Using seasonal mass-balanced models of the Algoa Bay ecosystem to investigate African penguin and small pelagic fish interactions

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Declaration

I, Emily Weigum, hereby declare that the work on which this dissertation/thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university.

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Abstract

Ecopath with Ecosim is a modeling software that allows the creation of mass-balanced models of the trophic flows of an ecosystem to explore the past and present impacts of fishing and environmental change on the trophic flows of a given food web. Currently, Algoa Bay supports the world's largest breeding colony of endangered African penguins (*Spheniscus demersus*). The breeding success of African penguins is largely dependent on the availability of their food, mainly anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*). African penguins breed year-round however, peak breeding season begins during the summer months (January to March) in Algoa Bay, when penguins begin building up fat reserves and laying eggs. In order to investigate the interaction between the small pelagic fish and penguin population, mass-balanced trophic models of the Algoa Bay ecosystem were constructed using the software Ecopath with Ecosim. Input parameters were derived from data compiled from published literature and survey data collected by DAFF (Department of Agriculture, Forestry, and Fisheries; formerly Marine and Coastal Management, MCM) and SAEON (the South African Environmental Observation Network). Two seasonal models were created to depict the summer (January to March) and winter (June to August) seasons from 2010-2014. Additionally, two seasonal models were created to represent a marine protected area where all fishery catch was set to zero. These static marine protected area models were created to investigate how the removal of fishery predation impacts the trophic structure of the Algoa Bay ecosystem by comparing ecotrophic efficiency values to those of the fished system. Two Ecosim simulations were used in fishery sensitivity analyses. The first, by setting all fishery catches to zero over a period of 30 years for each season to investigate the sensitivity of trophic groups to the removal of fishing pressure. The second, by setting fishery mortalities of anchovy and sardine to levels reported in the west coast (also over a period of 30 years) to investigate the sensitivity of trophic groups to an increase in small pelagic fishing pressure.

Seasonal differences were observed with an increase in primary production and zooplankton biomass in the summer season compared to the winter season. The increase in plankton biomass resulted in an approximately 3x greater summer total system throughput, and total net primary production. Transfer efficiencies were higher than the average of 10% for aquatic ecosystems at trophic levels II and III with the seasonal averages being 17% and 19%

respectively. The greatest seasonal change in modeled biomass occurred at trophic level III with summer biomass being 72% larger, indicating that small pelagic fishes benefit the most from the increase in summer plankton biomass.

Linefish ecotrophic efficiency values were smaller in the marine protected area models in the summer and winter respectively, reflecting the reduced mortality on linefish under MPA conditions. Although the removal of fisheries resulted in an overall drop in predation pressure of 27% in the static MPA models, predation by other predatory trophic groups in the bay increased by 13% as a result of their subsequent biomass increases after the removal of fishery predation. Ecosim results showed the greatest change in biomass occurred in linefish which increased in both seasons when fishery catch was set to zero. The increase in linefish biomass can be attributed to the removal of fishery pressure on themselves and their prey, and may be an indication that linefish are overexploited in the bay. As a result of the biomass increase of some predator groups, some lower trophic level fish groups decreased despite the removal of fishery pressure. The results of the marine protected area analyses indicate that fisheries do not necessarily only have direct impacts on a target species as food-webs can have moderating effects.

When fishing mortalities for sardine and anchovy were increased to west coast values, African penguins had the largest decrease in modeled biomass followed by other seabirds. Although, the observed decrease in modeled biomass of African penguins over the 30-year period does not fall within IUCN criteria for major concern, African penguins are already listed as endangered. An added decline of 10% on the largest breeding colony could have major implications on the future of the species.

This study was a preliminary attempt at constructing mass-balanced trophic models of the Algoa Bay ecosystem, highlighting seasonal differences while investigating the possible impact of implementing a marine protected area in the bay and the sensitivity of trophic groups to fishing. Future research is needed to improve the more uncertain model parameters; however, these models are a good base for future work and the application of spatialized modeling of the bay using EcoSpace.

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Acknowledgments

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Chapter 1: Introduction and Literature Review

1.1 Study Context

Trophic modeling approaches such as Ecopath with Ecosim (EwE) are powerful tools for analyzing exploited marine ecosystems (Christensen and Walters 2004). EwE allows for the creation of simple or complex models of the trophic flows of an ecosystem, providing an overview of feeding interactions and resources contained in the system (Christensen *et al*. 2005). This allows the user to explore past and present impacts of fishing and environmental changes on the trophic flows of a given food-web (Christensen and Walters 2004), to address fishery management and policy issues, and to analyze marine protected areas (Coll *et al*. 2009). This can be useful as it places fisheries in an ecosystem context, treating fisheries as top predators which not only impact the target species but can have a cascading effect on multiple species, and on fisheries (Coll et al. 2009). This can aid in making management decisions at the ecosystem level compared to the single-species approach (Shannon et al. 2008).

Ecopath was developed on the theory that food-webs are based on trophic flows between species, and the concept of mass balance and energy conservation (Polovina, 1984). After the first model was constructed in 1984, Ecopath was further developed (Christensen and Pauly, 1992) to consider trophic groups that feed across a range of trophic levels by incorporating fractional trophic levels (Odum and Heald, 1975). The dynamic modeling capability of Ecosim was introduced in 1995 (Walters *et al*. 1997), which allows the fitting of predicted biomasses to time-series data to investigate predator-prey interactions (Christensen *et al*. 2005).

African penguins (*Spheniscus demersus*) are endemic to the coasts of South Africa and Namibia and are currently listed as endangered on the IUCN red list (BirdLife International, 2018). The largest breeding colony of African penguins occurs in Algoa Bay, located on the Eastern Cape of South Africa (Pichegru, 2010). The breeding success of African penguins is largely dependent on the availability of their prey (Crawford *et al*. 2006), mainly anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*). In Algoa Bay, they breed throughout the year but the typical breeding season is from January to August, with peak egg laying occurring from January to March (Ralph, 2008). As Algoa Bay currently supports >50% of the global African penguin population (Crawford *et al*. 2014), understanding the trophic interactions around their food web in the bay is important when considering management policies aimed at protecting this vulnerable species. Currently there is no published EwE trophic model for Algoa Bay.

Forage fish are an important component of the ecosystem as they convert energy from lower trophic levels (phytoplankton and zooplankton) to energy for higher trophic levels (predatory fish, seabirds, cetaceans, etc. [Alder *et al*. 2008]). As a result of their position in the food-web, ecosystems dominated by small pelagic fish often show "wasp-waist" dynamics, where changes in their population size have major impacts on both their prey and predator species, i.e. control of trophic flows is from the "waist" up and down (Shannon *et al*. 2004). Therefore, fishing pressure on these species has the potential to impact all trophic levels of an ecosystem (Robinson, 2013).

1.2 Study Area: Algoa Bay

Algoa Bay, part of the Nelson Mandela Bay municipality (Figure 1.1) is located in the province of the Eastern Cape of South Africa bordered by Cape Recife on the west and Cape Padrone on the east (Karczmarski *et al*. 1999); the city of Port Elizabeth is situated in the sheltered Western section of the bay (Schumann *et al*. 2005). It is the easternmost and largest of several shallow bays along the south coast (Goschen and Schumann, 1988) and faces towards the Indian Ocean with the warm Agulhas current flowing 80km offshore and much cooler inshore waters (Chalmers, 2011).

Most of the bay is <50m deep (Karczmarski *et al*. 1999) with the deepest part of the mouth at approximately 73m (Goschen and Shumann, 1988). Water temperature in the bay typically ranges between 16°C in winter near the coast to as high as 25°C in summer further offshore (Schumann *et al*. 2005). The mean spring tide is 1.61m and neap tide is 0.51m (Karczmarksi *et al.* 1999). Freshwater inflow from rivers is limited within the bay with stable average salinity at about 35.2 ppt (Schumann, 1998).

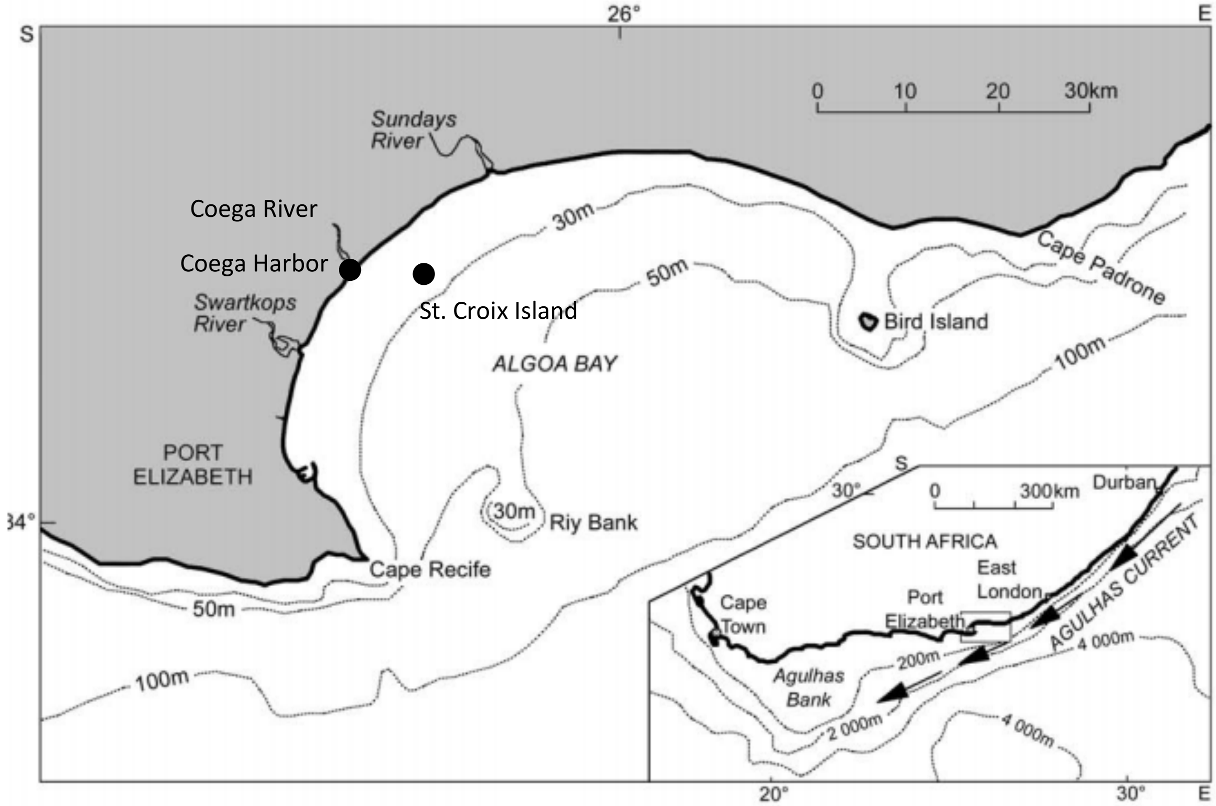


Figure 1.1 Map of Algoa Bay showing the bathymetry, prominent features, and location along the coast of South Africa (adapted from Schumann *et al.* 2005). Approximate locations of St. Croix Island and Coega harbor were drawn in using GPS coordinates.

1.2.1 Algoa Bay Islands

There are two main island groups located within the bay (Chalmers, 2011). On the western side, there are three outcrops: St. Croix (33°48S, 25°46E), Jahleel (33°48S, 25°42E), and Brenton islands (33°49S, 25°46E). St. Croix Island is the largest of the three outcrops (Randall *et al.* 1981) and currently supports the world's largest African penguin colony (Pichegru *et al.* 2010). It is 4km from the mainland with a maximum height of 59m and consists of rocky substrate (Randall *et al.*1981). The second island group is located on the eastern side near Cape Padrone (Chalmers, 2011). This group consists of Bird Island (35°51S, 26°17E) and Stag and Seal Islands (33°50S, 26°17E), and Black Rocks. Stag and Seal Island are connected by a land bridge during low spring tide. Bird Island is the largest in Algoa Bay at 19 ha, located 8.4km from the mainland with a maximum height of 5m. Bird Island is an important breeding area for African penguins, Cape gannets (largest colony in the world), and roseate terns (Randall *et al.* 1981).

The islands are all composed of Table Mountain Sandstone with the dominant vegetation being the fleshy herb *Mesembreanthemum aitonis* (Randall *et al.* 1981). They are of particular importance because they are the only islands along a 1,777km stretch of coastline from Cape Agulhas to Inhaca Island near Mozambique (Hutchings *et al*. 2013). As previously mentioned, they are important seabird conservation areas and support many keystone species, an important area for the threatened abalone stocks, and are an important breeding area for Cape fur seals (a primary food source for white sharks). In addition, the subtidal reefs around the islands support many endemic species of fish, invertebrates, and seaweeds (Chadwick *et al.* 2014). Three species of dolphins are also abundant in the bay: bottlenose, common, and humpback, along with several species of whales (Melly et al. 2017).

1.2.2 Algoa Bay Protected Areas

Marine protected areas (MPAs) are areas in the ocean that are given some form of protection for conservation purposes. The goals of MPAs are to conserve and protect biodiversity, allow for the recovery of exploited and threatened species, and to protect against the negative impacts of human activities such as mining and drilling (Edgar *et al*. 2007). The Bird Island Group MPA was declared in 2004 and surrounds Bird Island, Stag and Seal Island, and Black Rocks. The MPA includes the water, seabed, and airspace around the islands but not the islands themselves. Diving and anchoring in the MPA are not permitted due to abalone poaching (Chadwick *et al.* 2014). In addition, the proposed Addo National Park MPA (Figure 1.2) if instated would cover 137,773 ha from Cape Padrone to Coega Harbor (located at Coega River between Sundays River and Swartkops River, Figure 1.1) and encompass all islands within the bay (Hutchings *et al*. 2013). The zonation of the proposed MPA is depicted in Figure 1.2 below. The difference between the restricted and controlled zones are that the restricted zones prohibit fishing activity. Both restricted zones and controlled zones allow for all other activities listed in section 48A(1) of the Protected Areas Act if authorized in the terms of regulations listed in section 48A(2) of the act (Bill B-28, 2013). Refer to Figure 1.3 for a full list of prohibited activities listed in 48A(1). In October 2018, 20 new protected areas were announced (but not yet instated) by the Department of Environmental Affairs, which will increase South Africa's ocean protection from 0.4% to 5%, and includes the Addo National Park MPA (SANBI, 2018).

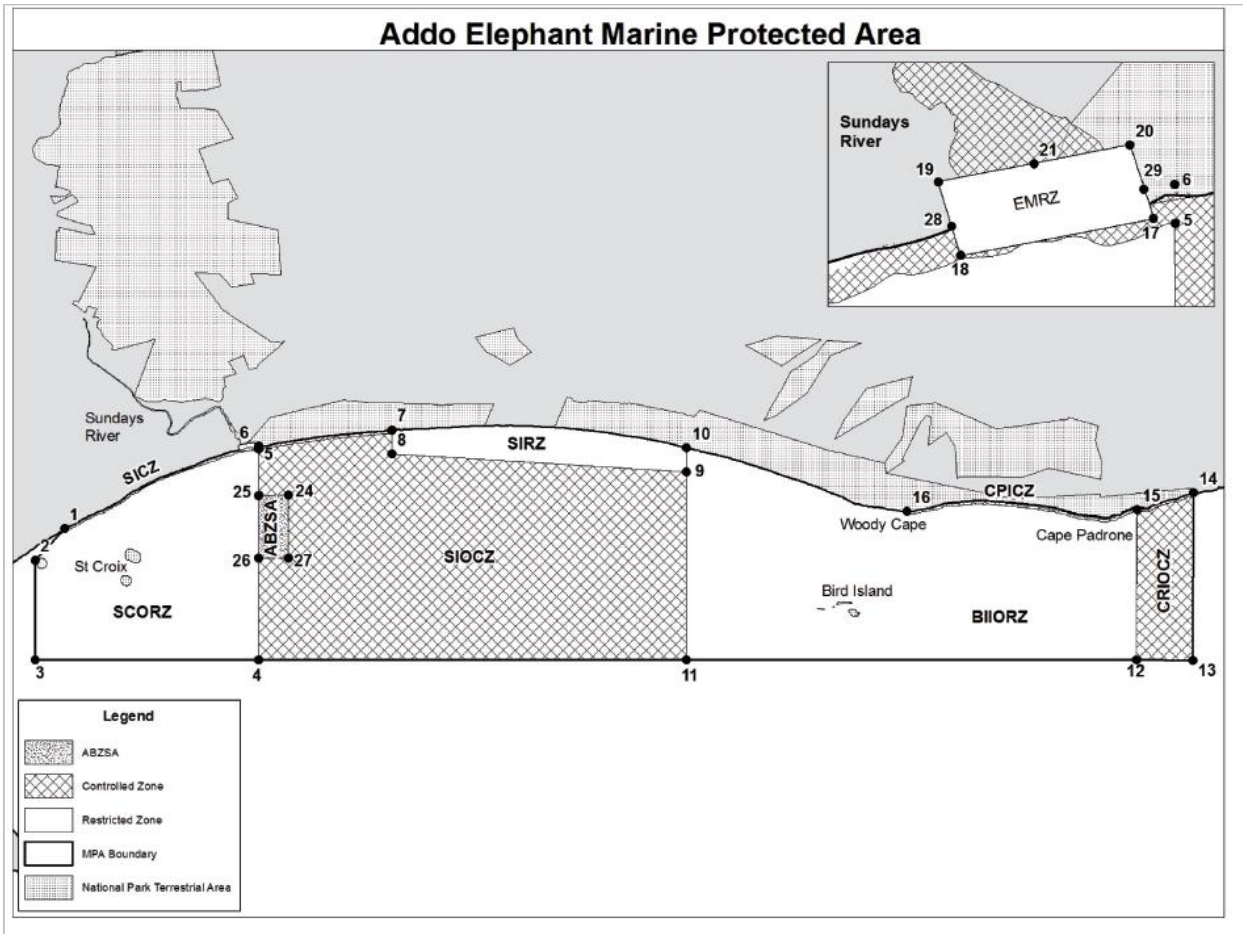
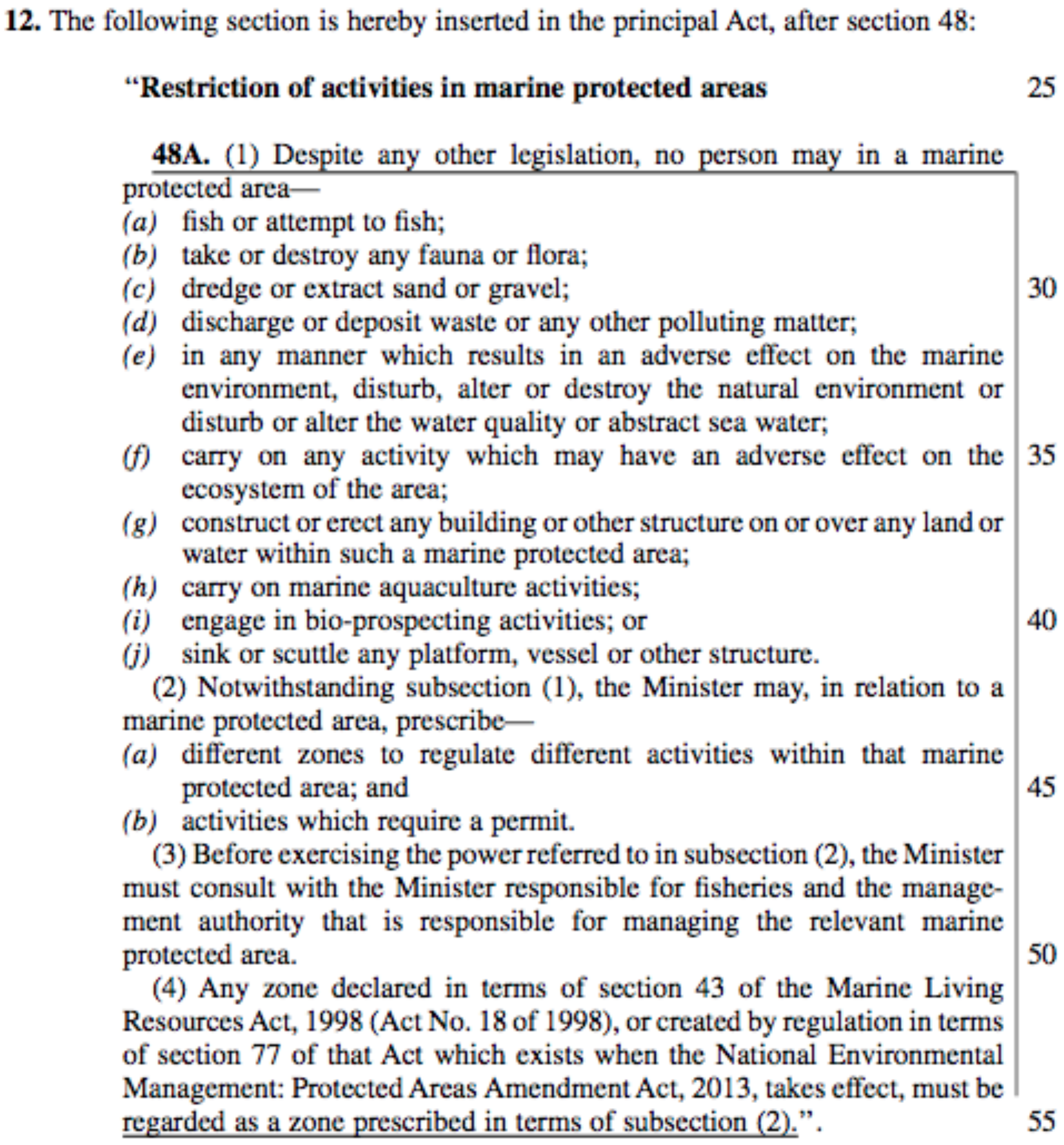


