014; Sink *et al.*, 2012b). The trawl footprint is currently in the vicinity of the proposed Port Elizabeth corals marine protected area (MPA) (Department of Environmental Affairs, 2014). The proposed MPAs in these cases aim to protect, along with other features, the cold-water corals that live in these areas. Trawling is not the only threat for cold-water corals; any form of mechanical disturbance will destroy these reefs, including threats from oil drilling and, increasingly, from proposed seafloor mining.

Seafloor mining represents a fast-growing threat to benthic habitats in South African waters; ninety percent of South Africa's exclusive economic zone was leased out for petroleum exploration (Sink, 2016). As of 2016, three prospecting rights for marine phosphate have been granted by the South African government (WWF-SA, 2016). Two of these leases allow for the prospecting of phosphate, rare earth metals and other metals excluding diamonds, petroleum or gas, using both non-invasive and invasive methods, including drilling, grabs and trenching. Both leases cover habitats that are known to include cold-water corals (Childs Bank, (Green

flash Trading, 2012a) and Browns Bank (Green flash Trading, 2012b)).

Benthic-pelagic coupling is important in the context of ecosystem management, as disturbance to the benthos can have a knock on effect on the pelagic organisms (Pilskaln *et al.*, 1998; Thrush and Dayton, 2002). Understanding the processes involved increases effectiveness of MPA planning and fisheries management by allowing for the targeting of important areas for protection. Without an understanding of how the benthic and pelagic systems are coupled, allowing any destructive activity to take place over certain habitats could have a cascading effect on other marine resources.

Tropical corals are susceptible to ocean acidification by reducing their ability to build coral skeleton, which is made of calcium carbonate ( $\text{CaCO}_3$ ). Cold-water corals also build calcium carbonate skeletons (Freiwald *et al.*, 2004). Ocean acidification has the potential to negatively impact cold-water corals (Roberts *et al.*, 2006). Ocean acidification is suspected to be taking place in South African waters, modelling predicts that the Benguela current could become unsuitable for calcium carbonate formation due to under-saturation of aragonite in the next three decades (Moloney *et al.*, 2013). Furthermore, an overall decrease in the growth rates of corals off the east coast is suggested to be related to the global trends for temperature change and ocean acidification (Hayman and Uken, 2015).

Threats to cold-water corals are growing, both in South Africa and globally, as nations explore ways to increase utilisation of marine resources. It is necessary to find ways of ensuring the sustainability of marine resources through effective management. In this light, understanding the effects of cold-water coral loss is increasingly urgent and important. The primary aim of this research is to determine whether trophic interactions drive benthic-pelagic coupling in cold-water coral systems. The secondary aim is to investigate whether fishing pressure, increased or decreased, triggers trophic-related benthic-pelagic coupling. The model is based on an existing model and data from the Southern Benguela ecosystem.

## Methods

### Model

A cold-water coral ecosystem model was developed using data for the Southern Benguela. The model code was written in Matlab using a customised version of the Ecosim model, as described in Chapter 2. The model was used to test a number of scenarios, described below, related to cold-water coral loss or damage and how it affects the rest of the ecosystem as a result of trophic interactions.

## Mediation links

Cold-water coral reefs may offer some model groups protection from predation (Freiwald *et al.*, 2004; Krieger and Wing, 2002). In this model only benthic groups were assumed to gain protection from the presence of the cold-water coral skeleton. These groups are: small *Merluccius capensis*, small *Merluccius paradoxus*, pelagic feeding demersal fish (which is the model group that contains the pelagic feeding demersal fishes that are not mentioned by name in the model), benthic feeding demersal fish, meiobenthos, and macrobenthos. The groups were given increased protection from predation, related to the biomass of the Cold-water coral group, assuming the relationship took the form of a sigmoid curve reaching a maximum protection of being two times less likely to be consumed than in the base state. The protection was assumed to apply to all predator-prey links except in the case of meio- and macro- benthos, which were not granted extra protection from each other, as they both live in close proximity regardless of the presence of the reef.

## Scenarios

The scenarios have been set up as experiments to answer the questions posed by the aims of the project.

### General scenario running procedure

Each scenario is applied to the model at year 20. The model run ends at 40 years and the biomass of each group at this point is compared to the biomasses just before the scenario conditions were applied. Results are presented as fractional change, thus values greater than one represent an increase in biomass between the start and end of the model run and values less than one represent a decrease.

### Scenario 1

The first scenario was designed to investigate the effects of damage to both the living Cold-water coral group and Cold-water coral skeleton group as might result from trawling or mining. In order to make the trends as pronounced as possible, the extreme case of complete removal of both groups was used. The biomass of the Cold-water coral and Cold-water coral skeleton groups are set to zero at year 20 and held there for the rest of the model run.

To isolate the effects of the trophic interactions between the living Cold-water coral group and the rest of the ecosystem, mediation effects were not present in scenario 1a. In scenario 1b mediation effects were present as the literature indicates that the physical structure of cold-water corals likely alters the predator prey interactions for fish living on the reef.

## Scenario 2

This scenario tests the effects that changes in fishing pressure on small pelagic fish groups might have on the cold-water corals. This scenario was used as it represents a method whereby the biomass of the small pelagic groups in the system might change. The small pelagic groups have some diet overlap with the corals feeding on zooplankton, thus this scenario was run to determine whether Cold-water coral growth is affected.

