Changes in food web structure and energy flow in kelp forest ecosystems on the south-west coast of South Africa following the invasion of *Jasus lalandii*.

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Declaration

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

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________22/04/2019________________

Date

Abstract

In the early 1990s the west coast rock lobster *Jasus lalandii* underwent an eastward shift in distribution into an area known as East of Cape Hangklip where they had previously been rare. This shift has also been termed an invasion and resulted in a complete change in the benthic community structure, changing from one state dominated by herbivores and encrusting algae, to another state dominated by lobsters, sessile species, kelp and understory foliose algae. Using the trophic modelling software Ecopath with Ecosim, baseline models of the pre- and Post-invasion systems were created to better understand trophic pathways between the two different states and assess how fishing pressure may have driven the shift in ecosystem state. Using the baseline models, different fishing management strategies were tested to see whether the post lobster-invaded ecosystem could be shifted back or close to the pre-invasion state. Baseline models that were developed to describe the shift in ecosystem state reflected an increase in the presence of kelp, sessile species and lobsters, and the decline of encrusting algae and herbivores. Furthermore, the baseline models reflect the Post-invasion system as more productive and less diverse than the pre-invasion system. Simulations using an Ecosim model showed that, with a reduction in fishing pressure on reef fish and abalone and a simulated increase in fishing pressure on rock lobster, reef fish and adult abalone recovered to pre-invasion levels, whereas juvenile abalone and urchin biomass did not recover, likely due to the difficulty in capturing non-trophic interactions in the trophic models. Further functional groups such as sessile species, turf and foliose algae, also did not return to the pre-invasion state. This study concluded that a reduction in fishing pressure on abalone and reef fish, and the removal of rock lobster through increased fishing pressure, would allow the post-invasion ecosystem to partially recover to the pre-invasion state, but not completely, suggesting a hysteresis effect. Further exploration of management strategies through model simulations is needed, including those that can account for non-trophic links.

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1 Introduction

Marine ecosystems are under severe pressure from overfishing and human-induced climate change (Halpern et al. 2008). Most vulnerable are those on the coastlines ,which are easily accessible and thus exploitable (Mead et al. 2013). Coastal ecosystems are both ecologically and socio-economically important, providing trillions of dollars’ worth of ecosystem goods (e.g. food and raw materials) and services (e.g. disturbance regulation and nutrient cycling) per year (Steneck et al. 2002; Harley et al. 2006; Hoegh-Guldberg & Bruno 2010; Smale et al. 2013; Vásquez et al. 2014; Bennett et al. 2016). As a result, it is imperative that we understand how marine ecosystems are affected by natural and anthropogenic stressors to try and mitigate negative impacts. In particular, the effects of exploitative fishing and climate change have been well documented (Tegner & Dayton 2000; Jackson et al. 2001; Scheffer et al. 2005; Daskalov et al. 2007; Möllmann et al. 2008) and there is strong evidence for their impacts on marine ecosystems globally (Hoegh-Guldberg & Bruno 2010; Poloczanska et al. 2013).

1.1 Global kelp forests and trophic interactions

Kelp forests can be found throughout temperate and sub-polar regions, dominating rocky reefs in intertidal and shallow subtidal upwelling zones (Steneck et al. 2002). These coastal systems are some of the most diverse and productive on Earth (Mann 1973; Brady-Campbell et al. 1984; Reed et al. 2008), providing vital ecosystem services worth billions of dollars annually (Beaumont et al. 2008; Blamey & Bolton 2018). Kelps are considered “ecosystem engineers” and play a key role in coastal systems, providing a complex habitat that hosts a wide variety of species, some of ,which are commercially important (Jones et al. 1994; Steneck et al. 2002; Smale et al. 2013). For these reasons, kelp forests across the globe have received a wealth of attention. Research has focused on trophic interactions within these systems (Estes et al. 2004; Graham 2004; Steneck et al. 2004; Halpern et al. 2006; Reisewitz et al. 2006; Branch & McClanahan 2008; Estes 2008; Fariña et al. 2008; Graham et al. 2008; Lorentsen et al. 2010; Wilmers et al. 2012; Steneck & Johnson 2014; Hamilton & Caselle 2015; Dunn et al. 2017; Vilalta-Navas et al. 2018; Pessarrodona et al. 2019), spanning the ecological effects of kelp (Ojeda & Santelices 1984; Reed & Foster 1984; Santelices & Ojeda

1984; Kennelly 1989; Kennelly & Underwood 1993; Edwards 1998; Melville & Connell 2001; Connell 2003; Irving et al. 2004; Irving et al. 2005; Toohey et al. 2007; Steneck & Johnson 2014; O'Brien et al. 2018; Layton et al. 2019), the effects of intensive grazing by sea urchins (Lawrence 1975; Breen & Mann 1976; Lang & Mann 1976; Hagen 1983; Dayton 1985a; Harrold & Reed 1985; Andrew 1993; Hagen 1995; Lauzon-Guay & Scheibling 2007; Norderhaug & Christie 2009; Vanderklift et al. 2009; Feehan et al. 2012; Filbee-Dexter & Scheibling 2014; Perreault et al. 2014; Hamilton & Caselle 2015; Morris & Blamey 2018; Christie et al. 2019), top-down control by predators (Estes & Duggins 1995; Estes et al. 1998; Tegner & Dayton 2000; Shears & Babcock 2002, 2003; Byrnes et al. 2006; Foster et al. 2006; Halpern et al. 2006; Heck & Valentine 2007; Bell et al. 2015; Dunn & Hovel 2019) as well as the ecosystem effects of overfishing in these systems (Steneck 1997; Steneck 1998; Babcock et al. 1999; Tegner & Dayton 2000; Ling et al. 2009; Braje et al. 2017; Pérez-Matus et al. 2017; Alongi 2018; Pita et al. 2018).

Environmental change, whether naturally or anthropogenically driven, can have an effect on species distribution, abundance patterns and community structure (Barry et al. 1995; Holbrook et al. 1997; McGowan et al. 1998; Perry et al. 2005; Ling et al. 2009; Lloyd et al. 2012; Pecl et al. 2017). A change in species abundance, particularly of predators, can strongly influence an ecosystem’s structure, function and resilience (Frank et al. 2005; Beschta & Ripple 2009; Ling et al. 2009; Estes et al. 2011), affecting the prey species as well has having indirect knock-on effects throughout the rest of the ecosystem (Steneck 1998; Jackson et al. 2001; Scheffer et al. 2005). This kind of top-down control is common in coastal kelp forest ecosystems (Estes et al. 1998; Steneck et al. 2002; Halpern et al. 2006; Watson & Estes 2011), whereas open-ocean marine environments are more typically controlled by resource availability (i.e. bottom-up control; Frederkisen et al., 2006; Richardson and Schoeman, 2004; Ware and Thompson, 2005). Research has shown that top-down control is most commonly documented in exploited systems (Frank et al., 2005; Worm and Myers, 2003), and this suggests that top-down control may be an indicator for biological instability and exploitation (Strong, 1992). Only in the past two decades have there been more cases of top-down control found in open-ocean systems, as many top predators have become overfished (Worm & Myers 2003; Frank et al. 2005; Scheffer et al. 2005; Heithaus et al. 2008; Baum & Worm 2009; Essington 2010; Pershing et al. 2015). Evidence suggests that human activity is modifying both bottom-up and top-down controlled systems (Scheffer et al. 2005; Ling et al. 2009), resulting in ecosystem shifts that may not be easily reversible (Frank et al. 2005).

Unfortunately, it is often the case that the over-exploitation of top predators has started long before the implementation of fisheries management (Jackson et al. 2001) or before scientists started collecting baseline data (Estes et al. 2011)and, as a result, historical data alone are impossible to rely on to assess whether ecosystem shifts occurred or not, let alone whether they occurred as a result of fishing out top predators (Blamey et al. 2014).

Sea urchins play a central role in the structure and functioning of kelp forest ecosystems (Estes & Palmisano 1974; Vadas 1977; Harrold & Reed 1985). Given their unique grazing abilities, they are notorious for transforming kelp forests into ‘urchin barrens’ dominated by encrusting corallines (Lawrence 1975; Breen & Mann 1976; Mann 1977; Tegner & Dayton 1991; Watanabe & Harrold 1991; Andrew 1993; Estes & Duggins 1995; Dayton et al. 1998; Steneck 1998; Steneck et al. 2002; Ling & Johnson 2009). Most cases of kelp deforestation originate from the Northern Hemisphere (Breen & Mann 1976; Tegner & Dayton 1991; Steneck 1997; Estes et al. 1998; Babcock et al. 1999; Ling & Johnson 2009), whereas in the Southern Hemisphere deforestation is less common (Steneck et al. 2002) as most urchin species here feed on drift kelp rather than attached plants (Castilla & Moreno 1982; Santelices & Ojeda 1984; Dayton 1985b; Day & Branch 2002; Vanderklift & Kendrick 2005). Predators including sea otters (Estes & Palmisano 1974; Watson & Estes 2011), fish (Shears & Babcock 2002; Steneck et al. 2002; Steneck et al. 2004) and clawed (Breen & Mann 1976) or rock (spiny) lobsters (Cowen 1983; Tegner & Levin 1983; Mayfield & Branch 2000; Shears & Babcock 2002; Ling et al. 2009) exert top-down control over the intense grazing pressure by urchins on kelp forest ecosystems.

1.2 Kelp forest ecosystems of South Africa

Along the coastline of southern Africa, kelp forests dominate the nearshore subtidal zone in the southern Benguela (Blamey & Bolton 2018), spanning from northern Namibia to just west of Cape Agulhas, South Africa (Bolton & Anderson 1997). From Cape Agulhas on the south coast, to Cape Columbine on the west coast, kelp forests are dominated by *Ecklonia maxima* in the shallows (to approximately 8m depth), whereas *Laminaria pallida* forms a sub-canopy growing beneath *E. maxima*, eventually replacing it in deeper waters (15-30m) (Blamey & Bolton 2018). North of Cape Columbine, and into Namibia, *L. pallida* progressively replaces *E. maxima*, dominating shallow wave-exposed areas (Rothman 2015).

Kelp forests along the west and south-west coasts are characterised by different benthic communities, with the distinction between the two coasts occurring at Cape Point (Field et al. 1980; Anderson et al. 1997; Leliaert et al. 2000). The West Coast rock lobster *Jasus lalandii*, as well as mussel species, *Choromytilus meridionalis, Semimytilus algosus* and *Aulacomya atra*, are characteristic of west coast kelp forest communities (Field et al. 1980; Branch & Griffiths 1988; Van Erkom Schurink 1990; Skein et al. 2018), where the substratum in the shallows is often dominated by dense red algae (Anderson et al. 1997; Zeeman et al. 2013). In contrast, kelp forests on the south-west coast (east of Cape Point) are dominated by herbivores, namely the urchin *Parechinus angulosus* as well as the abalone *Haliotis midae*, two turban snail species *Turbo samarticus* and *T. cidaris* and the winkles *Oxystele* spp (Field et al. 1980). In this region, the substratum is largely colonised by encrusting corallines, rather than red foliose algae (Anderson et al. 1997; Morris & Blamey 2018).

The West Coast rock lobster, *Jasus lalandii* is a significant and voracious predator in kelp forest ecosystems along the coast of South Africa (Pollock 1979; Mayfield et al. 2000a; Mayfield et al. 2000b; Mayfield et al. 2001; Van Zyl et al. 2003; Haley et al. 2011). Although the preferred prey of *J. lalandii* are mussels and urchins (Mayfield et al. 2000a; Mayfield et al. 2000b; Mayfield et al. 2001; Haley et al. 2011), in the absence of these species they do feed on a wide variety of unusual prey items such as sponge and barnacle recruits and thus are able to sustain themselves even in the absence of preferred prey (Barkai & Branch 1988). Historically, the center of abundance for the rock lobster has been on the west coast of South Africa. However, lobster catches on the west coast have dwindled due to heavy fishing pressure and a decline in growth rates from the late 1980s (Pollock et al. 1997). Although there is no single explanation for this slowed growth in rock lobsters, it is thought that a combination of a reduction in primary productivity, scarcity of preferred prey and an increase in frequency of low oxygen events have contributed to the lobster decline (Pollock & Shannon 1987; Shannon et al. 1992; Pollock et al. 1997; Mayfield et al. 2000b). The fate of the rock lobster population is now dire as recreational catch limits have progressively declined over the past two decades, illegal fishing has increased and the current exploitable biomass is estimated at < 2% of historic abundance (Johnston & Butterworth 2016).

1.3 The invasion of **Jasus lalandii** *into kelp forest ecosystems East of Cape Hangklip*

While *J. lalandii* has continued to decline on the west coast, in the early 1990s the rock lobster underwent an eastward shift in distribution, becoming more abundant in an area known as East of Cape Hangklip (EOCH), where they previously had been rare (Blamey et al. 2010; Blamey & Branch 2012). Similar geographic shifts have been reported for other coastal species including the kelp *E. maxima* (Bolton et al. 2012), sardine *Sardinops sagax* (Van der Lingen et al. 2001; Fairweather et al. 2006) and anchovy *Engraulis encrasicolus* (Van der Lingen et al. 2002). What drove the shifts in these cold-water species is largely unknown, although it is thought to be due to changing environmental conditions (Blamey et al. 2015). Cooling of inshore waters has been observed along the south coast (Roy et al. 2007), but long term data for this area are insufficient to make any definitive conclusions (Cockcroft et al. 2008). Until recently, the mechanism behind the lobster invasion was also uncertain, although a study by Blamey et al. (2013) determined that the invasion was likely due to adult migration rather than larval settlement. Furthermore, it was determined that these lobsters originated from the False Bay population (Matthee et al. 2008).

The EOCH region once hosted a lucrative wild-caught abalone (*Haliotis midae*) fishery (Hauck & Sweijd 1999; Hauck 2009) but in the mid-1990s illegal fishing escalated to such an extent that the recreational fishery was closed in 2003, followed by temporary closure of the commercial fishery in 2008 (Blamey et al. 2010; Blamey & Branch 2012). Concurrent to the rise in abalone poaching, *J. lalandii* invaded the EOCH region, having an indirect negative effect on the already perilously weakened abalone population by reducing the urchin population through predation (Blamey et al. 2010; Blamey & Branch 2012). Urchins and juvenile abalone have a unique relationship whereby urchins provide shelter and nutrients to juvenile abalone (Day & Branch 2000a, b). Given this relationship, the decline in urchin numbers (due to lobster predation) greatly influenced abalone recruitment and the eventual collapse of the population. As a result, the benthic community structure underwent a regime shift, changing from one dominated by herbivores (*Parechinus angulosus*, *Haliotis midae*, *Turbo* spp., *Oxystele* spp.) and encrusting coralline algae to an ecosystem dominated by rock lobster, sessile organisms and macroalgae (Blamey et al. 2010; Blamey & Branch 2012) (Figure 1).

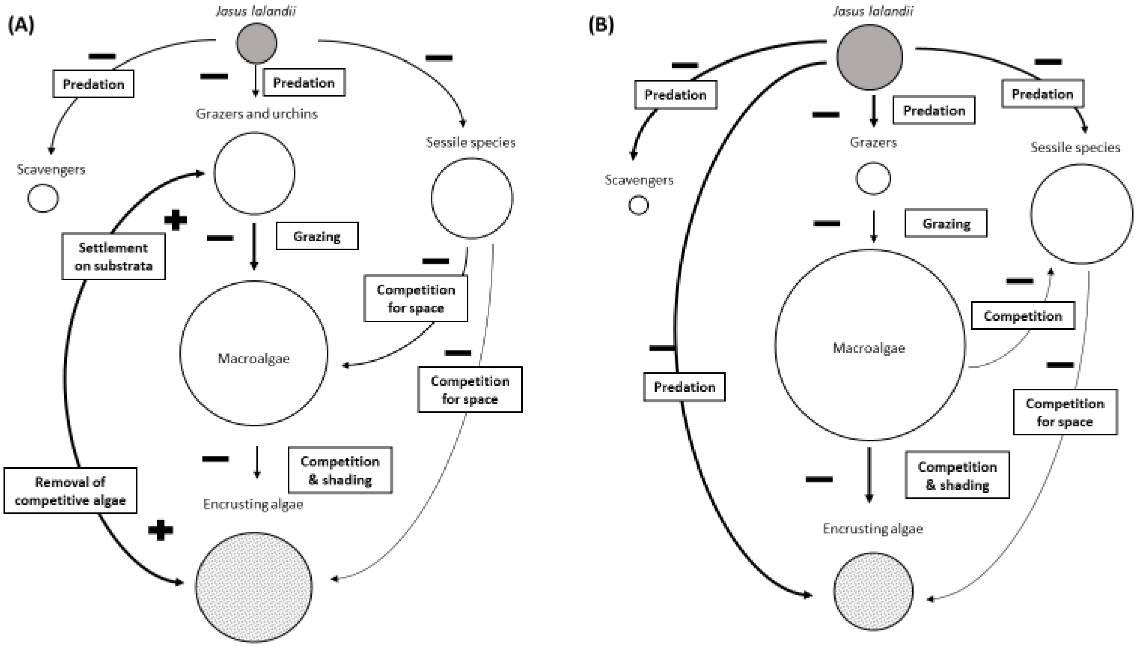

Figure 1: *A priori* conceptual flow model summarizing the interactions of the East of Cape Hangklip ecosystem in the (A) lobster pre-invasion and (B) lobster post-invasion states. The bold arrows imply strong effects. Positive (+) and negative (-) effects relate to the processes that appear in boxes. Size of the circles represents the relative biomass of different functional groups (g/m^2). Adapted from Blamey and Branch (2012).