Figure 1.2. The proposed Addo Elephant Marine Protected Area including zonation. BIIORZ = inshore and offshore restricted zone, SCORZ = offshore restricted zone, SIOCZ/CRIOCZ = inshore and offshore controlled zones, SIRZ = inshore restricted zone, CPICZ/SICZ = inshore controlled zones, EMRZ = Sundays River estuary restricted zone, and ABZSA = Algoa Bay zone for sustainable aquaculture (DEAT 2016).



12. The following section is hereby inserted in the principal Act, after section 48:

"Restriction of activities in marine protected areas

48A. (1) Despite any other legislation, no person may in a marine protected area—

(a) fish or attempt to fish;
(b) take or destroy any fauna or flora;
(c) dredge or extract sand or gravel;
(d) discharge or deposit waste or any other polluting matter;
(e) in any manner which results in an adverse effect on the marine environment, disturb, alter or destroy the natural environment or disturb or alter the water quality or abstract sea water;
(f) carry on any activity which may have an adverse effect on the ecosystem of the area;
(g) construct or erect any building or other structure on or over any land or water within such a marine protected area;
(h) carry on marine aquaculture activities;
(i) engage in bio-prospecting activities; or
(j) sink or scuttle any platform, vessel or other structure.

(2) Notwithstanding subsection (1), the Minister may, in relation to a marine protected area, prescribe—

(a) different zones to regulate different activities within that marine protected area; and
(b) activities which require a permit.

(3) Before exercising the power referred to in subsection (2), the Minister must consult with the Minister responsible for fisheries and the management authority that is responsible for managing the relevant marine protected area.

(4) Any zone declared in terms of section 43 of the Marine Living Resources Act, 1998 (Act No. 18 of 1998), or created by regulation in terms of section 77 of that Act which exists when the National Environmental Management: Protected Areas Amendment Act, 2013, takes effect, must be regarded as a zone prescribed in terms of subsection (2).".

Figure 1.3. Excerpt from the National Environmental Management: Protected Areas Amendment Bill listing the restricted activities in marine protected areas under section 48A(1), (Protected Areas Amendment Bill, 2013).

1.2.3 Seasonality in the Bay

Seasonal changes in the bay include increased frequency of easterly winds in the summer, which result in upwelling around Cape Recife of cold-water causing temperatures to decrease by 8°C during February and March (Beckley, 1983). Both northeasterly and southwesterly winds reach a maximum in speed and frequency in October and November, and a minimum in May, June, and July (Figure 1.4. [Goschen and Schumann, 2011]). Strong thermoclines are present in summer and temperature ranges of 10°C over a depth of 20m is common (Figure 1.5.). This thermocline is stronger close to the coastline and gets weaker further offshore (Swart and Largier, 1987). The thermocline dissipates in winter (Schumann *et al.* 2005), probably due to less heating of the surface waters and greater stress induced by westerly winds caused when the sea surface temperature is greater than air. Upwelling occurs more frequently in the summer due to the increased easterly winds (Figure 1.6., Goschen and Schumann 2011).

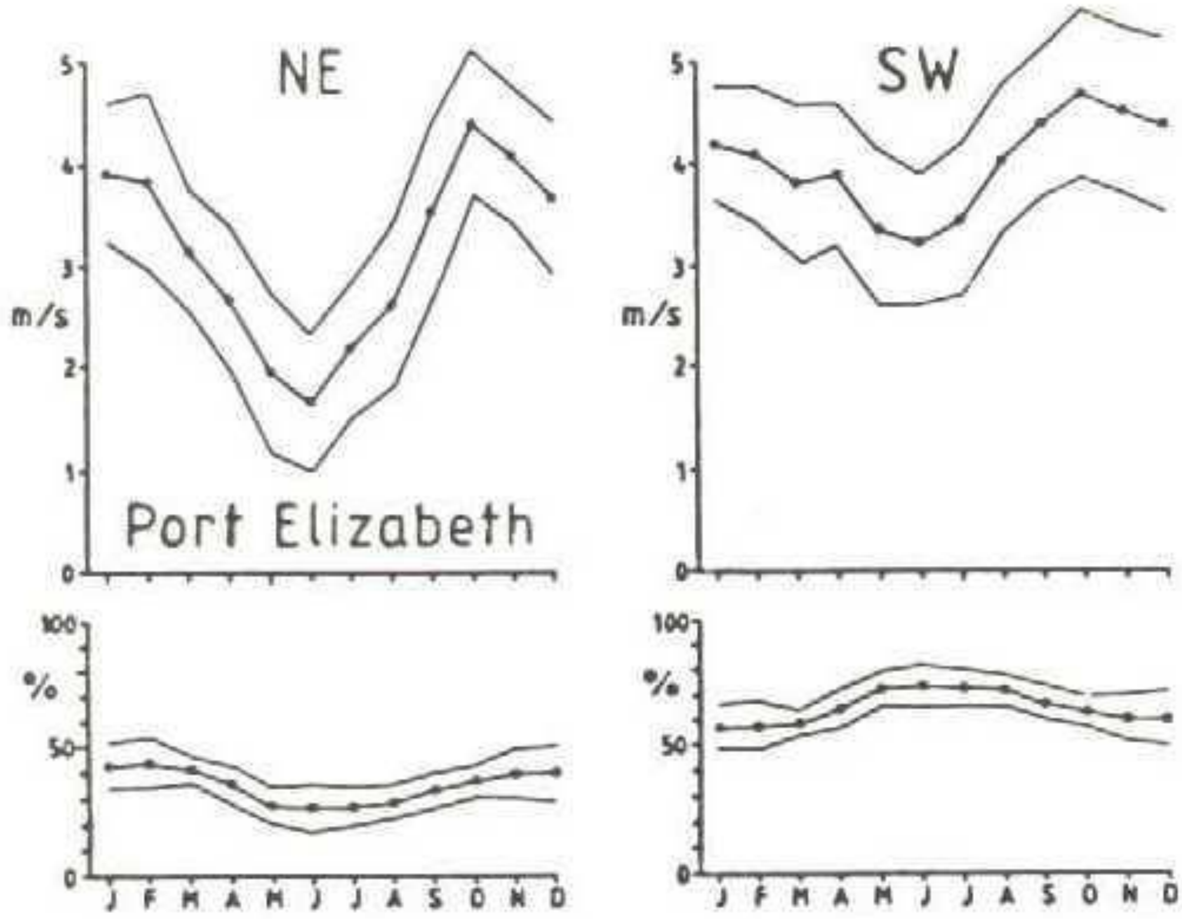


Figure 1.4. Monthly variation from January 1950 to September 1988, of the mean wind velocity (m/s, top panel) and percent occurrence of the Northeasterly (NE) and Southwesterly (SW) winds near Port Elizabeth (bottom panel). Standard deviation is shown in the outermost lines. Taken from Schumann and Martin 1991.

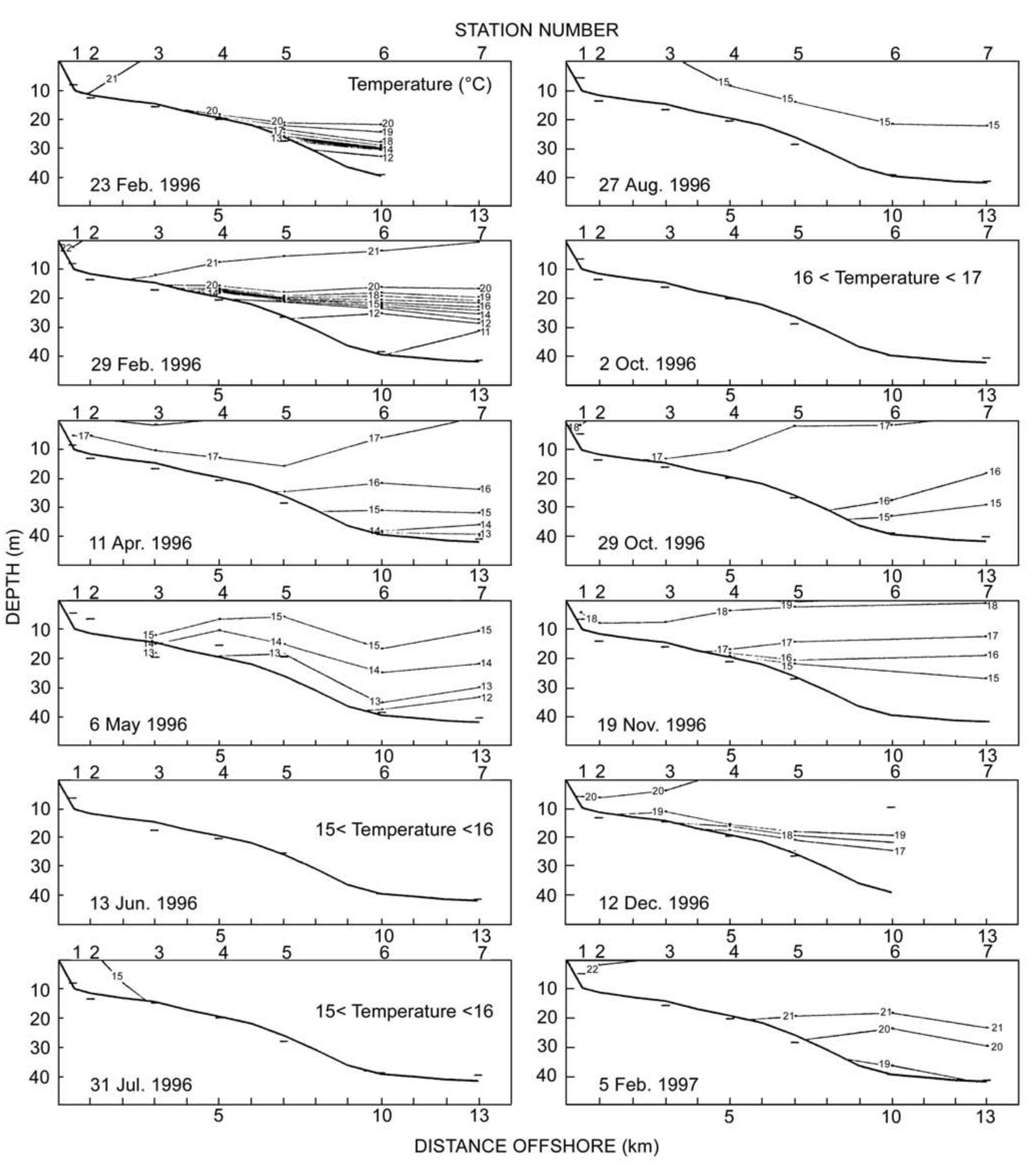


Figure 1.5. Temperature profiles by depth and distance from shore taken in an area 10km north of Port Elizabeth Harbor in the Western section of Algoa Bay from February 1996-1997 (Schumann et al. 2005).

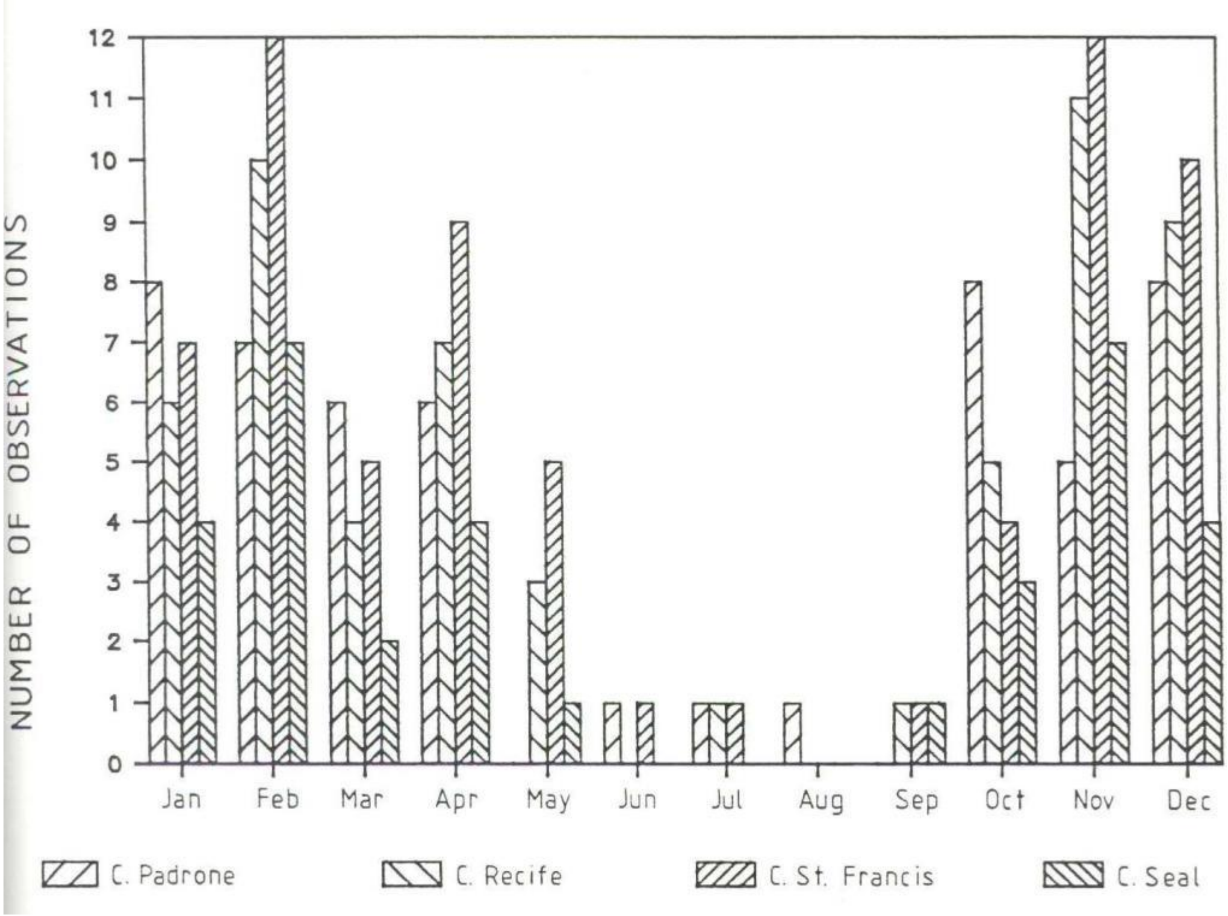


Figure 1.6. The frequency of upwelling events caught on satellite recordings by month from 1985-1990 at Cape Padrone, Cape Recife, Cape St. Francis, and Cape Seal (Goschen and Schumann, 2011).

1.3 African Penguins

1.3.1 Distribution and Population Trends

The African penguin is endemic to South Africa and Namibia. In South Africa, breeding locations occur in both the Western Cape province and the Eastern Cape province (Crawford *et al.* 2011). The largest breeding colony currently occurs in Algoa Bay on St. Croix Island and another on Bird Island (Pichegru *et al*. 2010) which together hold >50% of the global population (Crawford *et al*. 2014).

African penguins were abundant in the early 20th century. Originally believed to have been in the millions, by 2009 population estimates were at an all-time low of 26,000, which resulted in them being listed by the IUCN from vulnerable to endangered (Crawford *et al.* 2011). Factors contributing to their collapse are the commercial exploitation of their eggs, the mining of seabird guano which is important for their breeding nests, contamination by oil spills, and competition with the small pelagic purse-seine industry for food (Shannon and Crawford, 1999). Currently, African penguins are still listed as endangered on the IUCN Red List, with a population estimate of 50,000 individuals showing a decreasing population trend (BirdLife International, 2018).