The fishing pressure was altered on four small pelagic groups: cape anchovy, sardine, red-eye and other small pelagic fish. In scenario 2a the fishing pressure was increased to twice the base catch per unit biomass of each group. In scenario 2b the fishing pressure was decreased to half that of the base catch per unit biomass of each group. In both scenarios a and b mediation effects were assumed to be present.

## Scenario 3

This artificial scenario is designed to disentangle the trophic related changes from the loss of cold-water corals, from the mediation driven changes that result from the loss of cold-water coral skeleton. The scenario is partly based on the effects of ocean acidification, but the living Cold-water coral is not altered. Despite the ecological inaccuracy of not decreasing the living Cold-water coral, this is done in order to better examine the interactions between the Cold-water coral skeleton group and the ecosystem. Thus, this scenario should not be considered ecologically accurate. However, it provides an important insight into the way the model functions and the ecosystem wide effect of the Cold-water coral skeleton group. As the Cold-water skeleton group only interacts with the rest of the system by mediation effects, this scenario is only run with mediation effects present.

A loss term was added to the Cold-water coral skeleton group. The rate of cold-water coral skeleton loss is set to 0.2 of its current biomass annually. This term is applied at each time step, as with all other loss terms in the model. The cold-water coral skeleton loss is assumed to not contribute to the detritus pool, as it is made primarily of calcium carbonate.

# Results

## Scenario 1

The results for scenario 1a (figure 3.7) show that the complete removal of cold-water corals and their skeletons has little to no effect on the rest of the ecosystem as a result of trophic interactions. The biomass of the mucus group quickly falls to zero, as there is no production from the Cold-water coral group. The mucus pool is quickly depleted due to consumption by sponges and export from the system. The lateral import group, which contains both live and dead zooplankton and other particulate organic matter that is utilized by the Cold-water coral

group as a source of nutrients, increases by around 1.5 times as the Cold-water coral group is its main predator. The increased lateral import would be unlikely to accumulate in the system due to the currents.

The slight decrease in the biomass of sponges represents the effect of mucus loss. The change in sponge biomass is insufficient to trigger any other major biomass changes in its predators. The relative biomass of the Tube worm group increases, which is in response to changes in prey availability. The model does not include any prey switching terms and thus the loss of cold-water corals results in a slight increase in prey for tube worms.

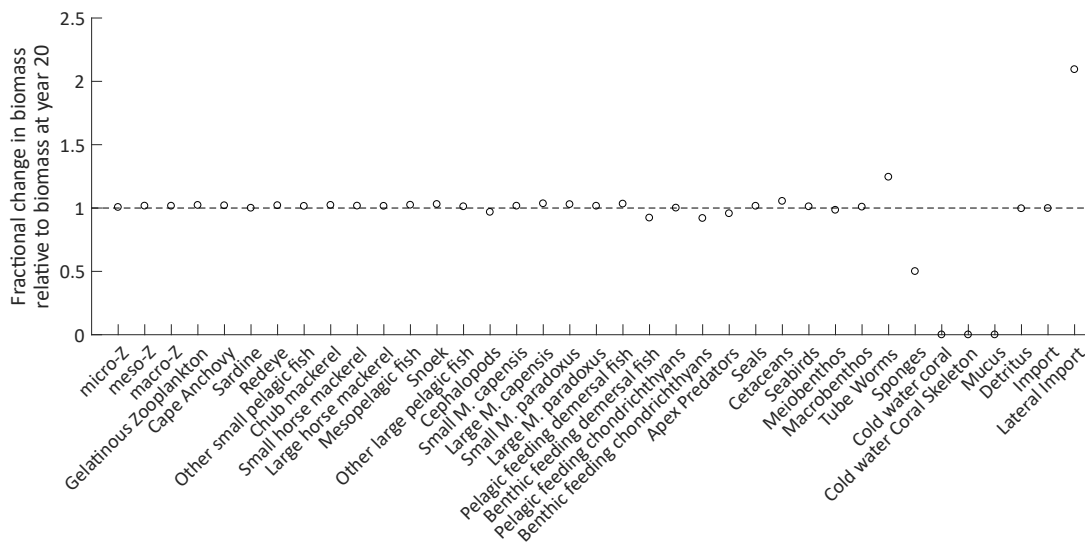


Figure 3.7: Results of the model for scenario 1a showing the fractional change of each group’s biomass between the end of the model run (year 40) and the start (year 20). All cold-water coral and cold-water coral skeleton were removed.

When mediation effects are included (scenario 1 b) the system response is notably different to those in scenario 1a (figure 3.8). The responses by the Tube worm and Sponge groups are similar to those in scenario 1a. The relative biomass of the Macrobenthos group decreases, while the relative biomass of the Meiobenthos group increases by a small amount.

The largest change in relative biomass that is not also present in scenario 1a, is for the Small *M. capensis* and Small *M. paradoxus*. The Cold-water coral skeleton group offers protection to both Small *M. capensis* and Small *M. paradoxus*. The loss of Cold-water coral skeleton thus directly contributes to increased predation on these two groups and a reduction in their relative biomass. The relative biomass of both the Benthic and Pelagic feeding demersal fish groups decrease as well. These two groups are also protected from predation by the presence of the Cold-water coral skeleton group. Because each of these four groups have multiple predators, no reciprocal increase in relative biomass is seen in scenario 1a or b. However, the relative biomasses of the Other large pelagic fish, Cephalopods, and Pelagic and Benthic feeding chondrichthyans increase slightly. All of these groups are predators of at least two of the four groups

that decreased.