Predators of *J. lalandii* include reef fish (Nepgen 1982; Buxton & Clarke 1989), fur seals *Arctocephalus pusillus* (David 1987), otters *Aonyx capensis* (Somers 2000a; Somers 2000b), the bank cormorant *Phalacrocorax neglectus* (Hockey et al. 2005) and possibly small sharks (Blamey et al. 2014). At pristine levels, reef fish and fur seals were likely the most important predators of *J. lalandii* (Blamey et al. 2014). However, in the 18th, 19th and early part of the 20th centuries, uncontrolled fishing of fur seals caused a significant population depletion (Shaughnessy 1984) and reef fish have shown signs of over exploitation long before 1980, with noticeable declines in commercial line fish catch per unit effort (CPUE) in the EOCH region (Attwood & Farquhar 1999; Griffiths 2000). Using an ecosystem model, Blamey et al. (2014) argue that predation of rock lobster by reef fish at pristine densities (in addition to other predators e.g. fur seals) would likely have prevented a sustained lobster invasion and a regime shift would not have occurred.

1.4 Using trophic models to explore ecosystem shifts

Modelling is a useful tool for understanding the complex interactions between species in ecological systems, and provides information used to test hypotheses and help develop appropriate management strategies. The mass-balanced modelling approach, Ecopath with Ecosim, is a whole-ecosystem modelling approach that was first applied by Polovina (1984) to a coral reef ecosystem at French Frigate Shoals in the Northwestern Hawaiian Islands. Further developments were made by Pauly, Christensen and Walters over the next three decades (Coll et al. 2015). The Ecopath model provides a snapshot of an ecosystem using information about biomass, production, consumption, migration and feeding relationships of species to create a baseline model (Christensen & Walters 2004). Most models created using Ecopath have been designed to analyse fisheries and have been based on shelf and open ocean species, rather than temperate reefs/rocky shores, for example, although exceptions include the work by Ortiz et al. (2013), Sadchatheeswaran (2017) and Vilalta-Navas et al. (2018).

Often, there is no one best-suited model for any particular system and multiple models of the same system can help explore model uncertainty and can be more effective in the management of a system (Fulton et al. 2015; Melbourne-Thomas et al. 2017). Previous work by Blamey et al. (2013) used a model of intermediate complexity for ecosystem assessment (MICE; previously known as a minimally realistic model) to explore the rock lobster driven regime shift dynamics in kelp forest ecosystems EOCH. Unlike whole ecosystem models such as Ecopath with Ecosim (EwE), these models only represent the species believed to have the most important interactions with the target species (Blamey et al. 2013). In this case, lobster, urchin and abalone were the sole components of the model developed by Blamey et al. (2013) ,which was later expanded upon by Blamey et al. (2014) to include reef fish. However, MICE do not examine trophic pathways between all species nor how these pathways change over time or in response to disturbance. As such, there is a need to further explore these changes in kelp forests EOCH to better understand how fishing pressure may impact shifts between two ecosystem states and compare predictions with other models.

My study expands on the work by Blamey et al. (2013, 2014) by using EwE to develop two food-web models for a kelp forest ecosystem EOCH on the south-west coast of South Africa. The aim of this study is to create pre-and post-lobster invasion baseline models using historic and recent benthic community data, in an attempt to better understand what drives this kelp forest ecosystem between two states, and to explore how fishing pressure might affect these shifts. This information is then used to test different or opposing management strategies that may bring the ecosystem back, or close to, a pre-invasion state.

2 Methods

2.1 Study area

An Ecopath model was developed for the Betty’s Bay kelp forest ecosystem before and after a rock lobster invasion. Betty’s Bay (34°22′08″S, 18°54′20″E, Figure 2) is located on the south-west coast of South Africa, in a transition zone between the cooler-temperate west coast and the warm-temperate south coast (Bolton 1986). Part of Betty’s Bay is protected by a Marine Protected Area (MPA) that spans 3.2km of coastline and covers an area of 20.14km^2 (Turpie et al. 2009). A wide diversity of habitats is represented within the area of the MPA, including unique benthic assemblages associated with kelp (Roberson et al. 2015). Surface reaching kelp forests cover approximately 1,034,004m^2 at Betty’s Bay (Tarr 1993) and occur on rocky reefs, usually between 0-10m depth, comprising mainly *Ecklonia maxima*, with *Laminaria pallida* occurring as a sub-canopy and replacing *E. maxima* at greater depths. During the early 1990s, kelp forests in this region experienced an ‘invasion’ of the rock lobster *Jasus lalandii* and were transformed from a grazer-dominated system to one dominated by lobsters, understory algae, and sessile invertebrates (Blamey et al. 2010). The shift to a post-invasion kelp ecosystem has persisted in this region ever since (Laura Blamey, University of Seychelles, pers. comm).

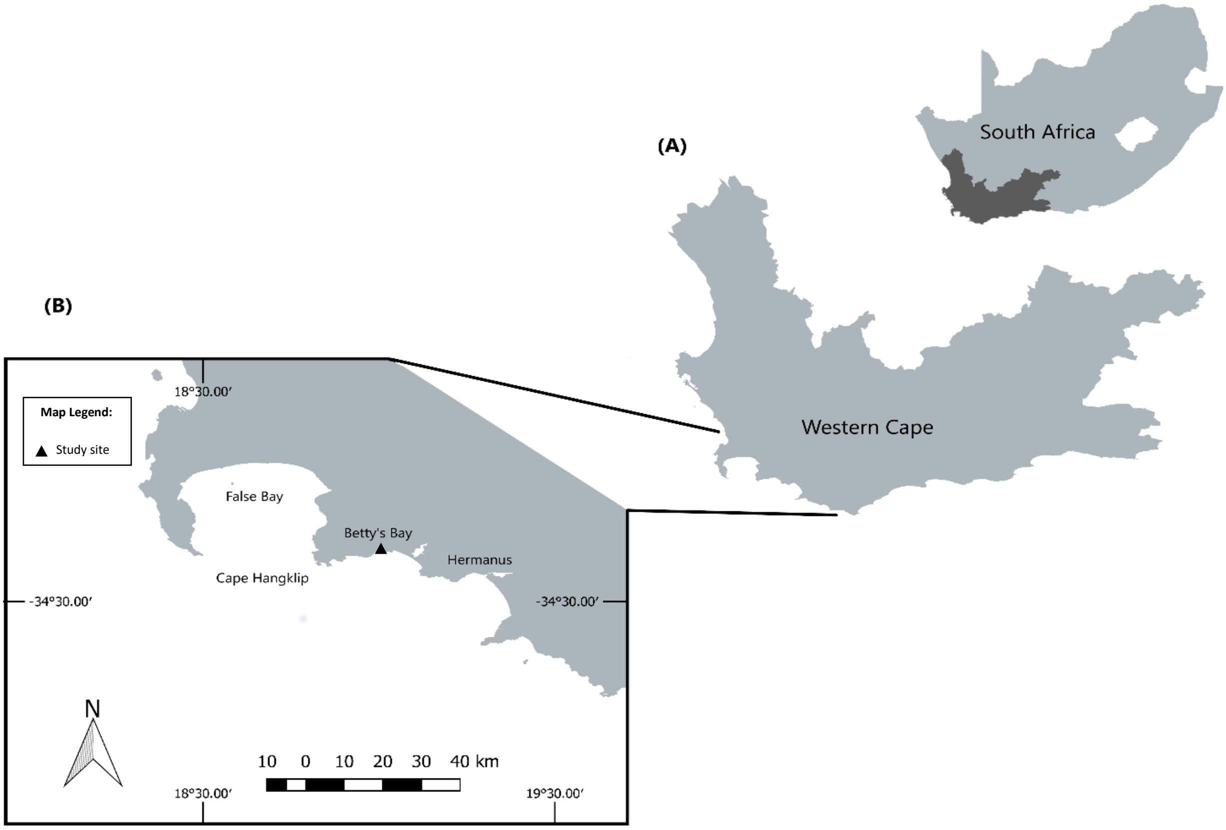

Figure 2: Map of (A) the Western Cape and (B) the south-west coast including Betty's Bay and Hermanus in the East of Cape Hangklip region.

2.2 *Ecopath model*

Baseline models for both pre-and post-invasion ecosystems in Betty's Bay were built using Ecopath with Ecosim (EwE) version 6.5 (Christensen et al. 2005). Ecopath is a whole ecosystem modelling approach, where individual species or taxonomic/functional groups, resources and their interactions are represented in a mass-balanced food web (Christensen & Walters 2004). The Ecopath model is balanced by two master equations (Christensen et al. 2005): one to describe the production term (Equation1), and one describing the energy balance for each group (Equation 2) (Christensen & Walters 2004).

1) Production (P) of each group (i) is described as the sum of predation mortality ($M2_i$) on prey with biomass (B_i), total fishery catch (Y_i), net migration (E_i), biomass accumulation (BA_i) and other mortality (MO_i).

$$P_i = B_i.M2_i + Y_i + E_i + BA_i + MO_i \qquad \text{Equation 1}$$

The production equation can use information about predator consumption rates and diets concerning a given prey to estimate the predation mortality for a group (Christensen & Walters 2004). Alternatively, if the predation mortality for a given group is known, the equation can be used to estimate the consumption rates for one or more predators as prey mortality is predator consumption (Christensen & Walters 2004).

To parameterize the model, Ecopath sets up a system of linear equations – one for each species/taxonomic group; each equation includes four parameters, one of ,which Ecopath will estimate for each group (Christensen & Walters 2004). These parameters are: biomass (B), production/biomass (P/B), consumption/biomass (Q/B) and ecotrophic efficiency (EE) – the proportion of production used in the system (Christensen et al. 2005). At least three parameters must be entered for all groups, in addition to catch rate for fished groups, net migration rate, biomass accumulation rate, assimilation rate and diet compositions (Christensen & Walters 2004).

Once all the missing parameters have been estimated to ensure mass balance between groups, energy balance is ensured by using Equation 2 below (Christensen & Walters 2004).

2) The energy balance of a group is described as the consumption (Q) of each group (i) being equal to the sum of its production (P_i), respiration (R_i) and unassimilated food (U_i), where respiration (R_i) is the amount of assimilated food not recycled through consumption by other groups (Christensen et al. 2005).

$$Q_i = P_i + R_i + U_i \qquad \text{Equation 2}$$

The energy balance calculation can be used to estimate respiration as the difference between consumption and production (Christensen & Walters 2004). This term is useful in the application of fisheries analysis where respiration is rarely given whereas the other terms are usually available (Christensen & Walters 2004).

2.3 Functional groups

2.3.1 Pre-invasion model

The pre-invasion baseline model is made up of 35 groups (Table 1) based on dominant species recorded by Field et al. (1980) and other important species/groups known to occur in this system. In addition to important species-based groups, several functional/taxonomic groups were included in the model, based on information for specific species as detailed in the footnote to Table 1.

The abalone, *Haliotis midae* was split into two stanzas: adult and juvenile based on shell size. Juveniles are classified as having a shell length between 3-35mm; anything larger is classified as an adult and anything smaller is regarded as a recruit (Day 1998). The stanzas for this species were required due to the important interaction between juvenile abalone and the urchin *Parechinus angulosus* (Day & Branch 2000a) , as well as legal and illegal fishing of adult abalone.

2.3.2 Post-invasion model

The post-invasion baseline model is made up of 25 groups (Table 1), based on dominant species recorded by Blamey et al. (2010) and other important species/groups known to occur in this system (Table 1).

Table 1: Functional groups and important species used in the pre-and post-invasion ecosystem models of the Betty's Bay kelp forest. Groups/species that are the same across both ecosystems are in bold, and those omitted from either the pre-or post-invasion systems were not recorded in the surveys carried out by Field et al. (1980) and Blamey et al. (2010) respectively. Common names are provided in brackets and used in the text.

Pre-invasion	**Post-invasion**
***Chrysoblephus laticeps* (Red Roman)**	***Chrysoblephus laticeps* (Red Roman)**
***Chrysoblephus gibbiceps* (Red Stumpnose)**	***Chrysoblephus gibbiceps* (Red Stumpnose)**
***Cymatoceps nasutus* (Poenskop)**	***Cymatoceps nasutus* (Poenskop)**
***Chrysoblephus cristiceps* (Dageraad)**	***Chrysoblephus cristiceps* (Dageraad)**
Cryptic fish[a]	**Cryptic fish**[a]
Herbivorous fish[b]	**Herbivorous fish**[b]
Omnivorous fish[c]	**Omnivorous fish**[c]
Carnivorous fish[d]	**Carnivorous fish**[d]
Jasus lalandii (rock lobster)	***Jasus lalandii (rock lobster)***
Argobuccinium argus (Pustular triton)	–
Thias spp. *(Dog whelk)*	–
Decapods[e]	**Decapods**[e]
Marthasterias africana (Spiny starfish)	–
***Oxystele* spp.**[f]	***Oxystele* spp.**[f]
Juvenile abalone	–
Adult abalone	–
Parechinus angulosus (Urchin)	–
Turbo cidaris	***Turbo cidaris***
Turbo sarmaticus	***Turbo sarmaticus***
Limpets[g]	–
–	Bryozoans[j]
Other sessile spp.[h]	–
Other echinoderms[i]	–
Anemones[k]	**Anemones**[k]
Polychaetes[l]	–
Sponges	**Sponges**
Tunicates[m]	**Tunicates**[m]
Sea cucumbers	–
Kelp[n]	**Kelp**[n]
Foliose algae[o]	**Foliose algae**[o]
Turf algae[p]	**Turf algae**[p]
Encrusting algae[q]	**Encrusting algae**[q]
Microalgae	**Microalgae**
Zooplankton	**Zooplankton**
Phytoplankton	**Phytoplankton**
Detritus	**Detritus**

a) *Clinus* spp., (b) *Sarpa salpa*, (c) *Spondyliosoma emarginatum*, *Pachymetopon blochii*, *Pachymetopon grande*, *Diplodus sargus capensis* (d) *Pachymetopon aeneum*, (e) *Plagusia chubrus*, *Paguristes gamianus*, other decapods, (f) *Oxystele sinensis*, *Oxystele tigrina*, *Oxystele variegata*, (g) *Cymbula compressa*, *Cymbula miniate*, *Scutellastra longicosta*, *Scutellastra barbara*, *Scutellastra tabularis*, (h) *Aulacomya ater*, *Comanthus wahlbergi*, *Tropiometra carinata*, *Austromegabalanus cylindricus*, *Balanus amphitrite*, *Balanus venustus*, *Notomegabalanus algicola*, (i) *Henricia ornata*, *Ophuiroidea*, (j) *Bugula dentata*, *Bugula neritina*, *Margaretta triplex,* (k) *Pseudactinia flagellifera*, *Bunodosoma capensis*, (l) fan worm, tube worm, (m) *Pyura stolonifera*, compound ascidians, other tunicates, (n) *Ecklonia maxima*, *Laminaria pallida*, (o) *Delisea flaccida*, *Gigartina insignis*, *Pachymenia cornea*, *Botryocarpa prolifera*, *Anthophycus longifolius*, *Epymenia capensis*, *Phyllymenia belangeri*, *Axillariella constricta*, *Bartoniella crenata*, *Gelidium capensis*, *Sargassum longifolium*, *Plocamium corallorhiza*, (p) *Caulerpa filiformis*, *Caulerpa holmesiana*, *Codium lucasii capense*, *Amphiroa ephedraea*, *Arthrocardia corymbose*, *Hypnea ecklonii*, *Jania verrucose*, *Plocamium beckerii*, (q) *Heydrichia woelkerlingii*, *Leptophytum foveatum*, *Hildenbrandia rubra*, other encrusting algae.

2.4 Parametrization of the baseline model

As explained in section 1.2 above, an Ecopath model requires estimates of three out of four basic parameters: biomass (B), production biomass ratio (P/B), consumption biomass ratio (Q/B) and ecotrophic efficiency (EE; the proportion of production used in the system).

For all benthic species/groups, biomass estimates (g/m^2) were derived from field work done by Field et al. (1980) in 1978/1979 (pre-invasion) and Blamey et al. (2010) in 2005/2006 (post-invasion), with the exception of all fish, microalgae, zooplankton and phytoplankton in both models.

Predatory reef fish found in kelp forests along the south-west coast include Red Roman (*Chrysoblephus laticeps*), Red Stumpnose (*Chrysoblephus gibbiceps*), Dageraad (*Chrysoblephus cristiceps*) and Poenskop (*Cymatoceps nasutus*) among others, and the decision to include them in both models was largely based on the study by Blamey et al. (2014). Red Roman and Red Stumpnose are known to feed on rock lobsters, although they are not likely a large component of their diet (Nepgen 1982). Dageraad and Poenskop are likely to feed on lobsters opportunistically.