In 2008, the Island Closure Task Team made up of representatives of the Department of Agriculture, Forestry, and Fisheries (DAFF), the Department of Environmental Affairs (DEA), and various NGOs, proposed paired, alternating years of no-take zones for fishing around the four largest breeding colonies (Robben, Dassen, St. Croix, and Bird Islands). The goal was to assess the impacts of fishing activities on penguin survival (McInnis, 2016) with alternative closures of adjacent pairs of islands to purse seine fishing for a period of 3 years at a time. Accordingly, a 20km area around St. Croix Island was closed to purse-seine fishing in January 2009 and again in 2010, while the area around Bird Island remained open. One of the aims was to study the foraging behaviour of adult penguins raising chicks at both sites to test whether a small no-take zone would benefit penguins relying on small pelagic prey. A preliminary study found that the no-take zone resulted in a decreased foraging effort of 25-30%, and a decrease in energy expenditure by 43% while there was an observed shift in foraging effort from outside to inside the no-take zone (Pichegru et al. 2010, Pichegru *et al*. 2012). This study suggested that African penguins may benefit from marine protected areas in Algoa Bay and that purse-seine fishing may have had a negative impact on their foraging behaviour (Pichegru et al. 2010), strengthening the need for the development of a trophic model for Algoa Bay to help examine the different impacts the small pelagic fishery has on the population there. The initial feasibility study is being continued as a full experiment to increase the data set for more comprehensive analyses.

1.3.2 Breeding Biology

African penguins demonstrate high mate and nest fidelity (Randall, 1983). They breed throughout the year but the typical breeding season is from January to August, with peak egg laying occurring from January to March (Ralph, 2008). Clutch size typically ranges from 1-2 eggs, which are incubated for 38-41 days by both parents, and the nesting period ranges from 64-105 days (McInnis, 2016). Each breeding pair shares the care of their chicks as one stays by the nest while the other forages for food (Pichegru *et al*. 2012). Most small pelagic fishery catches are taken during the pre- and early breeding season from January to March (McInnis, 2016) the bulk of which is made up of sardine according to the DAFF fishery catch reports listed in methods Section 2.3.3. This is an important time for breeding penguins as they need to build up fat reserves and improve body condition to cope with the approaching breeding effort (McInnis, 2016).

1.3.3 Diet and Foraging Behaviour

Anchovy and sardine dominate the diet of African penguins (Crawford *et al*. 2011) comprising more than 90% of their diet (Durant *et al*. 2010). Penguins forage inshore and during the breeding season their foraging range is restricted to 20-40km from their colony (Wilson 1985, Pichegru *et al*. 2012). They are visual pursuit hunters (Wilson 1985) and typically dive at depths between 10-70m (Pichegru *et al*. 2010). Breeding success is greatly influenced by the abundance of food (Crawford *et al*. 2006) as more energy is expended the further from the nest the penguin has to forage, and subsequently less resources are delivered to the chicks (Crawford *et al*. 2011). Peak spawning for sardine and anchovy occurs during the spring and summer months (Costalago *et al*. 2018) which coincide with pre- and early breeding season for African penguins (McInnis, 2016).

1.4 Small Pelagics

1.4.1 Distribution and Population Trends

Small pelagic fish species that occur in the bay include sardine, anchovy, redeye round herring (*Etrumeus whiteheadi*), and horse mackerel (*Trachurus trachurus capensis*). Pelagic species distribution is largely determined by the distribution of their food source: phytoplankton and zooplankton (Chalmers, 2011). Most of the adult biomass occurs along the southern west coast along the Agulhas bank and extends east to Port Alfred (Coetzee *et al*. 2008). Recently, there has been an observed shift (Figure 1.7) in relative abundance of sardine and anchovy from the west to east (Coetzee *et al*. 2008, van der Lingen *et al*. 2002). The eastward shift of anchovy biomass may be attributed to better feeding conditions and therefore better condition of fish East of Cape Agulhas relative to those West of Cape Agulhas. The condition of eggs and larvae are impacted by the condition of the adult spawners, therefore eggs and larvae produced by spawners

East of Cape Agulhas in recent years may have a higher probability of survival than those produced by fish West of Cape Agulhas (Van Der Lingen *et al*. 2002). The eastward shift of sardine has been linked to lower exploitation rate, improved habitat conditions, increased reproductive output, and the potential effects of higher temperatures on growth rates and survival of early life history stages (Coetzee *et al*. 2008, Watermeyer *et al*. 2016). According to Potter 2014, and based on DAFF surveys, there were approximately 20,000-40,000 tonnes of anchovy in Algoa Bay from 2010-2012, and 50,000-70,000 tonnes of sardine (Figure 1.8).

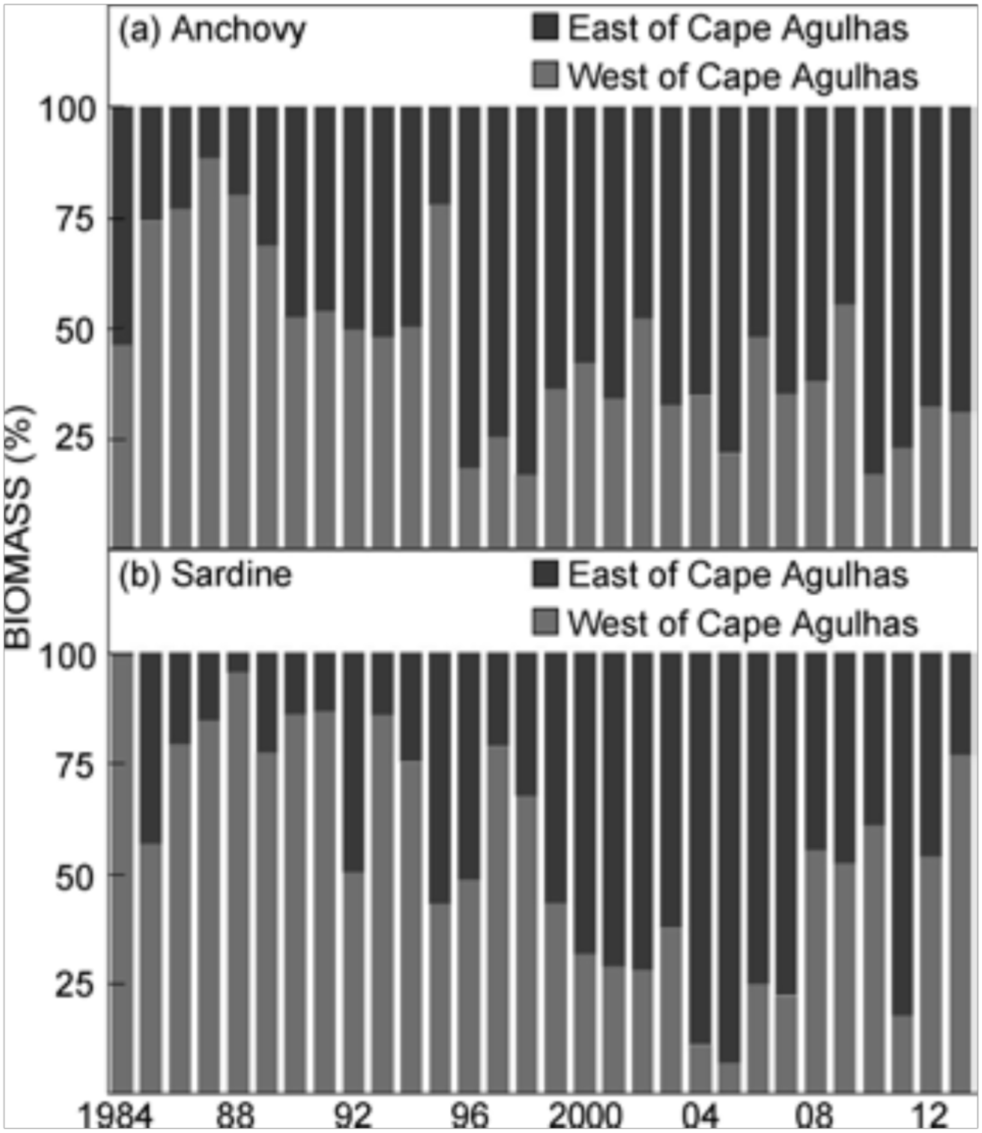


Figure 1.7. Percentage of total biomass (t) of anchovy (a) and sardine (b) found West of Cape Agulhas and East of Cape Agulhas based on data collected by DAFF stock assessment surveys (DEAT 2014).

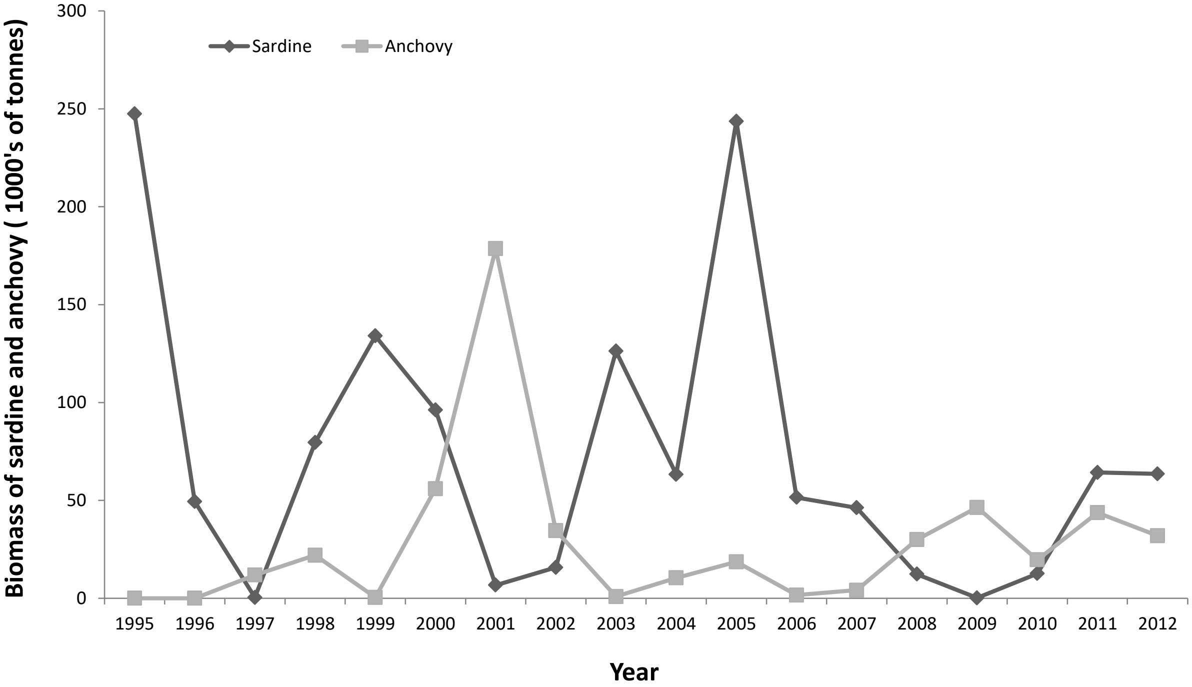


Figure 1.8. Biomass (1000 tonnes) of sardine and anchovy calculated from DAFF acoustic spawner biomass surveys from 1995-2012 within Algoa Bay, South Africa (Potter, 2014).

1.5 Fishery Activities in Algoa Bay

1.5.1 Small Pelagic Fishery

The small pelagic purse-seine fishery is the largest in South Africa in terms of landed catch and second in terms of value. Sardine, anchovy, and redeye account for >90% of the purse-seine catch (DEAT, 2014). The majority of fishing effort occurs along the West coast but there are a few small vessels based in Port Elizabeth that fish in the bay and the Eastern Cape (Chalmers, 2011). The small pelagic fishery began fishing around Algoa Bay in the 1990s and since 2000, catches have increased fivefold (Pichegru *et al*. 2012). Although approximately only 8% of all small pelagic fishery vessels operate in Algoa Bay (Chalmers, 2011), the population of African penguins has decreased by half in the 21st century alone, warranting concern about competition for food with the purse-seine fishery (Potter, 2014). According to DAFF acoustic survey reports, out of five stratums, the stratum enveloping Algoa Bay contained between 10-51% of all sardine spawner biomass between 2010-2014 with an average of 26% between all years. For anchovy, these numbers range from 11-54% with an average of 32% of all spawner biomass. Therefore, although fishing effort in Algoa Bay is relatively small, there is potential for the fishery to have an impact on small pelagic fish populations and in turn, their predators.

1.5.2 Linefishery

The linefishery in Algoa Bay consists of a recreational and a commercial sector (Chalmers, 2011). In South Africa, 54-57% of known linefish stocks are considered overexploited or collapsed (Mann, 2013, DAFF, 2016). In 2006-2007, there were 15 commercial rights holders operating in the bay regularly out of a total of 80-87 in the entire Eastern Cape region (Chalmers, 2011). Recreational fishing activities take place on the shore or in skiboats. Chalmers 2011, estimated an average of 1.01 anglers/km^2 of coastline but this estimate was as high as 2.9 anglers/km^2 in other studies (Mackenzie, 2005). A total of 375 recreational fishing vessels were identified between three launch sites in the bay between the years of 2006-2009 (Chalmers, 2011). The DAFF fishery report states that the protection MPAs provide for juvenile and spawning stock is of increasing importance in the recovery of some of the most endangered species (DAFF, 2016, IUCN, 2019).

1.5.3 Chokka Squid Fishery

The chokka squid (*Loligo vulgaris*) fishery is primarily based in the Eastern Cape with the most catches occurring from Plettenberg Bay to Port Alfred (Britz et al. 2001). A gradual increase in fishing effort has been observed in Algoa Bay since the establishment of the commercial fishery in the 1980s. Despite this increase in effort, catch per unit effort (CPUE) has been declining slowly, which may be an indication of a local depletion in stock. Contribution of landings from Algoa Bay to national landings has remained consistent since the 1990s at approximately 15-24% of total catch (Chalmers, 2011).

1.5.4 Inshore Demersal Fishery

Inshore demersal trawling is mostly focused in the eastern sector of the bay, as the average spatial distribution of commercial effort from 1983-2015 was concentrated east of Bird Island, and in the inshore areas between Cape Infanta and Mossel Bay (Currie, 2017). Contribution of landings from Algoa Bay (6-11% from 2002-2006) do not contribute significantly to the national landed catch, but CPUE and landings have shown a decline from 2003 onwards suggesting decreasing stocks and fishing pressure exceeded sustainable harvest levels (Chalmers, 2011).

1.5.5 Demersal Shark Fishery

The demersal shark fishery generally operates in shallow waters (<100m) and mainly targets two species: the smooth-hound (*Mustelus mustelus*) and soupfin (*Galeorhinus galeus*) sharks, with other species generally taken as bycatch (De Silva and Bürgener, 2007). Data for this fishery are unreliable and misreporting is thought to occur. From the year 2006-2007, only one vessel was active in Algoa Bay (Chalmers, 2011). Data limitation and poor understanding of stock dynamics increase the vulnerability of these species and increase their susceptibility to overexploitation (Chalmers, 2011).

1.6 Study Aims and Objectives

The aim of this study was to create first-prototype mass-balanced trophic models of Algoa Bay for the summer and winter seasons, as well as depicting the ecosystem if a marine protected area were to be implemented in the bay using the modeling software Ecopath with Ecosim. These models were used to examine the interactions between the small pelagic fish and African penguin populations.

The different elements of this study included:

1) Seasonal models depicting summer and winter conditions
2) Static MPA models demonstrating an “extreme MPA case” where fishery catches are set to zero for all fisheries operating in Algoa Bay
3) Temporal fishery sensitivity analyses using Ecosim where fishery catch is set to zero to represent an extreme MPA case for both the summer and winter models as well as analyses where small pelagic fishery catch is increased to west coast levels.

Additionally, seasonal differences and differences between the non-MPA and MPA model trophic structures were investigated. This work also serves to create a baseline for future use and further development of an ecosystem model for Algoa Bay.

1.7 Hypotheses

I hypothesize that eliminating fishery catches will have a positive impact on African penguin and small pelagic fish biomass, and that this impact would be greater in the summer season when fishing pressure is highest. Secondly, I hypothesize that increasing the fishery mortalities of sardine and anchovy to that of west coast levels will have a negative impact on African penguin modeled biomass. Lastly, trophic group sensitivity to fishing pressure will not be direct as the ecosystem will have a moderating effect on these sensitivities. For example, eliminating fishing pressure on predator groups will increase predator biomass in the bay and therefore increase predation on lower trophic level groups.

Chapter 2: Methodology and Derivation of Model Input Parameters

2.1 Ecopath Equations

The Ecopath model assumes the system is in a steady state, and that for each of the living groups in the system, the input equals the output. Therefore,

$$Q = P + R + U \qquad \text{Eq. 1}$$

Where Q is consumption, P is production, R is respiration, and U is the unassimilated food (Christensen and Pauly, 1992). The production term for each model group can then be split into components, expressed by the equation:

$$P_i = Y_i + B_i * M2_i + E_i + BA_i + P_i * (1 - EE_i) \qquad \text{Eq. 2}$$

Where, P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), B_i is the total biomass of (i), $M2_i$ is the total predation rate for (i), E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate of (i), $P_i * (1 - EE_i)$ is the “other mortality” for group (i) also known as $M0_i$. EE is the ecotrophic efficiency which is the fraction of production that is “used up” in the system. The value ranges from 0 to 1, with 0 indicating no predation (or fishing) pressure, and 1 representing considerable predation (or fishing) pressure (Christensen *et al.* 2005).

Equation 2 can then be re-expressed as:

$$B_i * \left({}^{P}/_{B}\right)_i * EE_i - \sum_{j=1}^{n} B_j * \left({}^{Q}/_{B}\right)_j * DC_{ji} - Y_i - E_i - BA_i = 0 \qquad \text{Eq. 3}$$

Where, P/B_i is the production/biomass ratio, Q/B_i is the consumption/biomass ratio, and DC_{ji} is the fraction of prey (i) in the average diet of the predator (j).

For parameterization, Ecopath sets up as many linear equations as there are groups in a model. Using this set of linear equations, Ecopath can solve for one of the following parameters: biomass, production/biomass ratio, consumption/biomass ratio, or eutrophic efficiency (EE

[Christensen and Walters 2004]). If all four parameters are entered, then Ecopath will estimate biomass accumulation or net migration. If only three basic parameters are entered, then the following parameters must be entered for all groups: catch rate, net migration rate, biomass accumulation rate, assimilation rate, and diet compositions (Christensen et al. 2005).