In addition to the groups mentioned above, Redeye and Mesopelagic fish have a small increase in relative biomass. Neither of these groups feed on mediated groups. Redeye and Mesopelagic fish are found in the diets of Small *M. capensis*, Small *M. paradoxus*, and Pelagic feeding chondrichthyans. Their increase is thus due to a decrease in predation pressure from the Small *M. capensis* and Small *M. paradoxus*. The increase in relative biomass of the Pelagic feeding chondrichthyans results in increased predation by this group, however this is insufficient to negate the reduction in predation pressure by the Small *M. capensis* and Small *M. paradoxus* groups.

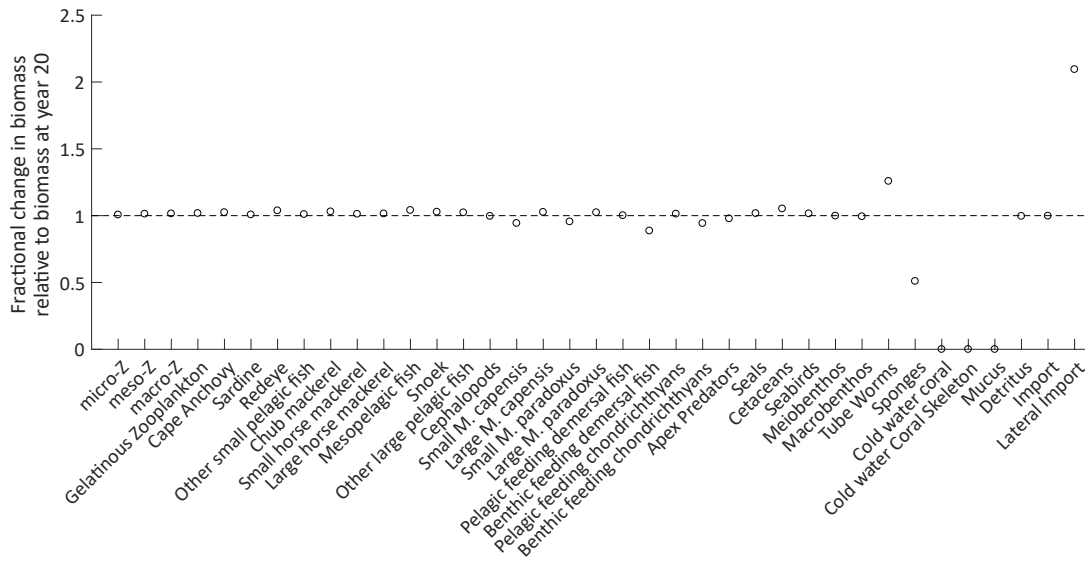


Figure 3.8: Results of the model for scenario 1b showing the fractional change of each group’s biomass between the end of the model run (year 40) and the start (year 20). All cold-water coral and cold-water coral skeleton were removed and mediation effects are present.

## Scenario 2

The results for scenario 2a (figure 3.9) show that increased fishing pressure on the small pelagic groups does not change the relative biomass of cold-water corals notably.

The relative biomass of the Tube worms increases more than that of the Cold-water coral group. The Cold-water coral group relies on Lateral import more than the Tube worms which is thus more resistant to changes in the surface production. The biomass of the Sponges decreases slightly in response to the fishing pressure; this change is most likely the response to increased predation on the Sponge group. The change in predation on the Sponge group is the result of an increase in the relative biomass of the Benthic feeding demersal fish and Macrobenthos groups. The relative increase in the Benthic feeding demersal fish group is due to changes in the relative biomass of the groups predators, mainly Seals and Apex Predators. The driving

changes behind the changes in the relative biomass of the Seal and Apex predator groups are discussed in greater detail later in this section.

The decreases in the relative biomasses of the Cape anchovy and Sardine groups are the direct result of increased fishing pressure on these groups. The Redeye group is more resistant to the increased fishing pressure as, while the pressure was doubled on all groups, the original catch rate of the Redeye group was relatively low. The biomass of the other Small pelagic fish group increases despite the increased fishing pressure on the group because, as with the Redeye group, the fishing pressure on the Other small pelagic fish group is low. The diet of the Other small pelagic fish group is made up only of zooplankton groups, thus the reduction in competition for food outweighs the increase in fishing pressure.

The biomass of the Snoek and Other large pelagic fish decreases. Both of these groups have diets that consist of more than 10% Cape anchovy, thus their decrease in biomass is driven by a decrease in prey abundance. Likewise, there are noticeable decreases in the biomasses of the Apex predators, Seals, Cetaceans and Seabirds groups. The Seals, Cetaceans and Seabirds groups have diets that consist of a fair amount (15-30%) of Cape anchovy. The Cetaceans and Seabirds also feed on Sardines. These decreases in prey abundance result in the observed decrease in biomass. The Apex predator group does not feed on any of the small pelagics, but it does feed on Cetaceans. Thus the decrease in the relative biomass of the Apex predator group is due to the decrease in relative biomass of the Cetacean group.

The increase in the relative biomass of the Small *M. capensis* group is due to a reduction in the relative biomass of its two largest predators, Snoek and Large *M. capensis*. However, these changes are muted slightly by the reduction in prey, as the Cape anchovy, Sardine and Redeye groups make up around 6% of the Small *M. capensis* group's diet.

