

Optimal sampling and spatiotemporal change in epibenthos at a sub-Antarctic Marine Protected Area

By
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Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in the Faculty of Science at Stellenbosch University



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December 2017

Declaration

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December 2017

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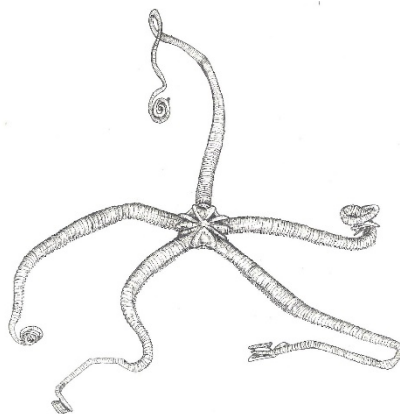
Acknowledgements

I would firstly like to thank my supervisors Dr Charles von der Meden, Dr Tammy Robinson and Dr Lara Atkinson for their invaluable guidance, support and encouragement and Professor Isabelle Ansong for her role in making this project possible. The South African Environmental observation Network (SAEON) and the South African National Antarctic Program (SANAP) provided funding for this project, as well as the Department of Botany and Zoology, Stellenbosch University.

I would also like thank the Department of Environmental Affairs; Dr Hans Verheye, Captain Syndercombe, as well as the officers and crew of the *SA Agulhas II* for their invaluable assistance during the cruise. Thank you to the biologists, oceanographers and technicians on-board the *SA Agulhas II* during the 2015 cruise for their insights and assistance during sampling.

Thank you to Emeritus Professor George Branch and authors of Branch et al. 1993a for the use of their historical images. I am highly appreciative of the authors of Chao et al. 2009 and Weissgerber et al. 2015 for the provision of their supplementary material.

Finally I would like to thank the friends and family who supported me through the writing of this thesis.



Abstract

There have been notable regional and temporal changes in many biological systems around the Prince Edward Islands (PEI) in the Southern Ocean, but little work has focused on epibenthic assemblages. The aim of this study was to investigate spatial and temporal changes in the epibenthos, as they may be important indicators of change. During the austral summer of 2013 and 2015, a benthic towed camera system was employed to survey benthic habitats around Marion and Prince Edward Islands. This photographic sampling survey was conducted to align with a previous epibenthic photographic survey completed between 1984 and 1989. As marine photographic surveys have a propensity to underrepresent the species richness present, investigations into the optimal sampling intensity required per substrate type were conducted initially in order to ensure rigorous representative sampling. Historical photographic data of epibenthic assemblages in the upstream and downstream regions of the islands were then compared to data from the new photographic surveys to assess changes in regional species composition over time.

Due to the various challenges associated with using underwater photography as a sampling method, identifying an optimal photographic sampling intensity for the epibenthos at the PEIs was imperative to this study. To achieve this, species-area relationships were used in conjunction with substrate type to determine the number of samples needed for given thresholds of species representation to be reached. The asymptotic richness estimator Chao 2 was used to compare the species richness detected in an area to a statistical estimation of the possible total species present. The point where species accumulation curves started to decelerate was identified as the point where a 20% increase in samples results in <5% increase in the number of new species observed. Points of deceleration were subsequently compared among substrate types. Substrate type was not found to be an accurate predictor of epifaunal species richness at the PEIs. There was no difference in the species area curves among substrate

types and all curves accelerated at the same rate irrespective of substrate type. An average of 20 samples was required to reach a point at which at least 80% of the total asymptotic richness had been sampled. A strategy using this sampling intensity can, therefore, be applied across substrate types at the PEIs.

With the required sampling intensity determined, historical and resampling surveys in the upstream and downstream regions of the PEIs were compared. The Shannon-Wiener index indicated that diversity differed over time but did not differ between regions. In contrast, however, there were regional differences in Pielou's evenness index but no difference over time. There were significant differences in species composition between regions over time. The temporal differences in assemblages, however, were due to dispersion effects. The temporal change in benthic assemblages may mirror shifts in the prevailing primary productivity patterns at the islands. Climate-driven changes are thought to have caused variations in mesoscale oceanographic regimes and subsequent primary productivity patterns, which influence the benthos upon sinking. The photographic dataset compiled in this study provide the second permanent record of the epibenthic environment at the PEIs and will aid future monitoring studies in this region, especially in the face of imminent climate changes. The results of this study will advance the long-term understanding of the epibenthos at the PEIs.

Chapter 1: Introduction

1.1: General background

The importance of benthos to marine ecosystem functioning

Benthic ecosystem diversity, assemblage composition and distributions are controlled by a wide range of factors at different spatial and temporal scales and have high socio-economic value (Arntz et al. 1994; Snelgrove 1999; Levin et al. 2001; Thrush et al. 2006a; Glover et al. 2010). The diversity of benthic communities is crucially important in maintaining the health of ecosystems and in the provisioning of ecosystem services (Snelgrove 1999; Worm et al. 2012). The role of benthos in structuring ecosystems from the bottom up is central in maintaining ecosystem health as benthic assemblages form valuable trophic links to top predators such as fish, marine mammals and birds (Arntz et al. 1994; Moore et al. 2003; Simpkins et al. 2003; Smith et al. 2006). Benthic invertebrates also aid in nutrient cycling and oxygenation of sediments, where deposit feeding organisms, through burrowing and feeding, combine particulate organic carbon (POC) and oxygen within sediments (Snelgrove 1999; Rex and Etter 2010). The presence of these bioturbators may influence the abundance of organisms reliant on nutrients within sediments and thereby their presence or absence is important in structuring predator-prey interactions at the seafloor (Martinetto et al. 2005). Benthic organisms themselves also play an important role in increasing diversity, as habitat-forming species like large sponges and octocorals provide a source of food and increase habitat complexity and thereby the realised niches of many species (Ross and Quattrini 2007; Buhl-Mortensen et al. 2010, Wood et al. 2012).

Global processes affecting benthic species distributions

There are several well-established ecological patterns associated with biological assemblage distributions in the deep sea. One of these patterns is that light availability becomes limited with increasing depth, thereby reducing in efficiency and ultimately limiting the distribution of benthic primary producers (Rex and Etter 2010). Benthic communities are consequently reliant on production taking place near the surface (Grebmeier and Barry 91; Snelgrove 99; Smith et al. 2006; Thrush et al. 2006a). Surface productivity generates particulate organic matter (POM), which is mostly reprocessed within the aphotic zone by microbes and zooplankton grazing (Rex and Etter 2010, Perissinotto 1992). POM not grazed, sinks through the water column to provide a source of nutrients to benthic assemblages (Clarke 1988, Grebmeier and Barry 1991; Billett et al. 2001; Sumida et al. 2008). Due to variability in the amount of POM flux to deeper waters, there may be shifts in the composition of benthic communities across depth gradients (Barry et al. 2003). Additionally, due to limiting oxygen levels, limited light and restricted nutrients, very deep waters tend to be exceptionally energy deprived environments (Levin et al. 2001; Rex and Etter 2010). Primary production is also highly variable along geographic gradients, where areas of higher production are likely to be at higher latitudes and in coastal regions in which nutrient-rich upwelling occurs (Rex and Etter 2010). However, in other areas such as the Polar Regions, where reduced light availability limits production during winter months, primary production is highly seasonal (Clarke 1988; Clarke and Harris 2003). Primary production within the surface layers is, therefore, controlled by both spatial and temporal factors (Smith et al. 2006). Distributions of species and assemblages may be linked to these patterns of productivity (Dayton and Oliver 1977; Billett et al. 2001; Smith et al. 2006; Sumida et al. 2008) and productivity patterns can thus be used to improve understanding of observed ecosystem changes (Smith et al. 2006).

Habitat type may also be important in driving species diversity gradients, where the type of substrate influences the suite of organisms able to live in a given area (Smith et al. 2006; Schlacher et al. 2007; Levin et al. 2010; Compton et al. 2013). Certain sessile epifaunal organisms require hard substrates for attachment, while soft sediments are necessary for burrowing infaunal species. The species diversity of soft sediment communities is affected by the particle sizes of sediments, particularly for deposit feeders that are reliant on sediment type (Etter and Grassle 1992). Species richness may be reliant on the specific abiotic substrate features of an environment. Highly complex biogenic habitats tend to have high species diversity and as such are important in structuring species diversity gradients (Lindholm et al. 2004; Buhl-Mortensen et al. 2010; Nolan et al. 2017). Biogenic habitats are important in that they provide a source of shelter, or a point of attachment; additionally organisms are known to parasitise biogenic habitats or use them as a food source (Buhl-Mortensen et al. 2010). Habitat type can, therefore, be classified using a combination of factors, where the underlying substrate type influences the species diversity and may aid in the formation of biogenic habitats.

Many large-scale processes influencing diversity have been found to be affected, either directly or indirectly, by anthropological disturbances such as pollution or climate change. While this is decidedly true in many terrestrial environments, the deep sea was long thought to be a stable environment and not sensitive to disturbances taking place at the surface layer (Glover et al. 2010; Rex and Etter 2010). This is a misconception, as has been demonstrated by research on changes in ice cover in the Antarctic, where benthic diversity has increased following ice shelf collapse and the subsequent increase in availability of POM to the benthos (Massom and Stammerjohn 2010; Gutt et al. 2011). Changes in climate and subsequent changes in sea surface temperature have been found to influence primary productivity and subsequent nutrient flux to the deep sea, thereby influencing the diversity of benthic assemblages (Clarke and Harris 2003; Brown et al. 2010; Hoegh-Guldberg and Bruno 2010;

Ramirez-Llodra et al. 2011; Doney et al. 2012). As climate changes occur over decadal timescales it is imperative that long-term studies of benthic assemblages be implemented, particularly in light of the importance of the benthos to ecosystem function (Josefson 1990; Billett et al. 2001; Ruhl and Smith 2004; Ruhl 2007; Glover et al. 2010).

1.2: History and trends in benthic ecology research

The need for novel sampling techniques

The study of terrestrial ecosystems is different from that on marine benthic systems in that terrestrial habitat types and species assemblages are readily visible and community structure and influences thereon can be more directly observed and tested. The deep sea is the most understudied system on earth with 95% of the oceans as yet unexplored (Ramirez-Llodra et al. 2011). It is often difficult to determine the organisms comprising assemblages and the manner in which they are structured. This is due to the depths at which these communities exist as well as the time and cost of the specialised equipment needed to access and view these systems (Snelgrove 1999; Solan et al. 2003). The marine benthic environment is, therefore, extremely difficult to study and sampling apparatus has, until recently, been blindly dropped into what was presumed to be a relevant habitat (Rex and Etter 2010). Benthic sampling methods have traditionally relied on physical samples taken from dredges, trawls and grabs. These methods are, however, unable to determine the underlying assemblage structure present in seafloor habitats as organisms obtained are analysed without the context of their original habitat (Solan et al. 2003). Additionally, these methods are destructive and not ideal for large-scale sampling because valuable biogenic structures from assemblages may be removed or damaged, which is particularly problematic in sensitive habitats (Sheehan et al. 2010; Beisiegel et al. 2017). As sampling that collects physical specimens is more efficient on soft substrates, apparatus better suited to sampling on hard substrates is needed to study benthic assemblages

(Branch et al. 1993a; Strong et al. 2006; Williams et al. 2015). Assessments of offshore benthic assemblages have, therefore, lagged behind those of other biological systems due to the extreme technical difficulties associated with surveying and sampling deep underwater assemblages (Hoegh-Guldberg and Bruno 2010).

Non-destructive sampling techniques are able to detect spatial patterns and relationships between the characteristics of the physical habitat and the benthic assemblages. Underwater imagery has recently begun to offer promising possibilities for developing innovative insights into community structure as it is able to contextualise relationships among species (Adams et al. 1995; Solan et al. 2003; Williams et al. 2015). Photography as a sampling strategy is relatively non-destructive and hence ideal for repeat surveys in sensitive areas or areas that allow only limited destructive sampling methods such as Marine Protected Areas (MPAs) (Teixidó et al. 2002; Solan et al. 2003; Knight et al. 2014; Williams et al. 2015).

Photography as a sampling method

Photography has been used in assessing the impacts of trawling on ecosystems (Roberts et al. 2000; Lindholm et al. 2004; Althaus et al. 2009), for surveys of MPAs (Stevens and Connolly 2005), and is a valuable tool in estimating the richness and diversity of epibenthic communities (Roberts et al. 2000). Despite limited use of repeat photography to track long-term changes in deep marine benthic environments, repeat photography has been used to visualise long-term changes in the size of glaciers, vegetation cover and in populations of distinct terrestrial species (Reimers et al. 2014). Additionally, changes in habitat structure can be visualised using photographic comparisons of historical and resampled states. Photographic comparisons of intertidal rocky shores have been valuable in visualising the impacts of alien species (Reimers et al. 2014). Photography has also been instrumental in determining habitat degradation on a large scale, with comparisons of historical and resampled aerial photographs

of coral reefs being used to assess the scale of coral bleaching (Sweatman et al. 2011; De'ath et al. 2012; Andréfouët et al. 2013). The use of photography to track changes in habitat or population structure over time has, therefore, been successfully applied in both terrestrial and marine systems.

Photography of marine epibenthic assemblages requires that the design of the camera apparatus matches the conditions of the sampling environment. Factors such as depth, topography, oceanographic environment and the total area of sample sites should be considered when applying a photographic sampling approach (Barker et al. 1999). Due to the depths at which offshore benthic assemblages exist, it is not possible to use diver surveys as the depths exceed the limits of SCUBA. By implication, camera systems cannot be handheld and must be remotely operated or towed behind a ship. Sampling with towed camera imaging systems is beneficial in that sampling can be undertaken with fewer destructive impacts (Teixidó et al. 2002), which is especially valuable in MPAs where research is closely monitored in order to limit damaging research impacts. Photographic sampling has an added benefit in that photographs can be analysed by multiple biologists to answer a diverse array of questions, eliminating diver bias generated through sampling by untrained individuals, and provides a permanent record of community structure (Stobart et al. 2007).

A typical caveat of photographic sampling methods is that the true number and diversity of species in a community may be underrepresented as only organisms that are discernible in the photographs can be counted (Roberts et al. 2000; Solan et al. 2003). Species that are too small to be seen, infaunal species and species that are able to actively avoid the camera, are often overlooked (Thistle 2003). Additionally, identification of species in photographic sampling is often difficult if specimens for identification purposes are not collected simultaneously with photographs (Solan et al. 2003; Thistle 2003). Image analysis can also be extremely time consuming (Parravicini et al. 2009) and it is therefore necessary for sampling

methods to be optimised. The need to ensure accurate species representation and optimisation of sampling methods means that careful consideration of equipment and image-sampling procedures is required. The costs associated with sampling multiple environments means that there is increased pressure to take as few samples as possible while still ensuring the scientific integrity of the data. The species area relationship (SPAR), whereby the number of species detected increases with area until all possible species have been found, has proven to be beneficial in determining the quadrat size or the best total sampling area necessary to obtain an accurate representation of the species present (Connor and McCoy 1979; Barbour et al. 1987; Kipson et al. 2011). SPAR is thus an important factor to consider when determining the optimal number of photo-replicates needed to ensure an acceptable level of species representation (Kipson et al. 2011).

In South Africa, capacity in underwater photographic methods has grown with remotely operated vehicles (ROV), baited remote underwater video (BRUV) and towed benthic cameras allowing studies to be conducted in regions that are not accessible through SCUBA surveys (Bernard et al. 2014). ROVs can be deployed in deep waters and can remain underwater for long periods of time, however ROVs require trained technicians and are costly to operate (Knight et al. 2014). BRUVs are most suited to determining population numbers of mobile predatory taxa (Bernard et al. 2014). The South African Environmental Observation Network (SAEON) recently acquired a deep-water towed benthic camera system for the purposes of underwater surveys, long-term monitoring and trawl impact studies. This towed camera system has high definition video and photographic capabilities and is, therefore, ideal for surveying and recording epibenthic taxa of deep offshore sites at a lower cost than many other types of apparatus.

1.3: The Prince Edward Island archipelago

The Prince Edward Island (PEI) group (46°50'S and 37°50'E) is made up of two volcanic islands situated 2000 km southeast of South Africa and 950km west of the Crozet Islands (Fig. 1). These sub-Antarctic islands are positioned within an area of elaborate seafloor topography and lie in the pathway of the Antarctic Circumpolar Current (ACC). Marion Island has an area of approximately 270km² and is 19km southwest of the smaller Prince Edward Island, which encompasses a total area of 45km². A shallow basin, ranging in depth between 40-200m, separates these two islands. The Prince Edward Island group was claimed as a South African territory in 1947 and declared a Marine Protected Area (MPA) in 2013 (Lombard et al. 2007). The commercial Patagonian Toothfish fishery is the most noteworthy non-research activity occurring within the islands' exclusive economic zone (Pakhomov and Froneman 1999; Lombard et al. 2007; Chown and Froneman 2008b). However, sanctioned fishing does not occur within 22 km of the islands in accordance with the Marine Living Resources Act of 1998 (Chown and Froneman 2008b). Since adult fish have a bathymetric distribution below 1000m, both sanctioned and unsanctioned fishing are unlikely to have occurred in the shallower island region (Collins et al. 2010). The islands are, therefore, protected from direct human influences and are an ideal research site for both terrestrial and marine ecologists. The South African research base on Marion Island is home to a team of overwintering scientists, many of who research the island's large populations of top predators including penguins, seals and flying seabirds. The food resources of the highly productive marine environment sustain these large numbers of breeding predators (Ryan and Bester 2008). There is a known 'island-mass effect', where increased residence time of water masses in the shallow saddle between the islands, compounded by nutrient runoff from islands, facilitates large seasonal phytoplankton blooms in the downstream and inter-island region of islands (Boden 1988). These mesoscale

oceanographic conditions are reliant on the position and flow dynamics of the ACC and its associated frontal systems.

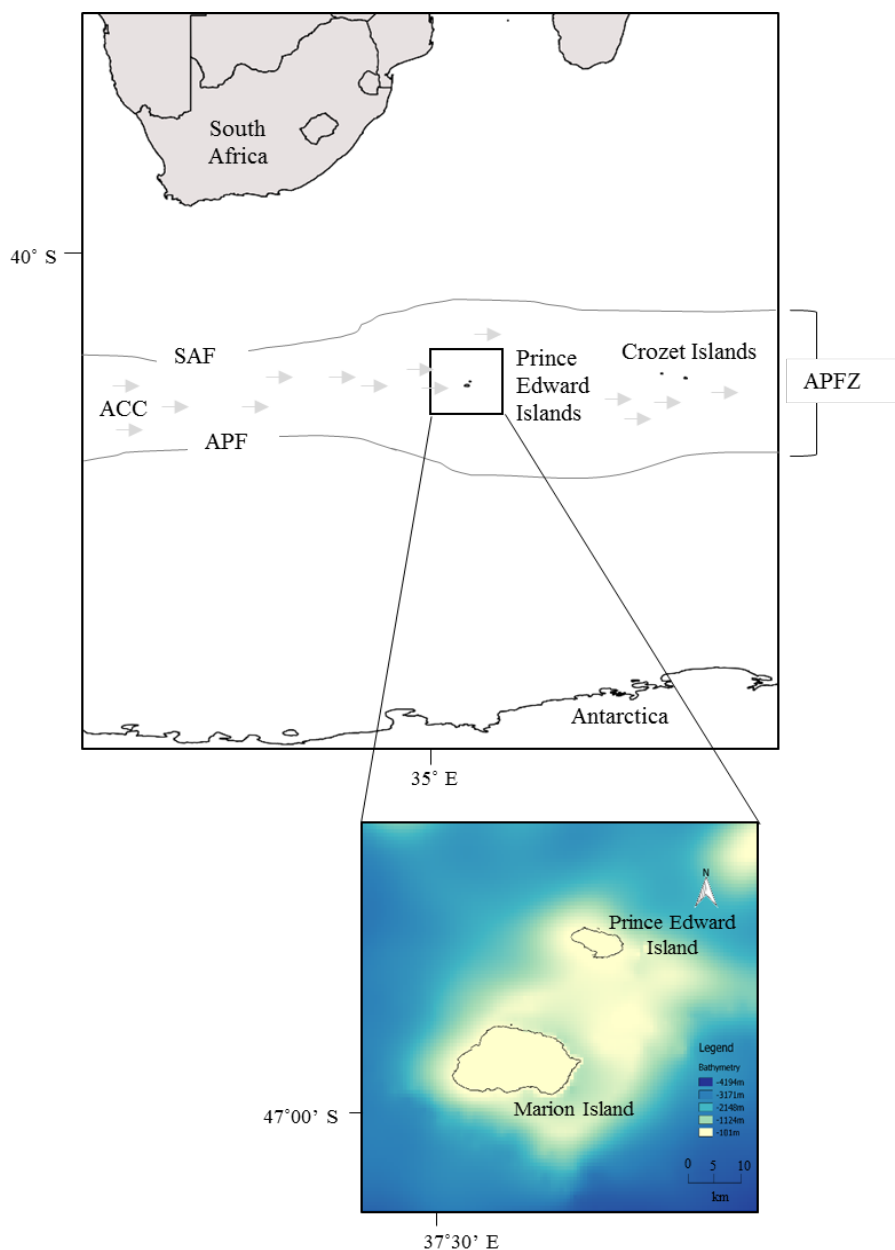


Figure 1.1 Position of sub-Antarctic Prince Edward Islands in relation to the closest landmasses in the Southern Indian Ocean (South Africa, Crozet Islands and Antarctica). The approximate positions of the two major fronts associated with the Antarctic Circumpolar Current (ACC) in relation to the PEIs are shown: the sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF). The direction of the ACC is illustrated by the grey arrows while the Antarctic Polar Frontal Zone (APFZ) is shown by the bracket.