2.2 Input Data

Four Algoa Bay mass-balanced models were created using the software Ecopath with Ecosim (EwE) version 6.5. All models were constructed to represent the time period from 2010-2014 and are characterized as:

I. Summer season (December – February)
II. Winter season (June – August)
III. Summer season if an MPA was implemented in the bay
IV. Winter season if an MPA was implemented in the bay

Twenty-seven trophic groups were used in the model representing the Algoa Bay ecosystem for the period of 2010-2014. The flow currency of the model is wet mass. See Appendix (Table A.1) for details of all input data and affiliated sources. Final diet composition input values and data sources can be also be found in the Appendix (Table A.2), and are discussed further in the next section. When possible, data collected in the 2010-2014 period were used however, for the trophic groups where 2010-2014 data were not available, older sources were consulted. The bay is an open system; therefore, the diet import option was used to account for migratory species. In addition, the biomass estimates of predator groups are representative of what are only present and feeding in the bay for the specific season modelled, and therefore adjust for the amount of prey consumed in the bay. Below I describe initial model parameters as derived from literature. Final (modified where necessary) input values for all models, and the final balanced versions can be found in Tables 3.1 and 3.2 of the results section.

2.3 Trophic Group Estimates

2.3.1 Plankton

Phytoplankton were separated into two size trophic groups (small <10µm, and large >10µm) based on size classes defined in Probyn (1992). Phytoplankton biomass estimates were taken from Dali (2010) and the proportion of the estimate attributed to the small and large size classes was 60% and 40% respectively (Lamont *et al*. 2018). The P/B value of large phytoplankton was taken from Shannon *et al*. 2003 (based on Brown *et al*. 1991), whereas small phytoplankton were assumed to have a higher turnover rate (set at 200/year).

Zooplankton biomass estimates were made from data collected by SAEON as part of the Pelagic Ecosystem LTER Programme. Zooplankton have been collected at 8 stations on a monthly basis since 2010. Oblique hauls were done using a 90µm net towed at a depth of 25m for all stations except station 7, which was towed at 55m. All size classes were collected together and reported as a total biomass. Because samples were not sorted into size classes, biomass contribution from each group (i.e. micro-, meso-, and macrozooplankton) was inferred from the proportions of zooplankton size classes reported in Shannon *et al*. 2003. The data were converted from dry weight (mg/m^3) to wet weight (t/km^2) by multiplying the dry weight by a factor of 6 to estimate wet weight (Jorgensen, 1979), and multiplying by the depth sampled. The data were also converted from mg/m^3 to t/km^2 for input into Ecopath. P/B values were taken from the published Southern Benguela model (Shannon *et al*. 2003), except for microzooplankton. The microzooplankton P/B value from the published Southern Benguela model was too high to be representative of the bay (ie. production exceeded a reasonable amount such that Ecopath was estimating a large annual biomass accumulation when all input parameters were entered), so a lower value was used, which was consistent with other ocean bay models (Christensen *et al*. 2009, Hutchings *et al*. 1995). Zooplankton diet composition data was taken from Shannon *et al*. (2003), based on Hutchings et al. (1991).

2.3.2 Benthic Producers, Meiobenthos, and Macrobenthos

Benthic producer biomass was estimated by EwE with the ecotrophic efficiency set to 0.500. An EE value of 0.500 was chosen because primary producers often have an EE value of 0.500 or lower, especially in ecosystems that have strong seasonal patterns (Heymans *et al*.

2016). The P/B values were taken from the published Southern Benguela model (Shannon *et al.* 2003). Meiobenthos and macrobenthos biomass was also estimated by EwE with the ecotrophic efficiency set at 0.950 for both. All other input values, as well as diet composition data, were taken from the published Southern Benguela model (Shannon *et al.* 2003).

2.3.3 Small Pelagic Fish

Anchovy and sardine were split into two groups representing recruit and spawning populations. Biomass estimates were calculated using the Department of Agriculture, Forestry, and Fisheries (DAFF) pelagic survey data from 2010-2014. The coast is divided into stratums, and acoustic survey data are being collected twice a year in November (spawner biomass survey) and May (recruitment survey). The biomass estimate (t) was divided by the stratum size (km^2) to obtain the biomass density, and the average over the 2010-2014 period was input in the model. A rough estimate of the stratum size covering Algoa Bay was estimated using Google Maps. It is important to note the 2013 anchovy summer biomass estimate was omitted in the calculation due to an abnormally high reported biomass which was therefore assumed not to depict "normal" conditions. For the summer model, the multi-stanza tool on Ecopath was used to estimate the biomass of recruits based on the spawning population. For the winter model, the recruit biomass was input and Ecopath estimated the spawner population using the multi-stanza tool due to data availability. This was done because the summer surveys are done to estimate the spawner population, and winter surveys are done to estimate the recruit population. The P/B, Q/B, and U values were all taken from the published Southern Benguela model (Shannon *et al.* 2003).

The input parameters for redeye round herring (DAFF survey reports and Chalmers, 2011 both indicate that redeye are indeed present in the bay) and the other small pelagics were all taken from the published Southern Benguela model (Shannon *et al.* 2003), and Ecopath estimated the biomass with an EE value set at 0.900. An EE value of 0.900 was chosen because it is assumed that most trophic groups in an exploited ecosystem (other than primary producers and large predators) will have an EE value close to 1 (Christensen *et al.* 2005).

Diet composition data was sourced from the current Southern Benguela model (Shannon, in prep). The proportion of the diet that is represented in the model to be "imported" (from outside Algoa Bay) was set to 50% for the winter season only do to the low seasonal productivity. This was necessary to achieve a balanced model as the winter primary production was not high enough to support the winter small pelagic biomasses.

Fishery yield was calculated from DAFF small pelagic fishery catch reports which provide monthly total catch (t) for all small pelagic species from 2010-2014 (Table 2.1). Total catch for the summer (Jan-Mar) months and winter (Jun-Aug) months for the stratum covering Algoa Bay were averaged over the modeled time period (2010-2014) for each species separately. The averaged total catch (t) was then divided by the stratum area (km^2) to obtain a fishery yield estimate (t/km^2) relevant for the bay. For some years, catch data was missing from November and December however, neither of these months fall within the modeled seasons (summer = Jan.-Mar., winter = Jun.-Aug.).

Table 2.1. Summary of the documents used to estimate fishery yield for small pelagic fish species in Algoa Bay.

Date Published	Document	Author
14/10/2010	MCM/2010/SWGPEL/44	Jan van der Westhuizen
14/12/2011	FISHERIES/2011/SWGPEL/91	Jan van der Westhuizen
13/12/2012	FISHERIES/2012/DEC/SWGPEL/65	Jan van der Westhuizen
31/10/2013	FISHERIES/2013/OCT/SWG-PEL/25	Jan van der Westhuizen
27/10/2014	FISHERIES/2014/OCT/SWG-PEL/56	Jan van der Westhuizen

2.3.4 Linefish

Linefish biomass was calculated by taking the average biomass estimate (in tonnes) for each linefish species from the years 1986-1990, and dividing by the study area (from Cape Agulhas to Port Alfred) to get a total biomass (t/km^2) for all linefish species (Smale and Badenhorst, 1991). Fishery yield, both recreational and commercial was calculated from data presented in Chalmers, 2011. The remaining input parameters were taken from the published Southern Benguela model (Shannon *et al.* 2003).

Diet composition data was taken from the current Southern Benguela model (Shannon, in prep). The proportion of the diet that is imported from outside the bay was estimated to be 50% for the seasonal models due to linefish having large home ranges and covering a large area over short periods of time (Griffiths, 2000). This import value was decreased to 40% for the MPA models because hypothetically there would be more prey available in the bay if it was closed off to all fisheries.

2.3.5 African Penguins

African penguin biomass estimate was calculated from the South African population estimate of approximately 20,000 breeding pairs in which >50% are found in Algoa Bay (Crawford *et al*. 2014). P/B was calculated from Crawford *et al.* 1991, and Q/B and U were taken from the current Southern Benguela model (Shannon, in prep).

Diet composition data was inferred from multiple diet studies in Algoa Bay (Crawford *et al*. 2011, Pichegru *et al*. 2012, and Randall and Randall, 1986). A summary of the estimated proportion of anchovy and sardine in African penguin diets in Algoa Bay, and the estimate used in the model (after balancing) is reported in Table 2.2 below. The proportion of diet imported from outside the bay was estimated from a foraging study which mapped the foraging area of penguins in Algoa Bay (Pichegru *et al*. 2012). The study mapped the foraging area of breeding penguins before the experimental closure of the purse seine fishery (described earlier in section 1.3.1) which was used to estimate the foraging area for the summer seasonal model. The maps depicting the foraging area of breeding penguins after the experimental closure were used to estimate the import values for the MPA models. These maps showed that when the bay was closed to fishing, penguins reduced their fishing effort 25-30%, and shifted their main foraging areas from outside to within the area closed to fishing (Pichegru *et al*. 2010), therefore in the MPA models, the import values were decreased from the seasonal models by 30%. The proportion of imported diet was assumed to be higher (from 30% in summer to 50%) for the winter models due to the decrease in productivity during the season, and because penguins are not bound to their nests as they are during peak breeding season.

Table 2.2 The reported estimates for the proportion of anchovy and sardine in African penguin diet in Algoa Bay, and the estimates used in the current model. The average column represents the average percent contribution to diet reported across the three diet studies examined (Crawford et al. 2011, Pichegru et al. 2012, and Randall and Randall, 1986).

	Model Input Used	Crawford *et al.* 2011		Pichegru *et al.* 2012	Randall and Randall 1986	Average
		St Croix	Bird Is.			
Anchovy	51%	29%	57%	97%	56%	60%
Sardine	16%	44%	39%	3%	23%	27%

2.3.6 Other Seabirds

Seabird biomass estimates were compiled from a variety of published data (Crawford *et a*l. 1991, Crawford *et al*. 2006, Crawford *et al*. 2009, Whittington *et al*. 2006, Spearpoint *et al*. 1988, and Mclachlan 1980). Species included in this group include the Cape gannet (*Morus capensis*), Cape cormorant (*Phalacrocorax capensis*), white-breasted cormorant (*Phalacrocorax carbo*), kelp gull (*Larus dominicanus*), and a few tern species. All other input values were taken from the published Southern Benguela model (Shannon *et al*. 2003).

Diet composition data was taken from Crawford *et al*. 2011, and the diet proportions were averaged between the Cape cormorant and Cape gannet due to data availability, and because those two species make up a good portion of the seabird trophic group biomass estimate. The proportion of the diet imported from outside the bay was estimated from Cape gannet foraging data (Pichegru *et al*. 2007), in which Algoa Bay makes up approximately 40% of their total foraging area. More recent publications (Botha *et al*. 2017, Thiebault *et al*. 2014) suggest an even lower use of the bay by Cape gannets, however as the trophic group is a combination of many seabird species, this value was used. For the winter models, this import proportion of 60% had to be increased to 80% to balance the model.

2.3.7 Elasmobranchs

Benthic elasmobranch biomass estimates were calculated from benthic research trawl surveys reported in Chalmers (2011). All other input values (P/B, Q/B, and U) were taken from the Southern Benguela model (Shannon *et al*. 2003). Fishery yield estimates were calculated from reported recreational and commercial catch data (Chalmers, 2011). The apex chondrichthyan trophic group is composed of biomass estimates of 5 species; *Sphyrna zygaena*, *Carcharhinus brachyurus*, and *Carcharhinus obscurus* (Smale, 1991), *Carcharodon carcharias* (Dicken *et al*. 2013), and *Carcharias taurus* (Smale *et al*. 2015). All other input values (P/B, Q/B, and U) were taken from the Southern Benguela model (Shannon *et al*. 2003). All input values for the pelagic elasmobranch trophic group were taken from the Southern Benguela model (Shannon *et al*. 2003).

Diet composition data for the pelagic feeding and benthic feeding elasmobranchs were taken from the Southern Benguela model (Shannon et al. 2003). Apex chondrichthyan diet composition data was estimated from diet studies (Smale, 1991, Cliff *et al*. 1989) and an overall average for all species was used (excluding *Carcharias taurus* because data for Algoa Bay was not available). The proportion of imported diet was estimated from data presented in Chalmers (2011) and monthly percent frequency data of sharks sampled inshore (in the bay) versus offshore (outside the bay) Smale (1991). Frequency data was used to estimate diet import in that if they are estimated as spending 52% of their time outside the bay, then 52% of their diet is imported.

2.3.8 Marine Mammals

Seal biomass was calculated from a population estimate of 4000 individuals on black rocks within the Bird Island group of Algoa Bay (Chalmers, 2011). All other input parameters were taken from the Southern Benguela model (Shannon *et al*. 2003). Seal diet composition estimates were derived from region specific (Table Bay to Algoa Bay) stomach content data (David, 1987). The proportion of seal diet considered imported was estimated from a foraging study in the northern Benguela, assuming seals in Algoa Bay would travel a similar distance from their breeding colony to forage for food (Skern-Mauritzen *et al*. 2009).

The cetacean trophic group consists of 6 species commonly found in Algoa Bay. These include: the Southern right whale (*Eubalaena australis*), humpback whale (*Megaptera novaeangliae*), Bryde's whale (*Balaenoptera brydei*), Indian Ocean bottlenose dolphin (*Tursiops aduncus*), Indo-pacific humpback dolphin (*Sousa chinensis*), and the long-beaked common dolphin (*Delphinus capensis*). All input values for the cetacean trophic group were taken from the published Southern Benguela model (Shannon *et al*. 2003). Diet composition data was taken from the current Southen Benguela model (Shannon, in prep). The proportion of diet imported from outside Algoa Bay was estimated from distribution data (Melly, 2011) averaged for all species represented in the trophic group.

2.3.9 EwE Estimates

Cephalopods, benthic-feeding fish, and pelagic-feeding fish biomass estimates were all made by EwE, when the ecotrophic efficiency was set at 0.900. As previously stated, an EE value of 0.900 was chosen because it is assumed that most exploited trophic groups (other than primary producers and large predators) will have an EE value close to 1 (Christensen *et al*. 2005). MPA model EE values for trophic groups in which Ecopath estimated biomass (i.e.

redeye, other small pelagics, etc.) were calculated by entering the seasonal model biomass estimate into the MPA model to generate an Ecopath EE estimate with fishery predation removed. The MPA biomass estimates for these groups were still calculated by setting the EE value to 0.900. For the cephalopods, all other input values were taken from the Southern Benguela model (Shannon *et al*. 2003). The pelagic-feeding and benthic-feeding fish trophic group Q/B values were calculated from FishBase (a global database of fish species, www.fishbase.org) while all other input values were taken from the Southern Benguela model (Shannon *et al*. 2003).

2.4 Balancing the Model

The initial models using input data collected from published and unpublished survey data mentioned above were unbalanced as biomass and production estimates were not high enough to support the ecosystem for some groups. Balanced models were achieved by slightly altering the diets of some trophic groups, mainly by altering the proportion of diet assumed to be consumed from outside the bay (ie. considered as "imports" to the system being modeled), and in the proportion of the diet between spawner and recruit groups for both sardine and anchovy in their predators' diets. Diet composition data was altered because it was generally the most uncertain input parameter (compared to the biomass estimates), and altering more reliable data should be avoided (Christensen *et al.* 2005). For example, out of the total contribution of anchovy to African penguin diet, how much is contributed by the spawner group versus the recruit group as such data is generally unknown or uncertain. Final diet composition input values and data sources can be found in the Appendix (Table A.2).

2.5 Ecosim

Ecosim was used to investigate changes in biomass for all trophic groups if fishing effort was reduced to zero for all fleets in the bay. While the proposed MPA does not cover the entire bay, this analysis is meant to represent an "extreme" MPA case, in order to explore maximum ecosystem responses to fishing. Ecosim was run for 20 years to achieve stable biomasses and then run for another 30 years with fishing effort set to zero for all fisheries. The biomass of each trophic group was recorded at the start and at the end of the 50-year period and expressed as a bar graph of percent increase or decrease (Figure 3.6) between the beginning and end of the simulation. Although using the seasonal models separately is unrealistic in terms of temporal dynamics, examining the effects of no take zones in Algoa Bay using the two seasonal models is useful in that patterns of likely ecosystem consequences can be identified for further detailed consideration and research.

In addition to setting fishery catch to zero, Ecosim was also used to investigate changes in biomass of trophic groups if fishing mortalities were increased for sardine and anchovy to simulate small pelagic fishing pressure on the west coast which is much higher than that of the east coast. Ecosim was again run for 20 years to achieve stable biomasses and then run for another 30 years with fishing mortalities increased to mortalities reported in a 2004-2008 southern Benguela model (Osman, 2010). The fishing mortality values used in the Ecosim analyses were 0.217 for sardine (static model value was 0.05 in summer and 0.01 in winter), and 0.0984 for anchovy (static model value of <0.001 in summer and <0.001 in winter). The biomass of each trophic group was recorded at the start and at the end of the 50-year period and expressed as a bar graph of percent increase or decrease (Figure 3.7) between the beginning and end of the simulation.

2.6 Data Analyses

Summary statistics were calculated for each model by Ecopath and reported to describe the ecosystem as a whole (Table 3.3). Total system throughput can be used to describe the size of the flow of the system and is expressed as: total system throughput = total consumption + total flow to detritus + total export + total respiration (Ulanowicz, 1986, Christensen *et al*. 2005).

Total biomass and transfer efficiency (TE) at each trophic level (TL) was calculated by Ecopath (Table 3.4) and the percent changes between the seasonal and MPA model as well as the summer and winter models were expressed in a bar graph (Figure 3.1). In Ecopath, primary producers and detritus are assigned a TL of 1, and consumers are assigned a TL of 1 + the weighted average of the TL of their prey (Christensen et al. 2005). Transfer efficiency refers to the fraction of total throughput at a discrete TL and the export and flow that is transferred from one TL to another (Ulanowicz, 1986, Christensen and Walters, 2004). Relative consumption of production by small pelagics and large predator trophic groups was estimated by Ecopath and visualized in a pie chart to highlight differences between seasons (Figure 3.2). Mixed trophic impact analyses (Ulanowicz and Puccia, 1990) were calculated for select trophic groups (Figures 3.3 and 3.4).

Chapter 3: Results

3.1 Basic Estimates

Plankton showed seasonal variation with zooplankton total (all size groups combined) biomass (t/km^2) being 5.4x greater and phytoplankton total (small and large) biomass being 3.2x greater in the summer (Tables 3.1 and 3.2). According to DAFF survey data, anchovy were the dominant small pelagic fish species in Algoa Bay during the 2010-2014 period. Anchovy and sardine biomass also varied by season with the anchovy spawner biomass being 1.9x greater, and sardine spawner biomass being 1.5x greater in the summer model. Small pelagic fish trophic levels ranged from 2.526 (anchovy and sardine recruits) to 3.662 (redeye), and the highest trophic level group was apex chondrichthyans with a trophic level of 4.929 (Tables 3.1 and 3.2). Ecotrophic efficiency (EE) values were generally higher in the winter model with the exception of sardine spawners. Differences between EE values compared between seasonal and MPA models are discussed in detail in section 3.6 below (Figure 3.5).