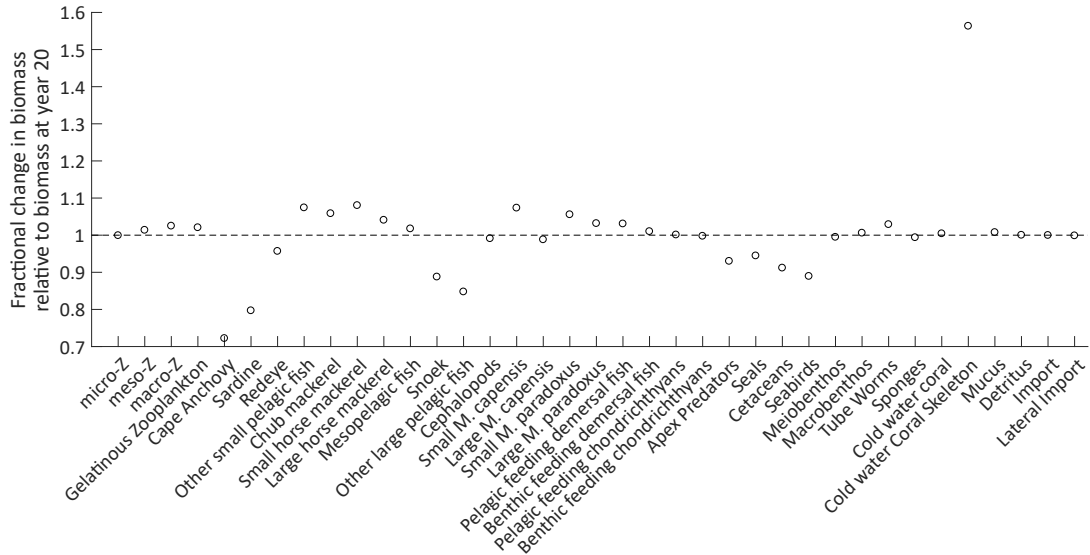


Figure 3.9: Results of the model for scenario 2a showing the fractional change of each group’s biomass between the end of the model run (year 40) and the start (year 20). The catch per unit biomass of the small pelagics are increased two-fold and mediation effects are present.

When the fishing pressure is decreased on the small pelagic groups in scenario 2b (figure 3.10), nearly the exact opposite of what is observed in scenario 2a is seen. The exact opposite of the reasons discussed for the changes in relative biomass observed as a result of scenario 2a apply to the results of scenario 2b. This is because the fishing pressure change used in scenario 2b is the exact inverse of that used in scenario 2a. The one exception to this is the Small *M. capensis* group, which does not decrease by the same amount it increases in scenario 2a. The increase in prey availability for Small *M. capensis* does not account for this, as it is identical to the decrease in prey availability used in scenario 2a and thus a mirrored response would be expected. Small *M. capensis* is one of the groups that is offered protection from predation by the presence of the Cold-water coral skeleton group. As the Cold-water coral groups are not disturbed by the increase in pelagic fishing pressure, the Coral skeleton group, which grows at a constant rate over time, is able to offer protection to certain groups. This accounts for the muted decrease in the biomass of Small *M. capensis*.

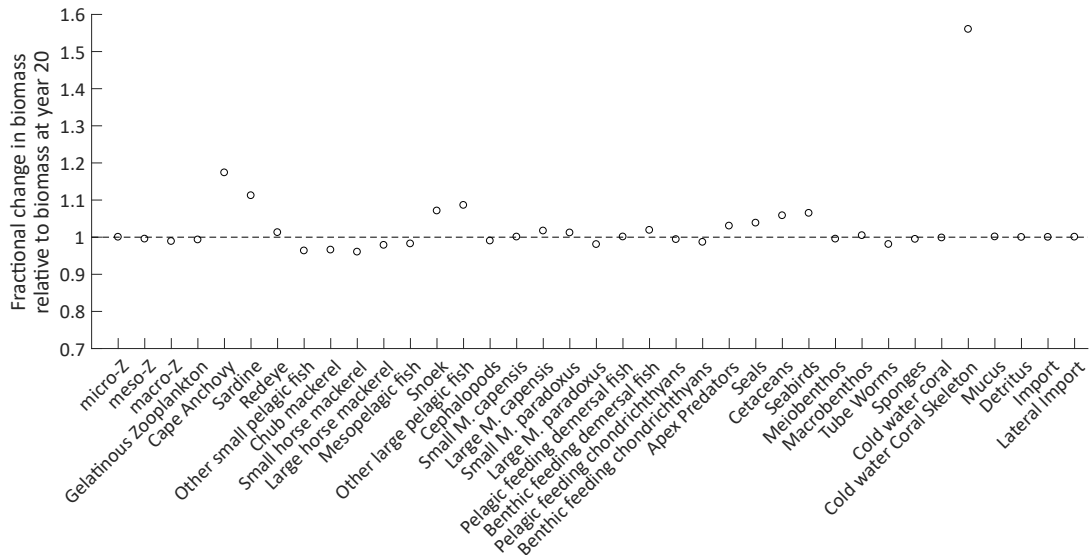


Figure 3.10: Results of the model for scenario 2(b) showing the fractional change of each group’s biomass between the end of the model run (year 40) and the start (year 20). The catch per unit biomass of the small pelagics are decreased to half their original values and mediation effects are present.