Between the 1960s and the 1990s, there has been a 1.2°C increase in air temperature on the islands (Sumner et al. 2003). Due to the impending impacts of climate change at sub-Antarctic islands (Smith 2002), it is imperative that continuous monitoring studies be undertaken in order to study the effects such changes may have on benthic community structure. Additionally, there has been limited research on the sub-Antarctic benthos at the Prince Edward Island archipelago (Lombard et al. 2007) and most research to date has been conducted using destructive sampling methods such as dredges (Branch et al. 1993a; Kaehler et al. 2000; Allan et al. 2013). Few studies included non-destructive sampling methods, but Beckley and Branch (1992) studied the sublittoral benthos in three areas using SCUBA surveys, while deeper waters were surveyed photographically in the 1980s by Branch et al. (1993a). These two studies recorded highly diverse inter-island epibenthic assemblages.

Higher air temperatures on southern ocean islands have been coupled with changes in weather conditions at the islands as well as an approximate 1.4°C increase in sea surface temperatures between 1953 and 2003 (Smith 2002; Mélice et al. 2003). Sea temperature fluctuations due to changing climate tend to change zooplankton community structure, thereby changing zooplankton grazing patterns and influencing the amount of POC flux to the benthos (Kirby et al. 2007). Additionally, temperature is important to the growth of invertebrate larvae and influences larval dispersal and settlement (Harley et al. 2006; Kirby et al. 2007). Changing temperatures may result in species range shifts as well as changes in species interactions and life history traits (Harley et al. 2006; Doney et al. 2012) which are expected to affect benthos abundance and distributions (Harley et al. 2006, Doney et al. 2012). Information on the present state of benthic habitats, based on rigorous sampling methods, is therefore needed so that climate change effects may be reliably identified and appropriate management actions implemented. This understanding is crucial for the conservation of representative species,

habitats and ecosystem functioning within pristine areas such as the PEI MPA (Lombard et al. 2007).

Physical oceanographic conditions of the Prince Edward Island archipelago

Marion and Prince Edward Islands are situated directly within the Antarctic Polar Frontal Zone (APFZ) which is bordered by the Sub-Antarctic Front (SAF) in the north and the Antarctic Polar Front (APF) to the south (Fig. 1) (Ansorge and Lutjeharms 2002). These two frontal systems, associated with the ACC, form a barrier between colder Antarctic surface water and warmer sub-Antarctic surface water with a transitional zone known as the Antarctic Polar Frontal Zone (APFZ) (Ansorge and Lutjeharms 2002; Ansorge et al. 2012). The fronts separating these two water masses are not static and their highly variable nature is crucial to the formation of the small and large scale oceanographic conditions around the islands (Ansorge and Lutjeharms 2002). The northern front, the SAF, is of particular importance within this system. The position of the ACC and its related frontal systems have been found to be gradually shifting southwards in response to climate changes (Hunt et al. 2001; Gille 2002; Downes et al. 2011). This has resulted in an alteration in the flow rate of the ACC within the APFZ (Downes et al. 2011). The three regions around the PEIs, the upstream region (west of Marion Island); the inter-island region (between the two islands) and the downstream region (east of Marion Island) are likely to experience different inflows of primary production dependent on the position of the SAF and the subsequent variations in oceanographic conditions (Boden 1988; Perissinotto and Duncombe Rae 1990; Pakhomov and Froneman 2000; Perissinotto et al. 2000; Durgadoo et al. 2010).

There tend to be short-term variations of the location of the main oceanographic fronts associated with the PEIs. In instances when the northern front, the SAF, is further north of the islands, the APFZ will be broader and the region is dominated by strong frictional forces as a

result of weak interactions between the islands and slower moving currents (Pakhomov and Froneman 1999; Pakhomov et al. 2000a; Ansorge and Lutjeharms 2002). The interactions between the islands and the ACC, as well as the interplay between the frontal systems and complex bottom topography, are crucial in the formation of anti-cyclonic eddies in the shallow basin separating Marion and Prince Edward islands as well as in the downstream region (Perissinotto and Duncombe Rae 1990; Froneman and Pakhomov 1998; Ansorge et al. 1999; Durgadoo et al. 2010). These eddies increase the residence time of water bodies within the inter-island region. The terrestrial environment of the Prince Edward Islands is characterised by strong winds, high precipitation and sub-Antarctic temperatures (Smith and Lewis Smith 1987). The high levels of rainfall on the islands (Smith and Lewis Smith 1987) result in a large nutrient input into the marine environment, largely through guano enriched runoff from the large numbers of breeding predators on the islands and nearshore kelp detritus (Perissinotto and Duncombe Rae 1990; Kaehler et al. 2006; Treasure et al. 2015). This characteristic situation of a retained water body resulting from eddies and nutrient input has typically resulted in large phytoplankton blooms being generated in the shallow basin between the two islands (Boden 1988; Perissinotto and Duncombe Rae 1990; Hunt et al. 2001; Kaehler et al. 2006; Treasure et al. 2015). The plankton biomass in the inter-island region may, therefore, be up to three times higher than that found in the open ocean (Pakhomov and Froneman 2000; Pakhomov et al. 2000b). However, the zooplankton communities at the islands consume <10% of the phytoplankton generated during bloom conditions resulting in a large amount of phytoplankton being made available to the benthos via sedimentation (Perissinotto 1992). Under these conditions, food quality increased in the downstream and inter-island regions (Allan 2011), which may benefit from kelp detritus in addition to phytoplankton (Kaehler et al. 2006; Allan 2011).

When the SAF is closer to the islands, and the APFZ is narrower, there is a weaker interaction between the oceanographic conditions and the islands themselves. In these instances, flow-through conditions become dominant, and residence times of water masses are short lived (Pakhomov and Froneman 1999; Perissinotto et al. 2000). Eddies and subsequent phytoplankton blooms have been found to be less intense. In the absence of strong nutrient retention and decreased Chlorophyll-a concentrations, there is a transition toward allochthonous production where planktonic food sources are brought into the island region through the movement of the ACC (Perissinotto et al. 2000; Hunt et al. 2001; Allan et al. 2013). Benthic communities may, therefore, become more reliant on primary production originating in the ACC (Allan 2011). The presence of phytoplankton species originating from blooms, and zooplankton species common to the inter-island region, in the downstream region is strong evidence for the direction of movement of water masses (Pakhomov et al. 2000b). Further evidence of the direction of water movement is seen in the presence of zooplankton species of Antarctic origin within the APFZ that had been displaced due to the formation of eddies (Bernard et al. 2007). The changing position of the SAF is, therefore, influential in the formation of productivity regimes at the PEIs and can have direct ecological consequences for this sub-Antarctic MPA (Hunt et al. 2001; Allan et al. 2013). In other systems, direct effects of long-term variations in nutrient supply to the benthos has been known to alter the abundance of benthic organisms (Ruhl 2007). Because of this, the epibenthic assemblages in the upstream region of the island (West) may have developed a different composition to the benthos downstream (East) and in the inter-island region over time.

The study of the benthos within the PEI region is important as benthic assemblages provide not only a direct indication of regional productivity, but also form an important component within marine food webs. For example, the benthic shrimp *Nauticaris marionis* is

a major component of the diet of Gentoo (*Pygoscelis papua*), Macaroni (*Eudyptes chrysolophus*) and Rockhopper (*Eudyptes chrysocome*) penguins as well as Imperial Cormorants (*Phalacrocorax atriceps*) and Crozet shags (*Phalacrocorax melanogenis*) (Arntz et al. 1994; Crawford et al. 2014). *Nauticaris marionis* has also been found to be a major dietary component of sea-stars (Perissinotto and McQuaid 1990) and, along with epifaunal polychaetes, forms an important food resource for the nototheniid fish, *Gobionotothen marionensis* (Blankley 1982; Bushula et al. 1998; La Mesa et al. 2004). Conversely, these benthic shrimps have been found to feed primarily on benthic suspension feeders (Perissinotto and McQuaid 1990; Vumazonke et al. 2003). The fact that both the bottom dwelling shrimp and the nototheniid fish are important prey species for inshore feeding pelagic predators indicates a vital link between benthic assemblages and pelagic predators at the Prince Edward Islands. Changes in the structure of benthic assemblages due to decreasing primary productivity may, therefore, have effects on population sizes of top vertebrate predators at sub-Antarctic islands (Weimerskirch et al. 2003; Allan et al. 2013; Crawford et al. 2014). Epibenthic assemblages are, hence, an important trophic link at the Prince Edward Islands and changes in the composition of the assemblages should be closely monitored in order to prevent bottom up effects to ecosystem functioning.

The underlying need for this research

Increases in Southern Ocean sea surface temperatures have been recorded (Mélise et al. 2003; Rhein et al. 2013) and along with sea surface height and salinity, have indicated a poleward shift in the ACC and the disruption of regional primary productivity patterns (Gille 2008; Allan et al. 2013). As benthic assemblages are crucial to the health of ecosystems and the maintenance of food web structures, it is necessary to determine whether the benthos is changing, as well as the magnitude of these changes (Smith et al. 2006; Allan et al. 2013).

There is, therefore, a need to establish baseline conditions at the Prince Edward islands using non-destructive monitoring techniques against which future impacts, including those due to climate change, can be measured (Lee and Chown 2009). This would enable managers to make informed decisions regarding this highly complex system. Photography of benthic habitats can potentially serve as a tool for acquiring such information to support management actions for protected marine ecosystems (Stevens and Connolly 2005, Schlacher et al. 2010, Kipson et al. 2011, Beisiegel et al. 2017), as permanent photographic datasets can be constructed (Parravicini et al. 2009). The current situation at the PEIs is unusual in that historical benthic photographs captured between 1984 and 1989 (Branch et al. 1993a) can be compared to current and future studies. Due to the unique oceanographic setting and their status as an MPA, the Prince Edward Island group offers an ideal system to study long-term ecological changes in epibenthic assemblages.

1.4: Overall aims

This project has the overarching aim of assessing present day epibenthic assemblages around the PEIs to provide a comprehensive baseline dataset that will enable informed decisions to be made regarding the future conservation of this MPA and improve our understanding of benthic ecology and responses to long-term change. To achieve this, underwater photography was employed to survey epibenthic assemblages and the following sub-aims were addressed:

- 1) To determine the optimal number of photographs required for a representative sample of epibenthic diversity in different substrate types at the Prince Edward Islands (Chapter 2). These results then informed the methods adopted in Chapter 3 and will enable future studies to optimally allocate scarce research resources in a way that secures representative data from these offshore assemblages.

2) To determine whether there has been a change in the species composition and abundance of epibenthic assemblages in two regions (upstream and downstream) in light of notable changes in various biological and oceanographic systems around the Prince Edward Islands over time. This was accomplished in Chapter 3 by comparing modern photographic samples with equivalent historical photographs obtained in 1984-1989.

Chapter 2: Species curves and determining an optimal sampling intensity

Abstract

The complexity of benthic substrates is one of several factors affecting species richness of epibenthic assemblages and is likely to influence the species area relationship (SPAR). Recently, underwater photography has been applied to non-destructively sample sensitive seabed areas. Photographic sampling, however, may underrepresent total species richness. This study tested the SPAR across substrate types to identify an optimal photographic sampling intensity for benthic habitats at the Prince Edward Islands (PEIs). Based on these results, recommendations for an optimal sampling intensity at the PEIs could be advanced. Species accumulation curves were constructed for 13 sites that represented four pre-defined substrates. The points of deceleration and total estimated asymptotic richness (Chao 2 richness estimator) were determined for each accumulation curve and compared among substrates. The effect of substrate type on the average rates of species accumulation was tested. No significant differences were detected between the points of deceleration, total asymptotic richness, and rate of species accumulation among substrates. Sampling an average of 20 (± 4.7 SD) photographs ($\sim 15\text{m}^2$ transect) per site was identified as an appropriate sampling intensity in this region, as 80% of species were identified at this point. Sites with fewer species may require more samples than species-rich sites, as such sites took longer to reach the points of deceleration. Results suggest that substrate type alone was not considered to be a strong predictor of species richness, and habitat-forming biological assemblages should be characterised in addition to substrate type. The determination of an appropriate sampling intensity in this study is important for ongoing monitoring at the islands, where it may be more profitable to sample more sites at a lower sampling intensity than few sites at a high intensity.

2.1: Introduction

Factors regulating species richness in benthic assemblages

Benthic assemblage richness is known to be determined by a variety of abiotic factors (Levin et al. 2001; Rex and Etter 2010). Over large scales these factors include oceanographic regimes and regional productivity patterns (Dayton and Oliver 1977; Levin et al. 2010; Rex and Etter 2010). At a local scale, species richness can depend on habitat complexity, which may primarily be reflective of substrate type, as well as habitat-forming biota dependent on specific abiotic substrates (Smith et al. 2006; Schlacher et al. 2007; Zajac 2008; Levin et al. 2010; Compton et al. 2013; Nolan et al. 2017). More complex abiotic substrates may have an increased species richness as species are able to share space due to the diversity of niches available (Bazzaz 1975; Douglas and Lake 1994; Levin et al. 2010). Substrate type is known to affect assemblage composition as certain groups of benthic epifauna; for example, Octocorallia require hard substrates for attachment (Mortensen and Buhl-Mortensen 2004). Deposit feeders are reliant on organic matter within soft sediments for nutrition and selectively consume particles of particular sizes (Etter and Grassle 1992). The substrate type of a specific site is, therefore, important in community assembly and it is imperative that underlying substrates are classified before surveys and analyses begin (Thrush et al. 2006b).

Species area relationships

A well-established pattern in ecology is that the number of new species discovered will increase as the area sampled increases, until the point where all possible species in the area have been detected (Arrhenius 1921; Schoener 1976; Connor and McCoy 1979). This curvilinear relationship between area and the number of species is known as the species area relationship (SPAR). This increase in the total number of species comes about as larger areas

tend to have a greater number of habitat types, thereby supporting species suited to a variety of niches as well as the higher probability of encountering a species not yet sampled (Scheiner 2003). The general species area relationship can be represented in two ways, either through a species area curve or a species accumulation curve, both representing ways of statistically representing the number of species in a given habitat. Species accumulation curves differ from species area curves as in the former, the observed species are not necessarily plotted against area but rather against some measure of sampling effort, such as numbers of quadrats (Colwell et al. 2004), or in the case of this study, numbers of photographs. The curves also differ in that species accumulation curves take the identity of the recorded species into account while species area curves simply log the number of new species found, irrespective of organism identity (Ugland et al. 2003; Thrush et al. 2006b).

The relationship between the number of species recorded in an area and the area sampled has been applied in various ways (Neigel 2003; Scheiner 2003; Kipson et al. 2011; Foster et al. 2013). Species curves are commonly used in conservation planning during the design of nature reserves and Marine Protected Areas (MPAs) (Neigel 2003, Desmet and Cowling 2004, Foster et al. 2013), especially those facing rapid size reductions (Connor and McCoy 2001). This is done in order to set conservation priorities, to maintain species representativeness, and to protect vulnerable populations (Neigel 2003; Desmet and Cowling 2004). Additionally, these curves have been used by ecologists to determine the optimal quadrat or sample size when designing sampling methodology and, more recently, to determine the minimum number of samples in coral reef communities to capture significant change in assemblages (Connor and McCoy 1979, 2001; Barbour et al. 1987; Scheiner 2003; Kipson et al. 2011).

Asymptotic richness estimators

Using species richness as a comparison tool is not always ideal in that the observed number of species usually falls short of the true species richness (Longino et al. 2002; Gotelli and Colwell 2011; Colwell et al. 2012). Asymptotic richness estimators provide one method of handling this problem and have typically been applied to systems where the species accumulation curve does not reach an asymptote (Gotelli and Colwell 2001). These estimators are a statistical tool to approximate the total species present and those not yet sampled in an area (Chao et al. 2009). Richness estimators are beneficial in that they give estimations of how much sampling is needed to reach an acceptable level of representation of species richness (Basualdo 2011). There are various non-parametric estimators of asymptotic richness that can be utilised to approximate the total species present in a sample. The estimator Chao 2, which makes use of replicated incidence-based data, is one such measure and takes into account rare species as well as the total species in the sample, to estimate the total richness of a sample (Chazdon et al. 1998; Chao et al. 2009; Basualdo 2011). This richness estimator is, therefore, valuable in the description of assemblages within heterogeneous habitat types (Chao 1987; Yurkov et al. 2011) and has been found to be an accurate predictor of species richness (Colwell and Coddington 1994).

Species area relationships and photography

Deep benthic habitats are not easily sampled and destructive sampling methods such as dredges, grabs, sleds and trawls are often used, but inevitably miss *in situ* species-species interactions and associations (Solan et al. 2003; Knight et al. 2014; Williams et al. 2015). Non-destructive sampling methods are more appropriate for sampling in sensitive habitats such as the Prince Edward Island MPA. Underwater photographic sampling methods have recently begun to be used more frequently in sensitive areas despite concerns that the sampling methods

may under-represent the species richness of the sampled area (Teixidó et al. 2002; Solan et al. 2003; Knight et al. 2014; Williams et al. 2015). There are often both cost and time constraints to photographic sampling, and there is a requirement for photographic sampling to be optimised. As with physical sampling techniques, SPAR can be used to determine the optimal number of sample photo-replicates needed to obtain an accurate representation of the diversity of an assemblage. A photo-replicate may be an accurate representation of the area sampled in that the total sampled area can be calculated from a known frame size or points within the frame that are a known distance apart (Strong et al. 2006). A single photo-replicate can, therefore, be equated to a quadrat and the total area sampled related to the total number of standardized photo-replicates analysed (Scheiner 2003).

The photographic survey conducted in this study provides a baseline photographic dataset that can inform long-term studies on the benthic environment of this region. As photo-sampling could potentially under-represent the taxa present in an environment, it is important that the photo-sampling method is tested. Testing the number of photo replicates required to produce a reliable SPAR in various substrate types will ensure that studies at the PEIs obtain sufficient samples to satisfy appropriate species representation. Species area relationships should be determined for different substrate types, as substrate type may be a strong predictor of species richness. The aim of this component of the study is to utilise photographs from various sites with different substrate types and calculate the species area relationship to optimise sampling strategies at the PEIs. In addressing the stated aim, two hypotheses were tested: 1) the estimated total species richness will differ among substrate types, and 2) the rate of species accumulation will be affected by substrate type. The results of this chapter will inform the sampling design for Chapter 3 of this thesis and optimise future photographic sampling within the Prince Edward Island archipelago.

2.2: Methods

Photographic surveys of sub-Antarctic epibenthic assemblages were conducted at sites around the Marion (-46°45'S, 37°50'E) and Prince Edward Island (-46°38'S, 37°56'E) group aboard the *SA Agulhas II* during annual voyages in April - May of 2013 and 2015. Photographic sites were chosen based on a sub-set of locations sampled photographically between 1984 and 1989 and described by Branch et al. (1993a). The selection of historical sites was chosen based on four *a-priori* defined substrate types namely mud, gravel, gravel-mud, and partial rock-sand (Fig. 2.1, Table 2.1, Appendix A Plate 1). Logistical constraints resulted in substrate types being represented by an uneven number of sites and not all sites could be sampled in the same year. Still images were captured using a towed camera system, the SAEON *Ski-Monkey III*. The camera was mounted at a 30° angle and at an approximate height of 90cm above the substratum. Within the custom-built waterproof housing, a Canon DSLR 550D digital camera captured both HD video and high-resolution still images (18 megapixel). The camera housing was equipped with two on-board LED lamps to illuminate the sea floor. All camera work was undertaken between sunrise and sunset due to vessel regulations applicable in close proximity to the islands. The camera was lowered off the stern of the ship by a stainless steel electro-mechanical sea cable that incorporates two copper conducting cores. The conducting cores enabled the camera settings and shutter to be controlled from the surface in response to a live feed, viewed on a computer screen. At each site the camera was towed behind the vessel for twenty minutes while the ship moved at a speed of 0.5 knots along approximately the same depth contour, giving a transect length of about 300m. During each twenty minute transect, non-overlapping photographs were taken along the entire transect length opportunistically, as visibility permitted.