Table 3.1. Basic estimates output for the summer model (top value) and summer MPA model (bottom value with asterisk) of the Algoa Bay ecosystem representing the 2010-2014 period (initial input values are in bold, values in italics were estimated by EwE). When both model estimates were the same, only one value was reported. Table key: TL = trophic level, B = biomass (t/km^2), P/B = production/biomass (/yr), Q/B = consumption/biomass (/yr), P/Q = production/consumption (/yr), U = unassimilated consumption, EE = ecotrophic efficiency, Y = fishery yield (t/km^2/yr).

Trophic Group	TL	B	P/B	Q/B	P/Q	U	EE	Y
Phytoplankton (Small)	*1.000*	**37.97**	**200.00**				*0.294*	
Phytoplankton (Large)	*1.000*	**25.32**	**154.4**				*0.041*	
Benthic Producers	*1.000*	*4.019* *5.525**	**15.00**				**0.500** *0.607**	
Microzooplankton	*2.053*	**7.009**	**150.00**	*600.000*	**0.250**	**0.200**	*0.874*	
Mesozooplankton	*2.526*	**7.550**	**40.00**	*133.333*	**0.300**	**0.350**	*0.826* *0.837**	
Macrozooplankton	*2.866*	**12.50**	**13.00**	*31.707*	**0.410**	**0.200**	*0.370* *0.378**	
Gelatinous zooplankton	*3.293*	**4.545**	**0.584**	*1.669*	**0.350**	**0.200**	*0.342* *0.388**	
Anchovy Recruits	*2.526*	**4.822**	**1.200**	**16.27**	*0.074*	**0.350**	*0.831*	

							*0.875**	
Anchovy Spawners	*3.547*	**7.510**	**1.200**	**12.30**	*0.098*	**0.200**	*0.734*	**<0.001**
							*0.769**	**0.000**
Sardine Recruits	*2.526*	**0.991**	**1.200**	**24.60**	*0.049*	**0.200**	*0.774*	
							*0.880**	
Sardine Spawners	*2.910*	**4.180**	**1.200**	**13.97**	*0.086*	**0.350**	*0.684*	**0.209**
							*0.675**	**0.000**
Redeye roundherring	*3.662*	*2.811*	**1.200**	**14.04**	*0.085*	**0.350**	**0.900**	**<0.001**
		*3.191**					*0.979**	**0.000**
Other small pelagics	*3.612*	*4.204*	**1.000**	**10.00**	*0.100*	**0.350**	**0.900**	**0.009**
		*4.446**					*0.952**	**0.000**
Linefish	*4.169*	**0.800**	**0.480**	*8.000*	**0.060**	**0.200**	*0.943*	**0.114**
	*4.193**						*0.744**	**0.000**
Cephalopods	*3.623*	*0.765*	**3.500**	*10.000*	**0.350**	**0.200**	**0.900**	**0.037**
	*3.626**	*0.849**					*0.980**	**0.000**
Pelagic-feeding fish	*3.959*	*0.720*	**1.000**	**5.040**	*0.198*	**0.200**	**0.900**	**0.016**
	*3.974**	*0.858**					*1.017**	**0.000**
Benthic-feeding fish	*3.304*	*3.441*	**1.000**	**5.921**	*0.169*	**0.200**	**0.900**	**0.027**
	*3.328**	*3.724**					*0.936**	**0.000**
Ben. Elasmobranchs	*3.429*	**0.711**	**1.000**	**10.000**	*0.100*	**0.200**	*0.649*	**0.022**
	*3.433**						*0.664**	**0.000**
Pel. Elasmobranchs	*4.505*	**0.582**	**0.500**	**4.500**	*0.111*	**0.200**	*0.157*	
	*4.543**						*0.165**	
Apex chondricthyans	*4.929*	**0.022**	**0.500**	**5.000**	*0.100*	**0.200**	*0.000*	
	*4.936**							
Seals	*4.436*	**0.417**	**0.946**	**19.31**	*0.013*	**0.200**	*0.082*	
	*4.442**						*0.117**	
Cetaceans	*4.367*	**0.080**	**0.600**	**10.000**	*0.060*	**0.210**	*0.239*	
	*4.368**						*0.339**	
Penguins	*4.235*	**0.024**	**0.200**	**96.98**	*0.002*	**0.200**	*0.000*	
	*4.237**							
Other seabirds	*4.198*	**0.298**	**0.123**	**123.00**	*0.001*	**0.260**	*0.000*	
	*4.197**							
Meiobenthos	*2.000*	*7.525*	**4.000**	**33.00**	*0.121*	**0.100**	**0.950**	
		*9.751**						
Macrobenthos	*2.161*	*35.456*	**1.200**	**10.00**	*0.120*	**0.100**	**0.950**	
		*46.001**						
Detritus	*1.000*	**50.00**					*0.260*	
							*0.270**	

Table 3.2. Basic estimates output for the winter model (top values) and winter MPA model (bottom values with asterisk) of the Algoa Bay ecosystem representing the 2010-2014 period (initial input values are in bold, values in italics were estimated by the model). When both model estimates were the same, only one value was reported. Table key: TL = trophic level, B = biomass (t/km^2), P/B = production/biomass (/yr), Q/B = consumption/biomass (/yr), P/Q = production/consumption (/yr), U = unassimilated consumption, EE = ecotrophic efficiency, Y = fishery yield (t/km^2/yr).

Trophic Group	TL	B	P/B	Q/B	P/Q	U	EE	Y
Phytoplankton (Small)	_1.000_	**13.71**	**200.00**				_0.161_	
Phytoplankton (Large)	_1.000_	**5.877**	**154.4**				_0.032_	
Benthic Producers	_1.000_	_3.969_ _4.207*_	**15.00**				**0.500**	
Microzooplankton	_2.053_	**1.308**	**150.00**	_600.000_	**0.250**	**0.200**	_0.992_	
Mesozooplankton	_2.526_	**1.696**	**40.00**	_133.333_	**0.300**	**0.350**	_0.980_ _0.960*_	
Macrozooplankton	_2.866_	**2.000**	**13.00**	_31.707_	**0.410**	**0.200**	_0.872_ _0.929*_	
Gelatinous zooplankton	_3.293_	**4.545**	**0.584**	_1.669_	**0.350**	**0.200**	_0.288_	
Anchovy Recruits	_2.526_	**2.520**	**1.200**	**16.27**	_0.074_	**0.350**	_0.916_ _0.941*_	
Anchovy Spawners	_3.547_	**3.925**	**1.200**	**12.30**	_0.098_	**0.200**	_0.837_ _0.866*_	**<0.001** __0.000*__
Sardine Recruits	_2.526_	**0.660**	**1.200**	**24.60**	_0.049_	**0.200**	_0.928_ _0.947*_	
Sardine Spawners	_2.910_	**2.723**	**1.200**	**13.97**	_0.086_	**0.350**	_0.586_ _0.614*_	**0.032** __0.000*__
Redeye roundherring	_3.662_ _3.696*_	_2.069_ _1.986*_	**1.200**	**14.04**	_0.085_	**0.350**	**0.900** _0.918*_	**<0.001** __0.000*__
Other small pelagics	_3.612_ _3.613*_	_3.201_ _3.433*_	**1.000**	**10.00**	_0.100_	**0.350**	**0.900** _0.967*_	**<0.001** __0.000*__
Linefish	_4.169_ _4.195*_	**0.800**	**0.480**	_8.000_	**0.060**	**0.200**	_0.964_ _0.740*_	**0.123** __0.000*__
Cephalopods	_3.623_ _3.625*_	_0.742_ _0.760*_	**3.500**	_10.000_	**0.350**	**0.200**	**0.900** _0.921*_	**0.037** __0.000*__
Pelagic-feeding fish	_3.959_ _3.964*_	_0.572_ _0.556*_	**1.000**	**5.040**	_0.198_	**0.200**	**0.900** _0.877*_	**0.013** __0.000*__
Benthic-feeding fish	_3.304_ _3.305*_	_3.397_ _3.391*_	**1.000**	**5.921**	_0.169_	**0.200**	**0.900** _0.893*_	**0.025** __0.000*__
Ben. Elasmobranchs	_3.429_	**0.711**	**1.000**	**10.000**	_0.100_	**0.200**	_0.657_ _0.618*_	**0.028** __0.000*__
Pel. Elasmobranchs	_4.505_ _4.537*_	**0.582**	**0.500**	**4.500**	_0.111_	**0.200**	_0.157_ _0.156*_	
Apex chondricthyans	_4.929_ _4.933*_	**0.022**	**0.500**	**5.000**	_0.100_	**0.200**	_0.000_	
Seals	_4.436_ _4.437*_	**0.417**	**0.946**	**19.31**	_0.013_	**0.200**	_0.082_	
Cetaceans	_4.367_ _4.368*_	**0.080**	**0.600**	**10.000**	_0.060_	**0.210**	_0.239_	

Penguins	_4.235_ _4.237*_	**0.024**	**0.200**	**96.98**	_0.002_	**0.200**	_0.000_
Other seabirds	_4.197_ _4.205*_	**0.290**	**0.123**	**123.00**	_0.001_	**0.260**	_0.000_
Meiobenthos	_2.000_	_7.429_ _7.458*_	**4.000**	**33.00**	_0.121_	**0.100**	**0.950**
Macrobenthos	_2.161_	_35.012_ _35.138*_	**1.200**	**10.00**	_0.120_	**0.100**	**0.950**
Detritus	_1.000_	**50.00**					_0.262_ _0.262*_

3.2 Summary Statistics

All summary statistics were 3.0-3.4x higher in the summer model compared to the winter model except for the total biomass excluding detritus (1.8x higher), the total catch (1.7x higher). The mean trophic level of catch and omnivory index which were both lower in summer. Summary statistics are for both seasons and are found in Table 3.3 below.

Table 3.3. Ecopath output summary of statistics for the summer and winter Algoa Bay models, and the difference between them expressed as a change from winter to summer. All flows are expressed in t/km^2/year, and total biomass (except detritus) is t/km^2.

Parameter	Summer (S)	Winter (W)	(S vs W)
Σ consumption	6650	1973	3.4x
Σ exports	8065	2672	3.0x
Σ respiratory flows	3566	1192	3.0x
Σ flows to detritus	10899	3618	3.0x
Total system throughput	29180	9454	3.1x
Σ production	13192	4099	3.2x
Mean trophic level of catch	3.406	3.760	0.9x
Total net primary prod.	11564	3709	3.1x
Net system production	7997	2517	3.2x
Total biomass (except detritus)	174	98	1.8x
Total catch	0.433	0.258	1.7x
Omnivory Index	0.525	0.652	0.8x

3.3 Total Biomass and Transfer Efficiency

Total biomass was higher in the summer model for all TLs. The highest total biomass occurred at TL I and decreased with increasing trophic levels for both seasons. The greatest percent change between the seasons occurred at trophic level III with a 71% higher total biomass in the summer compared to winter (Figure 3.1A).

Transfer efficiency was highest at TL III and lowest at TL VI for both seasons. Overall there was little difference in transfer efficiencies between seasons, but the largest difference of a 44% higher TE in the summer model, occurred at TL VI (Figure 3.1B).

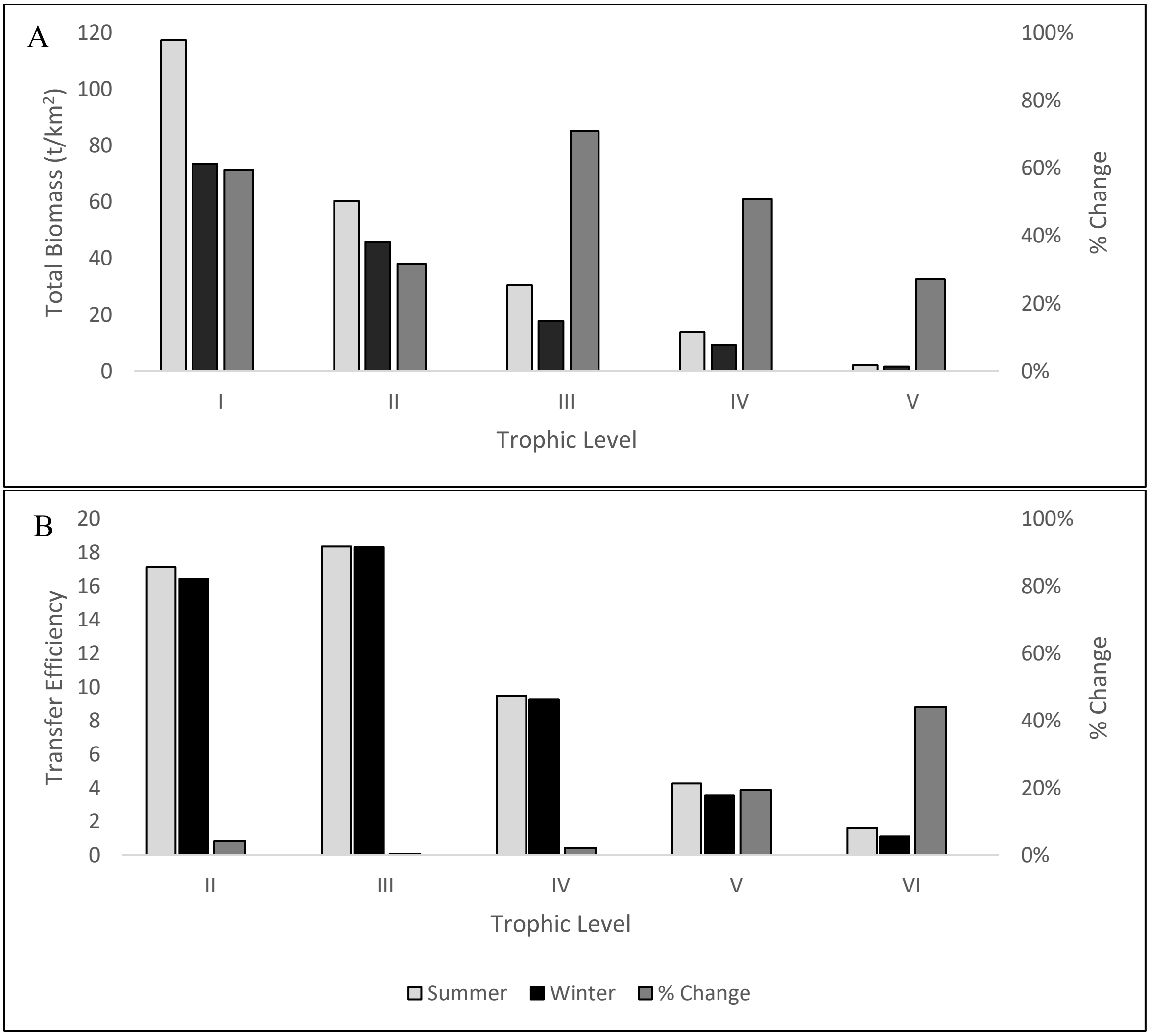


Figure 3.1. A) Total biomass (t/km^2) at discrete trophic levels (left axis) for the summer and winter models, and the percent change between winter and summer (right axis). B) transfer efficiency at discrete trophic levels for summer and winter (left axis), and the percent change from winter to summer (i.e. summer with respect to winter) (right axis).

3.4 Consumption

Small pelagic fish consumed the greatest proportion of total production in both seasons with anchovy consuming the most at 40% and 30% in the summer and winter respectively. Seabirds consumed the second greatest proportion of production in both seasons, but was 4% higher in winter. Other fish (linefish, pelagic feeding teleosts, benthic feeding teleosts) consumed the third greatest proportion of production in the winter season, which was 4% more than in the summer. Other fish, elasmobranchs, and marine mammals all consumed a greater proportion of production in the winter compared to the summer season. In contrast to linefish and aforementioned predators, small pelagic fish consumed a greater proportion of production in the summer than the winter season (78% in summer vs 68% in winter).

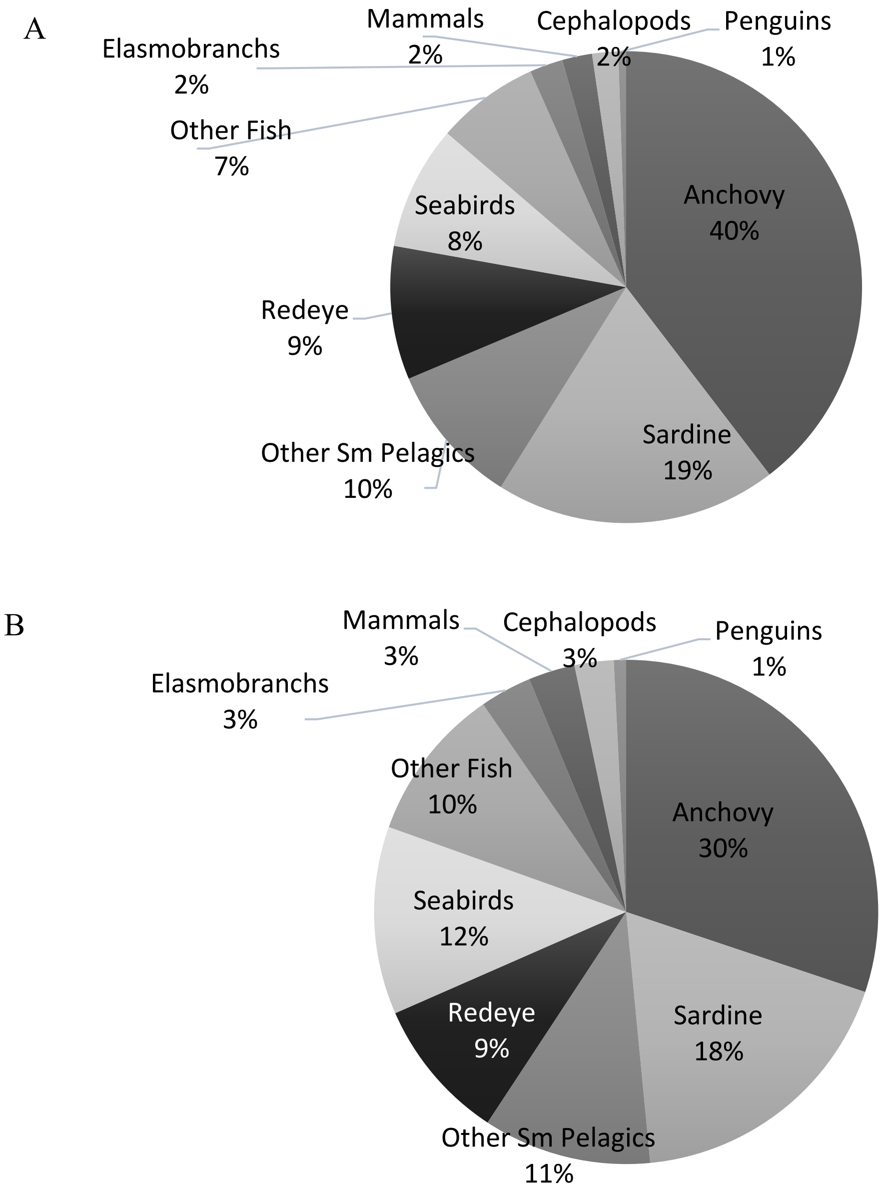


Figure 3.2. Relative consumption for each trophic group in Algoa Bay calculated by EwE for the A) summer model and B) winter model.