### Scenario 3

The results for scenario 3 show that increased ocean acidification, or any process that leads to an increased loss of Cold-water coral skeleton, leads to changes in the relative biomass of the groups that rely on the Cold-water coral skeleton for protection.

The results for scenario 3 (figure 3.11) are similar to those for scenario 1b (figure 3.8). The biomass of the Cold-water coral group is not altered in this scenario, but Cold-water coral skeleton loss was set to 20% of its biomass. As a result, the relative biomass of the Lateral import group does not change. The relative biomass of the Tube worms group does not increase as substantially in scenario 3 as it did in scenario 2b. This is because the living Cold-water coral group is unaltered and thus food availability for the Tube worms does not increase. Likewise the relative biomass of Sponges increases slightly in scenario 3, where it decreases in scenario 1b. As the living component of the Cold-water coral is unaffected in scenario 3, the increase in biomass of the Sponges is due to a slight decrease in predation pressure and the fact that Mucus production remains the same. The reduction in predation pressure is present in both scenarios 1b and 3, however the loss of the living Cold-water coral group in 1b results in Sponges not having access to coral mucus as a carbon source.

The changes in the relative biomass of the Meio- and Macrobenthos are very similar between scenarios 1b and 3. This is indicative of the driver of these changes being changes in predation pressure, related to the groups that are offered protection by the Cold-water coral skeleton, rather than trophic links between the living Cold-water coral group and the rest of the ecosystem.

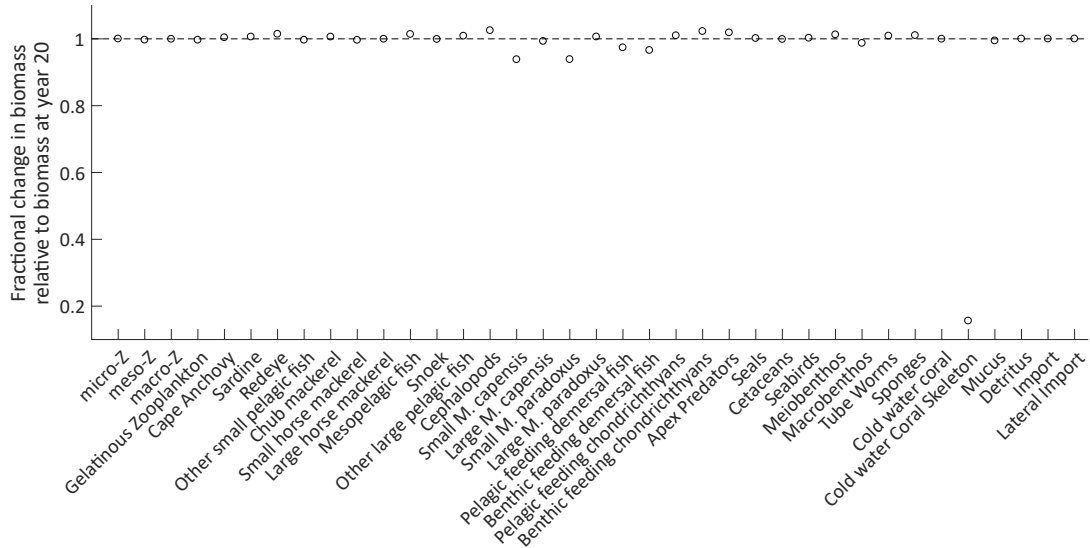


Figure 3.11: Results of the model for scenario 3 showing the fractional change of each group’s biomass between the end of the model run (year 40) and the start (year 20). Cold-water coral skeleton is lost at a rate of 20% per annum and mediation effects are present.

## Discussion

The results of the model show that the removal of Cold-water coral and Cold-water coral skeleton from the ecosystem has an impact on the other functional groups. The system-wide response to the removal of Cold-water coral skeleton is only present in scenarios where it is assumed that the Cold-water coral skeleton mediates the predator-prey interactions of other groups. This indicates that there are no trophic pathways from the Cold-water coral group that are sufficient to significantly alter the wider ecosystem. Furthermore, the changes in relative biomass of the other functional groups in the coral-disturbance scenarios were not sufficient to conclude that the trophic interactions considered in this model are the primary driver of increased abundance of fish observed on cold-water coral reefs. Observational studies of cold-water coral reefs indicate that the impact of removing cold-water coral from the system should have been much greater than what is observed in scenario 1 (Buhl-Mortensen *et al.*, 2017a; Costello *et al.*, 2005)

Tropical corals are ecosystem engineers, not just because they are autotrophic but also because of their role in providing habitat to reef organisms (Wild *et al.*, 2011). Cold-water corals are thus likely to be ecosystem engineers, as they also provide a habitat for organisms. Comparison between a cold-water coral reef and ship wreck found that more species associated with the cold-water coral reef than the ship wreck, suggesting that the complex 3-dimensional structure of the reef was more beneficial than the flat surfaces present on the shipwreck (Costello *et al.*, 2005). The model results cannot support or refute the hypothesis that the physical structure of cold-water coral reefs provides a refuge from predation to some fish groups (Costello *et al.*, 2005; Roberts *et al.*, 2006). However, when this hypothesis is assumed to be true, the results

show at most a 10% decrease in the mediated groups when corals are removed, coupled with an increase in their predator's relative biomass. This does not account for the increased abundance and richness observed on cold-water coral reefs in the North Atlantic (Costello *et al.*, 2005; Husebø *et al.*, 2002).