In the absence of biomass data, commercial line fish catch data (Henning Winker pers. comm., the Department of Agriculture, Forestry and Fisheries (DAFF)) were used as indices of abudance for for Red Roman and Red Stumpnose for the EOCH area, spanning the period from 1985-2014. Pre-invasion biomass was calculated using catch data by dividing the catch for the region (in grams) by the area of kelp forest/reef habitat (zone D in m^2 taken from Blamey et al. (2010)) for these species from 1985-1995 and post-invasion biomass was calculated from 1996-2014. Biomasses of Dageraad and Poenskop were estimated by the model due to a lack of information available.

Small reef fish such as cryptic (*Clinus* spp.), herbivorous (*Sarpa salpa*), omnivorous (*Spondyliosoma emarginatum, Pachymetaopon blochii, Pachymetopon grande, Diplodus sargus capensis)* and carnivorous fish (*Pachymetopon aeneum*) were also included to complete the models. Biomass estimates for these fish were made from commercial catch data by DAFF between Gordon's Bay and Hermanus by dividing the catch in grams by the area (zone D) in m^2; data were only extracted for the Bettys Bay and Cape Hangklip regions.

Production/biomass (P/B) and consumption/biomass (Q/B) values were sourced from the literature or using data from areas comparable to Betty's Bay, as well as from the nearby region (Appendix Table 3, Table 4). Parameters for functional model groups that included multiple species (e.g. other sessile species and other echinoderms in the pre-invasion model, and turf algae in both models) were calculated from key species comprising these functional groups. Ecotrophic efficiency (EE) was estimated by the model for most groups, with the exception of Poenskop, Dageraad, small crustaceans and microalgae in both models, and phytoplankton and zooplankton for the post-invasion model. Ecotrophic efficiency values were entered manually for these species, enabling the model to estimate a sensible biomass. Biomass for phytoplankton and zooplankton were only estimated in the post-invasion model because values for a post-invasion system were unavailable, and the biomass would have changed between the pre- and post-invasion states. Similarly, biomass values were unavailable for Poenskop, Dageraad and small crustaceans so they were estimated. Finally, diet composition for each group was sourced using a combination of published studies and grey literature from adjacent or similar systems, as well as FishBase, SeaLife Base and Branch et al. (2010) (Appendix Table 5, Table 6, Table 7).

2.5 Catch data

Catch data for Red Roman and Red Stumpnose were obtained from DAFF for the EOCH region between 1985-2014. Catches for the pre-invasion (1985-1995) and post-invasion (1996-2014) periods were used in the pre- and post-invasion models (Table 2).

Catch data for Poenskop and Dageraad were unavailable for the EOCH region and thus had to be estimated. This was done using post-invasion (2003-2014) data that were available for the southern Benguela region for all four fish species. In addition, CPUE data for large sparids (a proxy for Poenskop and Dageraad) were available from 1985-2014 (Henning Winker. DAFF. pers. comm.). As a result, it was possible to use the DAFF data from the EOCH for Red Roman and Red Stumpnose, and the CPUE data for Poenskop and Dageraad to calculate the percentage change in catch (Red Roman and Red Stumpnose) and CPUE (Poenskop and Dageraad) between the pre- and post-invasion periods. This percentage change could then be applied to the post-invasion catch data for all four species for the southern Benguela to calculate the pre-invasion catch.

The catches (for the southern Benguela region) of Red Roman and Red Stumpnose were an order of magnitude greater than those of Poenskop and Dageraad in the pre-invasion system. As a result, Poenskop and Dageraad catches in the pre-invasion system were set at half those of Red Roman and Red Stumpnose (Table 2). Post-invasion catches for Poenskop and Dageraad were calculated using the percentage difference between pre- and post-invasion catch calculated using the large sparid CPUE data.

Catch data for abalone and rock lobster were also obtained from DAFF. From these data an average catch for each species for the pre-invasion period (1990-1995) was obtained in the pre-invasion model, whereas only the average catch for lobsters in the post-invasion period (2000-2014) was used in the post-invasion model given abalone legal catches had mostly ceased in this region. Abalone catch data comprised of commercial catch data and illegal estimated catches for both the pre-invasion period. A commercial fishery for rock lobster did not exist in the pre-invasion period, as a result only recreational data exists for that time, although recreation and commercial catch data is available for rock lobster in the post-invasion period.

Table 2: Relative landings/catch for all four reef fish species in the pre- and post-invasion models including sources.

	Relative Landings/Catch	**Source**
Pre-invasion Model		
Red Roman	1.00	DAFF EOCH data
Red Stumpnose	1.00	DAFF EOCH data
Poenskop	0.50	Estimated relative to Roman and Stumpnose data, based on catch ratio between these species from the DAFF southern Benguela data
Dageraad	0.50	Estimated relative to Roman and Stumpnose data, based on catch ratio between these species from the DAFF southern Benguela data
Post-invasion Model		
Red Roman	0.33	DAFF EOCH data
Red Stumpnose	0.33	DAFF EOCH data
Poenskop	0.25	Estimated as half the pre-invasion catch, based on a 50% change observed in the large sparids (proxy) CPUE data
Dageraad	0.25	Estimated as half the pre-invasion catch, based on a 50% change observed in the large sparids (proxy) CPUE data

2.6 System statistics

There are several statistics that describe an ecosystem. Some of, which can be used to assess the ecosystem state. This study presents: total system throughput, total primary production, sum of all consumption, the system omnivory index and the Shannon Diversity index.

Total system throughput is the sum of all flows in an ecosystem and can be used to identify the state of ecosystem maturity (Odum 1969; Christensen et al. 2005).

Total system throughput = total consumption + total respiration +total flows to detritus.
Equation 3

Total primary production is the summed primary production from all producers (Christensen et al. 2005). The sum of all consumption as also expressed in the system statistics and represents consumption by all groups in the ecosystem (Christensen et al. 2005). Production and consumption are often linked, i.e. if there is more production there is likely to be more consumption as a result.

The system omnivory index is a measure of how the feeding interactions between groups is distributed across trophic levels (Christensen et al. 2005). If the ecosystem is made up of more groups that have a diverse diet and feed across trophic levels, the omnivory index will be greater compared to system where groups diets are restricted.

The Shannon-Weiner index (or Shannon Diversity index) is the most commonly used diversity measure (Clarke et al. 2014). In Ecopath, this index represents the diversity of the whole ecosystem informed by species richness.

2.7 Mixed trophic impact

Mixed trophic impact plants are used to measure the direct and indirect interactions between groups in an ecosystem. Using these plots, it is possible to assess the affect that change in the biomass of one group will have on the biomass of other groups in an ecosystem (Christensen et al. 2005).

2.8 Ecosim

For the purposes of Ecosim, the single fishing fleet used in the Ecopath baseline models was split into a reef fish fleet (Red Roman, Red Stumpnose, Poenskop and Dageraad), a rock lobster fleet and an abalone fleet. Fishing pressures on fished groups were manipulated in the post-invasion model to determine whether it was possible to return close to a pre-invasion state. In the benthic community data collected by Blamey et al. (2010) no abalone were found in the post-invasion period. However, for the purpose of the Ecosim model simulations aimed at forcing changes in abalone, a small biomass of abalone (328.5 t/km^2 – roughly a third of the original pre-invasion biomass) was added into the post-invasion Ecosim model as there are catch data (DAFF) suggesting that abalone were still being caught in the EOCH area commercially and illegally up until 2006, and likely still illegally to the present day. Finally, to model the change in urchin biomass, a small urchin biomass was included in the post-invasion Ecosim model based on anecdotal evidence of urchins occurring under boulders during surveys in 2015/2016 (Laura Blamey, University of Seychelles, pers. obs.). The biomass was estimated as 10% of the pre-invasion biomass.

Fishing pressure on reef fish and abalone was reduced over a 20-year period (the time frame corresponding to the pre- versus post-invasion ecosystem state change, and ,which allowed model groups to stabilize after manipulation in simulations) in an attempt to determine whether the ecosystem would recover, returning close to the pre-invasion state. At the same time, model fishing pressure was increased for rock lobster to simulate a removal or reduction of lobster in the ecosystem. A model reduction in fishing pressure on abalone was not sufficient to spark an increase in biomass. In addition, modeling the interaction between abalone and urchin (which may lead to an increase in abalone biomass) using a forcing function or mediation was not possible as this relationship is non-trophic. Instead, a forcing function was applied to the abalone’s food source (foliose and turf algae) (Figure 3)

as there was a significant difference in the abundance of these algae between the pre- and post-invasion systems. The model forcing function increased the availability of these algae for all species, thus indirectly increasing abalone biomass in Ecosim simulations.

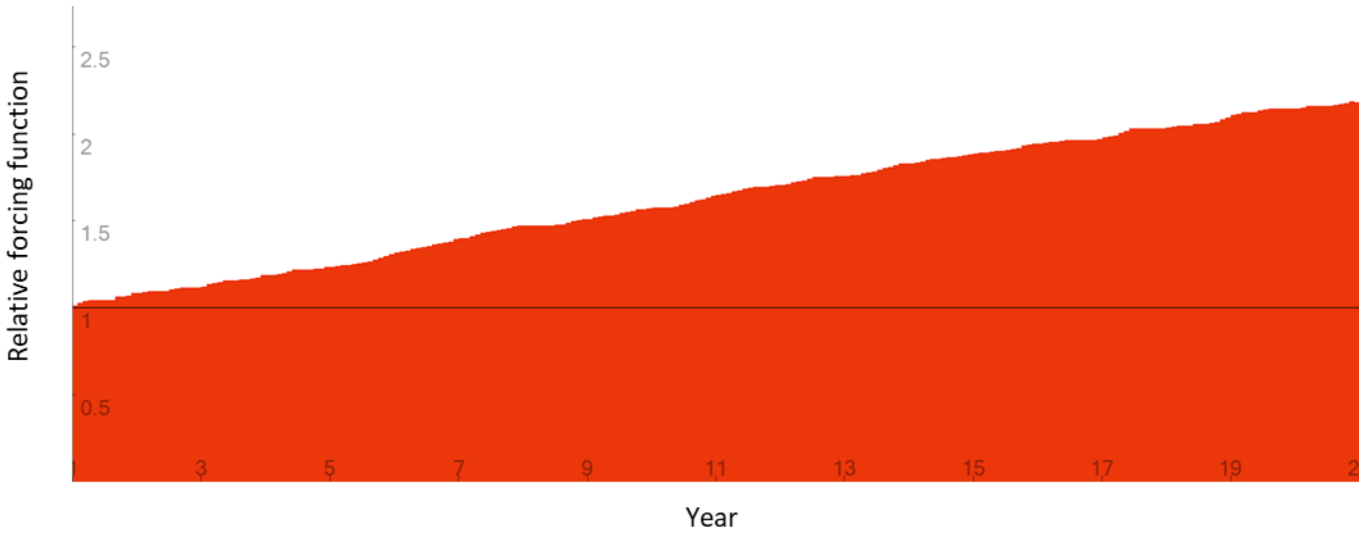

Figure 3: Forcing function applied to increase the biomass (t/km^2/year) of turf and foliose algae to indirectly lead to an increase in abalone biomass in the Betty's Bay kelp forest ecosystem.

Changes in fishing pressure were estimated from the difference in fished species biomass between the pre- and post-invasion systems (Appendix Table 10). Fishing pressure was adjusted accordingly in order to make the difference in biomass between fished species in the Ecosim model similar to those in the baseline Ecopath models. Thereafter, the difference in biomass between the other non-fished species was examined to see how they indirectly responded to the drivers of fishing pressure and whether or not they showed signs of returning to the pre-invasion state (Appendix Table 10).

3 Results

3.1 Ecopath

3.1.1 Baseline models

3.1.1.1 Balancing the baseline models

Initially, there was some difficulty in balancing the pre-invasion model. In order to get the model to balance, biomass of Dageraad and Poenskop were estimated by the model using an ecotrophic efficiency (EE) of 0.80 ,which assumes that a high proportion of the production of these two fish species is either removed via fishing or consumed by other predators (in this case the former applies). Microalgae biomass was also estimated by setting the EE at 0.90. Catch data for the rock lobster had to be lowered to balance the model. Initial rock lobster catch inputs were likely too high because the data were taken from 1990-1995, which includes high recreational catches as early as 1993, indicating that this is probably a transition period in the lobster invasion. Given that this period is supposed to be pre-invasion, such high catches like those recorded in 1993 overestimate catch in the post-invasion period. As a result, rock lobster catch was lowered to represent a pre-invasion state.

The post-invasion model balanced more easily and was achieved by setting the following EE: 0.80 for Dageraad and Poenskop (consistent with that adopted in the pre-invasion model) , 0.90 for microalgae and 0.99 for zooplankton and phytoplankton.

3.1.1.2 Pre-invasion baseline model

The balanced pre-invasion baseline model had a pedigree index of 0.64 and trophic levels ranging from 1.00 to 3.36 (Figure 4A). The pedigree index is a measure of uncertainty associated with the model input (Christensen et al. 2005). The index values for input data scale from 0 for data that is not rooted in local data up to 1 for data that are fully rooted in local data, and as a rule is better compared to data from elsewhere (Christensen et al. 2005). Primary producers and detritus were allocated to the lowest trophic level (TL 1.00), whereas the TL of benthic grazers, herbivorous fish and zooplankton ranged from 2.00 to 2.20. Filter and suspension feeders had TLs ranging from 2.00 to 2.91 and predators TL ranged from 3.00 to 3.36, with scavengers at a TL of 3.10 (Figure 4A). Top predators included carnivorous fish, Red Roman, Poenskop and Dageraad. Overall, trophic arrangement had a flat and linear topology, with most groups occupying the second trophic level (Figure 4A). Predator biomass was small, but evenly distributed and greater than that in the post-invasion model (Figure 4A, B). Strong interactions occurred between species mostly from the 1st and 2nd trophic levels, reflected by the energy flow between groups (see the colour and width of the line).

3.1.1.3 Post-invasion baseline model

The balanced post-invasion baseline model had a pedigree index of 0.71, reflecting the slightly more complete set of data available for the later period, and trophic levels ranged from 1.00 to 3.85 (Figure 4B). Primary producers and detritus were allocated to TL 1.00, whereas the TL of grazers, herbivorous fish and zooplankton ranged from 2.00 to 2.05. Filter and suspension feeders TL ranged from 2.00 to 2.88 and scavengers were at TL 2.31 (Figure 4B). Trophic level of predators ranged from 2.92 to 3.85. Top predators included Red Roman, Poenskop, Dageraad and carnivorous fish, all of which were low in biomass and instead the meso-predator *Jasus lalandii* was more abundant (Figure 4B). The post-invasion trophic arrangement was dominated by the lowest trophic levels (primary producers) and filter-feeding organisms along the second TL such as sponges, ascidians and bryozoans. Strong interactions occurred between species across all trophic levels.

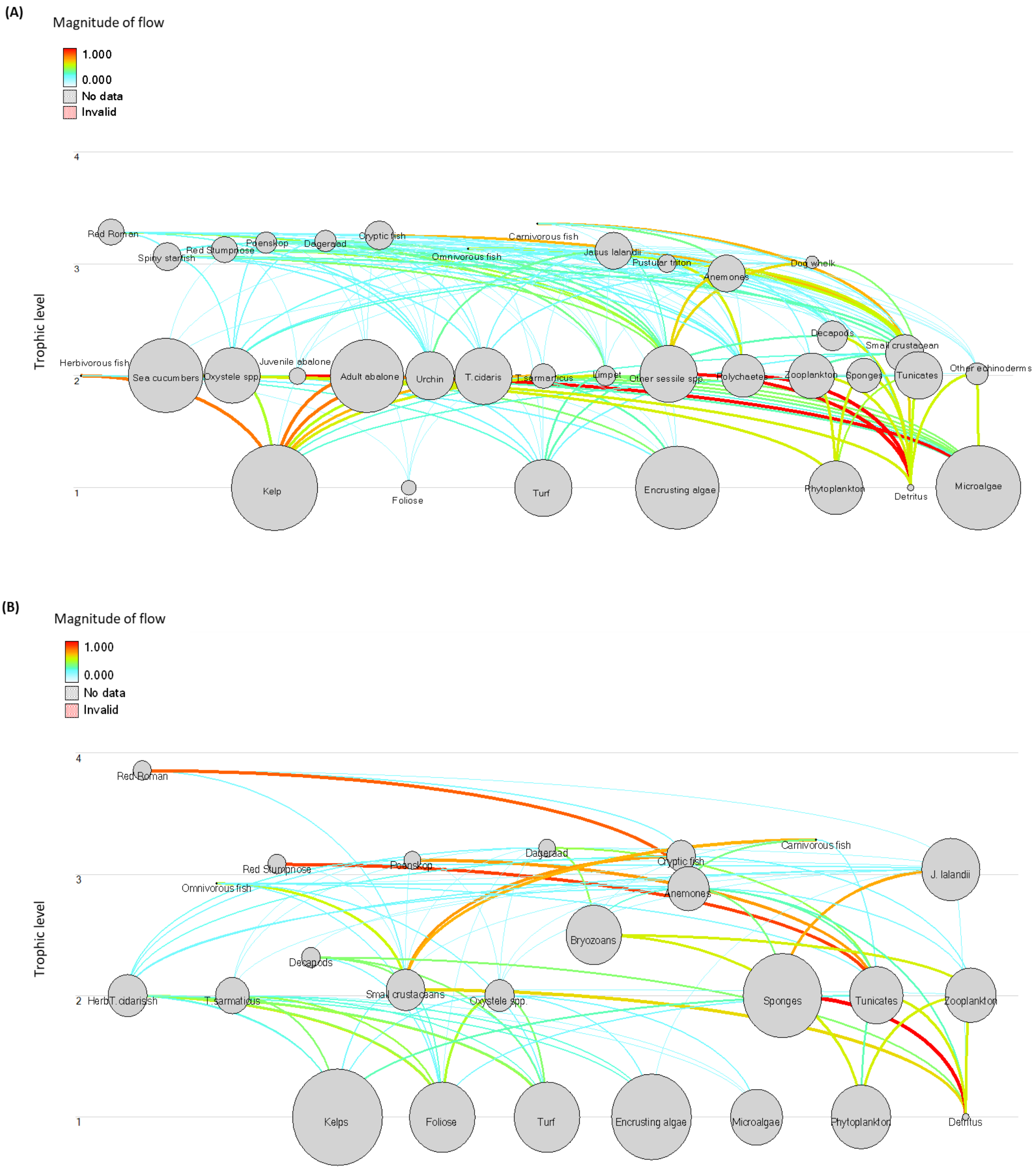

Figure 4: Trophic webs from (A) pre-invasion and (B) post-invasion ecosystem models showing trophic levels and relative biomass (indicated by size of circles) of taxonomic groups, and the strength of interaction/energy flow (width/colour of line in t/km^2) between groups in the Betty's Bay kelp forest ecosystem.