3.5 Mixed Trophic Impact Analyses

Mixed trophic impact analyses are reported below for select trophic groups. Small pelagic species and fisheries are described in Figure 3.3 while the larger trophic level groups (>4.0) are shown in Figure 3.4. Small pelagic fish species generally had negative impacts on lower TL groups and positive impacts on higher TL groups. The larger TL groups generally had negative impacts on other large TL groups while having mixed impacts on lower TL groups. Apex sharks had the largest negative impact than any other TL, which was on seals and cetaceans.

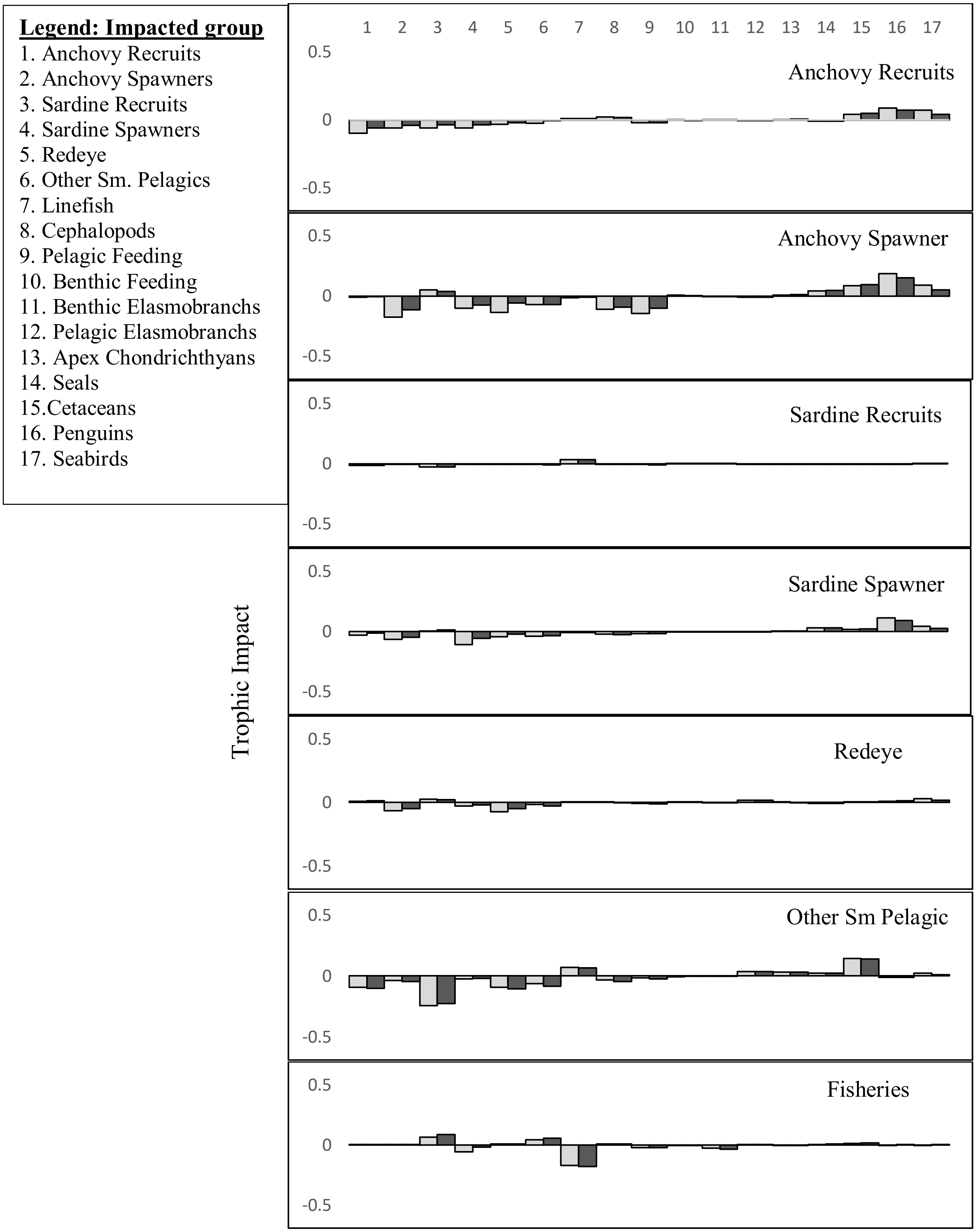


Figure 3.3 Mixed trophic impacts of small pelagic trophic groups, on other modeled trophic groups (listed in the legend). The y-axis is scaled from 0-0.5 with positive trophic impacts above the line and negative below. Light bars represent summer and dark bars represent winter.

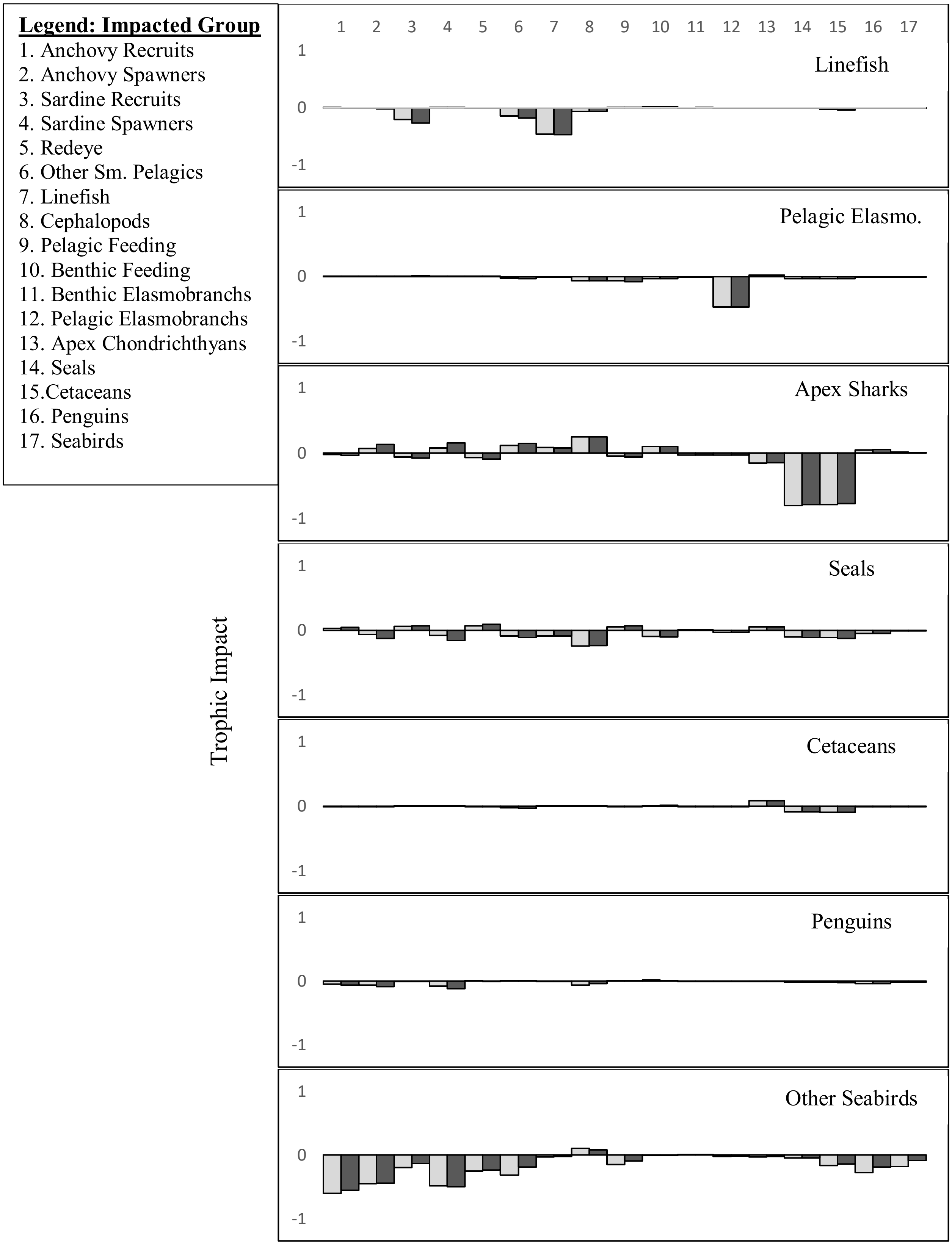


Figure 3.4 Mixed trophic impacts of select predator groups (TL>4), on other modeled trophic groups (listed in the legend). The y-axis is scaled from 0-1.0 with positive trophic impacts above the line and negative below. Light bars represent summer and dark bars represent winter.

3.6 Static MPA Model Ecotrophic Efficiencies

For the summer and winter MPA models, ecotrophic efficiency (EE) values were higher than the seasonal model for meso-, macro-, and gelatinous zooplankton, with the exception of winter mesozooplankton, which was 2% lower (Figure 3.5). EE values for anchovy and sardine recruits were also higher for both MPA models. For sardine spawners, EE values were higher in the winter MPA model (5%), and lower in the summer MPA model (-1%). Anchovy spawners had a higher EE value in the summer MPA model (5%), but a lower EE value in winter (-1%). Linefish had the greatest decrease in EE values observed in both seasons with a 21% and 23% smaller EE value in summer and winter respectively. Seals and cetaceans had the greatest percent increase in EE values at 43% and 42% larger values. Reported EE values can be found above in Tables 3.1 and 3.2.

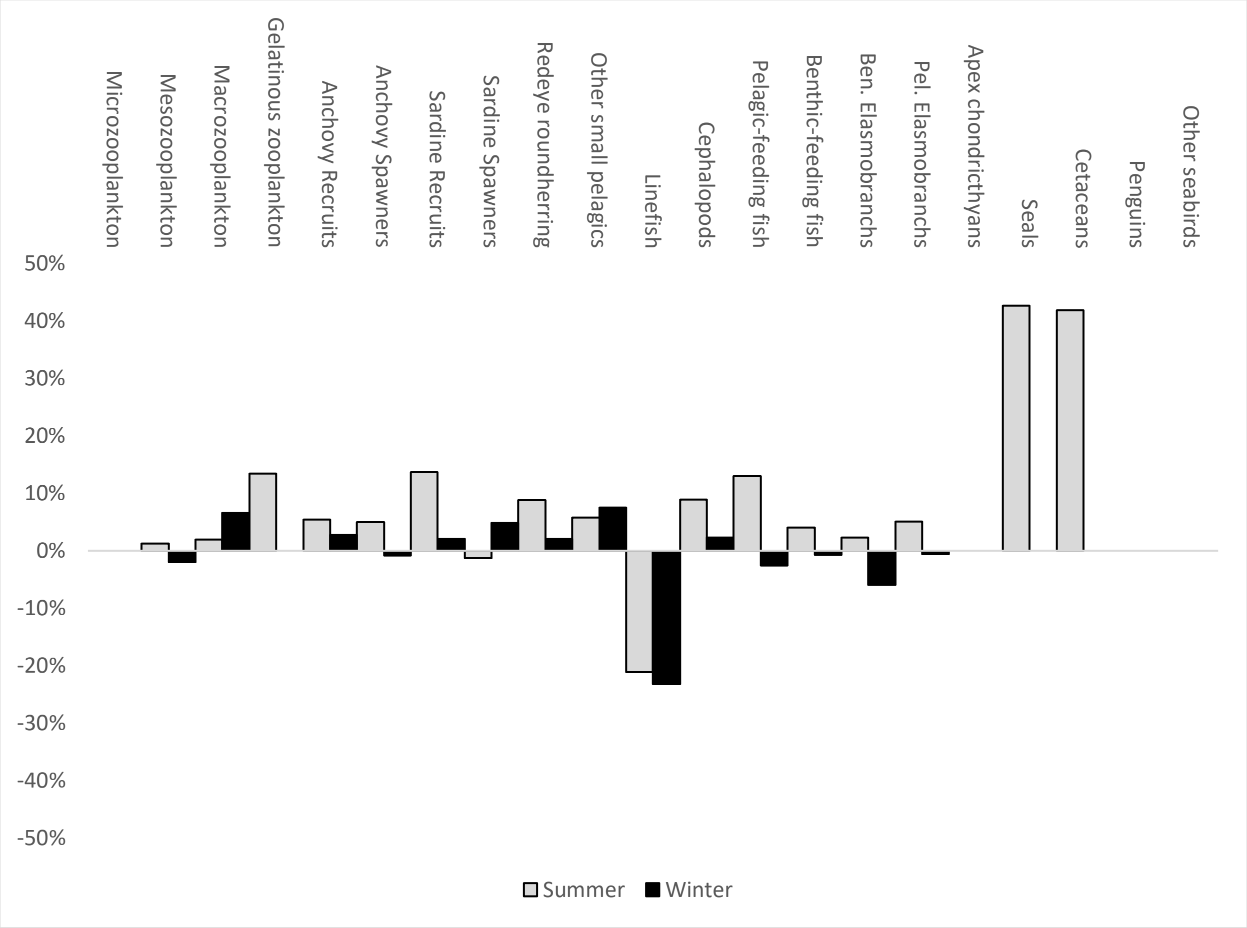


Figure 3.5. Percent change between the ecotrophic efficiency values of the seasonal and static marine protected area models. Bars below the line depict smaller EE values (less predation pressure) in the MPA model and bars above the line depict larger values (greater predation pressure).

3.7 Fishery Sensitivity Analyses Using Ecosim

3.7.1 Setting Fishery Catch to Zero

For the summer model, linefish had the greatest percent increase (18.9%, or 0.186t/km^2) in biomass after running Ecosim for 30 years with all fishery catch set to zero (Figure 3.5). Both anchovy recruits and spawners increased by a small amount, 0.4% and 0.3% respectively. Model sardine recruits decreased by 1.5% but spawners increased by 1.5%. Pelagic feeding fish and benthic elasmobranch biomass increased by 2.8% and 2.6% respectively. Model cetacean biomass decreased the most at 6.7%, and other small pelagic decreased by 6.4%. Penguin biomass showed a small increase of 0.5%.

For the winter model, linefish had the greatest percent increase of biomass after running Ecosim for 30 years at 19.4% or 0.193t/km^2 (Figure 3.5). Both anchovy recruits and spawners increased by 0.9% and 1.4% respectively. Model sardine recruits and spawners decreased by 6.6% and 1.3% respectively. Model pelagic feeding fish had the second largest increase in biomass at 4.3%, and benthic elasmobranchs increased by 3.3%. Model cetaceans had a large decrease of 8.1% and other small pelagics decreased by 6.4%. There was no change to penguin biomass in the model.

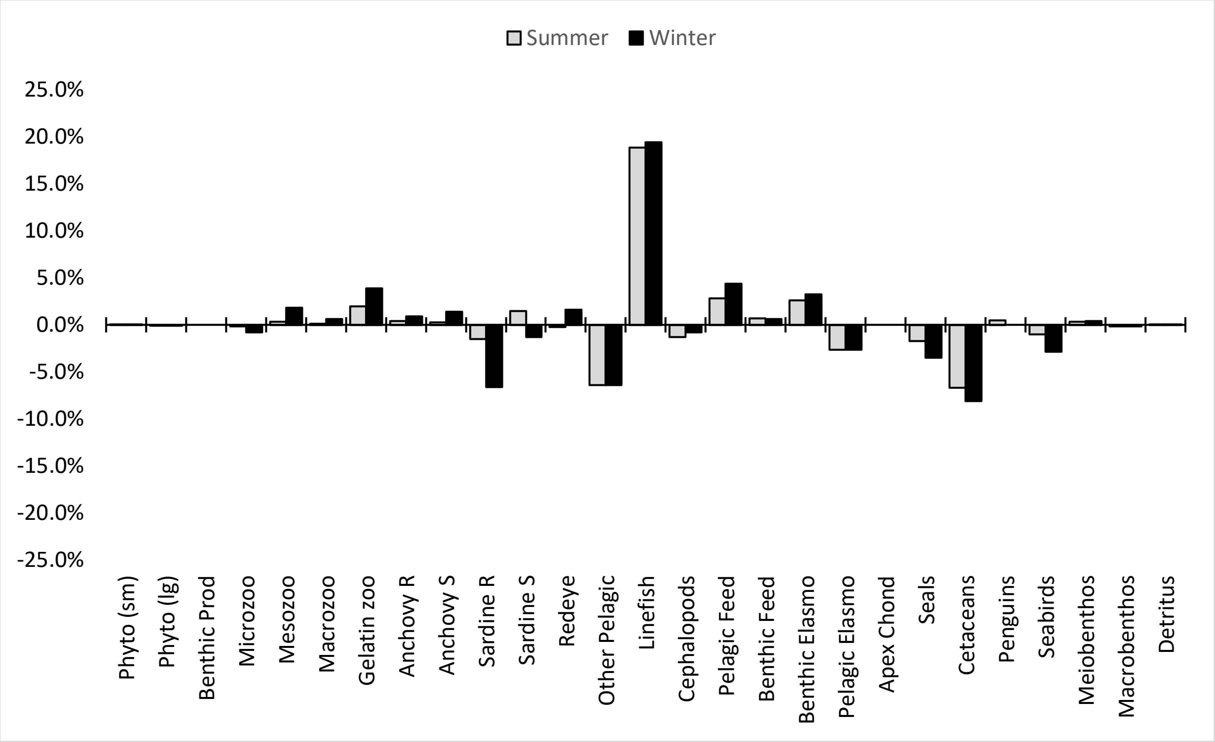


Figure 3.6. Biomass change expressed as percent increase or decrease for each trophic group in summer (grey) and winter (black) after running Ecosim for 30 years with fishery catch set at zero for all fleets.

3.7.2. Increased Fishing Mortalities

When modeled fishing mortalities were increased for sardine and anchovy to levels matching those of the west coast over a span of 30 years, sardine spawners had the largest biomass decrease in both summer (10.3%) and winter (15.1%; Figure 3.7). Of the top predator trophic groups, African penguins showed the largest biomass decrease in both seasons modeled, decreasing by 9.1% in summer, and 11.6% in winter. Other seabirds showed the second largest biomass decrease of 6.4% and 8.2% in the summer and winter models, respectively.