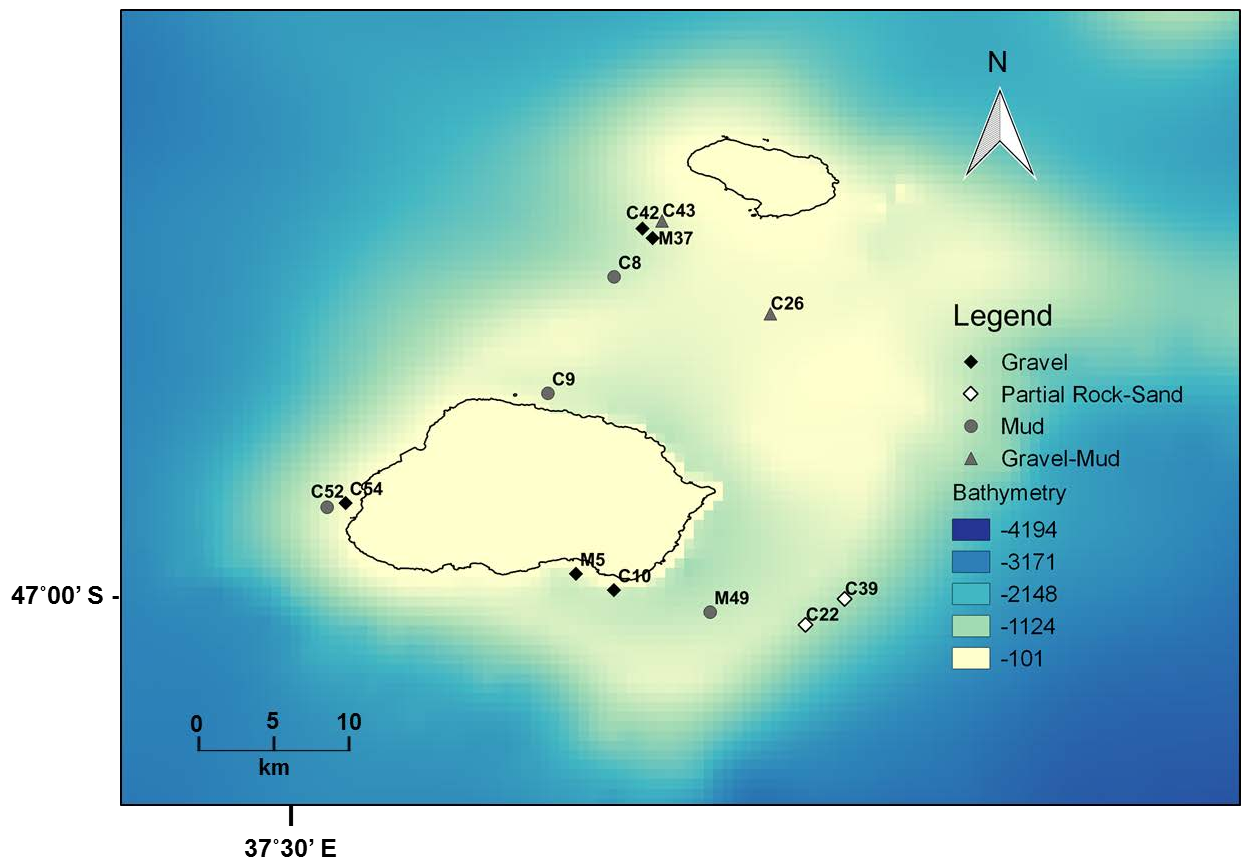


Figure 2.1 Location of sites sampled at the Prince Edward Islands. Pre-defined substrate types are represented by symbols, and colour intensity reflects different depths (m).

Table 2.1 Location, depth and the defining biological features of sites grouped by substrate type

<i>Substrate</i>	<i>Site</i>	<i>Depth (m)</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Average Transect area (m²)</i>	<i>Defining biological groups</i>
Mud	C52	383m	46 55.03°	37 34.03°	1.97	Hexacorallia, Bryozoa, Octocorallia, Hydrozoa
Mud	M49	283m	47 00.83°	37.9°	1.99	Malacostraca, Hexacorallia
Mud	C8	299m	46 43.02°	37 48.99°	3.86	Bryozoa, Polychaetae, Ophiuroidea, Octocorallia
Mud	C9	80m	46 49.09°	37 45.54°	1.93	Algae, Polychaeta, Bryozoa
Gravel-Mud	C43	225m	46 40.10°	37 51.49°	1.13	Bryozoa, Polychaeta, Porifera, Ophiuroidea
Gravel-Mud	M26	182m	46.75°	37.95°	1.95	Bryozoa, Hexacorallia, Brachiopoda
Gravel	M5	61m	46.98°	37.78°	2.09	Polychaeta, Hydrozoa, Hexacorallia
Gravel	C54	62m	46 54.81°	37 34.99°	1.78	Algae, Porifera, Hydrozoa
Gravel	C10	79m	46 59.35°	37 48.98°	1.88	Algae, Polychaeta, Hydrozoa
Gravel	M37	338m	46 68.33°	37.85°	1.93	Bryozoa, Polychaeta, Porifera
Gravel	C42	512m	46 40.50°	37 50.47°	1.78	Bryozoa, Hexacorallia
Partial rock- Sand	C39	403m	46 59.81°	38 01.04°	1.93	Bryozoa, Octocorallia, Ophiuroidea
Partial rock- Sand	C22	420m	47 01.16°	37 58.97°	1.41	Bryozoa, Porifera, Octocorallia

Image analysis

The camera was equipped with three lasers in a triangular configuration, a known distance apart (50cm at the base of the triangle). The three laser positions enabled image scaling and calculation of the total ground area in benthic photographs during photo-analysis, where the average size of the area of the photograph analysed was 0.83m² (\pm 0.12 SD). Prior to photo-analysis, sites were visually characterised and grouped into four substrate types out of the full range of all possible substrate types that may be present in the region. The four sampled substrates were categorised by classifying the two most common sediment types visible as the primary sediment type (encompassing >50% of the sample area) and, where present, the secondary sediment type (second most abundant sediment form). This technique was adapted from the method of sediment classification described by Knight et al. (2014), which was modified from Greene et al. (1999), in that the present study did not include the relief of samples. Photographic examples of each substrate type classified in this study are visually represented in Appendix A Plate 1.

The 30 degree oblique angle of the camera relative to the substratum enabled photographs to have a wider field of view than photographs taken perpendicular to the substratum (Wakefield and Genin 1987). This, however, was problematic when scaling the photographs as the area photographed in oblique images changes substantially with small changes in the orientation of the camera relative to the substratum. To overcome this issue, a calibrated grid of a constant size was overlaid on each photograph using the photo-analysis software CPCe to standardize the area analysed in each photograph (Kohler and Gill 2006). All images in each transect were reviewed and poor quality images removed. Usable images were limited to those where laser points were clearly visible and where sediment clouds did not obscure biota to any great degree. The total number of usable images differed among sites but a standardized maximum number of 33 images were analysed per site for construction of

species accumulation curves. Identification of biota was conducted from photographs and, where possible, confirmed using specimens collected in the same area by other researchers. All epibenthic organisms (> 1cm) were identified to species level where possible using Branch et al. (1991a, 1991b); Branch and Williams (1993); Branch et al. (1993b); Branch (1994); Branch and Hayward (2007). Following Davies et al. (2014) unknown taxa or taxa that could not be identified to species level in the photographs were separated into coded morpho-species.

Data treatment and statistical analysis

Sample-based species accumulation curves of mean species richness were constructed with 100 random permutations using incidence data in the statistical program EstimateS V9.1 (Collwell 2013). Species accumulation curves (Mao Tau) with non-overlapping $\pm 95\%$ confidence intervals were plotted against the sampling intensity (number of independent benthic images) for each substrate type. The non-overlapping $\pm 95\%$ confidence intervals of the sample based rarefaction curves were used to determine whether there were statistical differences at the tail end of curves (MacGregor-Fors and Payton 2013). To determine the point at which only a few new species were yet to be added, the points of deceleration were calculated. When a species accumulation curve starts to decelerate most of the species in a sample have been observed (Brandão et al. 2014). This point of deceleration is identified as the point where a 20% increase in the number of samples results in a less than 5% increase in the number of new species observed (Hortal and Lobo 2005; Kipson et al. 2011). Deceleration data were tested for normality and equal variances by using a P-P plot. The numbers of samples at which the points of deceleration of each curve were reached were compared across substrate types using a Kruskal Wallis one-way ANOVA.

Total estimated richness was calculated for each site following Chao et al. (2009) (see Appendix B for details). A Kruskal Wallis one-way ANOVA was conducted to determine whether the estimated Chao 2 asymptotic richness differed among sampled substrate types.

To test whether substrate type (categorical predictor) affected the relationship between observed species richness (dependent variable) and sampling intensity (continuous predictor), an analysis of covariance (ANCOVA) was conducted on sites grouped by substrate type. Sampling intensity and species richness data were log-log transformed in order to linearize the relationship (Rahbek 1997). The homogeneity of slopes of the log-log transformed data was tested, as was the homogeneity of variances, using a Cochran C Test (Quinn and Keough 2002). *Post hoc* Newman Keuls tests were used to determine significant differences in mean species richness among substrate types. All statistical analyses were conducted using Statistica V13 (Statsoft 2015).

2.3: Results

Species accumulation curves and points of deceleration

Several species accumulation curves within each substrate type had large degrees of overlap in their confidence intervals (Fig. 2.2). Likewise, there was considerable overlap in confidence intervals across substrate types. Confidence intervals of both partial rock-sand sites and the site with the highest species richness in the gravel-mud (C43) and mud substrates (C8) overlapped (Fig. 2.2). There were overlapping confidence intervals of the gravel substrate site with the highest species richness (C37) and the two partial rock-sand substrates. These curves did not overlap with the remaining mud, gravel-mud and gravel curves, the confidence intervals of which all overlapped with each other. While the within-substrate type confidence intervals largely overlapped, certain sites in the mud (C8) and the gravel (C37) substrates had

significantly different curves. Examining the confidence intervals within the gravel-mud substrate type revealed that the curves for the two sites did not have overlapping confidence intervals.

When comparing the sampling intensity at which points of deceleration of all curves occurred, a Kruskal-Wallis test found that they did not differ significantly among substrate types ($H = 2.46$, $n = 13$, $P = 0.48$ (NS), Fig. 2.3). The points of deceleration on the species accumulation curves in the mud substrate type ranged between 16 and 27 samples. The two species accumulation curves of the gravel-mud substrate type were significantly different in terms of their confidence intervals. However, the points of deceleration for these two curves were not different (Fig. 2.2b). In this substratum type, the lower species richness was found at site M26, for which the curve began to decelerate at 20 photographs. The site with the higher estimated richness in the gravel-mud substrate type had a steeper slope and started to decelerate at a sampling intensity of 18 photographs. In total, there were five gravel sites, all sites reached points of deceleration between 14 and 28 photographs (Fig. 2.2c). Site C42 had the slowest rate of acceleration and only reached the point of deceleration at 28 photographs. Within the partial rock-sand grouping, there was no significant difference between the species accumulation curves (Fig. 2.2d). The two partial rock-sand substrates were consistent and the points of deceleration at C22 and C39 were 24 and 26 samples, respectively (Table 2.2).

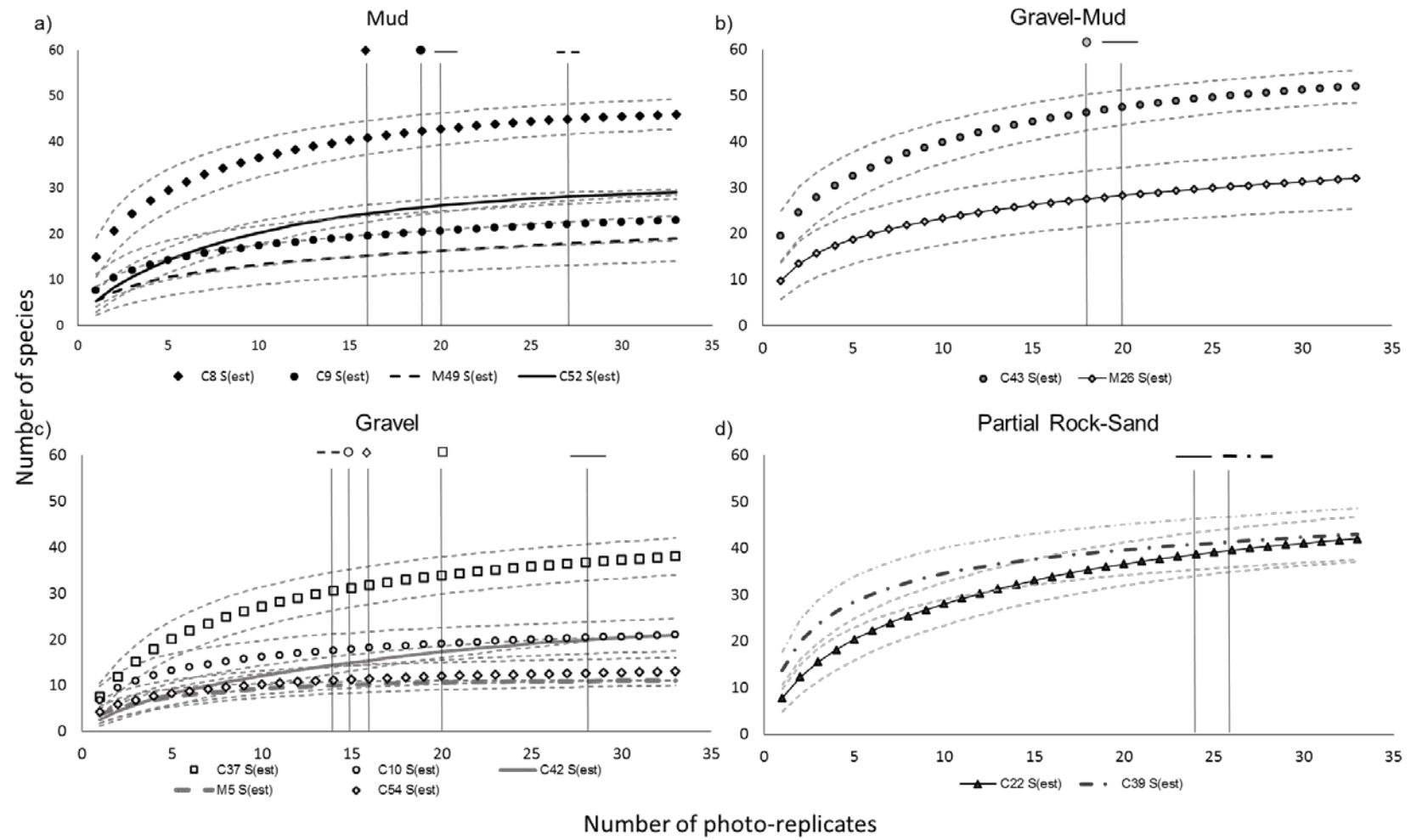


Figure 2.2 Species accumulation curves constructed from 100 random permutations of four substrate types: a) mud; b) gravel-mud; c) gravel; and d) Partial rock-sand. $\pm 95\%$ confidence intervals are represented by light grey dashed lines. Vertical lines represent the point of deceleration for each accumulation curve.

Table 2.2 The total number of observed species (S_{obs}) and the Chao 2 estimated asymptotic richness (S_{est}) in each of the sampled sites. ‘80% of S_{est} ’ refers to the number of photographs needed to reach 80% of the total estimated richness, while the number of photographs required to reach the point of deceleration is referred to as ‘sampling intensity required’.

Substrate	Site	S_{obs}	S_{est} (Chao 2)	80% of S_{est}	Sampling intensity req.
Mud	C52	28	30.2	19	20
Mud	M49	20	21.8	22	27
Mud	C8	47	50.3	14	16
Mud	C9	24	27	19	19
Gravel-Mud	C43	51	55.2	17	18
Gravel-Mud	M26	34	37.7	21	20
Gravel	M5	11	11.1	11	14
Gravel	C54	14	15.3	20	16
Gravel	C10	21	22	14	15
Gravel	M37	36	39.6	20	20
Gravel	C42	19	23.7	31	28
Partial rock- Sand	C39	45	48.1	15	26
Partial rock- Sand	C22	41	45.3	21	24

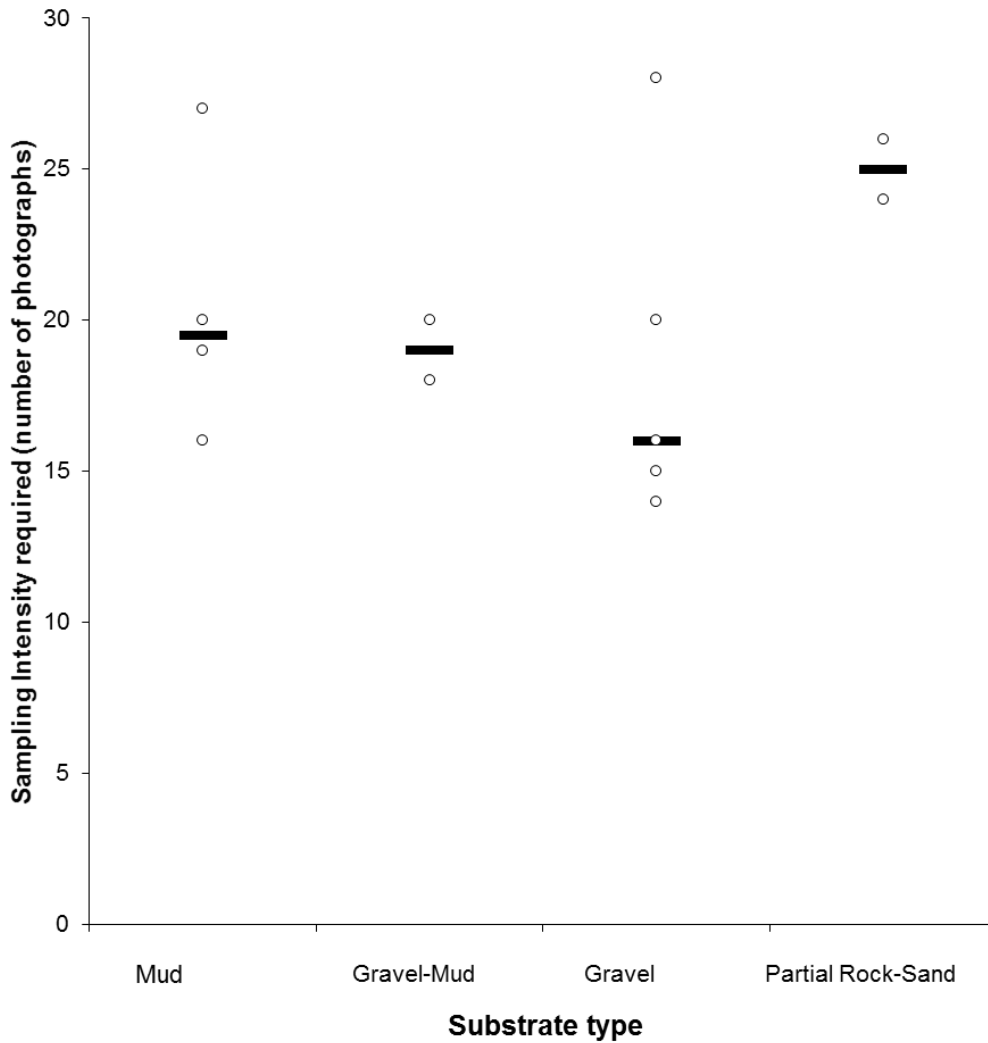


Figure 2.3 Plot comparing the number of photographs required to reach the point where species accumulation curves start to decelerate in each of the sampled substrate types. Black bars indicate the median points of deceleration per substrate type while dots represent site-specific points of deceleration.