3.1.2 The ecological role of groups in the model

3.1.2.1 Pre-invasion

Results from the Mixed Trophic Impact plot (Figure 4) suggested that groups with the greatest relative total impact on all other groups were *J. lalandii* , Red Roman, Red Stumpnose, adult abalone, kelp, other sessile species , small crustaceans and microalgae . Red Roman had a negative impact on spiny starfish, other echinoderms, limpets, anemones, sponge, and to a lesser extent rock lobster, decapods, carnivorous fish and encrusting algae. Conversely, they had a positive impact on sea cucumbers, other sessile species and a number of other gastropods. Red Stumpnose had a negative impact on tunicates, polychaetes, other sessile species, decapods, juvenile abalone, *J. lalandii*, Red Roman and themselves. On the other hand, Red Stumpnose had a positive impact on *T. sarmarticus*, sponge, other echinoderms, spiny starfish and dog whelks. Despite the reef fish; Red Romana and Red Stumpnose having strong impacts on various species, Poenskop and Dageraad had weak impacts in both the pre-and post-invasion models. The rock lobster *J. lalandii* had a strong negative effect on dog whelks, pustular tritons, *T. sarmaticus*, juvenile abalone, urchins and itself, and weaker negative effects on starfish and other grazers such as limpets and smaller snails (*Oxystele* spp.) It had a positive impact on tunicates and polychaetas. Adult abalone negatively impacted themselves, as well as kelp, foliose and turf algae, gastropods such as *T. cidaris* and *O. sinenesis*, spiny starfish and all predatory reef fish, including herbivorous fish. Adult abalone had a positive impact on the fishing fleet, and to a lesser extent on other echinoderms and anemones. Other grazers such as the *Turbo* spp. also negatively impacted kelp, foliose and turf algae, albeit to a weaker extent than abalone. Urchins showed weak negative impacts on other competitor grazers, and weak positive impacts on their predators - *J. lalandii* and various reef fish. Other sessile species negatively impacted sponges, other echinoderms, tunicates and themselves, and positively impacted dog whelks and to a lesser extent anemones and predatory reef fish. Small crustaceans negatively impacted zooplankton and their own group, and positively impacted phytoplankton, detritus, sea cucumbers, decapods, cryptic fish, omnivorous fish and carnivorous fish.

Algae such as kelp and microalgae had a weak to medium negative impact on turf, foliose and encrusting algae, as well as on themselves. Conversely, they had a positive impact on juvenile abalone, other echinoderms, herbivorous fish, adult abalone, urchins and *T. sarmaticus*.

3.1.2.2 Post-invasion

Results from the Mixed Trophic Impact plot (Figure 6) suggested that groups with the greatest relative total impact on all other groups were *J. lalandii*, tunicates, Red Roman, anemones, small crustaceans, bryozoans, *T. cidaris,* and sponges. Red Roman had a negative impact on anemones and itself, with weaker negative impacts on zooplankton, kelp and carnivorous fish. Conversely, Red Roman had a positive impact on tunicates, bryozoans and other reef fish. Despite Red Roman having strong impacts on various species in the post-invasion model, the remaining reef fish; Red Roman, Poenskop and Dageraad all had weak impacts. The rock lobster, *J. lalandii* had a negative impact on its own group, decapods, sponges, reef fish and a number of gastropods. The herbivorous snail, *T. cidaris,* had a negative impact on most of the algae including foliose algae, turf algae, encrusting algae and microalgae. Small crustaceans had a positive impact on cryptic fish, omnivorous fish and to a greater extent, carnivorous fish. Sessile species such as tunicates had a positive impact on predatory fish and a negative impact on kelps. Anemones also had a positive impact on predatory fish, but this was less compared to tunicates. Furthermore, anemones had a negative impact on bryozoans, tunicates and their own group. Bryozoans had a positive impact on phytoplankton and detritus, and a negative impact on zooplankton. Finally, sponges negatively impacted detritus and their own group.

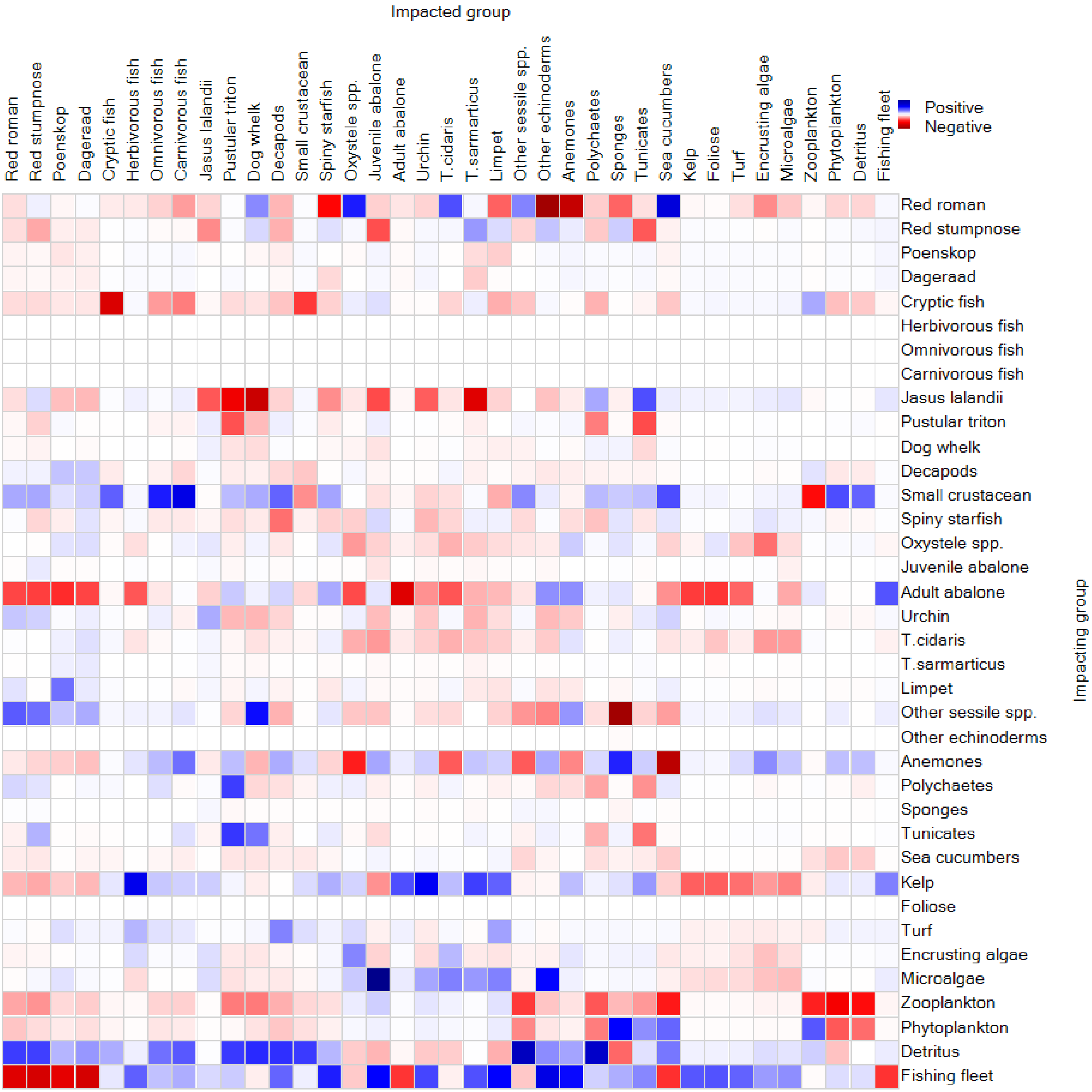

Figure 5: Mixed Trophic Impact diagram for all groups in the pre-invasion model of the Betty's Bay kelp forest, including the fishing fleet. Impacting group is shown on the right, while impacted group is shown on the top. Impact is either positive (blue) or negative (red) and strength of impact is indicated by tone of shading.

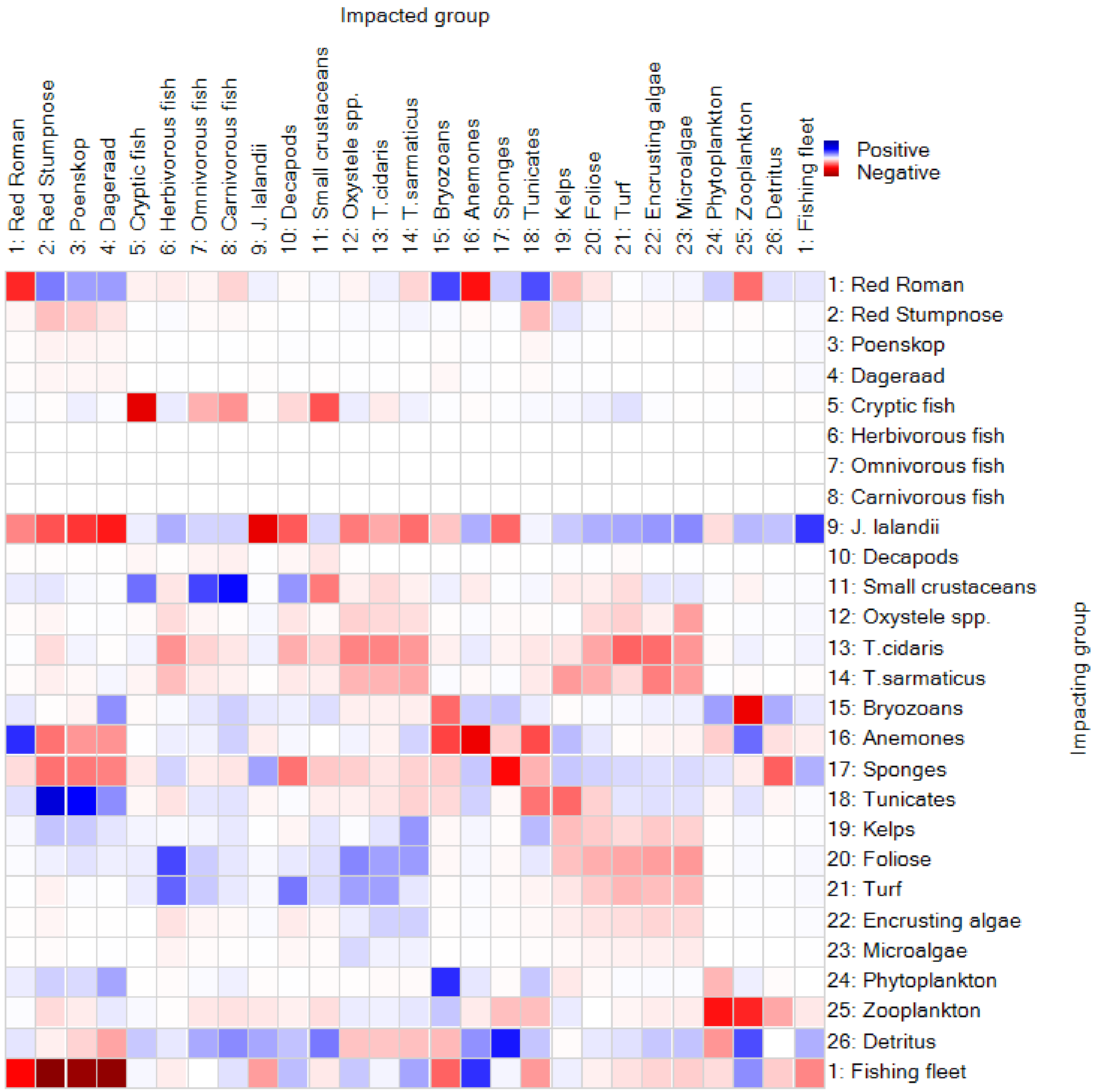

Figure 6: Mixed Trophic Impact diagram for all groups in the post-invasion model of the Betty’s Bay kelp forest, including the fishing fleet. Impacting group is shown on the right, while impacted group is shown on the top. Impact is either positive (blue) or negative (red) and strength of impact is indicated by tone of shading.

3.1.3 Structural and functional traits

Consumption, production, system throughput and the Omnivory Index were greater in the post-invasion system (Figure 7 A-D), whereas the Shannon Diversity Index was greater in the pre-invasion system (Figure 7 E).

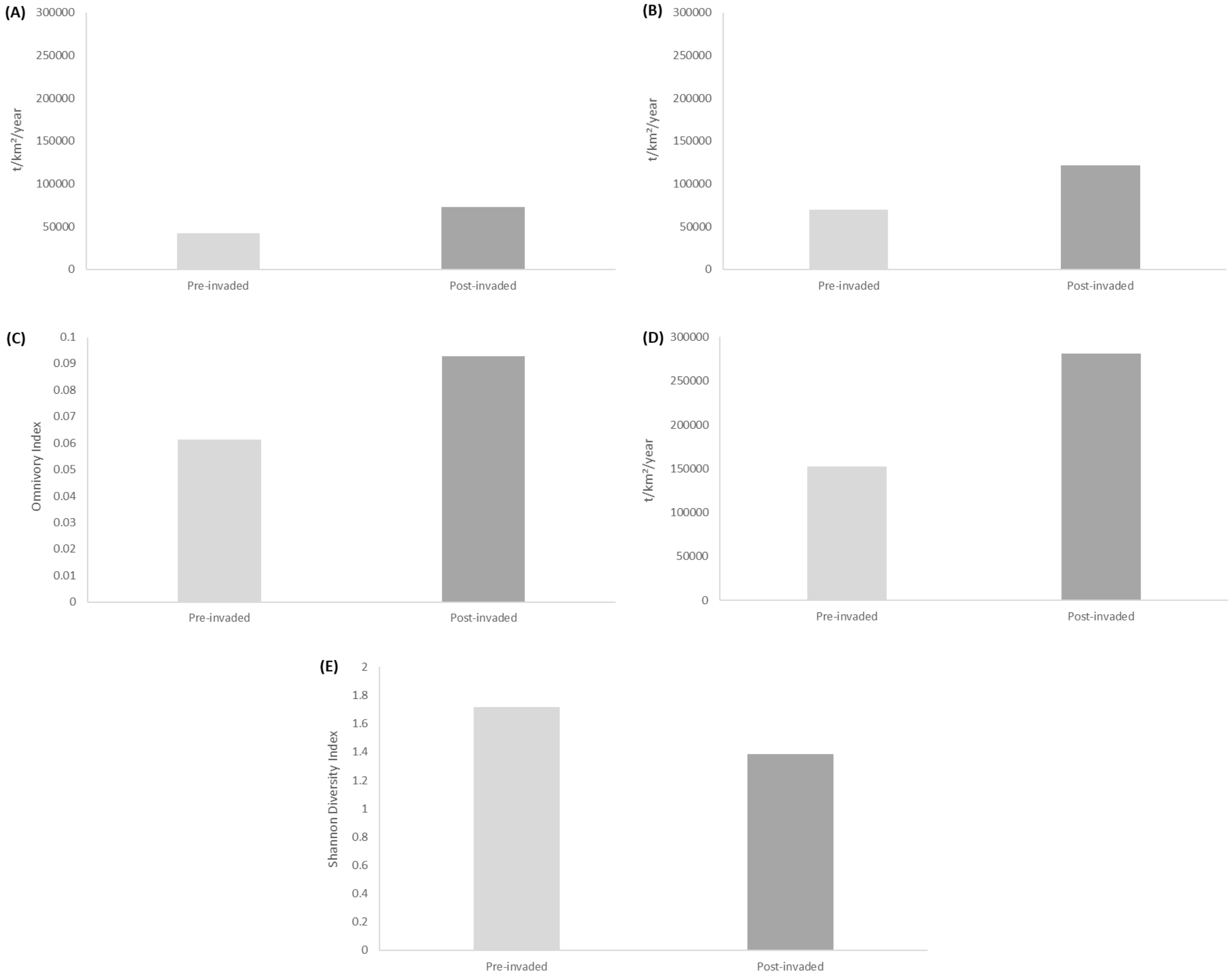

Figure 7 : System statistics for (A) total production, (B) total consumption, (C) total throughput, (D) omnivory index and (E) Shannon Diversity index for both pre- and post-invasion ecosystems in Betty’s Bay.