Norwegian fishers have indicated that they catch a greater number of fish using both long-line and gill nets close to cold-water coral reefs and that these catches decrease over damaged cold-water coral reefs (Fosså *et al.*, 2002). The fish species mentioned in their study would fall into the demersal fish groups in this model. The decrease in relative biomass of the groups as a result of cold-water coral skeleton loss (scenario 1 b) and 3) is small, but the species affected are supported by the literature. While these model results agree with observations from Norwegian reefs, the cold-water coral reef system modelled here has not been studied to determine whether the abundance of fish on the reef is different to the waters surrounding it. However, given the similarities among cold-water coral reefs, it is hypothesised that the abundance of fish on undamaged South African cold-water coral reefs would also be greater than the surrounding seafloor and damaged reefs. The fish species that show enhanced abundance on cold-water coral reefs are often commercially important (Costello *et al.*, 2005; Hall-Spencer *et al.*, 2002; Husebø *et al.*, 2002). The fish mediated in this study were chosen based on their life histories, but the groups contain commercially important species.

The sponge group was less reliant on the cold-water coral-derived mucus than Rix *et al.* (2016) suggested. The available data did not allow for a balanced model in which the sponge group was more reliant on the cold-water coral-derived mucus. The diets of sponges consist predominantly of migratory ultra-zooplankton, which in this model are included in the micro-zooplankton group. The customised EwE model used was designed to look for trophic interactions that might explain the increased abundance of fish on cold-water coral reefs and the role of reefs in benthic-pelagic coupling. The model did not include physical factors such as current flows and particle retention. Both the lack of detailed data regarding the diet of sponges in the system, and the nature of the model used may have negatively impacted the importance of the sponge loop in the simulations. The inclusion of more physical processes in the model could be used to determine whether mixing or other water flow-related processes increase the importance of the sponge loop in this system.

Changes in the pelagic groups altering the benthic groups are seen in the results for scenario 2. As cold-water coral relies more on lateral import than migrating zooplankton, in this model its relative biomass does not change as much as the benthic groups that feed primarily on zooplankton. This indicates that some benthic-pelagic coupling is present in this system. However, the relative changes in biomass for the affected groups are no greater than 10% of their original groups.

The trophic response of the system to live cold-water coral loss does not affect the relative biomasses of fish groups. The removal of Cold-water coral skeleton does affect the relative biomass of some of the fish groups, but it does not change their relative biomass by a notable amount. The trophic cascade that takes place in response to Cold-water coral skeleton loss is very small (scenario 3). It is thus suggested that the physical structure of the reef, both offering protection to fishes and altering the physical flows through the water column, is the primary driver of increased abundance. This agrees in part with the findings of Husebø *et al.* (2002) who concluded that *Sebastes* spp benefited most from the physical structure of the reef, rather than changes in diet.

The Ecotran model is a transformation of the EwE model, converting it into a bottom-up model (Steele, 2009). While EwE allows for benthic-pelagic coupling through foodweb interactions, it does not include physical mixing of nutrients and biomass within the system (Ruzicka *et al.*, 2018). The Ecotran model has been developed to allow for physical forcing and nutrient recycling, and its box structure allows for benthic-pelagic coupling to be better modelled (Steele and Ruzicka, 2011). Given the results of this model, an Ecotran model, with the necessary adjustments to account for the coral-related processes, would likely perform better at recreating the in situ observations.

As the species assemblage found on cold-water coral reefs is related to the local ecosystem and region in which the reef is found, direct observations of suspected cold-water coral reefs in South African waters would improve the results presented here. Increased data collection from the region in which cold-water coral reefs are identified in South African waters will enhance not just this model but allow for more detailed and correct processes to be included in future modelling studies.

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# Appendix A

Table A1: The basic inputs for the Ecopath model of the southern Benguela, including the additional groups used in this model. All figures are rounded to 3 decimal places. Biomass( $t\ km^{-2}$ ), PB = production to biomass ratio ( $y^{-1}$ ), QB = consumption to biomass ratio ( $y^{-1}$ ), EE=ecotrophic efficiency (ratio of energy flows out of the group to energy flows into the group), PQ = production to consumption ratio, Unassim is the fraction of consumption that does not contribute to production. Bold numbers represent values calculated by the Ecopath model, italicised numbers represent those solved using non-linear minimisation. This caption was adapted from de Haast *et al.* (2018)