Comparisons of asymptotic richness

The Chao 2 richness estimator was used to determine the estimated asymptotic richness of each site. No significant differences were found in total estimated species richness among substrate types ($H = 5.81$, $n = 13$, $P = 0.12$ (NS), Fig. 2.4). Among all sites, the minimum number of photographs required for the observed richness (S_{obs}) to be greater than 80% of the total estimated richness (80% of S_{est}) was after 11 photographs had been processed – for gravel at Site M3 (Table 2.2). Comparisons of the Chao 2 total estimated richness in mud sites found that 80% of the total estimated species richness was reached between 14 and 22 photographs. In the gravel-mud sites, 80% of the estimated richness was reached at 17 and 21 samples. There was high variability in both the gravel and partial rock-sand sites where 80% of total estimated richness was reached between 11 and 31 photographs in gravel sites and 15 or 21 photographs in partial rock-sand sites (Table 2.2).

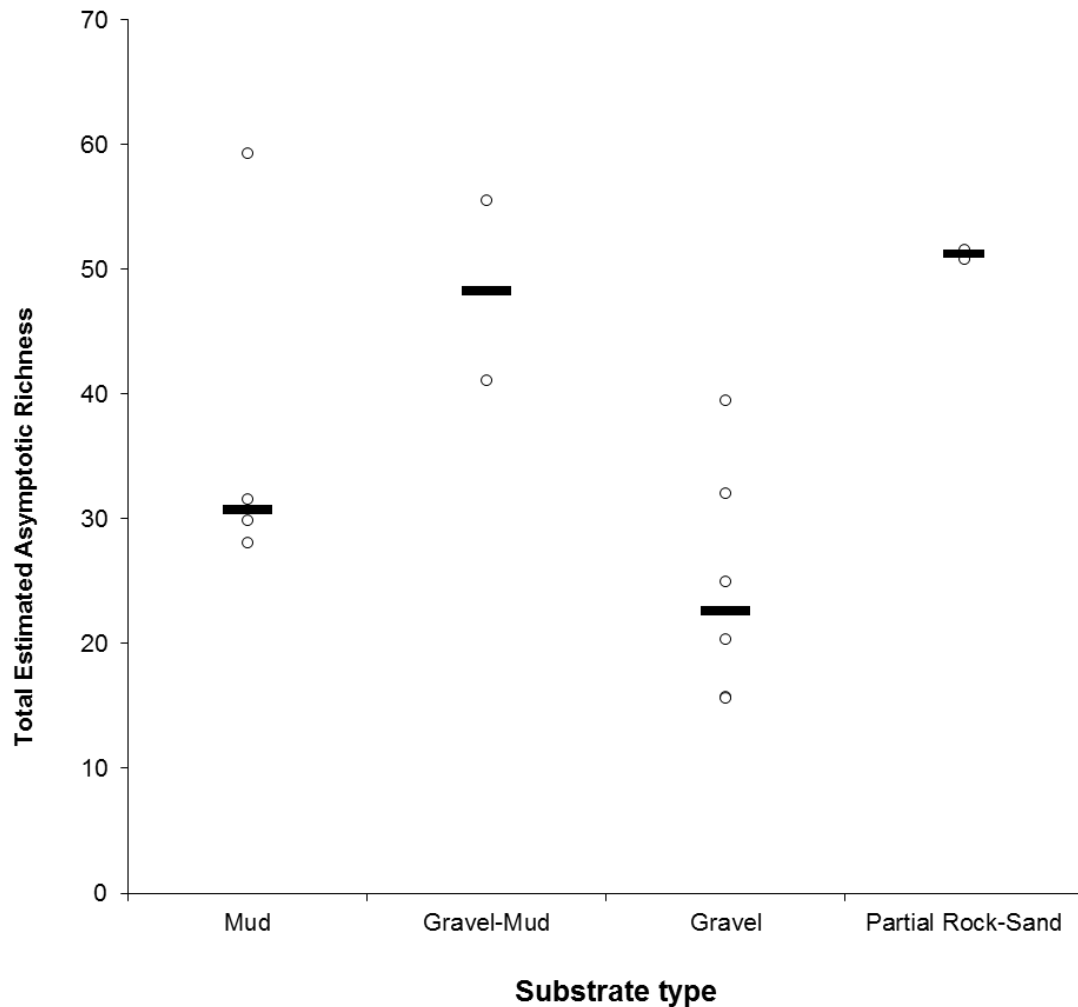


Figure 2.4 Plot showing the Chao 2 estimated total richness of sites compared across substrate types. Black bars denote median estimated species richness per substrate type while dots represent the site specific estimated total richness.

Rate of species accumulation per substrate type

In testing the homogeneity of slopes, the model found no significant interaction between substrate type and the covariate (sampling intensity) indicating that the rate of species accumulation was not affected by substrate type ($F_{3, 421} = 0.57$, $P = 0.6$, Fig. 2.5). The subsequent ANCOVA showed that substrate type had a significant effect on observed species richness ($F_{3, 421} = 16.76$, $P < 0.0001$, Table 2.3). *Post hoc* Newman Keuls tests demonstrated

no significant differences between the average species richness of partial rock-sand and gravel-mud substrate types ($P > 0.05$, Table 2.4). However, there were significant pairwise differences in the mean richness between all other substrate type combinations ($P < 0.001$, Table 2.4).

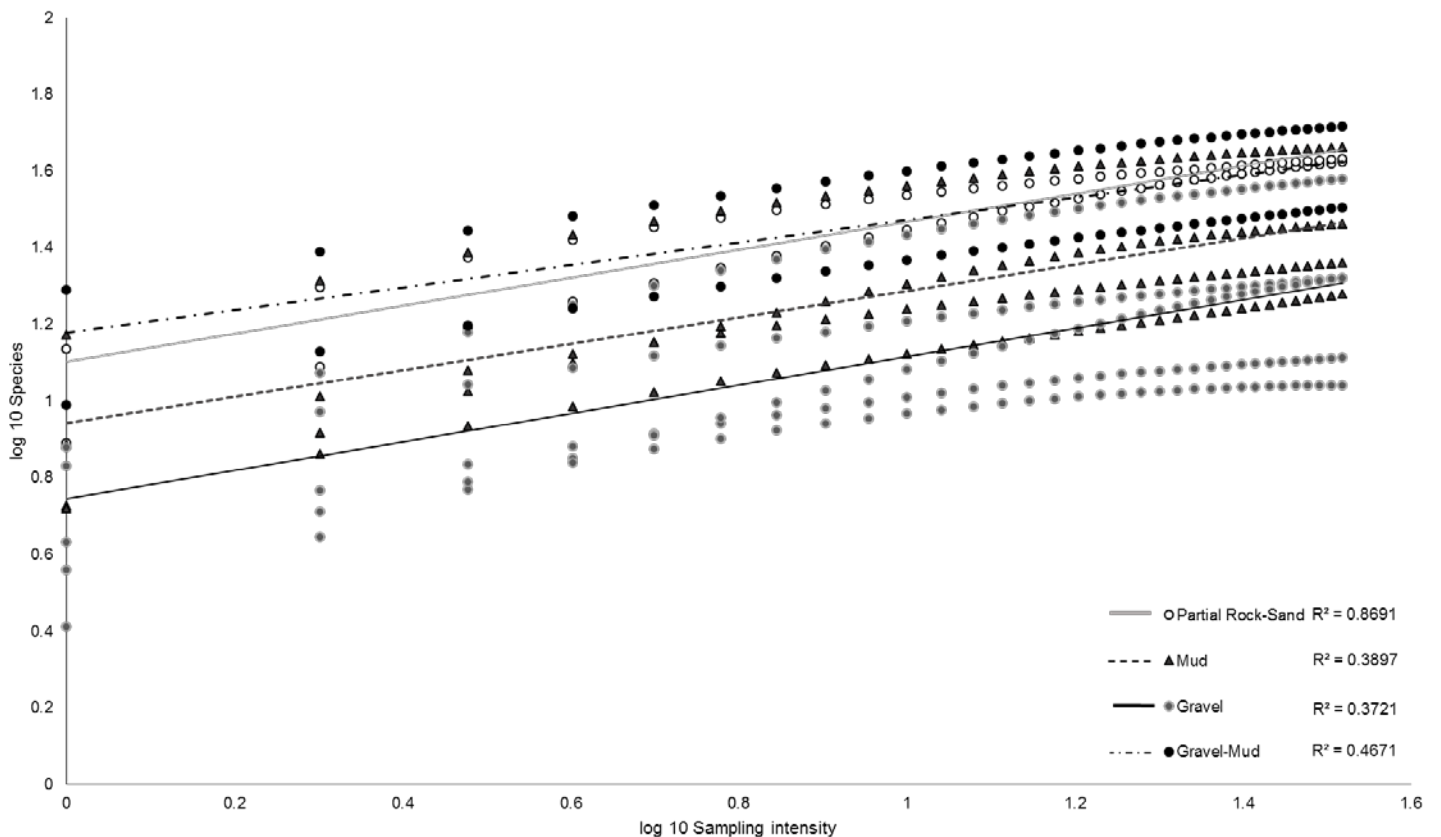


Figure 2.5 Scatterplot of the linear regression lines of log-log transformed species accumulation curves (number of samples against accumulated species) for each sampled substrate type (each sampled site is indicated on the plot by symbols). The type of substrate is indicated in the legend.

Table 2.3 Results of ANCOVA on the log-log of species accumulation curves. Significant results are indicated in bold.

	Sum of Squares	df	Mean Squares	F	P value
Covariate (Sampling Intensity)	7.07644	1	7.07644	314.302	P<0.0001
Substrate	9.01405	3	3.00468	133.454	P<0.0001
Error	9.54628	424	0.02251		
Total	25.63677	428			

Table 2.4 Pairwise *post hoc* comparisons of mean species richness among four substrate types.

Significant differences are indicated in bold.

Substrate type	P value
Gravel-Mud X Partial Rock-Sand	0.866605 (NS)
Mud X Gravel-Mud	P<0.0001
Mud X Gravel	P<0.0001
Mud X Partial Rock-Sand	P<0.0001
Partial Rock-Sand X Gravel	P<0.0001
Gravel-Mud X Gravel	P<0.0001

2.4: Discussion

Species accumulation curves were constructed for each of the four sampled substrate types at 13 sites at the Prince Edward Islands (PEIs) to identify and test for the effect of substrate type on differences in optimal sampling intensity. An optimal sampling intensity of an average of 20 (± 4.7 SD) photo-replicates was found and, along with substrate types, allowed recommendations to be made for sampling in the region. There was no difference among substrate types in the points of deceleration, the total estimated richness, or the rate of species accumulation in this study. In all substrate types, observed richness was close to asymptotic richness as all curves started to decelerate, indicating that less than 5% of species would still be found if a further 20 photographs had been processed. The Chao 2 richness estimator was used to demonstrate that at all sites, the observed species richness reached at least 80% of the total estimated richness between 11 and 31 photo-replicates. These species accumulation curves and the estimates of sampling intensity required to reach the point of deceleration are useful in informing a benthic sampling strategy at the PEIs. In this study, however, substrate type was not a strong predictor of differences in total estimated asymptotic species richness and, consequently, in species accumulation curves. The homogeneity of the linear substrate-specific slopes also confirmed that the rate of species accumulation was not dependent on substratum type. Substrate type did affect mean species richness, where gravel-mud and partial rock-sand substrates had similar high mean species richness's while mud had a low mean species richness.

Substrate type as a predictor of species richness

Abiotic substrate types are important when planning sampling strategies at unknown sites, as they may be simpler to characterise than biological data (Post 2008; Schlacher et al. 2010). Despite substrate complexity being a known driver of epibenthic diversity (Morais et

al. 2007; Schlacher et al. 2010), I did not find a significant difference in estimated asymptotic richness or required sampling intensity when comparing among substrate types. This may have been due to the four substrate types analysed being too similar to one another in terms of their complexity. My results, therefore, contrast with numerous other studies showing the use of abiotic surrogates to be a good indirect predictor of species richness gradients, particularly in cases where substrate type affected the attachment of habitat-forming biota (Stevens and Connolly 2004; Morais et al. 2007; Buhl-Mortensen et al. 2010; Levin et al. 2010). This may be because a combination of habitat type, major biological features and abiotic factors, will be a more robust predictor of species richness than substrate type on its own (Thrush et al. 2006b; Schlacher et al. 2010; Foster et al. 2013). Additionally, the habitat requirements of species and interspecific relationships may result in sites with comparable abiotic substrates having different species assemblages (Medina et al. 2013). Examination of the overlapping confidence intervals of species accumulation curves in my study revealed that the species-rich sites containing large assemblages of biogenic habitat-forming organisms, such as sponges, dense bryozoans and octocorals, were more similar to each other than to sites that were of the same substrate type but lacking in habitat forming organisms (Fig. 2.2, Table 2.1). The high species richness at these sites may be attributed to the heterogeneous nature of the substrate as well as the presence of large octocoral and bryozoan stands, which are also complex in structure. This heterogeneity would mean a greater diversity of habitat niches relative to more homogenous substrates, as it allows occupation by species normally prevalent on soft substrates as well as those more typical of rocky substrates (Griffin et al. 2009). Muddy sites containing biogenic habitat-forming organisms like bryozoans and octocorals (site C8) also had a greater estimated richness than muddy sites that did not host habitat-forming biota (Fig. 2.2, Table 2.1). At these sites positive biotic interactions may have allowed for a greater number of species to coexist. An example of this are the interactions between various species of ophiuroids (brittle stars)

including *Asteronyx loveni*, which was commonly found attached to octocorals (Appendix A plate 2b) (Fujita and Ohta 1988; Buhl-Mortensen et al. 2010). Habitat-structuring organisms such as calcareous bryozoans may also increase diversity by stabilising sediments; and the sites that had dense bryozoan abundance had a greater overall richness (Hageman et al. 2000). Examples of this from my study include the highly abundant tube-dwelling polychaete, *Lanice marionensis*. Research conducted on this genus has shown it to be an important habitat-structuring species as it stabilises soft sediments and changes bottom current flow dynamics, allowing a greater utilisation of space by other species (Rabaut et al. 2007; Van Hoey et al. 2008). Tube-building polychaetes also engineer ecosystems by increasing habitat complexity on homogenous substrates (Van Hoey et al. 2008). Similarly, Octocorallia often increase overall species richness as they create and facilitate microhabitats by providing refuges and points of attachment for other benthic invertebrates (Mortensen and Buhl-Mortensen 2004). Habitat-forming and structuring biota are able to facilitate positive species interactions and increase the niche space available to species, increasing the size of the realised niche (the actual space the species occupies) (Bertness and Callaway 1993; Bruno et al. 2003). Such interactions may explain why substrate type alone was not shown to drive species accumulation in this study. The biological structure of environments should be considered in tandem with abiotic factors when determining minimal sampling strategies.

The site that had the slowest rate of species accumulation was the deepest site (site C42 situated at 512m), located in the inter-island region, just south of Prince Edward Island. Due to the depth of this gravel site, it was not characterised by the large red algal stands common at the shallower gravel sites. The slope of the accumulation curve did not have a steep incline indicating that more rare species were yet to be found and more samples were required to reach point of deceleration (Baltanas 1992; Etnoyer et al. 2010). Such sites with few species may

require more samples than those with a greater species richness, as sites with steeper species accumulation slopes reach the total species richness faster (Schoenly and Barrion 2016).

Species accumulation curves and determining optimal sampling area

In this study, the asymptotic richness estimator showed that for an area to be sampled adequately, 20 photo-replicates ($\sim 15\text{m}^2$) would be required to reach 80% of the true species richness. Research conducted in species-rich Mediterranean coral outcrops and shallow rocky bottom assemblages found that transects between 25m^2 and 50m^2 were sufficient to obtain species representation (Kipson et al. 2011). Smaller sample areas (10m^2) have also been used in cold-water soft-sediment communities (Gray 2002). The minimum number of samples needed to obtain an accurate measure of species richness suggested in my study is therefore within the range of previous studies. A caveat when comparing observed richness with estimated richness is that all scarce species present in a study area are unlikely to be discovered and species accumulation curves simply *suggest* the point at which the most common species have been discovered. Consequently, species accumulation curves will most likely never reach absolute species richness as sampling larger areas will increase the probability of discovering a new species (Etnoyer et al. 2010).

No significant differences were observed in either species richness or rate of species accumulation among the different substrate types, and the number of samples required to accurately sample a substrate type in the epibenthic environment at the PEIs may be ubiquitous. As 80% of the species richness may be captured at a maximum of 30 photographs, it may be more effective to sample more sites at a lower sampling intensity (i.e. 20 samples) than sample fewer sites at a higher sampling intensity. Sites with few species and sites that are spatially heterogeneous (partial rock-sand substrate) may require more photographs as the species accumulation curves of such sites take longer to reach the point of deceleration (Baltanas 1992;

Scheiner 2003). However, the standard deviation of the number of photo-replicates needed to reach the deceleration points was 4.7, indicating that there were not large variations around the mean. This small standard deviation may indicate that at least five more photo-replicates may be required in species poor sites than in sites where the rate of species accumulation is faster. The average species richness differed between all substrate types except between the two substrate types that were a mix of hard and soft substrates (partial rock-sand and gravel-mud), reinforcing the idea that some substrates will take longer to reach total species richness. However, it is important to note that despite the heterogeneity of the partial rock-sand sites, the points of deceleration of species accumulation curves did not differ from other less heterogeneous sites at the PEIs in this study. Using at least 20 photo-replicates may, therefore, be adequate to sufficiently sample the species richness at the PEIs.

The functionality of the photographic sampling method and bias incurred.

There may have been a margin of under-sampling in shallow near-shore sites as dense algal stands there may have obscured small or cryptic species such as the hyper-benthic shrimp, *Nauticaris marionis* (Knight et al. 2014; Haley et al. 2016). The same could be said of sites characterised by dense stands of bryozoans and those that had large rock outcrops. Jørgensen and Gulliksen (2001) showed a margin of under-sampling using photographic methods in comparison to suction sampling (which would have included infauna as well as epifauna). The study found that semi-mobile species such as crustaceans, as well as smaller species like juvenile ophiuroids and bivalves, were often underestimated using photographic methods. However, Williams et al. (2015) found that, despite physical sampling methods being more efficient for organism identification, photographic methods provided higher estimates of epibenthic richness. The benefits of photographic sampling may outweigh the costs of missing

or misidentifying species. It is, however, clear that comparisons cannot be made across different methods of sampling.

Generally, differences in depth are likely to play an important role in the patterns of species richness found among and within sampled areas (Carney 2005). The depth range sampled in my study may have been too narrow to detect significant changes in species richness, as depth-related richness variations are usually only observed every three orders of magnitude in depth (McClain et al. 2010). Minor depth variations may impact the composition of benthic assemblages but have a limited influence on species richness (McClain et al. 2010). As my study was completed on a relatively narrow depth range (61 - 512m), protocols for sampling in deeper waters in the Prince Edward Island region cannot be inferred from my findings.

Despite abiotic surrogates, especially substrate type, being used in other diversity mapping studies (McArthur et al. 2010), no significant difference was found in the estimated richness across the substrate types sampled in this study. Additionally, Richmond and Stevens (2014) found that substrate was a poor predictor of assemblage structure compared to other abiotic surrogates like temperature and fishing effort. Due to biogenic habitat-forming organisms contributing significantly to species richness, future studies should take a more comprehensive approach to defining habitat, to include biological assemblages as well as other abiotic surrogates (Rabaut et al. 2007; Van Hoey et al. 2008; Buhl-Mortensen et al. 2010; Richmond and Stevens 2014).

2.5: Conclusions

In this chapter the number of photographs required to obtain an accurate representation of the true species richness was determined. There was high variability among the species

accumulation curves within different substrate types but substrate type did not drive patterns of species richness or accumulation. My results indicate suggest that an average of 20 (± 4.7 SD) photographs ($\sim 15\text{m}^2$ transect) is sufficient to capture 80% of the true species richness in a sample irrespective of the substrate type analysed at the PEIs. However, sites with fewer species may require more samples than those with greater species richness due to the increased probability of encountering rare species with greater sampling effort in sparsely populated sites. Partial rock-sand sites, which took longer to reach points of deceleration and had a higher estimated richness, required an average of 25 samples (± 1.4 SD), while substrates that did not take as long to reach points of deceleration required between 18 and 20 samples. Due to logistical sampling constraints, this study did not include the full range of possible substrate types that may be present at the PEIs. Sites consisting of sand or rock only were not sampled during either the 2013 or the 2015 survey. It is important to note that the sampling intensity suggested as being appropriate for the benthic environment of Prince Edward Islands may not be suitable as a global approach, as it is appropriate only to the specific abiotic and biotic benthic environments of the shelf region of Marion and Prince Edward Islands.