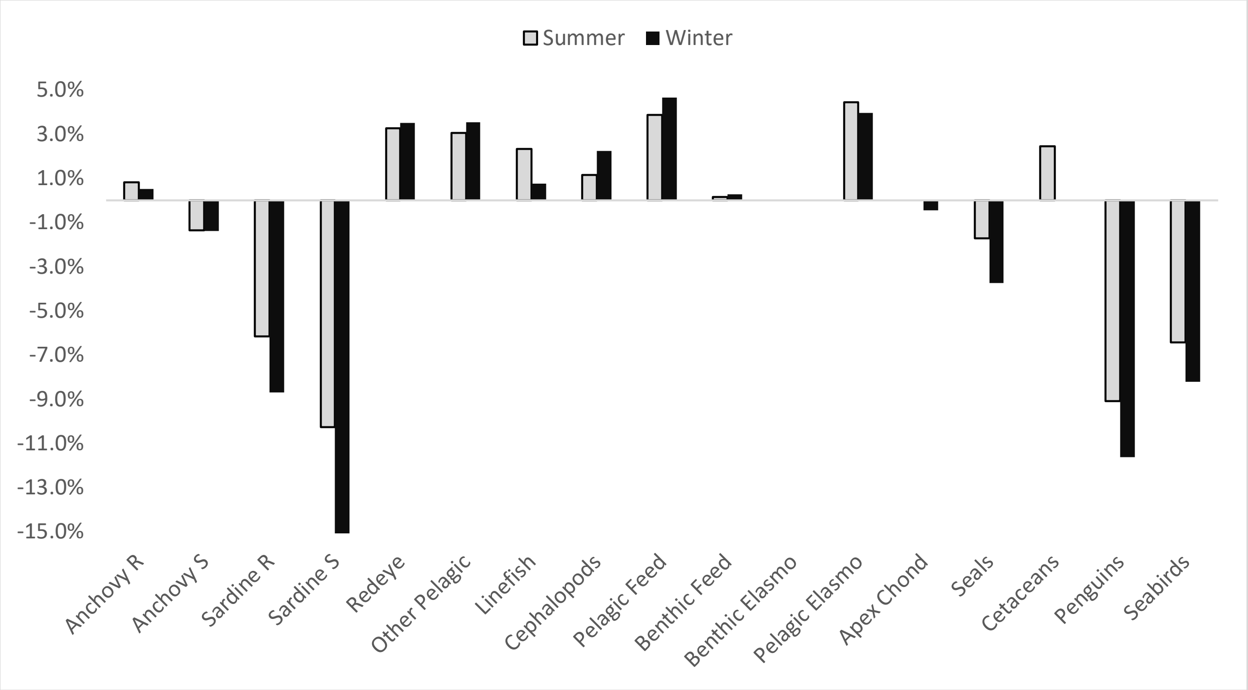


Figure 3.7. Biomass change expressed as percent increase or decrease for each trophic group in summer (grey) and winter (black) after running Ecosim for 30 years with fishery mortalities set to west coast levels estimated from Osman's (2010) Benguela model.

Chapter 4: Discussion

4.1 Model Uncertainty and Limitations

It is important to note that while these prototype mass-balanced seasonal Algoa Bay models have been constructed, there is some uncertainty with input parameter estimates. For example, data were not always available for the time period represented and some estimates were inferred from other models. While these models represent a good preliminary Ecopath model to investigate the trophic interactions and energy flows of the Algoa Bay ecosystem, model outputs should be viewed together with field studies and results of other types of analyses to build more confidence in the model results, ahead of possible recommendations for management advice.

In some cases (due to a lack of local data), model input parameters were taken from the southern Benguela model (Shannon *et al*. 2003). It is important to note this limitation in the model as there are likely differences in values between the two ecosystems. The southern Benguela model covers a vast area of 220,000km^2 (including Algoa Bay), and included the west coast's seasonal, pulsed, wind-driven upwelling that supports large biological productivity (Shannon et al. 2003), greater than that of the Algoa Bay system. Further development of the model by collecting more local data is recommended to improve model parametrization analogous with productivity in the bay.

One limitation of this study was the design of the Ecosim simulations. The design of the Ecosim sensitivity analyses may provide seasonal comparisons of trophic group sensitivity to fishing pressure however, it does not reflect the real world. For example, the Ecosim is run on a model which is only simulating one season's conditions, when in reality, the bay is experiencing all seasons (not just one) in a year. This allows for inferences to be made on the sensitivity of certain groups in winter versus summer but it may be useful for future studies to apply seasonal forcing on one model versus modeling seasons separately.

4.2 Seasonal Model Variation

4.2.1 Plankton Biomass

Plankton biomass was greater in the summer compared to the winter model estimates. Phytoplankton total biomass (small <10μm and large >10μm combined) was 3.4x greater (69% increase), and zooplankton total biomass (micro-, meso-, and macrozooplankton combined) was 5.4x greater (82% increase) in the summer model. These seasonal differences are consistent with the seasonality in wind resulting in strong easterly winds and upwelling occurring in the summer months (Schumann *et al.* 1991) compared to the strong westerly winds and downwelling which occurs in the winter months (Goschen and Schumann, 1995). Nutrient enrichment is influenced by wind direction and upwelling (Bakun and Parrish, 1991) which promotes the production of phytoplankton and zooplankton (Probyn *et al.* 1994, Daneri *et al.* 2000). Seasons with greater upwelling would be expected to be more biologically productive (Cury *et al.* 2000).

4.2.2 Small Pelagic Fishes

According to DAFF acoustic survey data, anchovy (48% increase) and sardine (35% increase) biomass was greater in the summer compared to the winter season (real-world biomass estimates). Increased summer biomass of anchovy and sardine is likely a result of the seasonal differences in their food source as plankton biomass is also greater in the summer season (Van der Lingen *et al.* 2006), as discussed in section 4.2.1 above. The greater increase in anchovy biomass in the summer compared to sardine biomass may be attributed to the greater increase in zooplankton compared to phytoplankton. While both species feed on phytoplankton and zooplankton, sardine diet relies more heavily on phytoplankton and smaller zooplankton (Van der Lingen, 2002) while anchovy feed more predominately on larger zooplankton.

Small pelagic fish consumed the greatest proportion of total production in both seasons with anchovy consuming the most at 39% and 24% in the summer and winter respectively.. These differences in diet could explain why anchovy are more abundant in Algoa Bay as there is a greater increase in their preferred found source of zooplankton compared to phytoplankton, which is more heavily consumed by sardine (Van der Lingen, 2002).

The greatest seasonal increase in total biomass occurred at trophic level III with a 72% higher total biomass in the summer model compared to the winter model (Figure 3.1). This increase in biomass suggests, again that the lower trophic level fishes (like the small pelagics) are greatly benefitting from the summer increase in primary production.

4.2.3 African Penguins

Pre- and peak egg laying of the breeding season for African penguins in Algoa Bay occurs during the summer months, from January to March (Ralph, 2008). This coincides with the warm summer temperatures, and the seasonal increase in plankton and small pelagic biomass in Algoa Bay associated with summer upwelling and strong easterly winds (Schumann *et al.* 1991). Penguin diet consists of species occurring from TLs 2.5 to 4.2. Model results showed a 24-47% higher summer total biomass at TLs II-IV compared to the winter total biomass. As breeding success is strongly dependent on food availability (Crawford *et al.* 2006), the model output therefore supports the idea that pre- breeding and peak egg laying time corresponds with the time of greatest food availability in Algoa Bay.

Relative consumption by African penguins was small at less than 1% of total production. Of the production consumed by African penguins, 60.4% and 43.2% of that consumption was on small pelagic fish in the summer and winter respectively. In summer, 39% of penguin consumption was on anchovy, and 16% was on sardine. In winter, 28% of consumption was on anchovy, and 11% was on sardine. The proportion of consumption that was taken from outside the bay was 30% and 50% in summer and winter respectively. The greater consumption of small pelagic fish in the summer highlights the importance of small pelagics in breeding success, in line with expectations.

4.2.4 Summary Statistics

All trophic summary statistics (Table 3.3) were approximately 3x greater for the summer model compared to the winter model with the exception of the mean trophic level of catch and total biomass excluding detritus. These differences can be attributed to the 69% increase in phytoplankton, and 82% increase in zooplankton between winter and summer. Comparing the Algoa Bay model statistics with other published models in terms of ecosystem size (ie. primary production, biomass, and total system throughput), the summer model was similar to the other bay models, while the winter model ranked much lower (Dalsgaard *et al.* 1997, Lin *et al.* 2004, Okey, 2006, Wolff, 1994). Seasonal differences cannot be compared between the bays because seasonal models do not exist for the other bays. The winter decrease in primary productivity greatly reduces the size of the ecosystem in terms of energy flow.

Omnivory index (OI) is calculated as the variance of trophic levels in a consumer's diet and is therefore an indication of whether the consumer is a specialist or generalist. If the consumer feeds on a single trophic level, the OI will be zero, if it feeds on a variety of trophic levels, the value will be large (Christensen *et al.* 2005). The system omnivory index (SOI) is the average OI of all trophic groups. The SOI was 24% lower in the summer model indicating that species diets were more specialized in the summer when production was high. In a real-world scenario, species may switch to a more generalist diet when food availability declines abruptly (Gerking, 2014), as observed with the decline in primary production during the winter season in Algoa Bay. Species may be displaying trophic adaptability in their diets in response to the seasonal change in food availability.

4.2.5 Total Biomass and Transfer Efficiency

Fractional biomasses were higher in the summer model for all trophic levels. This is expected as primary production is higher during the summer season. As previously mentioned in section 4.2.2., the largest change in total biomass occurred at TL III with a 72% larger biomass in the summer compared to the winter. This implies the lower trophic level fishes benefit the most from the seasonal boom in primary production. Trophic level II (herbivores) showed a lower percent change in total biomass with summer biomass only 32% larger than winter. This small increase in summer biomass may be attributed to the large increase that occurred at TL III (first-order carnivores).

Transfer efficiencies in Algoa Bay for the summer and winter models were both estimated higher than the means reported for 48 aquatic ecosystems which averaged around 10% for each TL (Christensen and Pauly, 1992). The highest transfer efficiencies occurred at trophic levels II and III with the seasonal averages being 16.8% and 18.7% respectively. As transfer efficiency describes the efficiency in which energy is transferred from one trophic level to the next (Christensen *et al*. 2005), these higher than average TEs suggest that zooplankton and small pelagic fish are important in the energy flow of the Algoa Bay ecosystem.

Transfer efficiencies were highest in the summer season with the greatest percent change occurring at the larger trophic levels (V-VII), which were 17-31% higher than the winter model. In the real world, trophic groups may display trophic adaptability in their diets in response to the summer increase in food availability, allowing them to be more selective in their prey by targeting more energy efficient food sources (Gerking, 2014). This is supported by the lower system omnivory index in the summer model, which indicates a more selective diet, as mentioned in the previous section 4.2.4.

4.2.6 Other Consumption

Notably, the consumption of other fish (pelagic-feeding, benthic-feeding, and linefish) was 11% higher in the winter model compared to the summer model. In addition, consumption of the other higher trophic level groups relative to other trophic groups modeled, was higher in the winter model while the lower trophic level fishes was lower. The low productivity in the bay during winter results in an increase in competition for food compared to the summer months when productivity is high. Additionally, there was a much larger decrease in small pelagic and lower trophic level fishes in the winter compared to the higher trophic level predators. Therefore, the ecosystem is more tightly constrained by predators during the winter months, resulting in a larger relative consumption by high trophic level groups. In contrast to the higher trophic level predators, the small pelagic fishes (sardine, anchovy, redeye, and other) all consumed a greater relative proportion of production in the summer. This can be attributed to the larger proportion of diet that was comprised of prey from outside the bay in the winter model due to lower primary production and zooplankton biomass in the bay in winter.

4.3 "Marine Protected Area" Model Analyses

4.3.1 Changes in Ecotrophic Efficiencies

Ecotrophic efficiency (EE) is the fraction of production that is "used up" in the system in terms of predation and fishery exploitation, for example. The value ranges from 0 to 1, with 0 indicating no predation (or fishing) pressure, and 1 representing considerable predation (or fishing) pressure (Christensen *et al.* 2005). The most drastic change in EE values occurred with linefish in both seasons, dropping by close to 20% when a model MPA is introduced (linefish EE dropped by 0.199 and 0.224 in summer and winter respectively), reflecting the currently high fishing pressure on linefish species in Algoa Bay. Real-world evidence that linefish are currently overexploited supports this model result (DAFF, 2016, Mann, 2013). According to the calculated fishery yield, 30.8% (seasonal average) of total linefish production is consumed by the fishery per year. Eliminating predation by fisheries, the ecotrophic efficiency indicates that 0.740-0.744 of linefish production would be utilized by predators in the bay. Although overall predation pressure on linefish was 26.5% lower in the MPA models, predation on linefish by other predators in the bay increased by 13.2% in the absence of fishing. According to mixed trophic impact (MTI) analysis, linefish have the greatest negative impact on other linefish (through predation). Therefore, eliminating predation from the fishery, predation from other linefish will also increase, which is why EE values are still relatively high in the MPA model.

Larger EE values for meso- and macrozooplankton were expected as predation by their predators (i.e. sardine, anchovy, and redeye) would increase with the removal of fishing pressure. Additionally, anchovy and sardine recruit EE values were larger in the MPA models but were smaller for the spawner population. This is partly due to the parameterization of the model as fishery yield was only input for spawning populations when realistically there would be fishing pressure on both recruits and spawners. However, the larger EE values are also an effect of increased predation by the previously fished species. For example, MTI analysis shows model linefish to have a relatively large negative impact on sardine recruits (Figure 3.4). Also, the proportion of predation outside the bay was lower (as import proportions were altered to reflect this) for some groups as foraging distances would be expected to decrease with the removal of fisheries, increasing predation pressure on the lower TL groups, which would be reflected in higher EE values. This increase in competition between predators on lower TL fishes could have negative implications for penguins, since previous studies have shown that an increase in predatory fish populations was inversely correlated to seabird abundance, which even effected the selection of feeding localities (Safina and Burger, 1985).

4.3.2 Fishery Sensitivity Analyses Using Ecosim: Zero Fishery Catch

In addition to the static MPA scenarios, the seasonal models were used in time-dynamic mode to track changes in the various model groups in the absence of fishing. The greatest percent change in biomass after running Ecosim with fishery effort set to 0, occurred in linefish. Linefish biomass increased 18.9% and 19.4% in the summer and winter respectively (Figure 3.3). This large percent increase in biomass reflects that the current fishing pressure is heavy on linefish in Algoa Bay, and reiterates that linefish may benefit from the implementation of a no-take marine protected area. Static MPA model results compliment the Ecosim sensitivity analyses as linefish EE values were smaller in the MPA models for both seasons, with a larger decrease occurring in the winter model.

Setting fishery catches to zero did not only have a direct impact on biomass for fished species. For example, winter modeled sardine spawner biomass decreased in winter when fishing pressure was removed, and other small pelagic modeled biomass decreased in both seasons. The food-web therefore has a moderating effect as predator biomasses are also affected by the reduction in fishery catches. These results lend support to the value of an ecosystem model over a single-species model, as changes in fishery catches result in indirect food-web effects which also impact the target species.

African penguin modeled biomass saw no change despite the removal of fishing pressure on their most important food sources (sardine and anchovy). This may be attributed to the fact that current fishing pressure on these species in Algoa Bay is relatively low. The large increase in linefish biomass (discussed above) may be creating competition for food which negates the removal of competition with the fishery. However, African penguins have a large overlap in diet composition with other seabirds (which decreased in modeled biomass), therefore an increase in competition with linefish alone may not explain the lack of change in modeled biomass observed in African penguins. According to MTI analyses, anchovy and sardine spawners have a larger positive impact on African penguins than other seabirds, which may explain the differences in sensitivities to zero fishery catches between the two model groups.

When Ecosim was run with fishing effort set to zero, other pelagic fish showed the greatest decrease in biomass, declining by 6.4% in summer and in winter. MTI analyses show that linefish (which increased in biomass when fishery catch was set to 0) have a relatively large negative impact on other small pelagics, attributed to predation. Alternatively, in the MTI analyses, fisheries had a small positive impact on other small pelagics. Additionally, anchovy and sardine spawners also have a negative impact on other small pelagic fish through competition. However, competition probably is less responsible for the decline in other small pelagic biomass because the main proportion of other small pelagic diet is on mesozooplankton, which had a slight increase in biomass in the winter season. The static MPA model supports the Ecosim results as EE values of other small pelagic fish were higher in both the summer and winter MPA models.

Model cetaceans decreased by 6.7% in summer and 8.1% in winter. The only predators of cetaceans in the model are apex sharks and since their biomass did not change with the Ecosim analyses, increased predation is not a cause for cetacean decline. The greatest contributing trophic group to cetacean diet in the model are other small pelagics, which also declined as discussed above. Therefore, the loss of their most important prey item in the model may explain the decrease in model cetacean biomass. Looking at the MTI analysis (Figure 3.3), other small pelagic fish have a large positive impact on cetaceans but not on the other larger predator groups. Therefore, some of the other model predators of other small pelagics still increased (such as linefish) despite the decline in prey. In the real world, predators do not have a fixed diet and would consume what is available to them. Opportunistic foraging behaviour is modelled in Ecosim in that relative consumption of prey groups depends on initial Ecopath base diet composition and on the relative changes in abundances of these prey groups over time. In other words, “new” prey items cannot be added to a predator’s diet in Ecosim simulations; it is only their relative contributions to a predator’s diet that changes. The trophic niches of linefish and whales would need to be understood better in order to improve model inputs and, in turn, increase confidence in the model outputs.

Modeled sardine recruits also decreased by 6.6% in winter only. The sensitivity of sardine recruits to a winter simulation only may be due to the large decline in other small pelagics. MTI analysis shows seasonal differences in other small pelagic impacts on sardine recruits, with a large negative impact in the summer and a small positive impact in winter. The large decrease in the other small pelagic group therefore would positively impact sardine recruits in summer only, while the opposite is true for the winter simulation. As a consequence of the model setup, fisheries also have a positive impact on sardine recruits as fishery catch was input for spawners only. In reality, there would be fishing pressure on both recruits and spawners. Further modifications to the model to address this issue is required in the future.