Group	Biomass	PB	QB	EE	PQ	Unassim
Import	101.930	143.467		0.59		
Lateral Import	7.249	10		0.5		
micro-Z	<b>10.022</b>	482	<b>1928</b>	0.95	0.25	0.2
meso-Z	<b>9.052</b>	40	<b>133.333</b>	0.95	0.3	0.2
macro-Z	<b>14.982</b>	13	<b>31.707</b>	0.95	0.41	0.2
Gelatinous Zooplankton	5	0.584	<b>1.669</b>	<b>0.152</b>	0.35	0.2
Cape Anchovy	3.573	1.2	12.3	<b>0.992</b>	<b>0.098</b>	0.2
Sardine	2.091	1.2	<b>12.371</b>	<b>0.992</b>	0.097	0.2
Redeye	<b>6.226</b>	1.2	<b>12</b>	0.99	0.1	0.2
Other small pelagic fish	0.364	1	<b>10</b>	<b>0.936</b>	0.1	0.2
Chub mackerel	0.455	0.8	<b>8</b>	<b>0.666</b>	0.1	0.2
Small horse mackerel	0.484	1.2	12	<b>0.665</b>	<b>0.1</b>	0.35
Large horse mackerel	1.937	1	10	<b>0.817</b>	<b>0.1</b>	0.3
Mesopelagic fish	<b>10.245</b>	1.2	<b>12</b>	0.99	0.1	0.35
Snoek	0.337	0.5	<b>5</b>	<b>0.989</b>	0.1	0.2
Other large pelagic fish	0.131	0.48	5.6	<b>0.899</b>	<b>0.086</b>	0.2
Cephalopods	1.364	3.5	<b>10</b>	<b>0.954</b>	0.35	0.2
Small M. capensis	<b>0.638</b>	2	<b>13.333</b>	0.999	0.15	0.35
Large M. capensis	1.127	0.8	<b>4.444</b>	<b>0.832</b>	0.18	0.2
Small M. paradoxus	<b>1.878</b>	13.333	<b>0.999</b>	0.15	0	0.35
Large M. paradoxus	1.067	0.8	<b>4.706</b>	<b>0.792</b>	0.17	0.2
Pelagic feeding demersal fish	<b>3.689</b>	1	<b>5</b>	0.99	0.2 0	0.2
Benthic feeding demersal fish	<b>3.704</b>	1	<b>5</b>	0.99	0.2 0	0.2
Pelagic feeding chondrichthyans	0.582	0.5	4.5	<b>0.987</b>	<b>0.111</b>	0.2
Benthic feeding chondrichthyans	0.873	1	<b>10</b>	<b>0.731</b>	0.1	0.2
Apex Predators	0.045	0.5	<b>5</b>	<b>0</b>	0.1	0.2
Seals	0.133	0.946	19.3	<b>0.427</b>	<b>0.049</b>	0.2
Caetaceans	0.082	0.6	10	<b>0.694</b>	<b>0.06</b>	0.21
Seabirds	0.012	0.123	118	<b>0.963</b>	<b>0.001</b>	0.26
Meiobenthos	<b>10.668</b>	4	<b>33.333</b>	0.95	0.12	0.1
Macrobenthos	<b>48.258</b>	1.2	<b>10</b>	0.95	0.12	0.1
Tube Worms	<b>0.4598</b>	1.2	<b>10</b>	0.95	0.12	0.1
Sponges	<i>9.149</i>	1.2	<b>12.121</b>	1	0.099	0.4
Cold water coral	<i>2.311</i>	1.2	<b>19.355</b>	<b>0.423</b>	0.066	0.1
Cold water Coral Skeleton	1					
Mucus	0.6					
Detritus	50					

Table A2: The diet matrix for the southern Benguela used in this model. Values are rounded to 4 decimal places, as such the column may not sum to 1 exactly. This caption was adapted from de Haast *et al.* (2018)