The results of this chapter are applied in the following chapter, and will be useful in future studies using photographic methods to sample benthic assemblages within the Prince Edward Island Marine Protected Area. Optimising the time spent sampling is important, as often there are logistical, technical, cost or environmental constraints associated with surveying benthic assemblages. More importantly however, this research will ensure that an acceptable level of species representation is obtained when sampling across different substrate types at the Prince Edward Islands.

Chapter 3: Spatial and temporal changes in epibenthic assemblages at the Prince Edward Islands in the Southern Ocean.

Abstract

The sub-Antarctic Prince Edward Islands are situated in the pathway of the easterly flowing Antarctic Circumpolar Current (ACC) which, along with its associated frontal systems, facilitates mesoscale oceanographic regimes in the inter-island and downstream region of the islands. Recent isotope studies on benthic invertebrates showed that frequent phytoplankton blooms in the inter-island region might have resulted in spatial and temporal differences in the quality of phytoplankton being made available as a food source for benthic invertebrates. It is, however, unknown whether these changes have translated into long-term alterations in the composition of epibenthic assemblages. To address this gap in knowledge, study sites in the upstream and downstream regions around the islands, photographed between 1984 and 1989, were re-sampled. Diversity and evenness indices and assemblage composition were compared spatially and temporally. Species diversity was found to have increased over time and the upstream region was found to have a higher evenness than the downstream region. There were significant differences in assemblage composition spatially and significant dispersion effects temporally. Characteristic regional primary productivity patterns may have been responsible for spatial differences in species composition. However, there may have been shifts in these productivity patterns as a result of climate change and subsequent temporal variations in assemblage composition. This work provides the second survey of epibenthos at the PEIs since 1993 and the results further develop the long-term understanding of the epibenthos in this region.

3.1: Introduction

The physical and biological environment of the Prince Edward Islands

Within the Indian sector of the Southern Ocean, the Prince Edward Islands (PEIs) are situated in the path of the easterly moving Antarctic Circumpolar Current (ACC). The Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) borders the ACC to the north and south respectively. The islands form an obstacle to water flow within the ACC, delineating the marine environment around the islands into three regions: upstream, downstream and the inter-island region (Froneman et al. 1999; Ansorge and Lutjeharms 2002). The PEIs are home to large breeding populations of top predators such as seals and seabirds (Pakhomov and Chown 2003; Ryan and Bester 2008) and are ideal systems in which to study both biological interactions as well as environmental change, as these southern ocean islands are not likely to be directly influenced by human activities (Bergstrom and Chown 1999; Smith 2002). Despite the sub-Antarctic generally being an area of low productivity, the ocean environment around the PEIs is extremely productive and supplies the large number of breeding predators with food resources (Laubscher et al. 1993; Pakhomov and Froneman 1999). There is a known ‘island mass effect’, where the runoff of nutrients from the islands, facilitated by a stable water column, forms phytoplankton blooms in the shallow basin between Marion and Prince Edward Islands (Boden 1988; Perissinotto and Duncombe Rae 1990). These phytoplankton blooms play an important role in various biological processes within the PEI environment by forming the foundation of the marine food web (Allan et al. 2013; Treasure et al. 2015). With recent evidence for shifting conditions at the islands, however, this influence of primary productivity may be changing.

Plankton studies focused in the immediate ocean environment around the Prince Edward Islands have documented regional differences in the abundance and structure of

plankton communities (Perissinotto et al. 1990; Froneman and Pakhomov 1998; Pakhomov and Froneman 1999). The upstream and downstream regions of the islands differ significantly in Chlorophyll-*a* concentrations, with the downstream environment having up to three times more Chl-*a* than the upstream region during bloom conditions (Froneman and Pakhomov 1998). Additionally, there are distinct differences in phytoplankton size classes between the upstream and inter-island regions of the islands. In the inter-island region, phytoplankton communities are composed of nano-phytoplankton (2-20 μm) and micro-phytoplankton (>20 μm), while the open waters surrounding the islands are dominated by pico-phytoplankton (< 20 μm) (Perissinotto et al. 1990; Froneman and Pakhomov 1998; Pakhomov and Froneman 1999). Zooplankton communities at the islands consume less than 10% of the total Chl-*a* standing stock within the inter-island region during phytoplankton bloom conditions and less than 25% in the open waters surrounding the islands (McQuaid and Froneman 2008). As such, a large amount of phytoplankton sinks through a stable water column and is made available to the benthos (Perissinotto and Duncombe Rae 1990; Perissinotto 1992; Kaehler et al. 2000; Glover et al. 2010; Treasure et al. 2015). During conditions of increased water movement, as occurs due to the influence of the SAF, there is a decreased rate of nutrient sinking and nutrients are advected into the system from the easterly flowing ACC (Allan et al. 2013). As a result, regional primary productivity patterns may have important direct implications for benthic assemblages and may influence species richness and diversity (Levin et al. 2010; Treasure et al. 2015).

The population dynamics of apex predators at the Prince Edward Islands may be directly influenced by regional changes in benthic assemblage composition. There have been notable long-term increases in the population sizes of top predators such as fur seals (*Arctocephalus tropicalis*); grey headed (*Thalassarche chrysostoma*) and wandering (*Diomedea exulans*) albatross; as well as King Penguins (*Aptenodytes patagonicus*), all of

which make use of offshore feeding grounds (Pakhomov and Chown 2003; Ryan and Bester 2008). The islands have also experienced decreases in the population sizes of species which are primarily limited to inshore feeding, such as Rockhopper penguins (*Eudyptes chrysocome*) and Gentoo penguins (*Pygoscelis papua*) (Pakhomov and Chown 2003; Crawford et al. 2009). Given the inability of these species to feed far offshore, declines in their populations may be due to changes in abundance of benthic prey in the area surrounding the islands (Lescroël and Bost 2006; Ryan and Bester 2008; Treasure et al. 2015).

Previous benthic research

The large populations of top vertebrate predators have been well studied, as have the plankton communities in the vicinity of the islands. However, benthic marine assemblages within the archipelago have not been studied to the same extent. The first collections of physical specimens of the marine benthic fauna of the PEIs were made on five separate occasions between 1873 and 1976 by four different research vessels of both French and South African origin (Branch et al. 1993a; Chown and Froneman 2008a). The South African specimens of benthic invertebrates collected prior to 1971 are described in Van Zinderen Bakker et al (1971). More recent surveys of epibenthic assemblages were conducted between 1984 and 1989 by Branch et al (1993a). As part of this series of surveys, benthic photographs were taken, in conjunction with dredged samples, to identify and classify benthic species and habitats around the PEIs. Various taxonomic keys were subsequently published using historical records and the data obtained from dredged samples (Branch et al. 1991a; 1991b; 1993b; Branch and Williams 1993; Branch 1994; Branch and Hayward 2007). In 1988 a SCUBA diving survey of epibenthic assemblages was conducted at 3 sites within the shallow nearshore region of Marion Island (Beckley and Branch 1992). This SCUBA survey also enabled validation of species identities and habitat types.

More recently, studies have investigated trophic relationships using stable isotope analyses from samples obtained from benthic invertebrates, (Kaehler et al. 2000; Allan et al. 2013; Richoux et al. 2016). Various studies have found that over time (20-25 year studies), benthic invertebrates, including the hyper-benthic shrimp, *Nauticaris marionis*, were significantly δC^{13} depleted indicating a shift in the source of nutrients being made available to the benthos (Pakhomov et al. 2004; Allan et al. 2013). Additionally, invertebrate species in the inter-island and downstream regions experience planktonic food sources of a higher quality than in the upstream region (Allan 2011). This was confirmed by Richoux et al. (2016) who found significant differences in the δC^{13} signatures of *N. marionis* between the inter-island and upstream regions of the islands. This change in isotope signature reflects that the source of food for benthic assemblages in the upstream and downstream regions have changed over time. As benthic assemblages are reliant on primary productivity generated at the surface layer for nourishment, seasonal variations in type and quality of productivity or short-term pulses of production may impact macrofaunal communities (Grebmeier and Barry 1991; Levin et al. 1999; Witte et al. 2003).

Previous research has, therefore, described notable changes in benthic food regimes at the Prince Edward Island Archipelago. However, not much focus has been directed towards the potential effects of such changes on benthic assemblage composition within each of the island regions over time. Comparisons of historical and recent data between regions can be used to quantify potential changes in the epibenthos. As a photographic dataset of the benthic habitats around the PEIs exists from a study conducted between 1984 and 1989 by Branch et al. (1993a), there is a valuable opportunity to resample the upstream and downstream regions to determine whether there have been changes in assemblage composition over decadal timescales. These historical photographs form a baseline dataset for continued, non-destructive monitoring at the sub-Antarctic Prince Edward Islands. The primary aim of this chapter was to

compare epibenthic assemblages in the upstream and downstream regions of the PEIs across time, between images taken between 1984 and 1989 and those of areas resampled in 2013 and 2015, to assess spatial and temporal changes. In addressing the stated aim, two hypotheses were tested: 1) the diversity of epibenthic assemblages would differ both temporally and spatially, and 2) there would be spatial and temporal changes in species composition.

3.2: Methods

Epibenthic assemblages were photographed during April/May in 8 separate surveys between 1984 and 1989 in the vicinity of Marion (46°45'S-37°50'E) and Prince Edward Islands (46°38'S-37°56'E) as described by Branch et al. (1993a). A photographic resampling survey was conducted aboard the *SA Agulhas II* during its annual relief voyages to the islands during April/May 2013 and 2015. The photographic equipment and camera orientation used to capture historical images differed from that used in the repeat surveys. Historical photographs were taken with an analogue (film) camera positioned perpendicularly to the substratum giving a plan view of the benthos, while photo-transects in 2013 and 2015 were taken at a 30 degree angle to the substrate (as described in Chapter 2). Historical photographic slides were digitized by high resolution scanning to allow the historical images to be processed the same way as resampled images. The locations of resampled study sites were chosen to best align with the locations used in the historical survey. The ground area photographed in each set of images was scaled, allowing standardisation of the area processed in each image (as outlined in Chapter 2). As substrate type may have an effect on the benthic biomass and diversity (Grebmeier et al. 1989), a similar range of substrate types were sampled in each study region (upstream and downstream). Each sampled region had an equal number of hard and soft substratum types (partial rock-sand, gravel, gravel-mud and mud sites). Six upstream sites and five downstream

sites with a depth range of between 61-420m were surveyed (Fig. 3.1). As each region (upstream/downstream) covered the same depth range, depth was treated as a constant variable and was not used to stratify samples. Camera work was conducted as per the methodology outlined in Chapter 2. The number of photographs processed per site was informed by the findings of Chapter 2 (Table 2.2). An average of 22(± 12 SD) historical sites and 27(± 3 SD) resampled photographs were sampled (Appendix C).

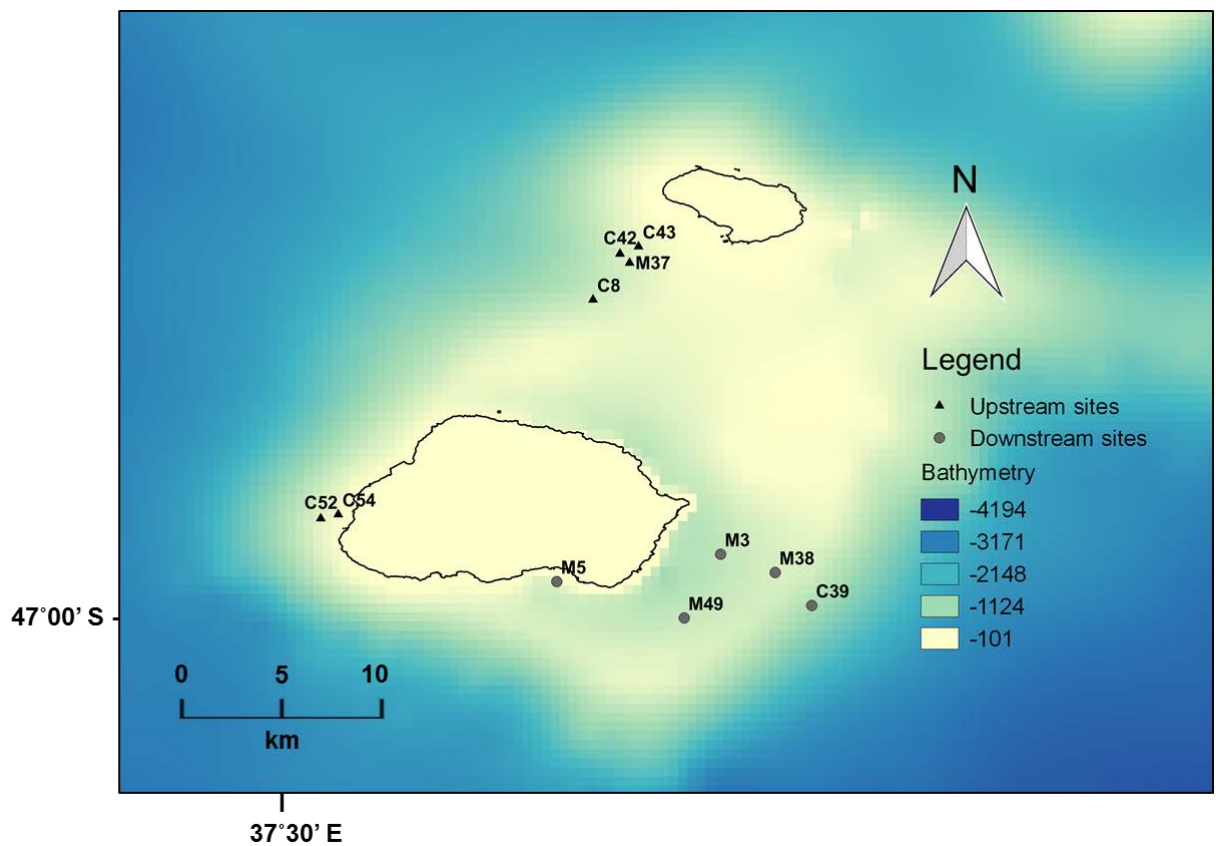


Figure 3.1 Location of the upstream and downstream sample sites in relation to the Marion and Prince Edward Islands. Triangles indicate upstream sites and grey circles indicate downstream sites. Shading reflects depth (m).

Image analysis

Two hundred and one historical and 264 resampled images were processed using Coral Point Count with Excel extensions (CPCe) (Kohler and Gill 2006) to determine species composition and estimate epibenthic abundances. In CPCe, a point-count grid of 80 points was overlaid onto each photograph and the epibenthic species under each point on the grid was identified to the lowest possible taxonomic level. From this, the abundance (percentage cover) of epibenthic organisms was estimated. Identifications were done using published taxonomic keys and photo-identification guides (Branch et al. 1991a; 1991b; 1993b; Branch and Williams 1993; Branch and Hayward 2007). Where species identification was not possible, a morpho-species was assigned as an operational taxonomic unit (OTU) code and identified to the lowest possible taxonomic level (Davies et al. 2014).

Data treatment and statistical analyses

Univariate statistics were completed using Statistica V13 (STATSOFT 2015). All multivariate statistical analyses were conducted using the PRIMER (Clarke and Gorley 2006) software and the complementary package PERMANOVA (Anderson et al. 2008).

Percentage cover data were fourth-root transformed to account for the effects of rare species. The diversity of assemblages was calculated using the Shannon Wiener diversity (Shannon and Weaver 1949) and Pielou's evenness indices (Pielou 1966). After testing for normality and equal variances by using a P-P plot, diversity and evenness indices were compared using a factorial ANOVA with fixed spatial (2-levels, upstream and downstream) and temporal factors (2-levels, historical and resampled).

To test for spatial and temporal differences in epibenthic assemblage composition, abundance data were compared using a two-way crossed permutation analysis of variance with

9999 permutations on a Bray-Curtis resemblance measure (PERMANOVA, Anderson 2005) with a fixed spatial factor of Region (2-levels, upstream and downstream) and a fixed temporal factor of Year (2-levels, historical and resampled). Pairwise tests were conducted in order to characterise the significant interactions. The sampling intensity at two stations from the historical survey was unavoidably lower than the resampled survey due to fewer usable images being available and the ideal number of photo-replicates, as advised in chapter 2, was not reached. However, the use of a conservative PERMANOVA design (Type III sum of squares) ensured that all design terms were treated independently, thus and eliminating the necessity of ensuring equal sample sizes (Anderson et al. 2008). Due to the sensitive nature of PERMANOVA to dispersion effects, a PERMDISP analysis was used to determine whether sites differed due to their variability in multivariate dispersion (PERMDISP, Anderson 2004). Patterns of epibenthic community structure were visualised using multi-dimensional scaling (MDS) plots based on a Bray-Curtis dissimilarity matrix. A group average cluster diagram with SIMPROF analysis was used to visualise the similarity between historical and resampled sites in the upstream and downstream regions. Canonical analysis of principal coordinates (CAP) was employed to determine how well the data fitted *a priori* groupings (resampled upstream, resampled downstream, historical upstream, historical downstream). A similarity percentage analysis (SIMPER; Clarke and Gorley 2006) identified the species responsible for driving differences between regions and across years. Only species that contributed >3% to the overall similarity or dissimilarity of the assemblage were reported on.

3.3: Results

Temporal and spatial diversity comparisons

Out of all 465 samples, 141 different morpho-species were observed. There was a significant increase in Shannon Wiener diversity over time ($P < 0.001$, Table 3.1a, Fig. 3.2a, b) but no difference in diversity between the upstream and downstream regions ($P = 0.6000$, Table 3.1a). There was no difference in Pielou's evenness over time ($P = 0.2000$, Table 3.1b). However, there was a significant difference in Pielou's evenness between regions, with upstream sites having a greater evenness than downstream sites ($P < 0.0500$, Table 3.1b, Fig. 3.3a, b).

Table 3.1 Spatial (upstream and downstream) and temporal (1984-1989 and 2013-2015) comparisons of **a)** Shannon Weiner diversity index (H') and **b)** Pielou's evenness (J'). Significantly different values are indicated in bold.

		<i>Df</i>	<i>Mean Squares</i>	<i>F</i>	<i>P</i>
a) <i>Shannon Weiner</i> (H')	Intercept	1	2209	12691	< 0.00001
	Temporal	1	2.141	12	< 0.0010
	Spatial	1	0.38	0.22	0.640 (NS)
	Temporal x Spatial	1	0.421	0.24	0.640 (NS)
	Error	514	0.174		
b) <i>Pielou's evenness</i> (J')	Intercept	1	497.375	256478 3	< 0.00001
	Temporal	1	0.0003	1	0.2317 (NS)
	Spatial	1	0.0010	5	0.0240
	Temporal x Spatial	1	0.000	0	0.9700 (NS)
	Error	514	0.0002		

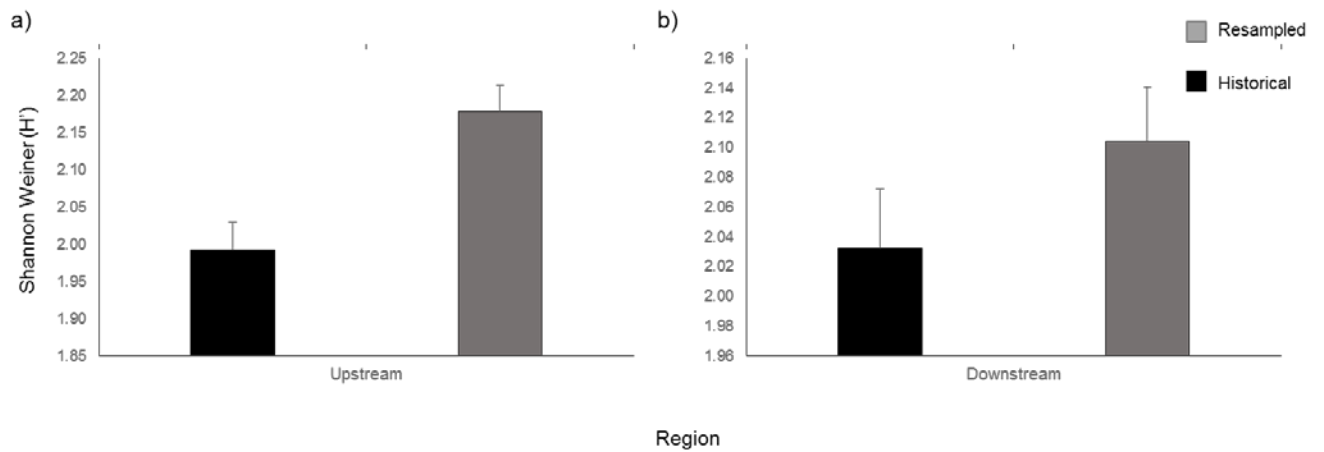


Figure 3.2 Mean Shannon Wiener diversity (+SE) showing significant temporal differences within the **a)** upstream sites and **b)** downstream sites.