3.2 Exploring the potential reversal of the lobster invasion using Ecosim

3.2.1 Difference in biomass (t/km^2) for fished groups and urchins

Fishing pressure was manipulated in the Ecosim post-invasion model in an attempt to return the ecosystem to a pre-invasion state. The relative change in biomass of fished groups between the pre- and post-invasion ecosystems was calculated for the baseline (Ecopath) and the simulation (Ecosim) models (Appendix Table 10). Among the fished groups, it was only possible to get similar relative change in biomass for rock lobster and adult abalone (Figure 8). Reef fish had a much greater relative change in biomass in the Ecosim models compared to Ecopath models, particularly for Poenskop and Dageraad (Figure 8 A). Rock lobster relative change in biomass was the same in both models (Figure 8 B), and similarly for adult abalone (Figure 8 C), whereas the relative change in biomass for juvenile abalone (Figure 8 C) and urchins (Figure 8 D) was much smaller in the Ecosim models compared to the Ecopath models.

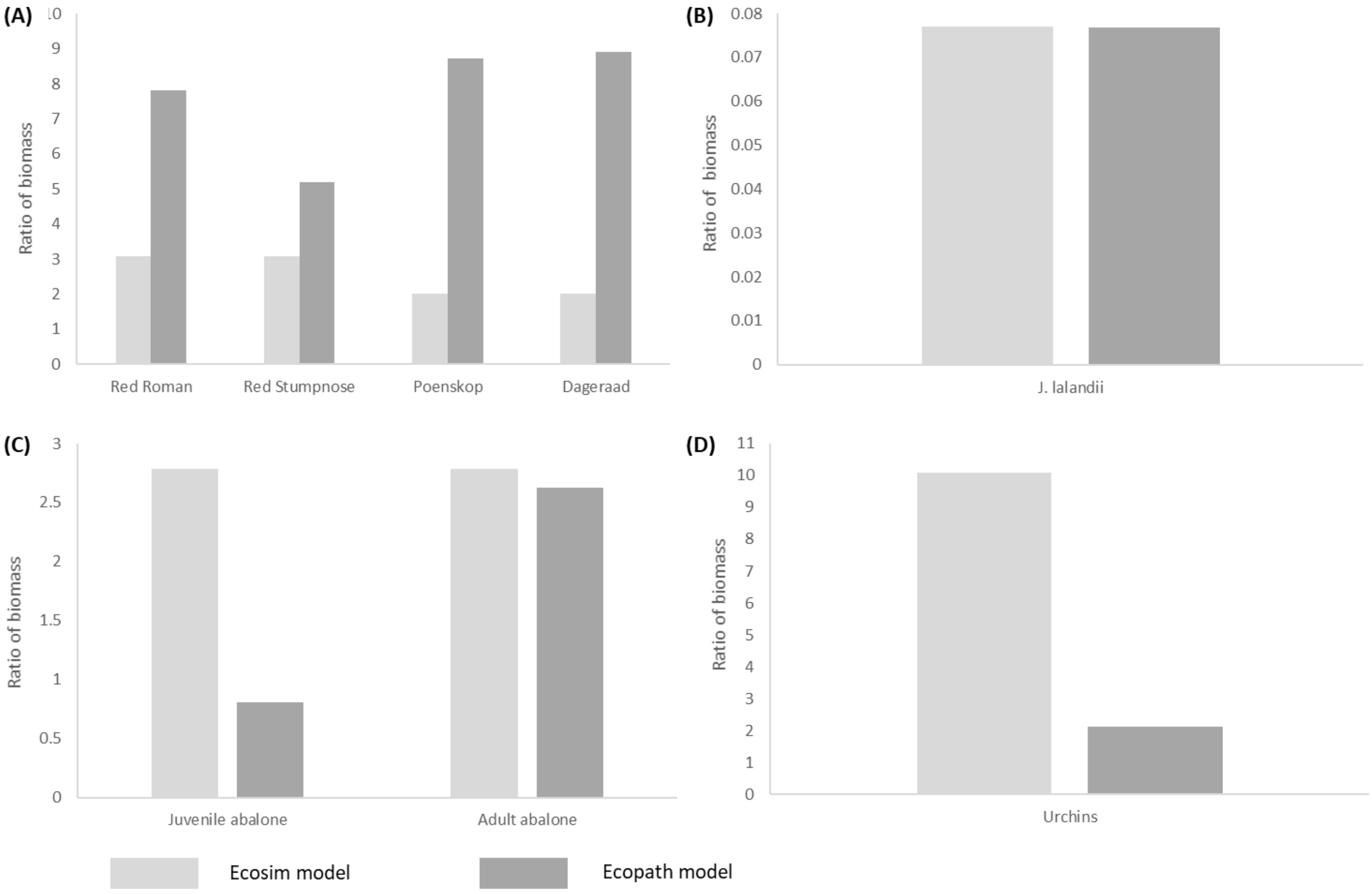

Figure 8: Relative change in biomass (ratio of biomass) of key groups in the pre-and post-invasion ecosystems in the Ecopath and the Ecosim models for (A) reef fish, (B) rock lobster (C) juvenile and adult abalone and (D) urchin in the Betty's Bay kelp forest.

3.2.2 Simulated annual catch for fished groups

Simulated fishing pressure was reduced for reef fish and adult abalone and increased for rock lobster. All fished groups showed an overall decline in catch over the simulated 20-year period (Figure 9). In the case of reef fish and adult abalone, catch declined to zero after 20 years in reef fish and 11 years in abalone. Rock lobster catch declined to 5.58 t/km^2 after 20 years as a result of increased hypothetical fishing on lobster in a model attempt to simulate a "reversed lobster invasion".

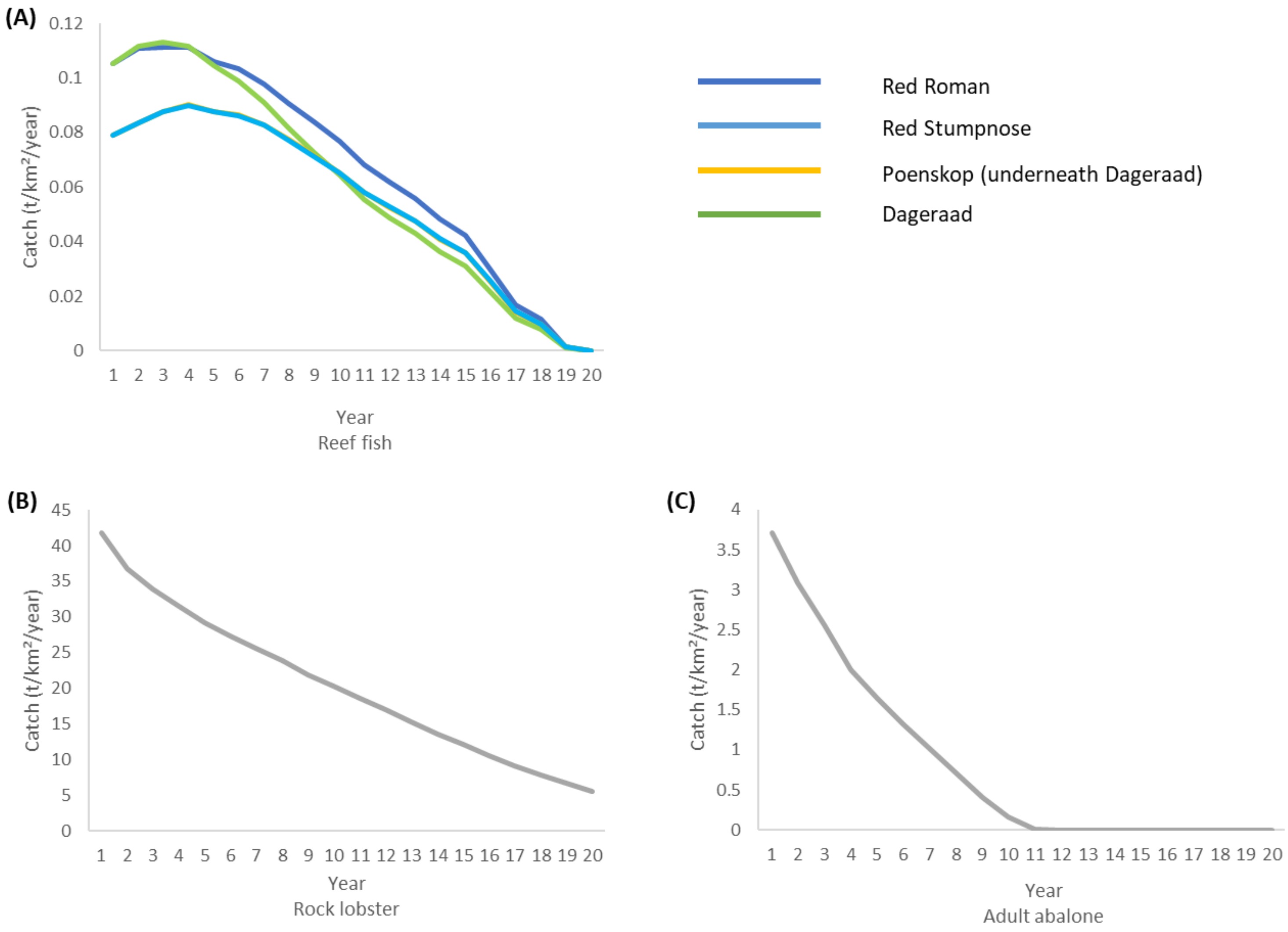

Figure 9: Annual model catch (t/km^2/year) for fished groups (A) reef fish, (B) rock lobster and (C) adult abalone, simulated using Ecosim in an attempt to model a hypothetical reverse in the lobster invasion in the Betty's Bay kelp forest.

3.2.3 Simulated annual biomass

3.2.3.1 Fished groups, juvenile abalone and urchins

Over the 20-year simulation period, there was an overall increase in model reef fish biomass (Figure 10 A). Red Roman increased from 0.92 t/km^2 to 7.22 t/km^2, Red Stumpnose increased from 0.92 t/km^2 to 4.80 t/km^2, Poenskop increased from 0.75 t/km^2 to 6.55 t/km^2 and Dageraad increased from 0.75 t/km^2 to 6.70 t/km^2. In contrast, rock lobster biomass consistently declined over the entire 20-year period (114.64 t/km^2 to 8.81 t/km^2), as intended in simulating a reversed lobster invasion (Figure 10 B), while adult abalone (338.47 t/km^2 to 887.94 t/km^2) and urchin biomass (4.21 t/km^2 to 8.94 t/km^2) also increased (Figure 10 C-D). Despite an initial increase in the first seven years, juvenile abalone biomass declined over the remaining 13 years (0.25 t/km^2 to 0.21 t/km^2) (Figure 10).

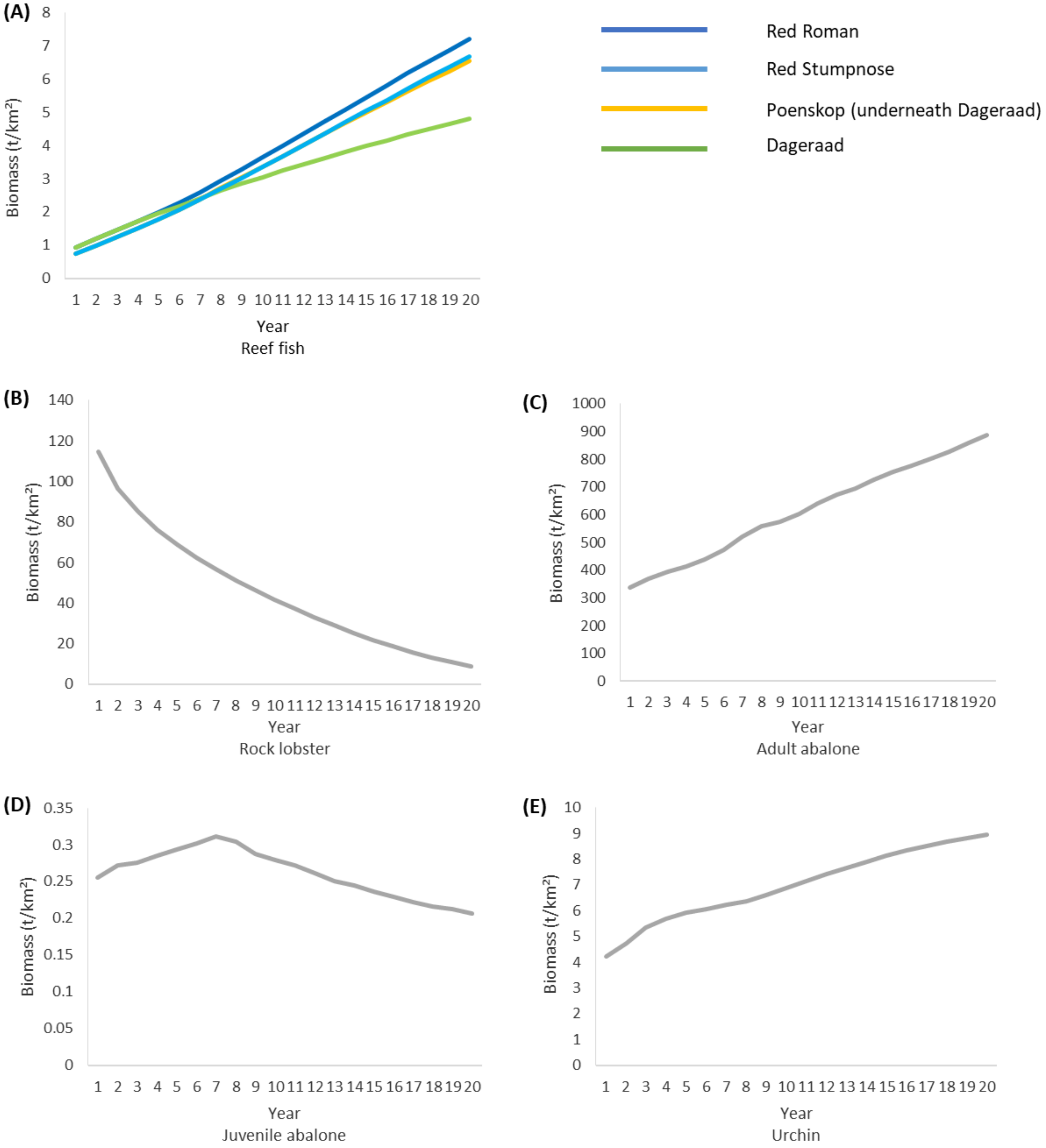

Figure 10: Annual biomass (t/km^2) for (A) reef fish, (B) rock lobster and (C) adult abalone and (D) juvenile abalone and (E) urchins, simulated using Ecosim in an attempt to model a hypothetical reverse in the lobster invasion in the Betty's Bay kelp forest.

3.2.3.2 Simulations of changes in other species/groups

Overall, biomass (t/km^2) in the remaining groups/species increased over the 20-year simulation period, with the exception of kelps, encrusting algae, microalgae and phytoplankton (Appendix Figure 11 A-X).

Biomass for all smaller reef fish i.e.: cryptic fish, herbivorous fish, omnivorous fish and carnivorous fish increased. Similarly, biomass increased for decapods, small crustaceans, *Oxystele spp*., urchins, *T. cidaris* and *T. sarmaticus*, bryozoans, anemones and sponges . Although biomass declined in most primary producer groups, biomass for foliose algae and turf algae increased. Finally, zooplankton biomass followed the general trend among groups and increased.

4 Discussion

4.1 The baseline models

Baseline models of the kelp forest ecosystem in Betty's Bay were built in Ecopath to demonstrate the trophic interactions between species/groups and to explore how these interactions changed following the invasion of *J. lalandii*.

Trophic webs provided a visual demonstration of how the trophic structure of the ecosystem changed as a direct or indirect result of the rock lobster invasion. Where the ecosystem had once been diverse and species/group rich and dominated by a high number of species, such as grazers, that occupy the 2nd trophic level, the ecosystem is now occupied by far fewer species/groups, with the 1st trophic level dominating, and all other species/groups dispersed more evenly over higher trophic levels. This change in trophic interactions may be due to the general loss of species/groups from the system, particularly grazers, resulting in greater primary production, and the remaining species preying on a wider range of species across more trophic levels due to the reduction or loss of their preferred prey. This suggestion is supported by the omnivory index ,which showed a higher index in the post-invasion ecosystem, indicating that species/groups are feeding across a greater number of trophic levels.