It is important to note that Ecosim was used in this case as a fishery sensitivity analysis and does not take into account the spatial dynamics of a marine protected area. Realistically, mobile marine species do not stay within the bounds of a marine protected area and would therefore be susceptible to fishery when not in Algoa Bay. However, although fishery catches occur outside the bay, the model has been parameterized to account for the portion of time the fish spend in the bay and the catches made in the bay during the modeled seasons. Additionally, the proposed MPA (detailed in the introduction section 1.2.2.) does not cover the entire area of the bay. The application of EcoSpace, the spatial and time-dynamic module designed for investigating the impact and placement of marine protected areas (Christensen *et al*. 2005) is recommended.

4.3.3 Differences Between Static MPA Models and Ecosim

For most trophic groups, changes in static MPA model EE values and Ecosim fishery sensitivity analyses results complimented each other. For example, groups with smaller MPA EE values generally had increased biomass after setting fishery catches to zero in Ecosim. The most obvious discrepancies occurred around some of the larger predator groups (such as cetaceans, seals, penguins, and other seabirds). There was no change in EE values observed in penguin and seabird trophic groups but there was a large increase in summer biomass for the same groups under the no-fishing Ecosim simulation. Additionally, seals and cetaceans had larger EE values in the summer MPA models only, but had large declines in both summer and winter biomasses in Ecosim. These discrepancies can be explained however, as the modelled increases/declines in biomass in the temporally-dynamic Ecosim simulation are likely a result of competition for resources in combination with changes in predation and fishing pressure, whereas changing EE values are a consequence of changes in predation and fishing pressure only.

Another obvious difference between changes in EE values and Ecosim results were observed with sardine recruits. Ecosim showed a large decline in winter biomass only, with no change in summer biomass, however, the summer MPA model had a much larger EE value which would indicate increased predation pressure and therefore an expected decrease in biomass in Ecosim. Again, these differences are likely attributed to the Ecosim sensitivity analyses incorporating increased competition for prey, in addition to increased predation pressure.

4.3.4 Fishery Sensitivity Analyses: Increased Fishing Mortalities

When sardine and anchovy fishery mortalities are increased to west coast levels reported in Osman, 2010, the greatest percent decrease in predator biomass occurs with penguins (9.1% and 11.6% in summer and winter respectively) followed by other seabirds (6.4% and 8.2%). Sardine biomass decreased by 10.4% and 15.1% in the summer and winter respectively while anchovy only decreased by 1.4% in both seasons (Figure 3.7). This result highlights the importance of sardine in penguin diet despite it contributing less to the diet composition of African penguins in Algoa Bay compared to anchovy.

According to the ICUN, a species must decline by more than 50% over a span of three generations in order to warrant major concern (BirdLife International 2018). It is important to note that African penguins are currently listed as endangered with a decreasing population trend of greater than 50% in three generations (BirdLife International, 2018). As Algoa Bay currently holds more than 50% of the global population (Crawford *et al*. 2014), an added decline of 10% to the largest African penguin breeding colony could be very damaging. Therefore, increasing fishing pressure in Algoa Bay to that currently occurring in the west coast could have serious implications for the future of the species. Additionally, the current model set up only considers fishing inside the bay. In reality, if fishing pressure on the east coast increased to levels on the west coast, the areas outside Algoa Bay would also experience increased fishing pressure and therefore less food availability when feeding outside the bay, meaning the actual penguin biomass decrease could be much larger than 10%.

4.4 Summary

Ecosystem modeling is a good tool for evaluating change in marine ecosystems, in particular to investigate past and present impacts of fishing and environmental change, and can aid in policy and management decisions. The aim of this study was to construct mass-balanced trophic models of the Algoa Bay ecosystem with a focus on African penguins and small pelagic fish interactions in order to: compare seasonal differences between summer (the beginning of peak breeding season) and winter, as well as compare how implementing a marine protected area in the bay would impact trophic flows and structure of the Algoa Bay ecosystem. Ecosim time-dynamic simulations were used on the seasonal models as a fishery sensitivity analyses by setting fishery catches to zero as well as increasing sardine and anchovy fishery mortalities in line with that occurring on the west coast where fishing pressure is greater. This work was a preliminary attempt to create seasonal, base models for the Algoa Bay ecosystem, providing a good overview of the trophic structure and energy flow in the bay.

There were strong seasonal differences between the summer and winter models which can be attributed to the increase in summer primary production associated with the strong easterly winds and upwelling. This high summer primary production results in larger biomass of lower trophic level fishes such as anchovy and sardine which coincides with the onset of peak breeding season for African penguins. This is important as breeding success is largely dependent on food availability. Summer model output resembles that of other published bay models, however the winter model output was much smaller in terms of ecosystem size.

Static marine protected area models and Ecosim time-dynamic simulation on the seasonal models suggest that linefish would benefit the most from the removal of fishing pressure in the bay, since they are currently heavily targeted. Setting fishery catch to zero did not result in a significant increase in African penguin and small pelagic biomass as may have been expected, and some other large predator groups showed a decrease in modeled biomass. This may be due to an increase in the modeled biomass of other predator groups (such as linefish) resulting in an increase in competition for food. This suggests that the sensitivity of trophic groups to fishing pressure is not direct. When sardine and anchovy fishery mortalities were increased to west coast levels, African penguin and other seabird modeled biomass decreased in both seasons. While the decrease in African penguin modeled biomass over the simulated 30-year span may not be large enough to warrant major concern according to IUCN standards, it could have serious implications for the future of this already endangered species. The results of these analyses highlight the importance of the ecosystem approach to fishery management and policy decisions.

Further detailed modelling and research is recommended. Future research areas to improve parametrization of the models should focus on more detailed and updated surveys of some trophic group biomass estimates, specific to Algoa Bay. For example, current data was not available for some model groups, or the data covered a much larger area encompassing Algoa Bay, making biomass and diet estimates more uncertain. While further research is needed to improve the more uncertain model parameters, these models are a good base for future comparisons, monitoring and analyses, and provide a well-researched and parameterized model base from which spatialized modelling of the bay using Ecospace can be explored.

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Appendix

Table A.1. Trophic group input data sources for all Algoa Bay models.

Trophic Group	Input Parameter	Comments	Source
Phytoplankton	B	Estimated	Dali 2010
(small and large)	P/B	In prep model	Shannon, in prep
Benthic Producers	P/B	S. Benguela model	Shannon *et al*. 2003
	EE	S. Benguela model	Shannon *et al*. 2003
Microzooplankton	B	Estimated	SAEON Pelagic Surveys
	P/B	Estimated	Christensen *et al*. 2009, Hutchings *et al*. 1995
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Mesozooplankton	B	Estimated	SAEON Pelagic Surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Macrozooplankton	B	Estimated	SAEON Pelagic Surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Gelatinous	B	S. Benguela model	Shannon *et al*. 2003
Zooplankton	P/B	S. Benguela model	Shannon *et al*. 2003
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Anchovy Recruit	B	Estimated	DAFF biannual surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	Ecopath estimate	Based on spawner Q/B
	U	S. Benguela model	Shannon *et al*. 2003
Anchovy Spawner	B	Estimated	DAFF biannual surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	DAFF, 2016
Sardine Recruit	B	Estimated	DAFF biannual surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	Estimate	FishBase
	U	S. Benguela model	Shannon *et al*. 2003
Sardine Spawner	B	Estimated	DAFF biannual surveys
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	Ecopath estimate	Based on recruit Q/B
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	DAFF, 2016
Redeye	P/B	S. Benguela model	Shannon *et al*. 2003
Roundherring	Q/B	Estimated	FishBase
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	DAFF, 2016

Other Small Pelagic	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	DAFF, 2016
Linefish	B	Estimated	Smale and Badenhorst 1991
	P/B	S. Benguela model	Shannon *et al*. 2003
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	Chalmers, 2011
Cephalopods	P/B	S. Benguela model	Shannon *et al*. 2003
	P/Q	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	DAFF, 2016
Pelagic-feeding fish	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	Estimated	FishBase
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	Chalmers, 2011
Benthic-feeding fish	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	Estimated	FishBase
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	Chalmers, 2011
Benthic elasmobranchs	B	Estimated	Chalmers, 2011
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
	Y	Estimated	Chalmers, 2011
Pelagic elasmobranchs	B	S. Benguela model	Shannon *et al*. 2003
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Apex chondrichthyans	B	Estimated	Dicken *et al*. 2013, Smale, 1991, Smale *et al*. 2015
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Seals	B	Estimated	Chalmers, 2011
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Cetaceans	B	S. Benguela model	Shannon *et al*. 2003
	P/B	S. Benguela model	Shannon *et al*. 2003
	Q/B	S. Benguela model	Shannon *et al*. 2003
	U	S. Benguela model	Shannon *et al*. 2003
Penguins	B	Estimated	Crawford *et al*. 2014
	P/B	Estimated	Crawford *et al*. 1991

	Q/B	In prep model	Shannon, in prep
	U	In prep model	Shannon, in prep
Other seabirds	B	Estimated	Crawford et al. 1991, Crawford et al. 2006, Crawford et al. 2009, Whittington et al. 2006, Shearpoint et al. 1988, and Mclachlan 1980
	P/B	S. Benguela model	Shannon *et al.* 2003
	Q/B	S. Benguela model	Shannon *et al.* 2003
	U	S. Benguela model	Shannon *et al.* 2003
Meiofauna	P/B	S. Benguela model	Shannon *et al.* 2003
	Q/B	S. Benguela model	Shannon *et al.* 2003
	U	S. Benguela model	Shannon *et al.* 2003
Macrofauna	P/B	S. Benguela model	Shannon *et al.* 2003
	Q/B	S. Benguela model	Shannon *et al.* 2003
	U	S. Benguela model	Shannon *et al.* 2003

Table A.2. Diet composition input data and sources for each Algoa Bay model (S = Summer model, S_MPA = Summer MPA model, W = Winter model, W_MPA = Winter MPA model).

Trophic Group	Prey	S	S_MPA	W	W_MPA	Source
1. Phytoplankton (Sm)						
2. Phytoplankton (Lg)						
3. Benthic producers						
4. Microzooplankton	1.	0.400	0.400	0.400	0.400	(Shannon *et al.* 2003)
	4.	0.050	0.050	0.050	0.050	
	27.	0.550	0.550	0.550	0.550	
5. Mesozooplankton	1.	0.500	0.500	0.500	0.500	(Shannon *et al.* 2003)
	4.	0.500	0.500	0.500	0.500	
6. Macrozooplankton	2.	0.330	0.330	0.330	0.330	(Shannon *et al.* 2003)
	4.	0.330	0.330	0.330	0.330	
	5.	0.340	0.340	0.340	0.340	
7. Gelatinous zooplankton	5.	0.640	0.640	0.640	0.640	(Shannon *et al.* 2003)
	6.	0.120	0.120	0.120	0.120	
	7.	0.040	0.040	0.040	0.040	
	27.	0.200	0.200	0.200	0.200	
8. Anchovy recruit	1.	0.250	0.250	0.125	0.125	(Shannon, in prep)
	2.	0.250	0.250	0.125	0.125	
	4.	0.500	0.500	0.250	0.250	
	I.	0.000	0.000	0.500	0.500	
9. Anchovy spawner	2.	0.050	0.050	0.025	0.025	(Shannon, in prep)
	4.	0.040	0.040	0.020	0.020	
	5.	0.570	0.570	0.285	0.285	
	6.	0.340	0.340	0.170	0.170	
	I.	0.000	0.000	0.500	0.500	

10. Sardine recruit	1.	0.250	0.250	0.125	0.125	(Shannon, in prep)
	2.	0.250	0.250	0.125	0.125	
	4.	0.500	0.500	0.250	0.250	
	I.	0.000	0.000	0.500	0.500	
11. Sardine spawner	1.	0.320	0.320	0.160	0.160	(Shannon, in prep)
	4.	0.320	0.320	0.160	0.160	
	5.	0.290	0.290	0.145	0.145	
	6.	0.070	0.070	0.035	0.035	
	I.	0.000	0.000	0.500	0.500	
12. Redeye roundherring	5.	0.600	0.600	0.300	0.300	
	6.	0.400	0.400	0.200	0.200	
	I.	0.000	0.000	0.500	0.500	
13. Other small pelagics	5.	0.388	0.466	0.388	0.388	(Shannon, in prep)
	6.	0.077	0.092	0.077	0.077	
	7.	0.014	0.017	0.014	0.014	
	8.	0.010	0.013	0.010	0.010	
	10.	0.005	0.006	0.005	0.005	
	12.	0.005	0.006	0.005	0.005	
	I.	0.500	0.400	0.500	0.500	
14. Linefish	6.	0.105	0.126	0.105	0.126	(Shannon, in prep), (Griffiths, 2000)
	8.	0.026	0.032	0.026	0.032	
	9.	0.039	0.047	0.039	0.047	
	10.	0.065	0.078	0.065	0.078	
	12.	0.025	0.030	0.025	0.030	
	13.	0.161	0.193	0.161	0.193	
	14.	0.028	0.034	0.028	0.034	
	15.	0.050	0.060	0.050	0.060	
	I.	0.500	0.400	0.500	0.400	
15. Cephalopods	5.	0.020	0.020	0.020	0.020	(Shannon, in prep), (Chalmers, 2011)
	6.	0.270	0.270	0.270	0.270	
	8.	0.030	0.030	0.030	0.030	
	10.	0.001	0.001	0.001	0.001	
	12.	0.050	0.050	0.050	0.050	
	15.	0.020	0.020	0.020	0.020	
	17.	0.100	0.100	0.100	0.100	
	25.	0.030	0.030	0.030	0.030	
	26.	0.379	0.379	0.379	0.379	
	I.	0.100	0.100	0.100	0.100	
16. Pelagic feeding fish	5.	0.006	0.007	0.006	0.006	(Shannon, in prep)
	6.	0.390	0.468	0.390	0.390	
	8.	0.001	0.001	0.001	0.001	
	12.	0.067	0.080	0.067	0.067	
	15.	0.012	0.014	0.012	0.012	
	16.	0.018	0.022	0.018	0.018	
	17.	0.006	0.007	0.006	0.006	
	I.	0.500	0.400	0.500	0.500	

17. Benthic feeding fish	5.	0.005	0.007	0.005	0.005	(Shannon, in prep)
	6.	0.026	0.037	0.026	0.026	
	8.	0.002	0.002	0.002	0.002	
	9.	0.001	0.001	0.001	0.001	
	12.	0.013	0.019	0.013	0.013	
	15.	0.011	0.015	0.011	0.011	
	16.	0.011	0.015	0.011	0.011	
	17.	0.017	0.024	0.017	0.017	
	18.	0.003	0.004	0.003	0.003	
	26.	0.412	0.576	0.412	0.412	
	I.	0.500	0.300	0.500	0.500	
18. Benthic elasmobranchs	15.	0.025	0.025	0.025	0.025	(Shannon *et al.* 2003)
	16.	0.004	0.004	0.004	0.004	
	17.	0.124	0.124	0.124	0.124	
	18.	0.050	0.050	0.050	0.050	
	26.	0.598	0.598	0.598	0.598	
	I.	0.200	0.200	0.200	0.200	
19. Pelagic elasmobranchs	9.	0.015	0.015	0.015	0.015	(Shannon *et al.* 2003)
	11.	0.008	0.008	0.008	0.008	
	12.	0.037	0.037	0.037	0.037	
	13.	0.091	0.091	0.091	0.091	
	14.	0.004	0.004	0.004	0.004	
	15.	0.144	0.144	0.144	0.144	
	16.	0.038	0.038	0.038	0.038	
	17.	0.144	0.144	0.144	0.144	
	18.	0.004	0.004	0.004	0.004	
	19.	0.015	0.015	0.015	0.015	
	I.	0.500	0.500	0.500	0.500	
20. Apex chondrichthyans	13.	0.016	0.022	0.016	0.016	(Smale, 1991), (Cliff *et al.* 1989)
	16.	0.003	0.004	0.003	0.003	
	17.	0.003	0.004	0.003	0.003	
	18.	0.221	0.315	0.221	0.221	
	19.	0.055	0.078	0.055	0.055	
	21.	0.078	0.111	0.078	0.078	
	22.	0.104	0.148	0.104	0.104	
	I.	0.521	0.318	0.521	0.521	
21. Seals	9.	0.088	0.088	0.088	0.088	(David, 1987), (Skern-Mauritzen *et al.* 2009)
	11.	0.048	0.048	0.048	0.048	
	13.	0.069	0.069	0.069	0.069	
	14.	0.007	0.007	0.007	0.007	
	15.	0.100	0.100	0.100	0.100	
	17.	0.078	0.078	0.078	0.078	
	26.	0.008	0.008	0.008	0.008	
	I.	0.601	0.601	0.601	0.601	

22. Cetaceans	5.	0.022	0.022	0.022	0.022	(Shannon, in prep), (Melly, 2011)
	6.	0.029	0.029	0.029	0.029	
	8.	0.066	0.066	0.066	0.066	
	9.	0.166	0.166	0.166	0.166	
	11.	0.051	0.051	0.051	0.051	
	12.	0.022	0.022	0.022	0.022	
	13.	0.212	0.212	0.212	0.212	
	15.	0.100	0.100	0.100	0.100	
	17.	0.034	0.034	0.034	0.034	
	I.	0.298	0.298	0.298	0.298	
23. Penguins	8.	0.125	0.178	0.089	0.107	(Crawford *et al*. 2011), (Pichegru *et al*. 2012), (Randall and Randall 1986), (Shannon, In prep)
	9.	0.266	0.380	0.190	0.228	
	10.	0.003	0.002	0.001	0.002	
	11.	0.155	0.223	0.112	0.134	
	12.	0.033	0.047	0.024	0.028	
	13.	0.022	0.032	0.016	0.019	
	14.	0.001	0.002	<0.001	0.001	
	15.	0.088	0.126	0.063	0.075	
	16.	0.001	0.001	<0.001	<0.001	
	17.	0.006	0.008	0.004	0.005	
	26.	<0.001	<0.001	<0.001	<0.001	
	I.	0.300	0.000	0.499	0.400	
24. Other seabirds	8.	0.098	0.098	0.049	0.049	(Shannon, in prep), (Pichegru *et al*. 2007)
	9.	0.132	0.132	0.066	0.066	
	10.	0.008	0.008	0.004	0.004	
	11.	0.066	0.066	0.033	0.033	
	12.	0.043	0.043	0.021	0.021	
	13.	0.047	0.047	0.024	0.024	
	16.	0.006	0.006	0.003	0.003	
	I.	0.600	0.600	0.800	0.800	
25. Meiobenthos	3.	0.050	0.050	0.050	0.050	(Shannon *et al*. 2003)
	27.	0.950	0.950	0.950	0.950	
26. Macrobenthos	3.	0.050	0.050	0.050	0.050	(Shannon *et al*. 2003)
	25.	0.080	0.080	0.080	0.080	
	26.	0.070	0.070	0.070	0.070	
	27.	0.800	0.800	0.800	0.800	
27. Detritus						