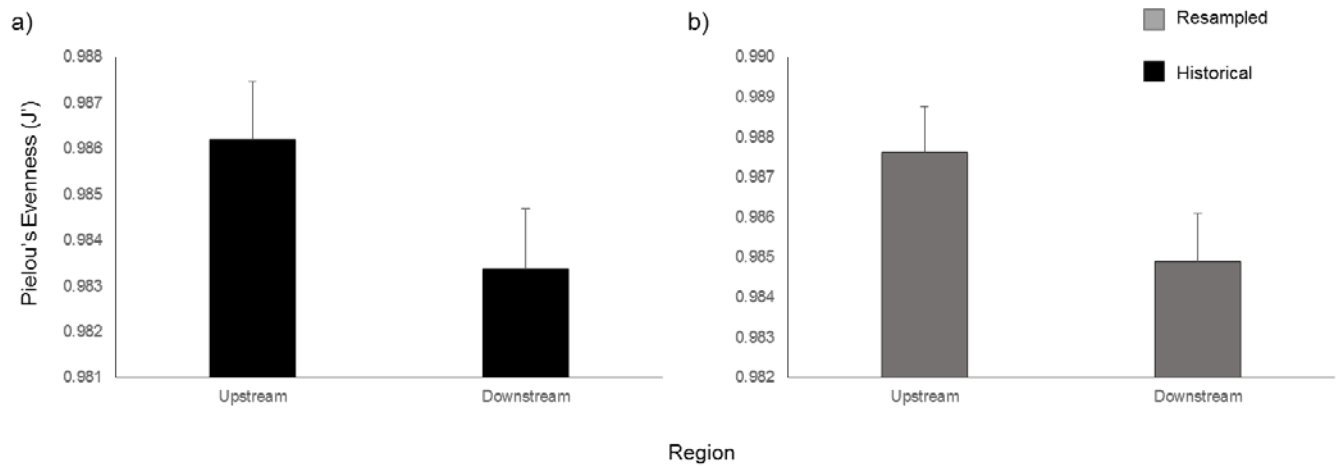


Figure 3.3 Spatial differences in mean Pielou's evenness (+SE) between **a)** historical sites and **b)** resampled sites. Historical surveys are indicated with black bars and resampled surveys are indicated with grey bars.

Temporal and spatial comparisons of benthic assemblages

PERMANOVA results of the temporal and spatial comparisons showed significant main effects of time and region on epibenthic assemblage composition (Table 3.2). A significant interaction effect was also found between these spatial and temporal factors (Table 3.2). All pairwise tests were significant ($P_{(Perm)} \leq 0.0001$) and the spatial-temporal interaction could not be resolved any further.

Table 3.2 PERMANOVA analysis of epibenthic assemblages between periods (historical and resampled) and regions (upstream and downstream), and their interaction.

<i>Factor</i>	<i>Df</i>	<i>Mean squares</i>	<i>Pseudo F</i>	<i>P value</i>	<i>Unique Perms</i>
Temporal (resampled x historical)	1	33230	18.987	0.0001	9942
Spatial (upstream x downstream)	1	42622	24.354	0.0001	9926
Temporal x Spatial	1	13696	7.8259	0.0001	9933
<i>All Pairwise tests significant P < 0.0001</i>					

A PERMDISP analysis was conducted to determine whether the statistical differences in tests of spatial and temporal factors were due to dispersion effects. There was a significant overall deviation from the group centroid of both factors (PERMDISP, $F_{(3,474)} = 35.45$, $P_{(Perm)} \leq 0.0001$). Significant results of pairwise tests indicated that within each region, there were significant dispersion effects over time (Table 3.3). There were, however, no dispersion effects of the spatial factor within either sampling event (Table 3.3).

Table 3.3 Test statistics for pairwise tests of dispersion (PERMDISP) between years (historical and resampled surveys) and regions (upstream and downstream sites). Significant values of $P < 0.050$ are indicated in bold and non-significant by (NS).

<i>Factor</i>	<i>T-value</i>	<i>P-value (perm)</i>
Resampled upstream, Resampled downstream	2.3454	0.029 (NS)
Resampled upstream, Historical downstream	7.6939	0.0001
Resampled upstream, Historical upstream	4.3517	0.0002
Resampled downstream, Historical downstream	7.0633	0.0001
Resampled downstream, Historical upstream	5.0676	0.0001
Historical downstream, Historical upstream	1.9278	0.075 (NS)

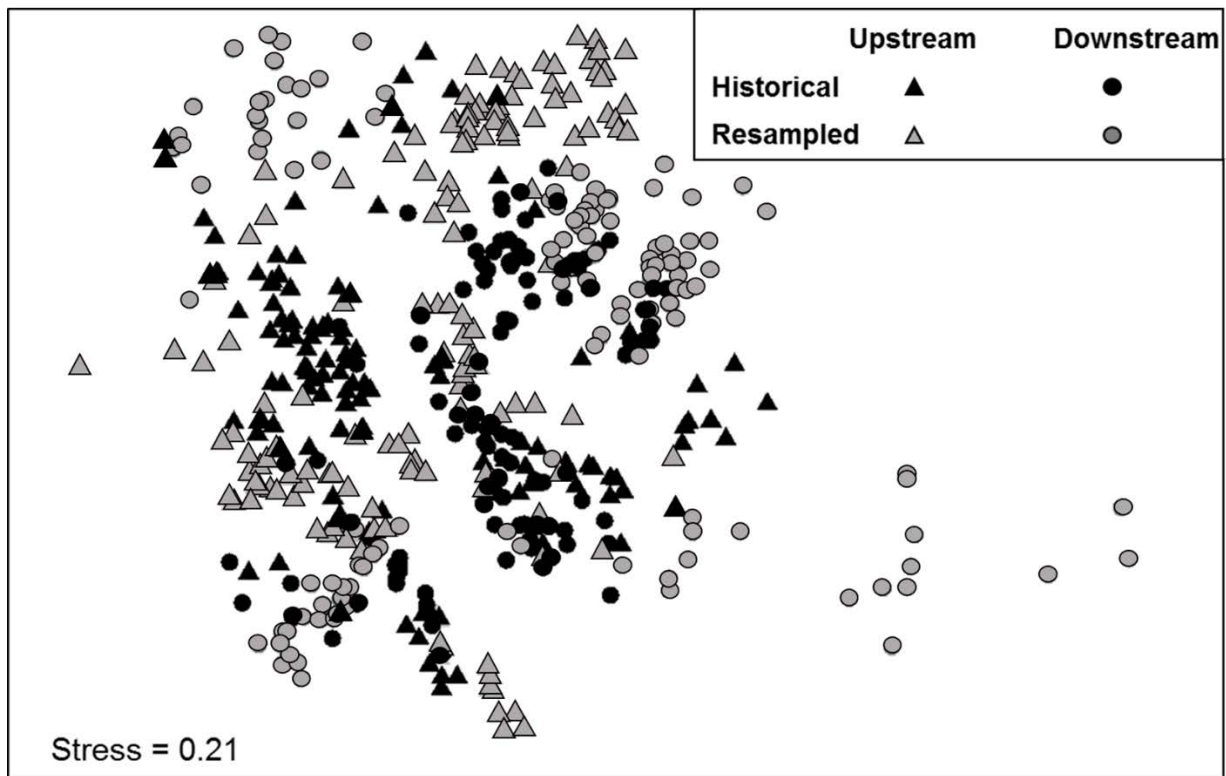


Figure 3.4 Multi-dimensional scaling (unconstrained) plot of percentage cover of epibenthic organisms showing the spatial (upstream and downstream) and temporal (historical and resampled) patterns.

The MDS plot did not show a clear separation between upstream and downstream groups in either sampling years (Stress = 0.21, Fig. 3.4). However, there was a significant difference in dispersion between the historical and resampled survey within the downstream region. The cluster analysis with SIMPROF found six statistically distinct groups (A to F) within the two main clusters, while three individual stations did not group (Fig. 3.5). The six groups had a similarity percentage of 42% (Fig. 3.5) but there was no clear separation between upstream and downstream sites over time. The cluster consisting of groups A and B was characterised by the shallow upstream and downstream sites in which red algae occurred.

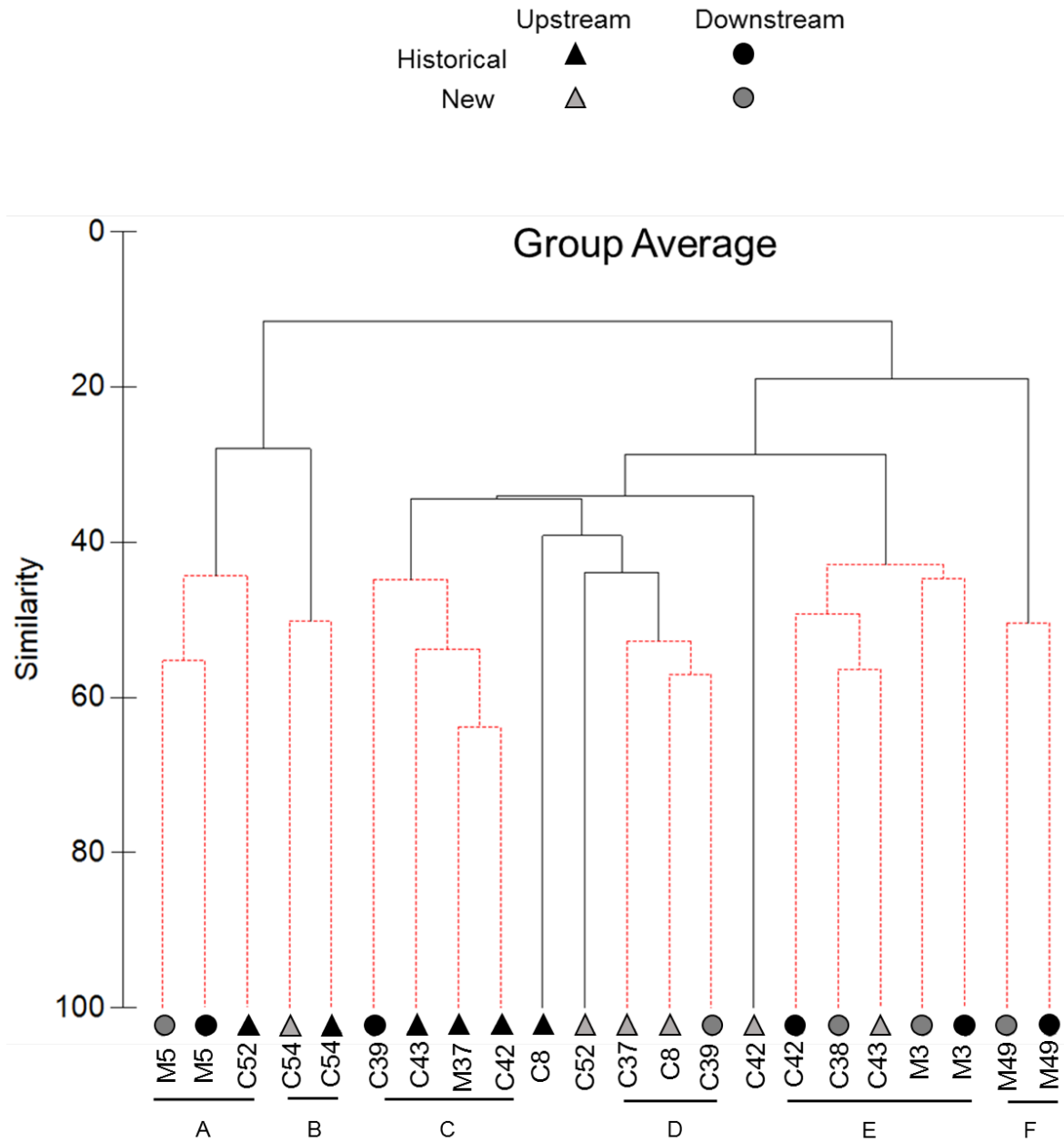


Figure 3.5 Group Average Cluster diagram with SIMPROF analysis of sites grouped by percentage similarity in epibenthic assemblage cover.

A canonical analysis of principle components (CAP) distinguished among the four *a priori* groups (historical downstream, historical upstream, resampled downstream and resampled upstream). There was a strong association between multivariate data and the groups underlying the hypothesis, as reflected by the high canonical correlation values (δ), particularly for the first two axes, $\delta = 0.80$ and $\delta = 0.68$ (Fig. 3.6). The third axis was weaker with a δ of 0.51. Overall, the success of CAP in classifying benthic assemblages according to the grouping factors was high and the chance that samples were properly assigned to their own group was 77% (percentage correctness). Resampled upstream (67%) and downstream (83%) assemblages both had a high chance of being correctly assigned to their specific group, as did the upstream (84%) and downstream (74%) historical assemblages. The CAP results improve confidence in the findings of PERMANOVA, as the results of the PERMANOVA more closely reflect the results of CAP rather than MDS.

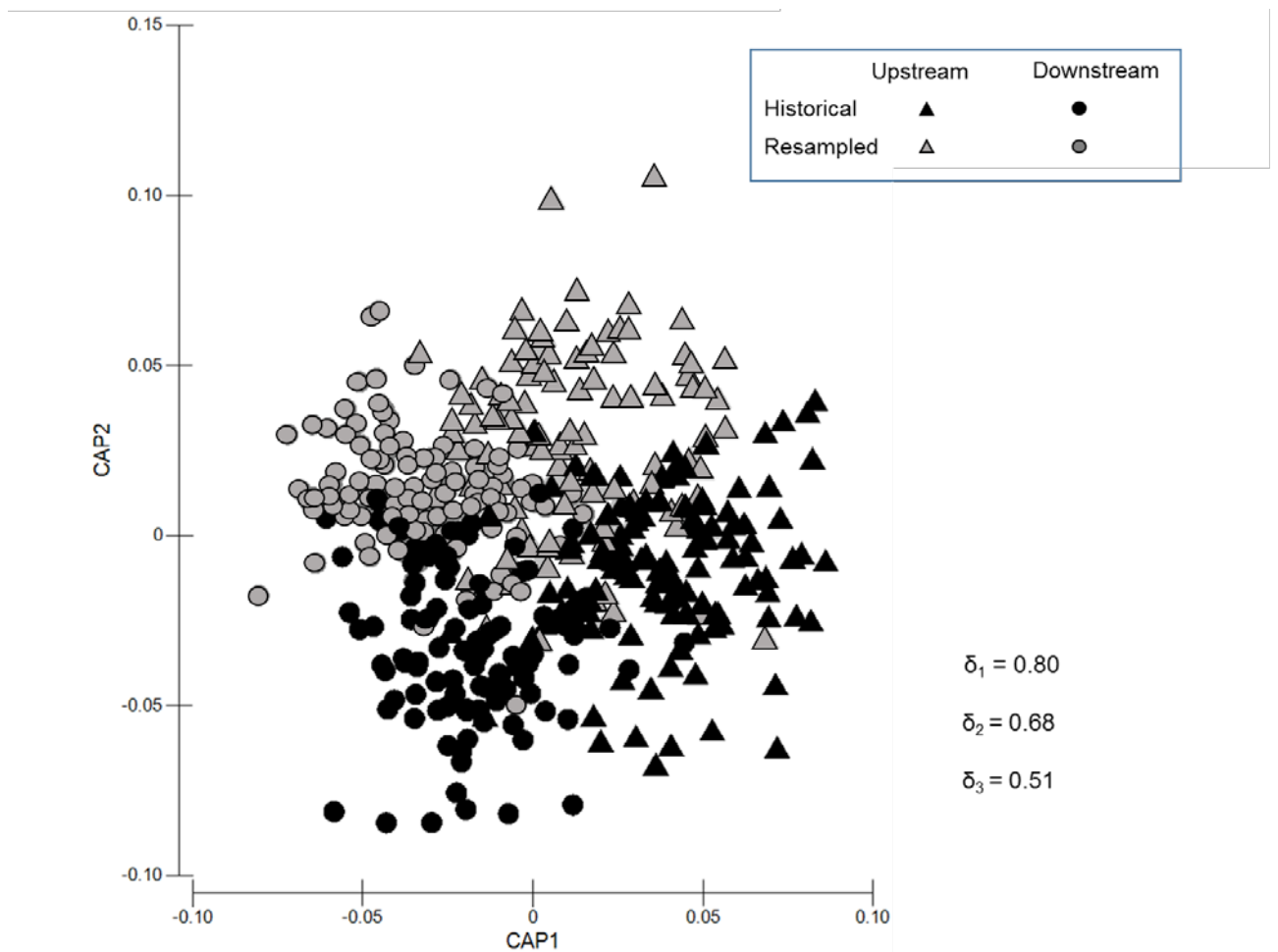


Figure 3.6 Canonical analysis of principal coordinates (CAP) of epibenthic assemblages from historical and resampled surveys in the upstream and downstream region of the PEIs. Values for δ are the canonical correlation coefficients.

SIMPER analysis showed that within the upstream region, resampled and historical assemblages had an average dissimilarity of 60.2% (Fig. 3.7). The most notable species contributing to this dissimilarity were tube-building polychaetes (*Lanice marionensis*), which increased in abundance over time. Additionally, two morpho-species of bryozoans, red algae, an encrusting sponge and two cerianthid morpho-species also contributed to dissimilarity in

the upstream region over time (Fig. 3.7a). Within the downstream region, dissimilarity between the historical and resampled assemblages had an average dissimilarity of 60.74% (Fig. 3.7b). The most notable species contributing to this dissimilarity was a species of bryozoan (*Cellaria malvinensis*) and the hermit crab (*Sympagurus dimorphus*) which both increased in abundance over time. The most notable species which decreased in abundance over time was and *L. marionensis*, two cerianthid morpho-types, the lollipop sponge (*Stylocordyla* sp.), one hydroid morpho-type, and the hyper-benthic shrimp *Nauticaris marionis*.

SIMPER analysis also showed that the average dissimilarity between upstream and downstream sites in the resampling survey was 64.15% (Fig. 3.8a). The most important species contributing to this similarity was *L. marionensis*, which had a higher abundance in the downstream region. Additionally, various bryozoan morpho-types and hermit crabs (*Sympagurus dimorphus*) also contributed >3% to dissimilarity. The dissimilarity between the upstream and downstream sites in the historical survey was 58.2% (Fig. 3.8b). The most noteworthy species contributing to this dissimilarity were *L. marionensis* (higher abundance in downstream region), various morpho-species of bryozoan, one cerianthid morpho-species, red-algae, *N. marionis*, the lollipop sponge (*Stylocordyla* sp.) and the hermit crab (*Sympagurus dimorphus*).