Kelp, turf and foliose algae proliferated in the post-invasion ecosystem model. This is likely due to the reduction in urchins and other benthic grazers as a result of increased predation by rock lobster and other predatory species ,which have been shown to keep grazer biomass in check and prevent overgrazing in some kelp forests (Mann & Breen 1972; Estes & Palmisano 1974; Cowen 1983; Tegner & Levin 1983; Mayfield & Branch 2000; Shears & Babcock 2002; Steneck et al. 2002; Steneck et al. 2004; Ling et al. 2009; Watson & Estes 2011; Norderhaug et al. 2014; Hamilton & Caselle 2015). As a result of the increase in algal biomass, the post-invasion ecosystem was much more productive than the pre-invasion system. The highly productive post-invasion system led to increased food availability for all specie ,which resulted in higher consumption rates in the post-invasion ecosystem. It has been determined previously that the post-invasion ecosystem has been disturbed or is in 'poor condition' following the lobster invasion (Blamey et al. 2010; Blamey & Branch 2012). This is based on the fact that the benthic community structure in the post-invasion system has changed to such a degree that it is no longer typical of a kelp forest ecosystem on the south-west coast of South Africa (i.e. grazer dominated; Field et al. (1980); Anderson et al. (1997); Blamey et al. (2010)). Given this information, one may expect to see these results reflected in the system throughput with a smaller throughput in the post-invasion system, indicating disturbance (Odum 1969; Odum & Barrett 1971; Christensen 1995; Christensen & Walters 2004). However, throughput was in fact greater in the post-invasion system. This is a result of high zooplankton biomass that was estimated in the post-invasion system. Zooplankton have a high turnover rate (Schneider 1992; Villarino et al. 2015) ,which increases the system throughput. In future work it may be possible to explore this result by introducing meio- and mesofauna groups to close the loop and lower the modelled system throughput.

In comparison to other modelled kelp forest ecosystems, the pre-invasion baseline model closely resembled the structure of the Isla Natividad kelp forest ecosystem on the Baja California Peninsula, modelled by Vilalta-Navas et al. (2018). Both ecosystems have a similar number of trophic levels and are dominated by invertebrates, abalone, sea snails, encrusting algae and kelp. The pre- and post-invasion baseline models also share similarities with models of kelp forest ecosystems on the Chilean coast (Ortiz 2008; Ortiz et al. 2013). Trophic levels are similar across both South African and Chilean ecosystems and the Chilean kelp forest ecosystems are dominated by kelps, red and green macroalgae, epifauna and grazers such as sea urchins and snails. These dominant groups were reflected in both the pre- and post-invasion ecosystems in my study of Betty’s Bay, where the pre-invasion ecosystem was dominated by grazers, epifauna (such as herbivores and grazers) and kelp and the post-invasion ecosystem was dominated by kelp, epifauna (such as sessile species) and red and green macroalgae.

4.2 Using Ecosim as a tool to explore the potential for reversing the lobster invasion

Overfishing of various marine resources along the south-western Cape coast, including linefish (Attwood & Farquhar 1999; Griffiths 2000; Winker et al. 2014) and abalone (DAFF 2016), is thought to have contributed either directly or indirectly to a shift in kelp forest ecosystem state (Blamey et al. 2014). As such, fishing pressure on fished groups in the post-invasion model was manipulated to explore potential drivers of the ecosystem shift, and whether it might be possible to return the ecosystem back or close to its pre-invasion state.

Model fishing pressure was reduced for reef fish and abalone, leading to an overall decline in catch for both groups, as was the actual situation in the pre-invasion ecosystem compared to the post-invasion state. Conversely, the (hypothetical) increased model fishing pressure on rock lobster invoked purely to model reduced lobster abundance, led to an overall decline in catch, due to the declining rock lobster biomass being insufficient to support such high levels of model fishing effort.

The reduced fishing pressure on reef fish in the post-invasion model, bolstered by an increase in prey availability (grazers, sessile species), enabled this group to recover to pre-invasion levels in the simulation. In fact, the reef fish biomass in the simulated pre-invasion model exceeded that of the pre-invasion Ecopath model. This result may be because despite best efforts, it was not possible to return the simulated fish biomass to the pre-invasion state due to differences in observed catch rates for the reef fish species that were not fully captured in the model simulations here as exploitation of all reef fish species were modelled under one model fleet. This could be explored further in future work.

Despite a reduction in model fishing effort for adult abalone, it was not possible for a change in hypothetical fishing alone to return the post-invasion abalone biomass to pre-invasion levels. Furthermore, even with the addition of a simulated decline in rock lobster biomass, abalone biomass did not recover to pre-invasion levels. This pattern of non-recovery is also reflected in Blamey et al. (2013), where abalone populations failed to recover despite the closure of legal (and simulated closure of illegal) abalone fisheries and the presence of rock lobsters. It was also not possible to model the shelter-provision relationship between urchin and abalone in Ecopath as this interaction is non-trophic. This may account for why it was not possible to restore model abalone biomass by reducing model fishing pressure alone. To partially address this, a model forcing function was applied to turf and foliose algae, increasing the availability of the algae for abalone only. Following this, model abalone biomass was able to recover to pre-invasion levels. In a future step, this non-trophic interaction could also be modelled by increasing the adult abalone biomass manually when “fitting” of the model to observed data for modelled groups. Fitting was not done in this study due to time constraints and limited availability of time series data sets that would be required to fit important modelled groups. Rather, this study is purely hypothetical and exploratory.

Despite the increase in simulated adult abalone, simulated juvenile abalone biomass declined, and failed to recover to pre-invasion levels. It is likely that without being able to model the urchin-abalone “habitat protection” interaction, model juvenile biomass will not recover. Furthermore, the forcing function applied to adult abalone did not affect juvenile abalone ,which feed mainly on microalgae.

Increased hypothetical model fishing pressure on rock lobster reduced their biomass to pre-invasion levels. Given the dire state of the rock lobster population in South Africa currently (Johnston & Butterworth 2016), removing rock lobster from the Betty’s Bay ecosystem by fishing them out would be highly controversial, but the rock lobster fishery was simply used as a proxy for the hypothetical removal or reduction of rock lobster abundance in that area. Instead, a better management option may be to restore predatory fish in the area, which (1) feed on rock lobster and (2) restrict lobster to crevices, thereby reducing their foraging area and their ability to feed on urchins and other grazers. As a result, an increase in predators to the area may change the foraging behavior of lobsters and limit their ability to feed across reefs, as has been shown elsewhere (Atkinson 2001).

In response to changes in simulated fishing effort, model urchin biomass increased from post-invasion levels, but not sufficiently to recover to pre-invasion levels. As previously mentioned, spatial competition is not well modelled in this study and likely explains model abalone recovery that falls below pre-invasion levels observed. It is probable that in the real world, the combined impact of increased reef fish, abalone and other grazers have suppressed the urchin biomass through predation (reef fish), competition for food (abalone and other grazers) and competition for space (abalone). Furthermore, a decline in kelp biomass in the pre-invasion ecosystem may also negatively impact urchin abundance as kelp is an important food source for urchin (Buxton & Field 1983).

Small reef fish showed mixed results in response to trophic change within the modelled ecosystem. Where cryptic and omnivorous fish increased in biomass, recovering to pre-invasion levels, herbivorous and carnivorous fish did not return to pre-invasion levels, despite an increase in modelled biomass. The success of cryptic and omnivorous fish is likely due to the increase in small crustacean biomass in the model. Herbivorous and carnivorous fish were not able to recover in the model, likely due to the increase in modelled abalone abundance sparking competition with herbivorous fish, and the reduction in kelp abundance, a main food source for herbivorous fish and abalone. The increased abundance of cryptic fish and decapods in the model would provide competition for the carnivorous fish, possibly leading to their inability to recover.

Model decapod and small crustacean biomass increased and recovered to pre-invasion levels, this recovery is likely due to the combined impact of a reduced modelled rock lobster abundance and increased food availability. A greater availability of algae, as well as detritus, in the pre-invasion ecosystem model would support the increase in decapod and small crustacean biomass. Furthermore, an increase in simulated small crustacean biomass would support the increase in decapod biomass.

Grazers such as *Oxystele* spp., *T. cidaris* and *T. sarmaticus* increased in biomass in the modelled simulation, likely due to greater food availability (turf and foliose). However, *Oxystele* spp. and *T. cidaris* did not recover to pre-invasion levels despite their increased biomasses, whereas *T. sarmaticus* did recover to pre-invasion levels. The *Oxystele* spp. and *T. cidaris* snails were possibly unable to recover to pre-invasion levels due to a greater presence of predatory reef fish in the pre-invasion ecosystem model, and possible competition with abalone and other grazers for food.

Sessile species (bryozoans, anemones, sponge, tunicates) continued to have a biomass greater in the simulated pre-invasion Ecosim ecosystem than in the pre-invasion baseline (Ecopath) ecosystem model. This result was unexpected because according to previous studies (Blamey et al. 2010; Blamey & Branch 2012), sessile species were reported to have proliferated in the observed post-invasion ecosystem whereas they were scarce in the observed pre-invasion ecosystem. It is possible that greater detritus and zooplankton availability, along with a reduction in rock lobster abundance allowed the sessile species biomass to remain high in the modelled pre-invasion system. Given that there were more urchin, abalone, snails and limpets moving about the reef and disturbing the settlement/growth of sessile species, biomass of sessile species may well not have remained high in reality. Since the implementation of the trophic model in this study did not capture non-trophic interactions such as disturbance to sessile species by mobile grazers, it is understandable that pre-invasion sessile biomass was overestimated in the model simulation.

Overall, algal biomass increased in the pre-invasion modelled ecosystem, a pattern contrary to what has been found in previous literature (Blamey et al. 2010; Blamey & Branch

2012). Model kelp biomass declined to pre-invasion levels in the model due to predation by grazers. In reality, competition for space with sessile species would also limit kelp abundance. In the simulation, turf and foliose algal biomass increased to levels greater in the pre-invasion ecosystem. This was an unexpected result given that previous literature has reported scarce understory algae in the pre-invasion system (Blamey et al. 2010; Blamey & Branch 2012), although the larger than expected simulated increase was undoubtedly a result of the forcing function applied to abalone-foliose and turf algae interactions, given that prior to the application of the forcing function, foliose and turf algae declined in the modelled pre-invasion ecosystem. Encrusting algae biomass was less in the pre-invasion model ecosystem than in the simulation back to pre-invasion, i.e. in the simulation encrusting algae did not recover to pre-invasion levels. In reality, the lower encrusting algae biomass pre-invasion would have occurred due to competition for space, as well as to encrusting algae being shaded out by turf and foliose algae. However, this conclusion is difficult to verify given that it is a non-trophic interaction and not captured by the model. Therefore, it may be that encrusting algae is not able to re-establish and recover to pre-invasion levels due to grazing by *T. cidaris* and *T. sarmaticus*. Microalgal biomass also declined and did not recover to pre-invasion levels in the simulation, possibly due to the increase of adult abalone biomass in the modelled pre-invasion system, as well as the presence of *T. cidaris*, both of ,which feed on microalgae.

Despite a decline in simulated biomass, phytoplankton levels remained greater in the pre-invasion system. This may be due to a reduction in predation by zooplankton as a result of an increase in model bryozoans ,which feed on zooplankton. Finally, simulated zooplankton biomass increased to above pre-invasion levels, possibly due to an increase in detritus availability in the pre-invasion ecosystem.

4.3 Summary

This study is now the first widely available Ecopath model for a South African kelp forest ecosystem. The focus was on a kelp ecosystem typical of the south-western coast of South Africa, before and after a rock lobster invasion. As expected, the pre-invasion model was species-rich and dominated by grazers at the second trophic level, while the post-invasion model had fewer species and was dominated by primary producers. There were a number of non-trophic interactions that were not captured in the model implementation in this study, such as competition for space, shading effects from canopy seaweeds and reef disturbance on sessile species from mobile grazers, amongst others. As such, an Ecospace model carefully modified to describe habitat effects (Sadchatheeswaran 2017), or a non-trophic or mixed modeling approach may be needed in future to capture these interactions e.g. the association between juvenile abalone and urchins and between abalone recruitment and encrusting algae (Day & Branch 2000b).

The purpose of the exploratory model simulation work done in this study was to plant a seed for future work. Resultant changes to the post-invasion kelp forest ecosystem in Betty’s Bay, following the manipulation of fishing pressure and the application of a trophic forcing function, suggest that the ecosystem will recover partly, but not completely, to the pre-invasion state. Findings of the trophic-based model investigations of this study may suggest a possible hysteresis effect at play, whereby the route required to return the ecosystem to its original state (reverse shift) differs from the route taken to reach the current state (forward shift; (Scheffer & Carpenter 2003)). After a 20-year period there was still unusually high abundances of sessile species and foliose and turf algae in the model. Urchin and grazers were scarce, and encrusting algae were less abundant than expected in a pre-invasion ecosystem. These findings are in agreement with the results from Blamey et al. (2013) who concluded that the invasion of *J. lalandii* caused a regime shift in the EOCH kelp forest ecosystems that was unlikely to be reversible within at least 50 years. Given that this study has only modelled changes over a 20-year period and the ecosystem is likely to experience hysteresis, a partial rather than full return to the pre-invasion state is a reasonable outcome.

Future recommendations for restoring the ecosystem include building up the reef fish stocks in the area as they may play an important role in controlling rock lobster predatory behavior in the system. In addition, the urchin population would have to be re-established to (1) reduce understory algae and allow for encrusting algae to recover ,which aid abalone recruitment (Day & Branch 2000b) and, (2) provide shelter for juvenile abalone (Day & Branch 2000b) and eventually, the establishment of an adult abalone population, in ,which both abalone and urchins then feedback to keep understory algae reduced and encrusting algae abundant. Although there are adjacent non-invaded kelp forest ecosystems that may be a source of abalone and urchin spawning biomass (Blamey et al. 2013), these stocks may need to be supplemented by clearing algae and seeding invaded reefs with juvenile urchin, and later abalone once the urchins have reach the right size to shelter the juvenile abalone. However, given that illegal fishing of abalone is still rife in South Africa, re-seeding of abalone is costly and should not be considered until the protection of the abalone once they mature can be assured.

Finally, these models were created for a kelp system along the south-west coast ,which differs in benthic community structure to kelp forests on the west coast. In the future, this model could be adapted for the west coast to provide a better understanding of the similarities and differences in kelp forest ecosystems between coasts, including testing hypotheses relating to ecosystem change and overfishing.

5 Appendix

Table 3: Ecopath parameters (P/B) (year^{-1}), (Q/B) (year^{-1}) and the respective sources for the various species/groups in the pre-invasion model for Betty's Bay. Shaded rows indicate age stanzas.

#	Group name	P/B (Z)	Q/B	Source
		Predators		
1	*C. laticeps*	0.50	5.00	Lynne Shannon pers. comm., Blamey et al. (2014)
2	*C. gibbiceps*	0.50	5.00	Lynne Shannon pers. comm., Blamey et al. (2014)
3	*C. nasutus*	0.48	0.86	Shannon et al. (2003) (for other large pelagic fish)
4	*C. cristiceps*	0.48	0.86	Shannon et al. (2003) (for other large pelagic fish)
5	Cryptic fish	2.40	15.60	Eddy et al. (2014)
6	Omnivorous fish	1.02	21.85	Okey et al. (2004)
7	Carnivorous fish	0.41	3.59	Eddy et al. (2014) (fish: invertebrate feeders)
8	*J. lalandii*	0.42	1.90	Pollock and Beyers (1981); Zoutendyk (1988a, 1988b)
9	*A. argus*	1.80	9.00	Lovvorn et al. (2015)
10	*Thias* spp.	2.16	7.48	Sadchatheeswaran (2017)
		Scavengers		
11	Decapods	0.82	4.10	Lovvorn et al. (2015)
12	*M. glacialis*	0.60	5.00	Ortiz et al. (2013)
		Herbivores		
13	Herbivorous fish	0.40	9.52	Eddy et al. (2014) (fish: herbivorous feeders)
14	*Oxystele* spp.	4.00	20.00	Ortiz et al. (2013)
15	Juvenile *H. midae*	2.00	131.01	Calculated by Ecopath
16	Adult abalone *H.midae*	1.50	15.00	Eddy et al. (2014)
17	*P. angulosus*	1.83	6.54	Sadchatheeswaran (2017)
18	*T. cidaris*	4.00	20.00	Ortiz et al. (2013)
19	*T. sarmaticus*	2.00	30.00	Ortiz et al. (2013)
20	Limpet	4.00	20.00	Sadchatheeswaran (2017)
		Sessile species		
21	Other sessile spp.	1.73	4.09	Calculated
22	Other echinoderms	1.04	2.95	Calculated
23	Anemones	1.53	4.88	Sadchatheeswaran (2017)
24	Polychaetes	4.75	13.66	Sadchatheeswaran (2017)
25	Sponges	3.44	14.89	Sadchatheeswaran (2017)
26	Tunicates	2.10	6.00	Ortiz et al. (2013)
27	Sea cucumbers	0.60	3.40	Eddy et al. (2014)

Table 3 continued.				
		Producers		
28	Kelp	10.00	0.00	Stobie (2002)
29	Foliose	13.00	0.00	Eddy et al. (2014)
30	Turf	10.72	0.00	Ortiz et al. (2013)
31	Encrusting algae	1.33	0.00	Stobie (2002)
32	Microalgae	1.00	0.00	Lovvorn et al. (2015)
33	Phytoplankton	154.40	0.00	Shannon et al. (2003)
		Zooplankton		
34	Zooplankton	136.63	658.46	Shannon et al. (2003)

Table 4: Ecopath parameters (P/B)(year^{-1}), Q/B) (year^{-1}) and the respective sources for the species/groups in the post-invasion model for Betty's Bay.