	micro-Z	meso-Z	macro-Z	Gelatinous Zooplankton	Cape anchovy	Sardine	Redeye	Other small pelagic fish	Chub mackerel	Small horse mackerel	Large horse mackerel	Mesopelagic fish	Snoek	Other large pelagic fish	Cephalopods	Small M. capensis	Large M. capensis	Small M. paradoxus	Large M. paradoxus	Pelagic demersal fish	Benthic demersal fish	Pelagic chondrichthyans	Benthic chondrichthyans	Apex chondrichthyans	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos	Tube Worms	Sponges	Cold-water corals				
Import	0.4	0.5	0.6	0	0.05	0.32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Lateral Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8			
micro-Z	0.2	0.5	0	0	0.04	0.32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.09	0.99	0.02			
meso-Z	0	0	0.4	0.64	0.57	0.29	0.6	0.81	0.0503	0.75	0.3894	0.4	0	0	0	0	0	0	0	0.0101	0.01	0	0	0	0	0.035	0.009	0	0	0.27	0	0.12				
macro-Z	0	0	0	0.12	0.34	0.07	0.4	0.16	0.6593	0.25	0.5192	0.6	0.1084	0.0874	0.2694	0.7293	0.0994	0.7675	0.2059	0.6502	0.05	0	0	0	0	0.035	0.1040	0	0	0.54	0	0.06				
Gelatinous Zooplankton	0	0	0	0.04	0	0	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Cape Anchovy	0	0	0	0	0	0	0	0	0.0181	0	0.0215	0	0.1238	0.2106	0.0299	0.0200	0.0795	0.0199	0.0010	0	0.005	0.0200	0	0	0.15	0.204	0.3011	0	0	0	0	0	0			
Sardine	0	0	0	0	0	0	0	0	0.0080	0	0.0050	0	0.2270	0.1580	0.0210	0.0110	0.0537	0.0130	0.0049	0.0020	0	0.0100	0	0	0.028	0.104	0.2201	0	0	0	0	0	0			
Redeye	0	0	0	0	0	0	0	0	0.0090	0	0.0649	0	0.0464	0.0790	0.0499	0.0300	0.0864	0.0491	0.0245	0.1058	0.025	0.0490	0	0	0.105	0.135	0.0650	0	0	0	0	0	0			
Other small pelagic fish	0	0	0	0	0	0	0	0	0	0	0	0.0258	0.0264	0	0	0.0050	0.0010	0.0147	0	0	0.0150	0	0	0.003	0.035	0.0550	0	0	0	0	0	0	0			
Chub mackerel	0	0	0	0	0	0	0	0	0	0	0	0.0108	0.0358	0	0	0.0199	0	0	0	0	0.0100	0	0	0.013	0	0.0040	0	0	0	0	0	0	0			
Small horse mackerel	0	0	0	0	0	0	0	0	0	0	0	0.0578	0.0537	0	0	0.0298	0	0	0	0	0	0	0	0.01	0	0.0300	0	0	0	0	0	0	0	0		
Large horse mackerel	0	0	0	0	0	0	0	0	0	0	0	0.0501	0	0	0	0.1570	0	0	0	0	0	0.0902	0.0100	0.025	0.022	0.27	0	0	0	0	0	0	0	0		
Mesopelagic fish	0	0	0	0	0	0	0	0.2553	0	0	0	0.1486	0.0253	0.0998	0.0779	0.0994	0.0797	0.3569	0.1512	0.05	0.2535	0.0100	0	0.007	0.042	0.1030	0	0	0	0	0	0	0			
Snoek	0	0	0	0	0	0	0	0	0	0	0	0.0021	0	0	0	0.0020	0	0.0049	0	0	0.0050	0	0.07	0.005	0	0.0020	0	0	0	0	0	0	0	0		
Other large pelagic fish	0	0	0	0	0	0	0	0	0	0	0	0	0.0011	0	0	0	0	0	0	0	0	0.0060	0	0.005	0.005	0	0	0	0	0	0	0	0	0		
Cephalopods	0	0	0	0	0	0	0	0	0	0	0	0.0144	0.1517	0.0499	0.0519	0.0447	0.0100	0.0980	0.0202	0.02	0.2004	0.0300	0	0.233	0.104	0.0650	0	0	0	0	0	0	0			
Small M. capensis	0	0	0	0	0	0	0	0	0	0	0.0196	0.0105	0.0219	0	0.1143	0	0	0.0040	0.001	0	0	0	0	0	0	0.1	0.001	0	0	0	0	0	0	0		
Large M. capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0402	0	0	0	0.002	0.0401	0.0100	0	0.022	0.009	0	0	0	0	0	0	0	0	0		
Small M. paradoxus	0	0	0	0	0	0	0	0	0	0	0	0.1238	0.0358	0.0778	0.0210	0.1490	0	0.1471	0.0161	0.008	0	0	0	0.1	0.018	0.0300	0	0	0	0	0	0	0	0		
Large M. paradoxus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0206	0	0.002	0.0501	0	0	0.018	0.008	0	0.018	0.008	0	0	0	0	0	0	0		
Pelagic feeding demersal fish	0	0	0	0	0	0	0	0	0	0	0	0.0413	0.0906	0	0.0490	0.0099	0.0498	0.0294	0.0302	0.02	0.0501	0.0500	0.01	0.035	0	0.0070	0	0	0	0	0	0	0	0		
Benthic feeding demersal fish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0100	0.0099	0.0100	0.0922	0.0101	0.02	0.1002	0.1998	0.01	0.079	0	0	0	0	0	0	0	0	0			
Pelagic feeding chondrichthyans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1002	0	0.1	0	0	0	0	0	0	0	0	0	0		
Benthic feeding chondrichthyans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0.0500	0.43	0	0	0	0	0	0	0	0	0	0	0		
Apex Predators	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Seals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.0037	0	0	0	0	0	0	0	0	
Cetaceans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.15	0	0	0	0	0	0	0	0	0	0	0	0	
Seabirds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0010	0	0	0	0	0	0	0	0	
Meiobenthos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.084	0	0	0	0	0		
Macrobenthos	0	0	0	0	0	0	0	0	0	0	0	0	0.0280	0.3196	0	0	0	0	0	0	0.6505	0	0.5320	0	0.065	0	0	0	0.07	0	0	0	0	0		
Tube Worms	0	0	0	0	0	0	0	0	0	0	0	0	0.0010	0.0010	0	0	0	0	0	0	0.001	0	0.0010	0	0	0	0	0	0.001	0	0	0	0	0		
Sponges	0	0	0	0	0	0	0	0	0	0	0	0	0.0050	0.0599	0	0	0	0	0	0	0.1305	0	0.1074	0	0	0	0	0	0.005	0	0	0	0	0	0	
Cold water Corals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mucus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0
Detritus	0.4	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.84	0	0	0	0		

Table A3: The layout of aggregated groups used in figure 2.3 to represent the flow of energy through the larger Ecopath model used in this study.

Aggregated group name	Group
Primary Producer	Import
Zooplankton	Microzooplankton Mesozooplankton Macrozooplankton Gelatinous zooplankton
Pelagic Consumers	Cape Anchovy Sardine Redeye Other small pelagic fish Chub mackerel Small horse mackerel Large horse mackerel Mesopelagic fish Snoek Other large pelagic fish Apex Predators Seals Caetaceans
Benthic Consumers	Cephalopods Small <i>M. capensis</i> Large <i>M. capensis</i> Small <i>M. paradoxus</i> Large <i>M. paradoxus</i> Pelagic feeding demersal fish Benthic feeding demersal fish Pelagic feeding chondrichthyans Benthic feeding chondrichthyans
Macrobenthos	Macrobenthos
Meiobenthos	Meiobenthos
Tube worms	Tube worms
Lateral Import	Lateral Import
Sponges	Sponges
Cold-water coral	Cold-water coral
Cold-water coral skeleton	Cold-water coral skeleton
Detritus	Detritus
Mucus	Coral Mucus