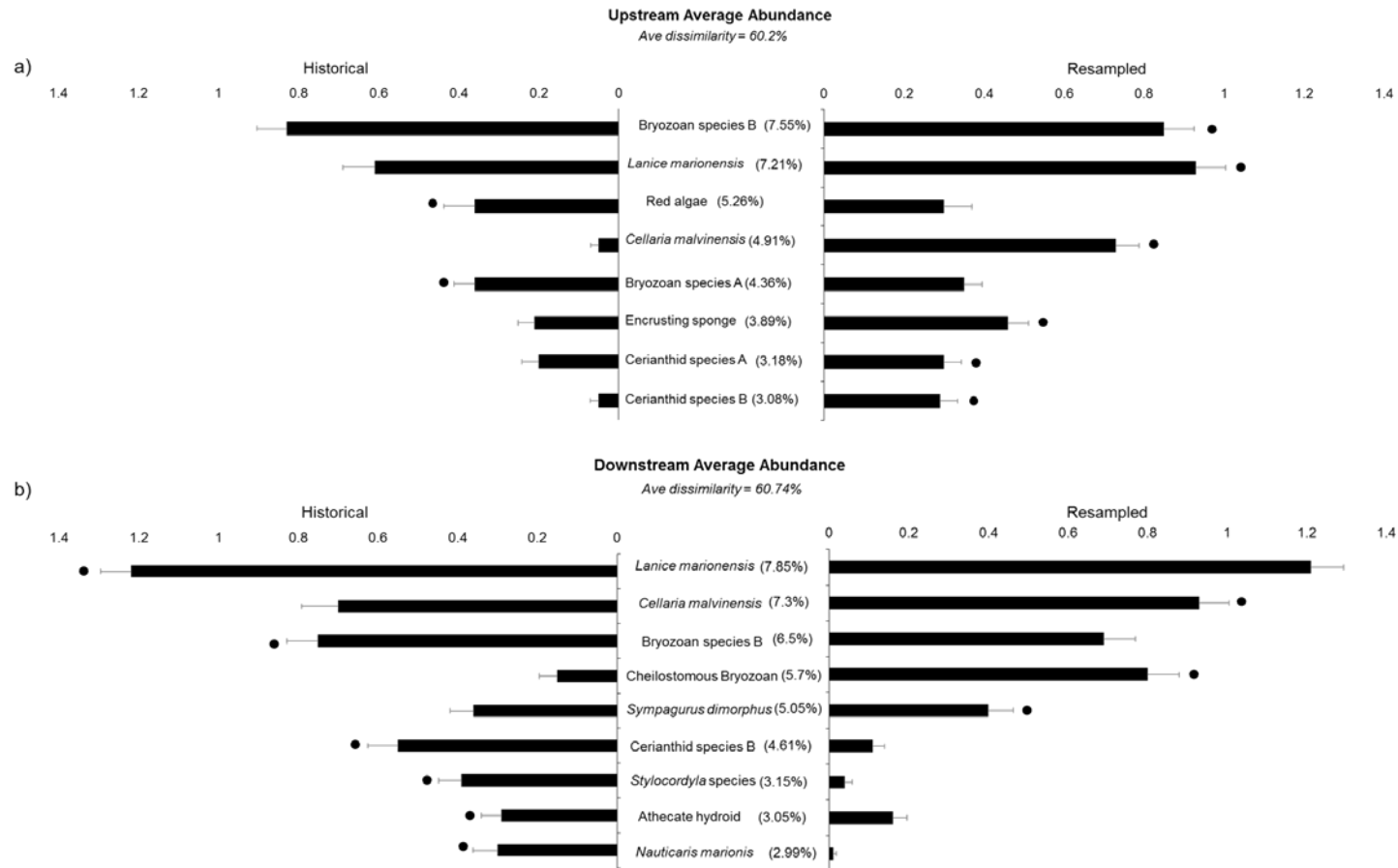


Figure 3.7 Average abundance of species contributing >3% to average dissimilarity between **a)** historical and resampled surveys within the upstream region, and **b)** historical and resampled surveys within the downstream region. Data were fourth root transformed and percentages in brackets reflect a taxon's contribution to dissimilarity. Black circles indicate which group (historical or resampled) had the greater abundance of a given species.

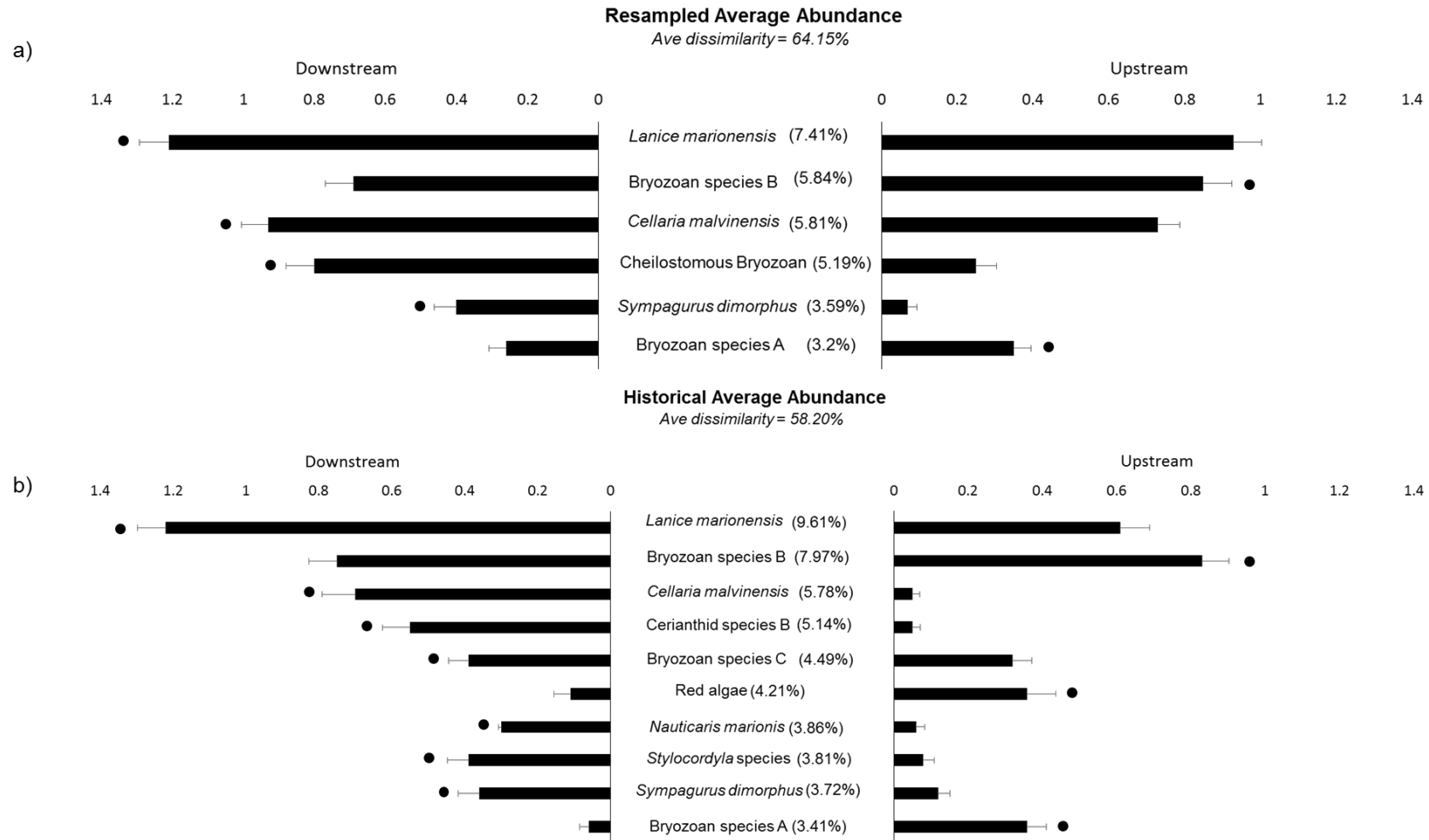


Figure 3.8 Average abundance of species contributing >3% to average dissimilarity between **a)** resampled downstream and upstream sites, and **b)** historical downstream and upstream sites. Data were fourth root transformed and percentages in brackets reflect a taxon's contribution to dissimilarity. Black circles indicate which group (historical or resampled) had the greater abundance of a given species.

3.4: Discussion

In this chapter, the assemblage structure of the epibenthos at the Prince Edward Islands was analysed to determine whether there have been temporal and/or spatial changes in diversity and assemblage composition. Epibenthic assemblages at sites in the upstream and downstream regions of the islands were compared between two sampling time periods separated by 26 years. There were significant differences in assemblage composition and diversity both temporally (between historical and resampled surveys) and spatially (upstream and downstream). Additionally, there was a significant interaction between the spatial and temporal factors. The changes detected in epibenthic assemblages at the PEIs in this study may reflect temporal and regional changes observed in other biological systems around the islands, such as spatial and temporal variations in plankton community structure as well the isotope signatures of benthic invertebrates (Pakhomov et al. 2000b; Hunt et al. 2001; Allan et al. 2013).

Broad-scale climatic changes have caused changes over time in the position of the fronts associated with the ACC in the surrounding area of the Prince Edward Islands (Hunt et al. 2001). The changing position of the SAF has important implications for biological productivity at the islands over inter- and intra-annual timescales. Over short time-scales (intra-annual cycles) the position of oceanic fronts are highly variable (Lutjeharms and Valentine 1984; Ansorge et al. 1999). Over longer time-scales (decadal cycles), climate change in the Southern Ocean has resulted in the gradual southward movement of the position of the SAF, which has had implications for localised primary productivity regimes (Hunt et al. 2001). This has been apparent in zooplankton community composition at the islands, which has changed over time with warmer-water (subtropical) species becoming more abundant than Antarctic species (Pakhomov et al. 2000b; Hunt et al. 2001). Due to changes in mesoscale oceanographic regimes resulting from alteration of the influence of the SAF, phytoplankton blooms may have

become less intense within the inter-island region (Hunt et al. 2001; Allan et al. 2013). This putative reduction in the frequency of phytoplankton blooms may have reduced nutrient availability to the benthos over time. Records show that there has been a decrease in the Chlorophyll-a concentrations in the island region since 1976 (Pakhomov and Chown 2003). Phytoplankton blooms are crucial to the ecological functioning of the island shelf ecosystems as the sedimentation of nutrients generated from these blooms supports benthic assemblages within the PEI region (Ansorge et al. 2012). The influence of declining *Chl-a* concentrations and productivity flux on the benthos has been associated with long-term changes in the δC^{13} isotopic signatures of benthic organisms at the PEIs (Allan et al. 2013). The present study corroborated the idea that persistent changes in productivity regimes are important in influencing benthic assemblages, as the downstream region had a lower evenness than the upstream region during both surveys, and diversity differed in both the upstream and downstream regions over time. This spatial change in evenness indicates that the upstream region had similar abundances across the range of species, while the downstream region had an uneven distribution of abundance across the species. The differences in evenness may be indicating that species adapted to the variable downstream environment have higher abundances than those that are not. The differences in diversity over time may reflect long-term changes in food supply to the benthos in the inter-island/downstream region (Pakhomov et al. 2004; Allan et al. 2013). In addition to differences in diversity, my study showed that species composition differed between the upstream and downstream regions within the historical survey and the resampling survey. Thus, my study may be indicative of persistent productivity patterns driving spatial differences in species composition.

Short-term and decadal changes

Despite seasonality in sea surface temperatures (Mélise et al. 2003), it was unlikely that strictly seasonal changes in epibenthic assemblages could have been an agent of change, as both historical and resampled photographs were taken during austral summer. Over intra-annual (seasonal) and short-term inter-annual (1-5 years) time scales, variations in benthic community structure are directed by community dynamics such as predation, disturbance, food availability, seasonal migration as well as larval settlement and recruitment (Glover et al. 2010). Benthic research in the North East Pacific has found no correlation between assemblage composition and food supply over short time-scales (24 month study period) (Lauerman et al. 1996; Ruhl and Smith 2004). Long-term studies, however, may be more useful in identifying epibenthic responses to environmental changes such as shifts in productivity regimes (Josefson 1990; Billett et al. 2001; Ruhl and Smith 2004; Ruhl 2007; Glover et al. 2010). Several multi-decadal (10-20 years) studies have found significant long-term changes in benthic assemblages as a result of changes in food supply over time (Josefson 1990; Billett et al. 2001; Ruhl and Smith 2004; Ruhl 2007; Glover et al. 2010). While changes in productivity regimes are known to be a result of the deterioration of sea ice in Polar Regions (Clarke et al. 2007), many of the decadal studies mentioned above showed that changes in productivity influenced the benthos, as a result of variations in oceanographic regimes and nutrient input (Josefson 1990; Billett et al. 2001; Ruhl and Smith 2004; Ruhl 2007).

Feeding modes

One of the epibenthic groups driving temporal differences within each region comprised scavenging hermit crabs. This may indicate that the downstream environment is more favourable to species that can benefit from multiple food sources and are not exclusively dependent on planktonic food sources. Overall, the tube-building polychaete, *Lanice*

marionensis, was more abundant in the downstream region than the upstream region. However, *L. marionensis* has decreased in abundance over time in the downstream region but increased in abundance in the upstream region. These tube-building polychaetes are able to filter both plankton and detritus from the water column (Fauchald and Jumars 1979). In addition to suspension feeding, *L. marionensis* is able to actively switch to deposit feeding when suspended food is limited (Rabaut et al. 2007; Allan 2011). The high abundance of this species may in part be due to their variable feeding modes enabling *L. marionensis* to switch facultatively to deposit feeding, or feed on low-quality food sources during flow-through conditions when there is less sedimentation of planktonic food sources (Allan et al. 2013). Allan et al. (2011) found that *L. marionensis* consumed increased amounts of dinoflagellates during flow-through conditions, which are common when diatom food sources become unavailable. Previous studies in other regions have found that higher abundances of a *Lanice* conspecific resulted in greater diversity of organisms as the tube worm facilitated niche expansion for other species by creating habitats and improving water quality (Eckman 1983, Rabaut et al. 2007, 2009; Van Hoey et al. 2008). This was not observed in the results of my study where the greater abundance of *L. marionensis* in the downstream region did not correlate with greater diversity of epibenthic species in the downstream region. This decreased diversity in the downstream region may have been as result of the lowered food quality in this region over time (Pakhomov et al. 2004; Allan et al. 2013).

Sponges and hydrozoans contributed to both spatial and temporal changes observed at the islands, but this is unlikely to have been due to changes in food supply. Hydrozoans may be able to consume zooplankton in addition to phytoplankton (Allan et al. 2013) indicating that they are not solely reliant on stable primary productivity regimes. Changes in primary productivity regimes were unlikely to have caused decreases in zooplankton abundances as zooplankton have been found to preferentially feed on allochthonous production (Perissinotto

1992). Additionally, sponges are only able to consume particles within the size range 0-20 μ m and are, therefore, unlikely to directly utilise the phytoplankton blooms at the islands, which are comprised of species greater than 20 μ m (Pile et al. 1996; Allan 2011). Two species of sponge, an encrusting sponge commonly found on hard substrates and a species of lollipop sponge (*Stylocordyla* sp.), had a higher abundance in the downstream region than the upstream region, but decreased in abundance in the downstream region over time. The higher abundances of this sponge species in the downstream region may be attributed to it not being wholly reliant on the variable phytoplankton blooms.

Trophic level implications

The changes in benthic assemblages measured in this study may have contributed towards the observed declines of top predators in the PEI region. My results showed that the average abundance of the hyper-benthic shrimp, *Nauticaris marionis*, decreased significantly in downstream sites over time. *Nauticaris marionis* forms a major dietary component of several species of inshore feeding seabirds such as Gentoo, Macaroni and Rockhopper penguins, Imperial Cormorants and Crozet shags (Perissinotto and McQuaid 1990). Decreases in *N. marionis* abundance in the downstream region may be attributed to the increasingly variable productivity regimes and the subsequent decrease in food quality in the lee of the islands (Pakhomov et al. 2004; Allan et al. 2013). Models of phytoplankton bloom conditions at the islands suggest that increased primary production would benefit the maintenance of benthopelagic coupling and that in the absence of bloom conditions, there could be a 25% reduction in benthic invertebrate secondary production (Gurney et al. 2014; Treasure et al. 2015). The decreases in the population sizes of inshore feeding pelagic predators may consequently be attributed to the decreases in the abundance of their benthic prey over time.

Potential caveats of this study

Despite the advantages of photographic sampling, species richness and diversity may have been underrepresented. Coral Point Count in excel (CPCe) uses a point count grid to estimate percentage cover of epibenthos. Despite the point intercept method being commonly used in photographic studies of invertebrates (Drummond and Connell 2005), there may be portions of the image where organisms are not sampled and the method may underestimate the abundance of species. Drummond and Connell (2005) compared the various sampling intensities used to estimate percentage cover of sessile intertidal invertebrates and reported no difference in richness estimation among 25, 50 or 100 point-intercepts. Drummond and Connell (2005) also found that estimates of percentage cover did not differ among photographic sampling, *in situ* sampling and laboratory sampling. Additionally, the previous chapter of this thesis analysed the species accumulation curves of various upstream and downstream sites and found that 20 photographs (± 4.7 SD) were sufficient to capture at least 80% of the species present in a given sample area, irrespective of substrate type. Despite concerns with photographic sampling, photographs retain the advantage that any errors incurred in this study by comparing spatial and temporal changes would have been consistent across the factors. Additional advantages of photographic sampling is that it is non-destructive and therefore ideal for sampling in the sensitive areas like the PEIs (Teixidó et al. 2002; Solan et al. 2003; Knight et al. 2014; Williams et al. 2015).

The most important non-research activity that occurs in the vicinity of the PEIs is fishery for the economically important Patagonian toothfish (*Dissostichus eleginoides*). Sanctioned fishing vessels most likely did not have large impacts on the sampled benthic assemblages as there is a moratorium on fishing within 22km from the islands and all sampling was undertaken at depths shallower than those commonly fished (CCALMR; Ryan et al. 2002;

Lombard et al. 2007; Collins et al. 2010). This fishery mainly supports long-line fishing, which has a less destructive impact on the benthos than other fishing methods, and as larger fish live in water deeper than 1000m it is unlikely that either sanctioned or unsanctioned fishing vessels had an impact on sampled benthic assemblages in the vicinity of the islands (Collins et al. 2010). Previously, fishing at the PEIs was seasonal (May to August), but to curb illegal fishing within the PEI EEZ, fishing was sanctioned for the entire year (Brandão and Butterworth 2002). This was done under the assumption that the presence of authorised vessels would deter unlawful fishing (Brandão and Butterworth 2002).

3.5: Conclusions

Despite the relative isolation of the Prince Edward Islands in the Southern Ocean, the threat of human-induced change remains a concern to ecologists (Halpern et al. 2008). Although this study may be considered a snapshot study, the results indicate that there have been both compositional and diversity changes of epibenthic assemblages at the Prince Edward Islands over 2.5 decades.

The results revealed that epibenthic assemblages at both upstream and downstream regions changed over time. Additionally, significant spatial differences in species composition within the historical and resampled survey likely reflect changes in prevailing productivity patterns. The alignment of spatial and temporal patterns is likely in response to both long-term differences in oceanographic conditions and subsequent changes in productivity regimes. As benthic invertebrates are reliant on sedimentation of nutrients from phytoplankton blooms, and the benthos is an important food source for top predators, changes in epibenthic abundances as a result of changing productivity regimes may have important impacts on higher trophic levels. Variations in the position of the SAF as a result of climate change may have important influences on the functioning of the Prince Edward Island ecosystem (Pakhomov et al. 2000b;

Ansorge and Lutjeharms 2002; Ansorge et al. 2012). It is imperative that investigations into long-term trends in epibenthic assemblages at the PEIs be established, especially in light of documented changes in productivity regimes in the region. However, as it is difficult to isolate inter- and intra-annual differences, future studies may benefit from sampling at shorter timescales in order to distinguish climate-change effects from natural variability. This work may be important in understanding the population dynamics of top predators at the PEIs. Additionally, this work furthers the understanding of epibenthic invertebrates at the Prince Edward Islands and the photographs provide a permanent record of epibenthic assemblages that will serve as a baseline for future repeat epibenthic surveys.

Chapter 4: Synthesis

The principle aim of this project was to assess present day epibenthic assemblages around the sub-Antarctic Prince Edward Islands using photographs taken with a towed benthic camera. Two more sub-aims were tested in this study. Firstly, the optimal photographic sampling intensity required to attain a representative sample of epibenthic diversity in various abiotic substrate types at the PEIs was determined. Secondly, as spatial and temporal changes have been documented in multiple biological and oceanographic systems at the PEIs, this study aimed to test whether changes had occurred in the species composition and abundance of epibenthic assemblages in the upstream and downstream regions over time.

Photography has recently become more frequently used as a sampling method to document and visualise change in community structure (Jørgensen and Gulliksen 2001; Solan et al. 2003; Kipson et al. 2011; Reimers et al. 2014; Williams et al. 2015). However, due to the various challenges associated with using photography, it was necessary for sampling strategies to be optimised. Epibenthic photographs from various sites, with different substrate types, were used to calculate the species area relationship (SPAR). Based on SPAR testing, the point where the species accumulation curve started to decelerate was determined. Species accumulation curves did not differ when compared across the sampled substrate types and an optimal number of 20 (± 4.7 SD) photo-replicates ($\sim 15\text{m}^2$) emerged as the recommended intensity for future long-term sampling at the PEIs (Chapter 2).