#	**Group name**	**P/B (Z)**	**Q/B**	**Source**
		Predators		
1	*C. laticeps*	0.50	5.00	Lynne Shannon pers.comm., Blamey et al. (2014)
2	*C. gibbiceps*	0.50	5.00	Lynne Shannon pers.comm., Blamey et al. (2014)
3	*C. nasutus*	0.48	0.86	Shannon et al. (2003) (for other large pelagic fish)
4	*C. cristiceps*	0.48	0.86	Shannon et al. (2003) (for other large pelagic fish)
5	Cryptic fish	2.40	15.60	Eddy et al. (2014)
6	Omnivorous fish	1.02	21.85	Okey et al. (2004)
7	Carnivorous fish	0.41	3.59	Eddy et al. (2014) (fish: invertebrate feeders)
8	*J. lalandii*	0.42	1.90	Pollock and Beyers (1981); Zoutendyk (1988a, 1988b)
		Scavengers		
9	Decapods	1.50	9.50	Ortiz et al. (2013)
		Herbivores		
10	Herbivorous fish	0.40	9.52	Eddy et al. (2014) (fish: herbivorous feeders)
11	*Oxystele* spp.	4.00	20.00	Ortiz et al. (2013)
12	*T. cidaris*	4.00	20.00	Ortiz et al. (2013)
13	*T. sarmaticus*	2.00	30.00	Ortiz et al. (2013)
		Sessile species		
14	Bryozoans	50.00	150.00	Thapanand et al. (2009)
15	Anemones	1.53	4.88	Sadchatheeswaran (2017)
16	Sponges	3.44	14.89	Sadchatheeswaran (2017)
17	Tunicates	2.10	6.00	Ortiz et al. (2013)
		Producers		
18	Kelps	10.00	0.00	Stobie (2002)

Table 4 continued.

19	Foliose	13.00	0.00	Eddy et al. (2014)
20	Turf	34.29	0.00	Ortiz et al. (2013)
21	Encrusting algae	1.33	0.00	Stobie (2002)
22	Microalgae	1.00	0.00	Lovvorn et al. (2015)
23	Phytoplankton	154.40	0.00	Shannon et al. (2003)
Zooplankton				
24	Zooplankton	136.63	658.46	Shannon et al. (2003)

Table 5: Dietary matrix showing prey (listed as left column) composition of predator diets (listed as top row) for the pre-invasion model of Betty's Bay. Shaded cells indicate potential cannibalism. The sum of all predator diet compositions are equal to 1.

	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	34
1	Red roman																													
2	Red stumpnose																													
3	Poenskop																													
4	Dageraad																													
5	Cryptic fish	0.040		0.050	0.002	0.100		0.000																						
6	Herbivorous fish																													
7	Omnivorous fish																													
8	Carnivorous fish																													
9	Jasus lalandii	0.040	0.080	0.020						0.044																				
10	Pustular triton			0.012	0.001					0.035																				
11	Dog whelk			0.012	0.001					0.035																				
12	Decapods	0.050	0.050	0.121	0.110	0.001		0.026		0.030					0.050															
13	Small crustacean	0.060	0.050	0.004	0.004	0.626		0.448	0.630	0.021			0.300		0.200															
14	Spiny starfish	0.080		0.030	0.118					0.028																				
15	Oxystele spp.			0.089	0.083					0.110		0.100			0.110										0.150					
16	Juvenile		0.040							0.027		0.020																		
17	Adults			0.040	0.060	0.021																								
18	Urchin	0.120	0.080	4.320	0.056	0.021		0.042		0.238					0.100															
19	T.cidaris			0.060	0.070	0.042				0.082					0.083										0.100					
20	T.sarmarticus			0.032	0.040					0.020																				
21	Limpet	0.060		0.260	0.047	0.021		0.008		0.030		0.030																		
22	Other sessile spp.	0.380	0.375	0.206	0.243	0.072		0.017	0.010	0.184		0.550			0.310										0.550					
23	Other starfish	0.001		0.000	0.000			0.000		0.000																				
24	Anemones	0.070						0.105	0.255	0.005																				
25	Polychaetes	0.100	0.117	0.011	0.024	0.042		0.087	0.035	0.033	0.500				0.100										0.010					
26	Sponges									0.019													0.020	0.020						
27	Tunicates		0.208		0.001			0.016	0.070		0.500	0.300			0.047															
28	Sea cucumbers			0.010				0.010																	0.020					
29	Kelp						0.749	0.050						0.150		0.400		0.750	0.750	0.430	0.620	0.500						0.160		
30	Foliose						0.001	0.000										0.000		0.000	0.000									
31	Turf						0.150	0.020					0.200	0.100		0.100		0.070		0.050	0.030	0.200								
32	Encrusting algae						0.100	0.010		0.059						0.300		0.050		0.200	0.050									
33	Microalgae															0.200	1.000	0.130	0.250	0.320	0.300	0.300		0.490						
34	Zooplankton					0.054								0.200											0.070					
35	Phytoplankton																										0.500	0.380	0.500	0.500
36	Detritus												0.500	0.550									0.980	0.490	0.100	1.000	0.500	0.460	0.500	0.500
37	Import				0.140			0.160																						

Table 6: Dietary matrix showing prey (listed as left column) composition of predator diets (listed as top row) for the post-invasion model of Betty’s Bay. Shaded cells indicate potential cannibalism. The sum of all predator diet compositions are equal to 1.

	Group	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**25**
1	**Red Roman**	▨																		
2	**Red Stumpnose**		▨																	
3	**Poenskop**			▨																
4	**Dageraad**				▨															
5	**Cryptic fish**	0.077		0.055	0.001	0.100		0.000												
6	**Herbivorous fish**						▨													
7	**Omnivorous fish**							▨												
8	**Carnivorous fish**								▨											
9	**J. lalandii**	0.050	0.077	0.050	0.020					0.099										
10	**Decapods**				0.000					0.004	▨									
11	**Small crustaceans**	0.071	0.053	0.004	0.004	0.680		0.482	0.630	0.021	0.300	▨								
12	**Oxystele spp.**			0.033	0.031					0.044			▨				0.010			
13	**T.cidaris**			0.113	0.080	0.120				0.104				▨			0.080			
14	**T.sarmaticus**			0.037	0.047					0.014					▨					
15	**Bryozoans**				0.338				0.030							▨	0.150			
16	**Anemones**	0.802						0.105	0.270								▨			
17	**Sponges**									0.648							0.280	▨		
18	**Tunicates**		0.870	0.678	0.347			0.073	0.070								0.220		▨	
19	**Kelps**						0.100					0.100	0.100	0.150	0.300				0.200	
20	**Foliose**				0.002		0.500	0.090			0.100	0.150	0.400	0.350	0.350				0.100	
21	**Turf**						0.400	0.091			0.300	0.150	0.300	0.300	0.150					
22	**Encrusting algae**									0.009			0.100	0.150	0.150					
23	**Microalgae**												0.100	0.050	0.050					
24	**Phytoplankton**															0.500			0.200	0.500
25	**Zooplankton**					0.100						0.050				0.500	0.070			▨
26	**Detritus**									0.057	0.300	0.550					0.190	1.000	0.500	0.500
27	**Import**			0.030	0.131			0.158												

Table 7: Diet of the various groups included in the pre-invasion model of Betty's Bay, and associated sources.

PRE-INVASION		
Groups	**Diet**	**Source**
Predators		
C. laticeps	Fish, decapods, macrura, bivalves, *Turbo* spp., *Oxystele* spp., whelks, limpets, brittle star, feather star, starfish, urchin, polychaetes, anemones	Nepgen (1982)
C. gibbiceps	Decapods, macrura, bivalves, juvenile abalone, brittle star, sea urchin, polychaetes, ascidians	Nepgen (1982)
C. nasutus	Decapods, abalone, limpets, *Oxystele* spp., *T.cidaris*, *T.sarmaticus*, whelks, *H.ornata*, *M.glacialis*, fish, macrura, brittle stars, feather stars, sea cucumbers, urchin, polychaetes, bivalves	Buxton and Clarke (1989)
C. cristiceps	Decapods,feather stars, starfish, brittle stars, gastropods, bivalves, echinoderms (urchin), cephelopods, polychaetes, bryozoans, ascidians, fish, chitons, sea spiders, algae, cirripedia , tanaidacea, isopods, amphipods, fish	Buxton (1987)
Cryptic fish		
Small herbivorous fish	Benthic algae	Lechanteur and Griffiths (2002)
Small omnivorous fish	Decapods, barnacles, sea cucumber, feather star, brittle star, urchin, whelks, limpets, sea anemone, polychaetes, fish	Lechanteur and Griffiths (2002)
Small carnivorous fish	Decapods, barnacles, ascidians, feather stars, bivalves, anemones, polychaetes, bryozoans	Lechanteur and Griffiths (2002)
J. lalandii	Sponge, barnacle, brown algae, small crustaceans, mussels, limpets, *Turbo* spp., *Oxystele* spp., winkles, urchin, lobster, crab	Pollock (1979); Mayfield et al. (2000a); Haley et al. (2011) (from SeaLife Base)
A. argus	Polychaetes (cape-reef worm), ascidians	Govan (1995) (SeaLife Base) (ascidian), Branch et al. (2010) (polychaetes)
Thias **spp.**	Ascidians, gastropods, cirripedia	Branch et al. (2010)
Scavengers		
Decapods	Molluscs, annelids, crustaceans (amphipods, copepods, isopods), echinoderms, bryozoans	Branch et al. (2010)
Small crustaceans	Algae, zooplankton, detritus	Branch et al. (2010)
M. africana	Molluscs, echinoderms, polychaetes, crustaceans	Verling et al. (2003) (from SeaLife Base)

Table 7 continued.		
Herbivores		
***Oxystele* spp.**	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)
H. midae (juvenile)	Benthic algae/seaweeds	Barkai and Griffiths (1986) (from SeaLife Base)
H. midae (adult)	Benthic algae/seaweeds	Barkai and Griffiths (1986) (from SeaLife Base)
P. angulosus	Benthic algae/seaweeds	Fricke (1979); Buxton and Field (1983)
T. cidaris	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)
T. sarmaticus	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)
Limpet	Benthic algae	Branch (1971); Espinosa and Rivera-Ingraham (2017)
Sessile species		
Other sessile species	Sponge and detritus	Branch et al. (2010)
Other echinoderms	Sponge, microalgae and detritus	(Branch et al. 2010)
Anemones	Bivalves, cirripedia, gastropods, tunicates,sea cucumbers, polychaetes, detritus	Kruger (1995)
Polychaetes	Particulate matter/detritus	Branch et al. (2010)
Sponge	Detritus/food particles suspended in the water column	Branch et al. (2010)
Tunicates	Phytoplankton, benthic algae (fragments), detritus	Tatián et al. (2008)
Holothuroidea (sea cucumbers)	Phytoplankton, detritus	Branch et al. (2010)
Zooplankton		
Zooplankton	Phytoplankton, detritus	Branch et al. (2010)

Table 8: Diet of the various groups included in the post-invasion model of Betty's Bay, and associated sources.

POST-INVASION		
Groups	**Diet**	**Source**
Predators		
C. laticeps	Fish, decapods, macrura, bivalves, *Turbo spp.*, *Oxystele* spp., whelks, limpets, brittle star, feather star, starfish, urchin, polychaetes, anemones	Nepgen (1982)
C. gibbiceps	Decapods, macrura, bivalves, juvenile abalone, brittle star, sea urchin, polychaetes, ascidians	Nepgen (1982)
C. nasutus	Benthic invertebrates, echinoderms, crustaceans,	Buxton and Clarke (1989)
C. cristiceps	Benthic crustaceans, molluscs, finfish/bonyfish, annelids	Buxton (1987)
Cryptic fish	Fish, decapods, small crustaceans, abalone, urchin, *T.cidaris*, limpet, polychaetes, barnacles, mussels, feather stars	Prochazka (1998)
Small herbivorous fish	Benthic algae	Lechanteur and Griffiths (2002)
Small omnivorous fish	Decapods, barnacles, sea cucumber, feather star, brittle star, urchin, whelks, limpets, sea anemone, polychaetes, fish	Lechanteur and Griffiths (2002)
Small carnivorous fish	Decapods, barnacles, ascidians, feather stars, bivalves, anemones, polychaetes, bryozoans	Lechanteur and Griffiths (2002)
J. lalandii	Sponge, barnacle, brown algae, small crustaceans, mussels, limpets, *Turbo* spp., *Oxystele* spp., winkles, urchin, lobster, crab	Pollock (1979); Mayfield et al. (2000a); Haley et al. (2011) (from SeaLife Base)
A. argus	Polychaetes (cape-reef worm), ascidians	Govan (1995) (SeaLife Base) (ascidian), Branch et al. (2010) (polychaetes)
***Thias* spp.**	Ascidians, gastropods, cirripedia	Branch et al. (2010)
Scavengers		
Decapods	Molluscs, annelids, crustaceans (amphipds, copepods, isopods), echinoderms, bryozoans	Branch et al. (2010)
Small crustaceans		
Herbivores		
***Oxystele* spp.**	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)
T. cidaris	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)
T. sarmaticus	Benthic algae/seaweeds/encrusting algae/microalgae	Branch et al. (2010)

Table 8 continued.		
Limpet	Benthic algae	Branch (1971); Espinosa and Rivera-Ingraham (2017)
Sessile species		
Bryozoans	Phytoplankton, zooplankton	Smithsonian Marine Station and Fort Pierce, 2017, SeaLifeBase (pers.comm)
Anemones	Bivalves, cirripedia, gastropods, tunicates, sea cucumbers, polychaetes, detritus	Kruger (1995)
Polychaetes	Particulate matter/detritus	Branch et al. (2010)
Sponge	Detritus/food particules supened in the water column	Branch et al. (2010)
Tunicates	Phytoplankton, benthic algae (fragments), detritus	Tatián et al. (2008)
Zooplankton		
Zooplankton	Phytoplankton, detritus	Branch et al. (2010)

Table 9: Biomass (t/km^2) for groups in the pre-and post-invasion ecosystems of the Ecopath models, and biomass for the start (post) and end (pre) ecosystems of the Ecosim model for Betty’s Bay. Important species are in bold.

#	*Group name*	***Baseline models (Ecopath)***		***Ecosim***	
		Biomass (Pre)	**Biomass (Post)**	**Biomass (end = Pre)**	**Biomass (start = Post)**
1	***C. laticeps***	2.436	0.792	7.218	0.923
2	***C. gibbiceps***	2.436	0.792	4.799	0.924
3	***C. nasutus***	1.302	0.651	6.554	0.751
4	***C. cristiceps***	1.302	0.651	6.699	0.752
5	Cryptic fish	3.410	3.410	11.018	3.463
6	Herbivorous fish	0.000	0.000	0.000	0.000
7	Omnivorous fish	0.000	0.000	0.000	0.000
8	Carnivorous fish	0.000	0.000	0.000	0.000
9	***J. lalandii***	9.912	128.550	8.814	114.638
10	Decapods	4.106	0.919	5.545	0.963
11	Small crustaceans	11.422	11.750	25.077	12.229
12	*Oxystele* spp.	103.497	3.764	24.954	4.213
13	**Juvenile *H. midae***	0.696	0.250	0.207	0.255
14	**Adult *H. midae***	914.981	328.547	887.938	338.473
15	***P. angulosus***	41.283	4.100	8.938	4.208
16	*T. cidaris*	119.342	12.327	47.385	13.551
17	*T. sarmaticus*	2.012	6.529	19.668	6.812
18	Anemones	9.333	15.758	39.262	15.750

Table 9 continued.

19	Sponges	6.893	1636.452	2486.897	1655.238
20	Tunicates	37.996	74.800	111.005	75.467
21	Kelps	4147.648	6268.636	6173.527	6269.904
22	Foliose	0.501	333.422	904.903	363.359
23	Turf	124.121	312.925	981.848	337.941
24	Encrusting algae	3146.869	1791.249	1483.440	1792.529
25	Microalgae	3497.260	1164.494	589.035	1167.642
26	Phytoplankton	76.938	153.946	140.494	153.571
27	Zooplankton	28.805	50.504	56.707	50.720

Table 10: Difference in biomass (t/km^2) between the pre-and post-invasion ecosystems for the Ecopath models for Betty’s Bay. Important species are in bold.