Research into the oceanography surrounding the PEIs has found long-term spatial and temporal changes in mesoscale oceanographic regimes and, consequently, shifts in productivity regimes (Froneman and Pakhomov 1998; Pakhomov and Froneman 1999; Pakhomov and

Chown 2003; Pakhomov et al. 2004; McQuaid and Froneman 2008; Allan et al. 2013). As many studies have noted, these kinds of oceanographic changes can have implications for many biological systems in the islands' region, from plankton community structure to changes in population dynamics of top predators (Pakhomov and Chown 2003; Crawford et al. 2009). However, as yet, not many studies have considered how benthic assemblages may have responded to these oceanographic changes and resultant changes in bottom-up effects on productivity patterns (Allan 2011). Historical epibenthic photographs were available from a previous benthic survey of the PEIs (Branch et al. 1993a). These, combined with resurvey photographs from 2013 and 2015, enabled spatial and temporal changes in epibenthic assemblages to be evaluated. The epibenthos in the upstream and downstream regions of the PEIs were compared over time using these historical and resampled images. Epibenthic assemblages differed between the upstream and downstream regions, and assemblages in both these regions changed over time. As the PEIs lie directly in the pathway of the easterly moving Antarctic Circumpolar Current, the oceanic environment surrounding the islands is separated into three distinct regions, which all experience varied nutrient levels and support different plankton size classes as a result of their characteristic productivity regimes (Perissinotto et al. 1990; Froneman and Pakhomov 1998; Froneman et al. 1999; Pakhomov and Froneman 1999; Ansorge and Lutjeharms 2002). This is partly due to the 'island mass effect', where nutrient runoff from the islands, compounded with mesoscale oceanographic regimes, facilitates large phytoplankton blooms in the inter-island region (Boden 1988). Moreover, eddies are created in the lee of the islands due to the obstruction of water flow by the islands, retaining primary productivity and influencing population connectivity in terms of the entrainment, recruitment and dispersal of larvae (Heywood et al. 1990; Wolanski et al. 1996; Blain et al. 2001). Spatial differences in the benthos were likely attributable to spatial differences in productivity patterns as a result of mesoscale oceanographic regimes affecting the biology of the islands. However,

temporal differences possibly reflected that there have been alterations in these patterns over time (Chapter 3). Previous studies have documented a gradual southward shift of the position of the sub-Antarctic front, and this has affected mesoscale oceanographic regimes at the islands over time, changing the origin of planktonic food resources (Hunt et al. 2001; Allan et al. 2013).

The results of Chapter 2 informed the sampling intensity used in Chapter 3 and will inform future epibenthic photographic work at the Prince Edward Islands. This will ensure that scarce resources are optimally allocated in surveys of epibenthos in this sensitive area. The work outlined in this thesis provides an important starting point for future benthic research at the PEIs and is the first epibenthic photographic survey since the 1980s (Branch et al. 1993a). This study will enable educated decisions to be made regarding the future conservation of the PEI marine protected area and improve our understanding of benthic ecology and potential responses to long-term change.

4.1: Photo-methodology

Despite the many benefits of photographic sampling (Adams et al. 1995; Teixidó et al. 2002; Solan et al. 2003; Stobart et al. 2007; Reimers et al. 2014; Williams et al. 2015), sampling benthic habitats is notoriously difficult, with problems ranging from inadequate sampling apparatus to the underrepresentation of species richness (Roberts et al. 2000; Solan et al. 2003; Knight et al. 2014; Williams et al. 2015). My study determined that in the region of the PEIs, an average of 20 (± 4.7 SD) photo-replicates ($\sim 15\text{m}^2$) can be used to reach a point where at least 80% of the total asymptotic richness had been sampled (Chapter 2). Testing revealed that this sampling intensity can be applied irrespective of substrate type at the PEIs. Other studies, using species area relationships in Mediterranean coral outcrops as well as soft bottom communities, have found that estimates of required sample size differed from those of my study by one order of magnitude (Gray 2002; Kipson et al. 2011). Additionally, similar number of photo-replicates

as was used in my study, have been used in studies of seamount benthic diversity (Williams et al. 2015). However, a study on various substrates in the North East Atlantic processed large sampling areas (80m² - 16170m²) and species accumulation curves were yet to start decelerating (Foster et al. 2013). That study processed habitats similar to those covered in my study, in that a mixture of hard and soft substrates were classified but differed in that sites that included biogenic habitats were analysed separately from those that did not. The recommendation provided in the current study may, therefore, be a low estimate and while it may not be necessary to increase the sample size of benthic photographs at the PEIs, caution should be exercised when translating the results of this study to different locations. The estimated sampling intensity recommended in this study is suitable for the PEI region as the species accumulation curves all reached points of deceleration irrespective of substrate type, indicating that only a few species were yet to be found. However, certain locations at the PEIs may require more photo-replicates than is recommended in this study. Deeper sites, spatially heterogeneous sites or any area where the species richness may be low, will require more photo-replicates as these areas contain more rare species and species will accumulate at a slower rate than those with higher richness (Baltanas 1992; Scheiner 2003). Taking these considerations into account, the work detailed in this study (Chapter 2) provides an optimised framework for future photographic sampling and monitoring at the PEIs and will enable the allocation of time spent on photo-analysis to be improved.

There are several important caveats of the photographic sampling outlined in this thesis. One of these limitations is that only visible species (species >1cm) could be characterised. While there are distinct benefits to visualising *in situ* species relationships and habitat context, species too small to be seen or infaunal species are overlooked. This disregards species that are vital to the health of ecosystems such as burrowing species. Several studies have used box corers or grabs in addition to photographic sampling to aid species identifications (Solan et al.

2003). My study was only able to classify species to morpho-species level, as physical specimens were not always collected. Future studies could, therefore, make use of a dredge or grab in conjunction with photography in order to collect specimens and conduct a genetic analysis of epibenthos. Despite these drawbacks, benthic imagery allows for the classification of extensive areas without disrupting or removing large habitat-forming organisms like corals or sponges (Beisiegel et al. 2017). Another limitation of the photographic sampling in my study is that only sedentary mega-benthos could be classified. Highly mobile species such as fish were excluded as they move away from the camera. As predatory fish are important top-down regulators of benthos invertebrate abundances, they are crucial to the understanding of ecosystem function. Previously, assessments of fish populations within the PEI region have been undertaken through destructive trawl surveys (Brandão and Butterworth 2002; Pakhomov et al. 2006). Baited remote underwater video (BRUV) has been used in many marine ecosystems to estimate the standing stock of a variety of mobile predatory species (Yau et al. 2001; Cappo et al. 2004; Watson et al. 2010). Future studies may, therefore, be able to elucidate the size of the commercially important Patagonian toothfish population and other predatory fish at the PEIs using non-destructive videography and aid in trophic studies at the islands.

4.2: Future directions of epibenthic studies at the Prince Edward Islands

It was long thought that the Antarctic and sub-Antarctic were one of the few undisturbed ecosystems left on earth due to their isolation from human populations. Many studies, however, have refuted this claim and have demonstrated veritable change in polar ecosystems both in pelagic as well as deep sea systems (Peck 2005; Halpern et al. 2008; Hoegh-Guldberg and Bruno 2010). Climate change is of major concern in polar systems, where increases in sea surface temperatures have resulted in increased glacial melting, changing oceanographic patterns and subsequent variations in primary productivity regimes (Clarke and

Harris 2003, Constable et al. 2014). Increases in global sea surface temperatures resulting from climatic changes may directly affect the abundance of benthic invertebrates by influencing settlement, dispersal and growth of larval stages (Harley et al. 2006). Additionally, environments may become more susceptible to invasive species and some organisms may shift their biogeographical range thereby changing the composition and diversity of ecosystems (Walther et al. 2002).

Due to the paucity of research and information about the deep-sea, it is highly likely that species can become extinct without our knowledge (Snelgrove 1999). Despite the ACC being a good biogeographic barrier to species movement (Clarke and Harris 2003), invasive species are still a major concern at the PEIs, and terrestrial invasions (insects, grasses, mice, and cats) have plagued biological systems at the islands (Chown and Froneman 2008b). Recently a new research base was built on Marion Island, and more trips to the islands were scheduled during construction. As a result of increased ship traffic in the vicinity of the islands (fishing and research vessels); the ability of some alien species to survive long ship journeys; and a changing climate, marine environments may become more susceptible to invasive spread (Bergstrom and Chown 1999; Smith 2002; Aronson et al. 2007; Lee and Chown 2007; Occhipinti-Ambrogi 2007, Constable et al. 2014). As impacts of alien species associated with invasive spread is a known threat to marine biodiversity, ecosystem services and the ecological functioning of marine food webs are likely to be negatively affected (Molnar et al 2008; Vilà et al. 2009; Worm et al. 2012; Mellin et al. 2016). The benthic surveys undertaken in this study in conjunction with previous benthic taxonomic and photography work will facilitate the assembly of a permanent baseline record of epibenthic species at the PEIs. Such baseline records will help characterise any changes caused by climate change species introductions or fishing (Reimers et al. 2014; Beisiegel et al. 2017).

Despite the population dynamics of top predators at the PEIs being well studied, not much research has analysed trophic relationships between top vertebrate predators and the marine environment. Models have suggested that changes in the abundance of benthic invertebrates could have deleterious impacts on higher trophic levels, especially in light of climate change (Gurney et al. 2014; Jones et al. 2014; Treasure et al. 2015). The present study corroborated these models (Chapter 3), and changes in assemblage composition were found to mirror other environmental changes taking place at the islands (Froneman and Pakhomov 1998; Pakhomov and Froneman 1999; Pakhomov and Chown 2003; Pakhomov et al. 2004; McQuaid and Froneman 2008; Ryan and Bester 2008; Allan et al. 2013). The work presented here forms a valuable starting point in the study of both bottom-up and top-down effects on trophic relationships at the PEIs. Future studies could also focus on the effects that climate changes and consequent changes in primary productivity regimes may have on the survival and recruitment of pelagic larvae of benthic invertebrates due to their dependence on food availability (Przeslawski et al. 2008).

As climate change has altered the availability of resources to the benthos, the manner in which communities are assembled may have changed. In many terrestrial plant communities, functional trait analysis has been suggested to be useful in determining community assembly in the face of disturbance (McGill et al. 2006; Cornwell and Ackerly 2009; Swenson and Weiser 2010). Functional trait analysis has also been found to be applicable in marine communities (Litchman and Klausmeier 2008; Edwards et al. 2013), and may be a more rigorous method to assess diversity change rather than comparing only taxonomic composition (Bremner et al. 2003). Applying such techniques could be an important next step in epibenthic studies at the PEIs.

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23:7-18.

Appendix A

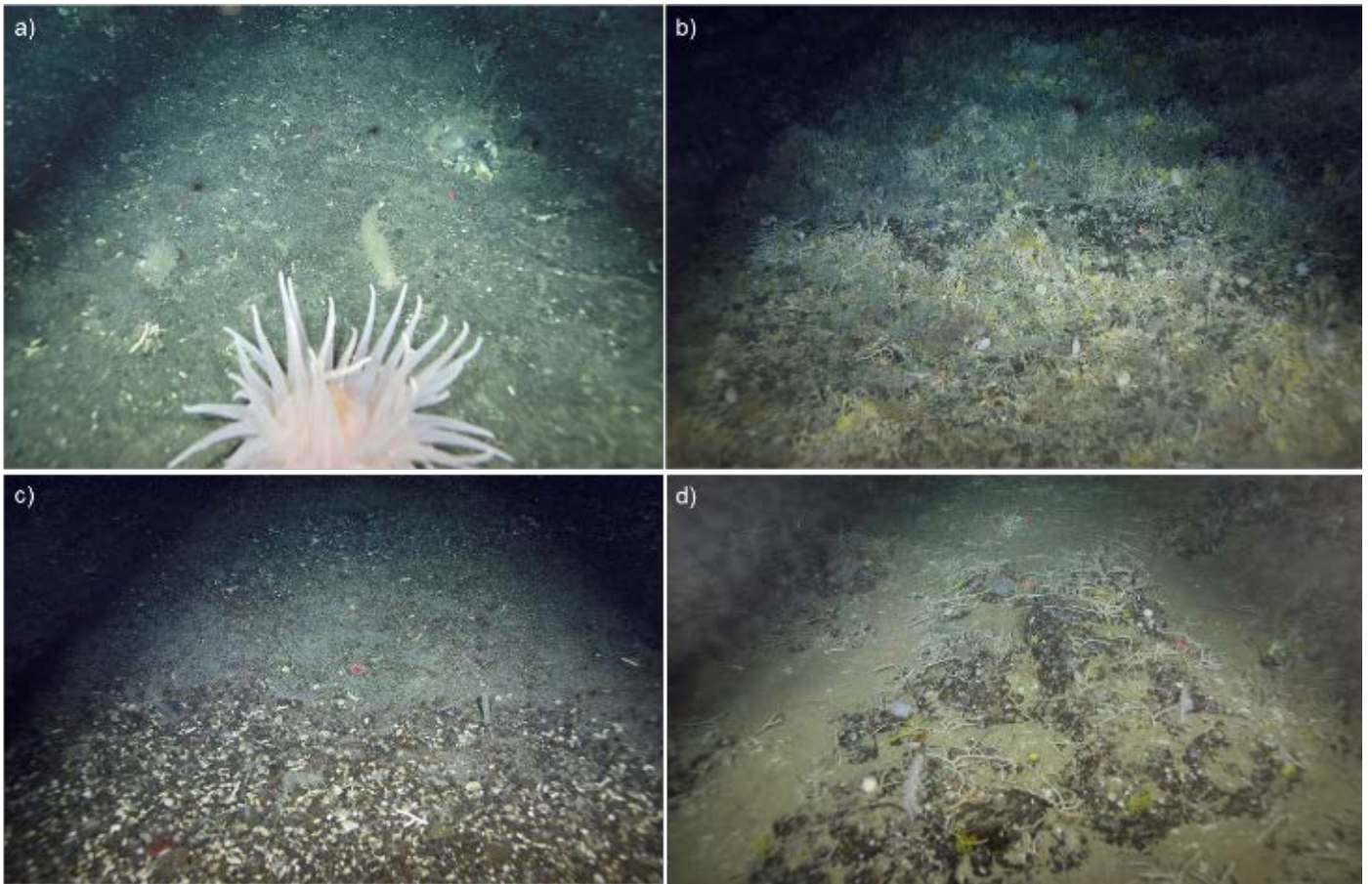


Plate 1) Examples of epibenthic assemblages at four classified substrates **a)** large anemone and holothuroid (*Synallactes challengerii*) on mud substrate (site C52) **b)** dense assemblage of bryozoans, sponges as well as ophiuroids and crinoids on gravel-mud substrate type (site C43) **c)** gravel substrate with pink anemone (site C42) **d)** bryozoans and encrusting sponges on partial rock-sand substrate (site C22)

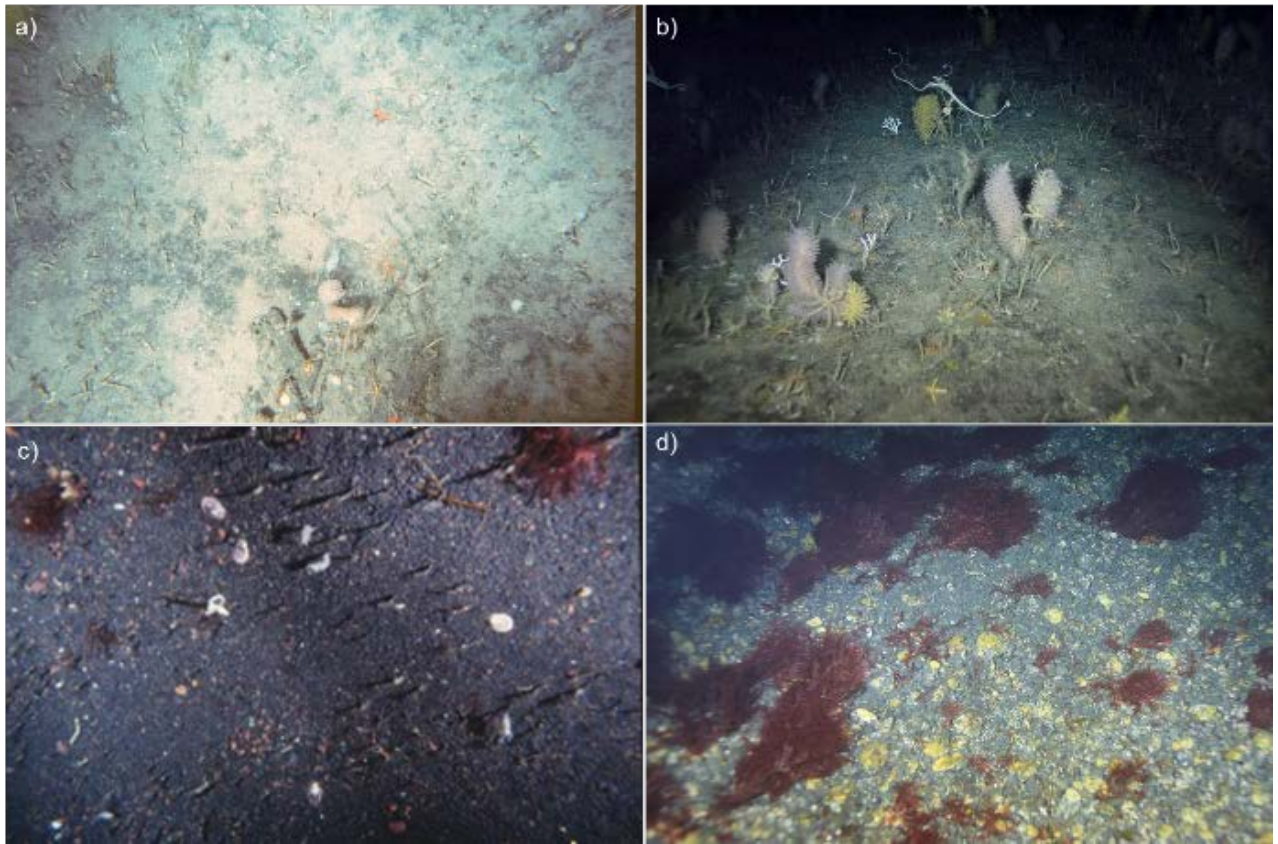


Plate 2) Examples of historical and resampled epibenthic assemblages **a)** historical image (site C8) of Octocorals (*Thouarella variabilis*) and ophiuroids and crinoids **b)** resampled image (site C8) of octocorals (*Thourella variabilis*), ophiuroids (*Asteronyx loveni*). **c)** Historical image (site C54) of tube dwelling polychaete (*Lanice marionensis*), red algae and aeolid nudibranch **d)** resampled image (site C54) of red algae and hyper-benthic shrimp (*Nauticaris marionis*).

Appendix B

The Chao 2 calculation uses the number of individuals that only occur once in a sample (uniques, Q_1), the recurring individuals (duplicates, Q_2) and the total number of observed individuals (S_{obs}) in order to calculate the estimated number of individuals in a sample (S_{est}). This equation adjusts for small sample sizes by incorporating the number of replicated samples into the equation (t).

$$S_{\text{est}} = S_{\text{obs}} + \frac{\left(1 - \frac{1}{t}\right)Q_1^2}{2Q_2}.$$

Appendix C

Table C1) Location, depth, and substrate type of a recent survey of the Prince Edward Islands with the number of photographs sampled in sites included in Chapter 3 analyses.

<i>Substrate</i>	<i>Site</i>	<i>Depth (m)</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Region</i>	<i>Number of photographs sampled in Chapter 3</i>	
						<i>Historical photographs</i>	<i>Resampled photographs</i>
Mud	C52	383m	46 55.03°	37 34.03°	Upstream	11	28
Mud	M49	283m	47.01°	37.90°	Downstream	44	30
Mud	C8	299m	46 43.02°	37 48.99°	Upstream	20	27
Mud	C9	80m	46 49.09°	37 45.54°	Inter-Island	N/A	N/A
Mud	M3	135m	46.95°	37.93°	Downstream	30	30
Mud	C38	204m	46.97°	37.98°	Downstream	25	30
Gravel-Mud	C43	225m	46 40.10°	37 51.49°	Upstream	9	20
Gravel-Mud	M26	182m	46.75°	37.95°	Inter-Island	N/A	N/A
Gravel	M5	61m	46.98°	37.78°	Downstream	N/A	N/A
Gravel	C54	62m	46 54.81°	37 34.99°	Upstream	N/A	N/A
Gravel	C10	79m	46 59.35°	37 48.98°	Downstream	N/A	N/A
Gravel	M37	338m	46.68°	37.85°	Upstream	36	26
Gravel	C42	512m	46 40.50°	37 50.47°	Upstream	21	30
Partial rock-Sand	C39	403m	46 59.81°	38 01.04°	Downstream	5	25
Partial rock-Sand	C22	420m	47 01.16°	37 58.97°	Downstream	N/A	N/A