#	***Group name***	***Baseline models (Ecopath)***	***Ecosim***
1	***C. laticeps***	**3.074**	**7.817**
2	***C. gibbiceps***	**3.074**	**5.196**
3	***C. nasutus***	**2.000**	**8.725**
4	***C. cristiceps***	**2.000**	**8.908**
5	Cryptic fish	1.000	3.181
6	Herbivorous fish	10.838	4.307
7	Omnivorous fish	1.558	2.972
8	Carnivorous fish	6.731	2.530
9	***J. lalandii***	**0.077**	**0.077**
10	Decapods	4.469	5.757
11	Small crustaceans	0.972	2.051
12	*Oxystele* spp.	27.499	5.923
13	**Juvenile *H. midae***	**2.785**	**0.809**
14	**Adult *H. midae***	**2.785**	**2.623**
15	***P. angulosus***	**10.069**	**2.124**
16	*T. cidaris*	9.681	3.497
17	*T. sarmaticus*	0.308	2.887
18	Anemones	0.592	2.493
19	Sponges	0.004	1.502
20	Tunicates	0.508	1.471
21	Kelps	0.662	0.985
22	Foliose	0.002	2.490
23	Turf	0.397	2.905
24	Encrusting algae	1.757	0.828
25	Microalgae	3.003	0.504
26	Phytoplankton	0.500	0.915
27	Zooplankton	0.570	1.118

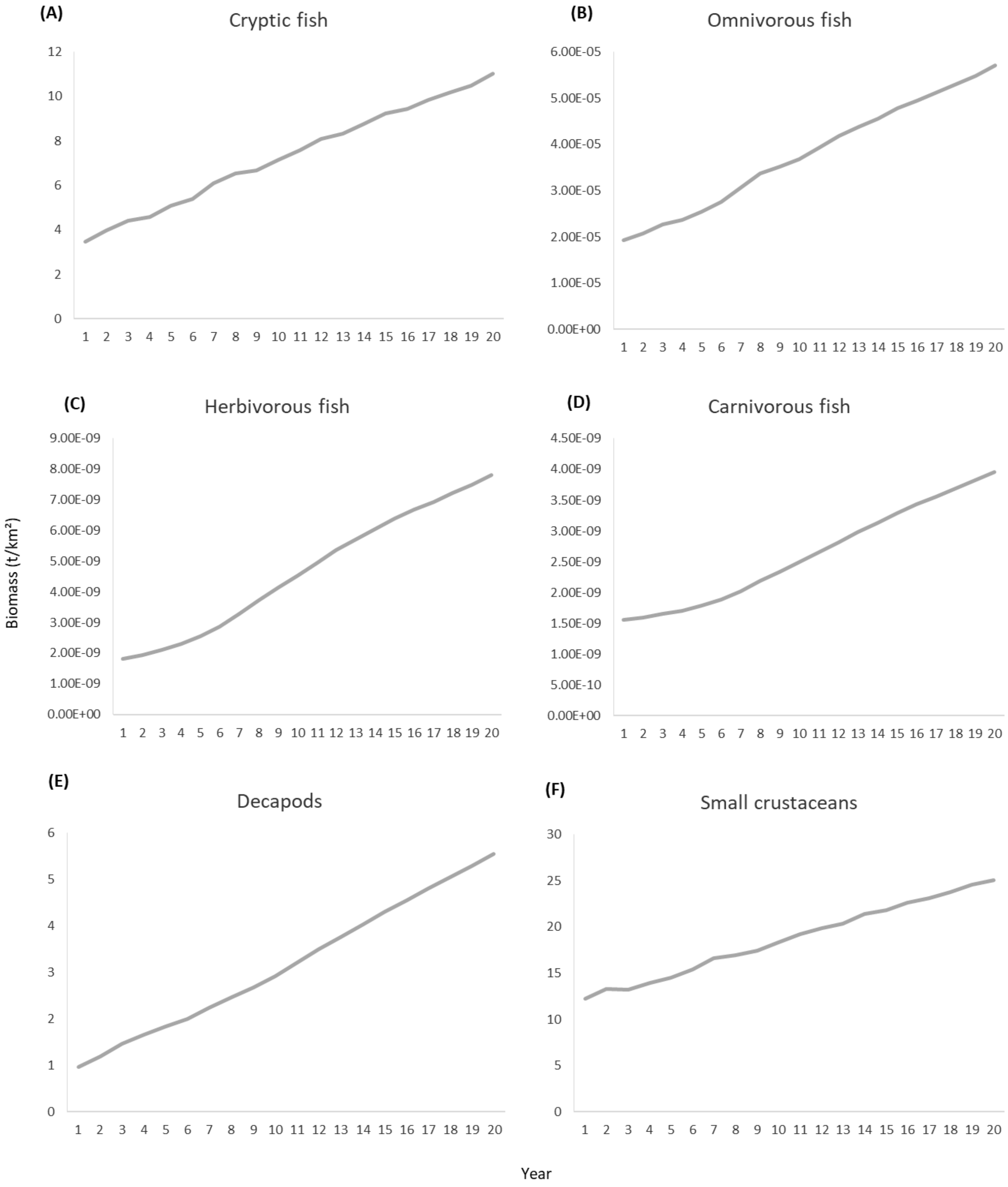

Figure 11 A-F: Annual biomass (t/km^2) over the 20-year simulation period for (A) cryptic fish, (B) omnivorous fish, (C) herbivorous fish, (D) carnivorous fish, (E) decapods and (F) small crustaceans in the Betty’s Bay kelp forest.

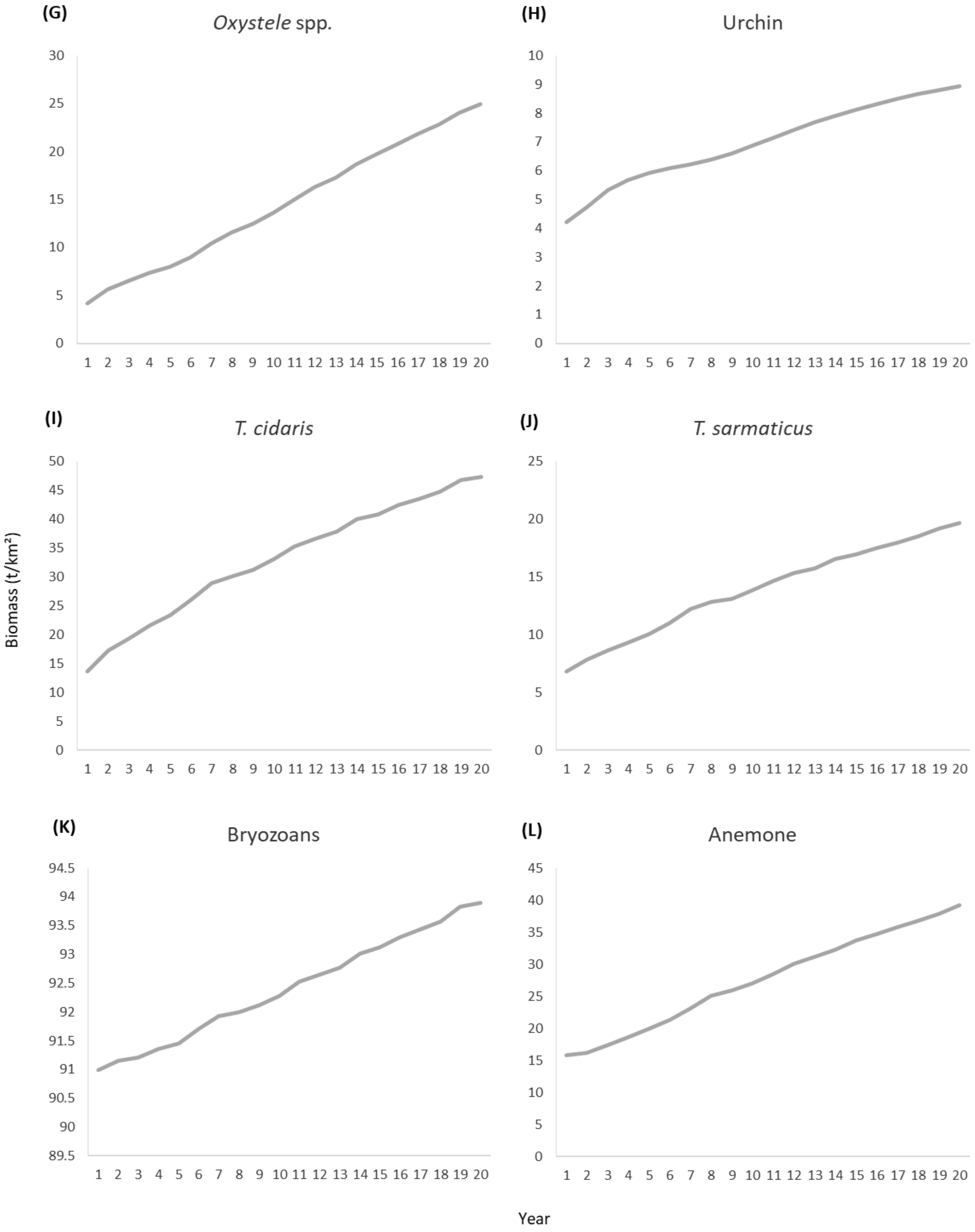

Figure 11: G-L: Annual biomass (t/km^2) over the 20-year simulation period (G) Oxystele spp., (H) urchins (*Parechinus angulosus*), (I) *T. cidaris*, (J) *T. sarmaticus*, (K) bryozoans, (L) anemones in the Betty's Bay kelp forest.

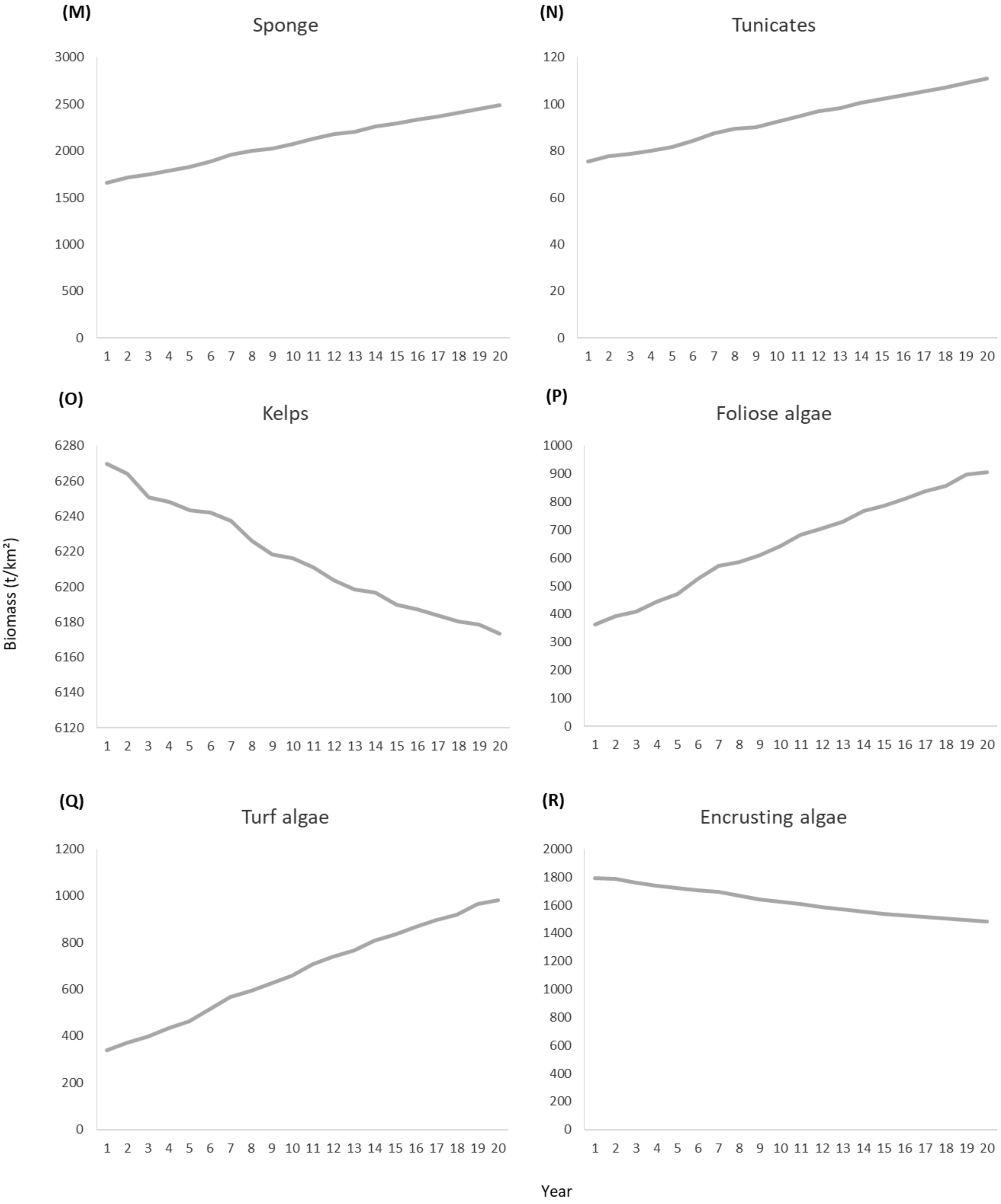

Figure 11 M-R: Annual biomass (t/km^2) over the 20-year simulation period for (M) sponges, (N) tunicates, (O) kelps, (P) foliose algae, (Q) turf algae, (R) encrusting algae in the Betty’s Bay kelp forest.

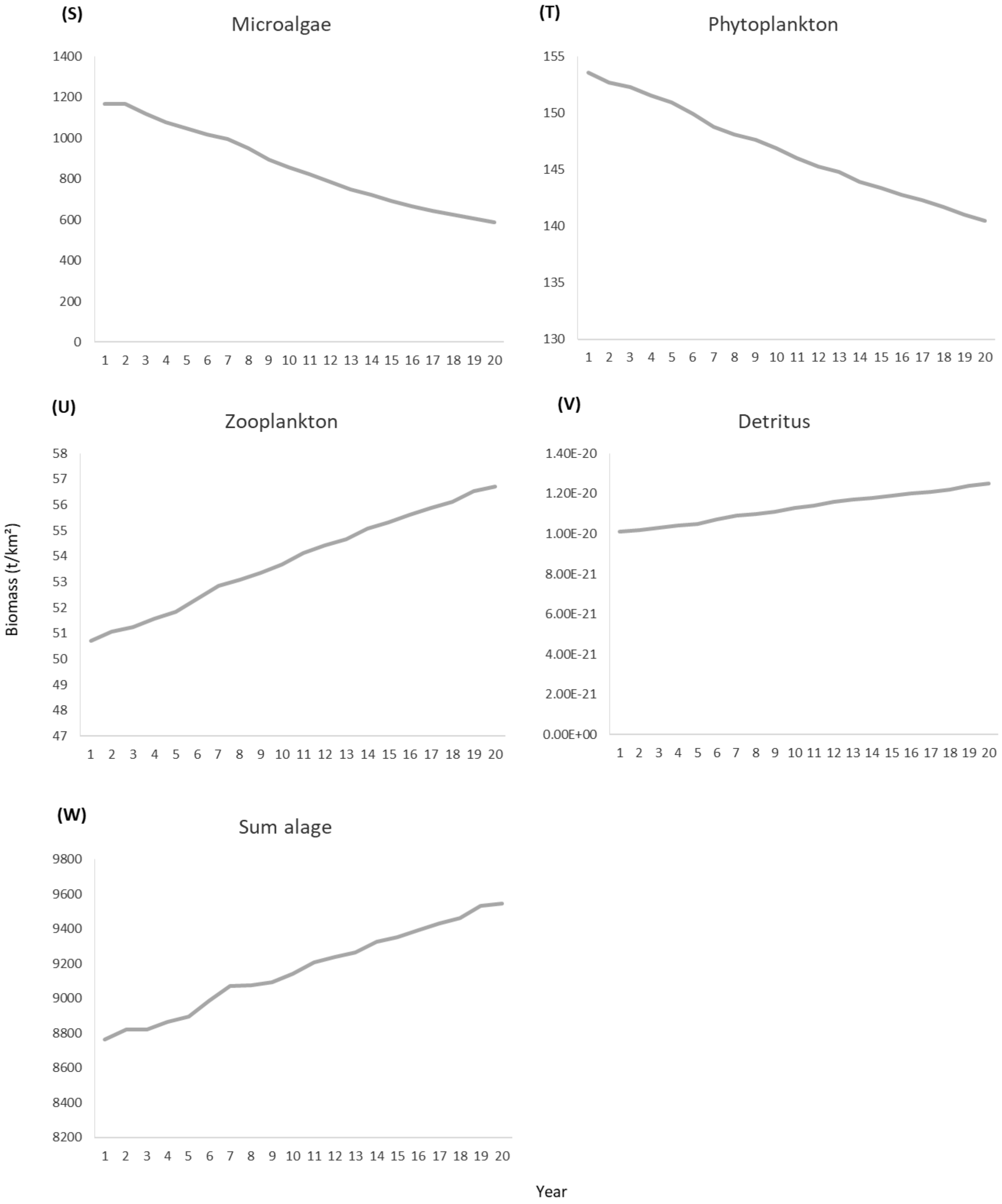

Figure 11 S-W: Annual biomass (t/km^2) over the 20-year simulation period for (S) microalgae, (T) phytoplankton, (U) zooplankton, (V) detritus, (W) sum algae in the Betty's Bay kelp forest.

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