Diversity and abundance of intertidal zone sponges on rocky shores of southern NSW, Australia: patterns of distribution, environmental impacts and ecological interactions

Caroline Cordonis Borges da Silva

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Diversity and abundance of intertidal zone sponges on rocky shores of southern NSW, Australia: patterns of distribution, environmental impacts and ecological interactions.

Caroline Cordonis Borges da Silva

Supervisor:
Andy Davis

This thesis is presented as part of the requirement for the conferral of the degree:

DOCTOR OF PHILOSOPHY

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University of Wollongong
School of Earth, Atmospheric and Life Sciences

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ABSTRACT

Sponges (Porifera) are among the most diverse and important components of sessile benthic communities. Sponge communities have a global range of distribution occupying a diverse array of aquatic habitats. They also play a range of ecological roles thus contributing to ecosystem functioning. Although the scientific evidence strongly supports the significance and widespread nature of these functional roles, sponges remain underappreciated in marine systems. This is the first study that identifies the sponge assemblage and investigates in detail the patterns of distribution and abundance of sponge taxa on rocky reef habitats of south-eastern Australia. It is also one of the few studies worldwide to uncover some of the processes responsible for influencing these patterns, such as smothering by sediment and spongivory.

The accessibility of rocky shores has rendered sponges susceptible to a wide range of anthropogenic stressors. Furthermore, pressure caused by a range of natural factors on various spatial and temporal scales, such as emersion in the air during low tide is exacerbated by human activities. Sponges tend to be avoided in ecological monitoring due to their taxonomic complexity, so while changes in the distribution, abundance and range limits of intertidal species have already been explored in previous studies, investigating patterns of abundance and distribution in a variety of poorly understood, yet key species is essential to understanding the ecological processes that affect populations.

The data presented in this study addresses the importance of taxonomic expertise to ensure adequate species description and identification of a challenging group of organisms. This study sought to fill knowledge gaps and enhance our understanding of a poorly described community associated with an ecosystem that faces unpredictable natural fluctuation and anthropogenic pressures. I have sought to investigate some of the key environmental factors affecting sponge taxa through quantitative surveys and manipulative experiments.

I recorded a total of 22 sponge species, restricted to five of the fourteen intertidal reefs I examined. Twelve taxa were established as new occurrences for the Illawarra region, with many of these previously undescribed. The most common species Callyspongia sp. was the most widely distributed. In contrast, other species had a markedly low abundance recorded among the reefs, with one or two individual sponges recorded at each reef. Sponges were uncommon, sparsely distributed, and these assemblages showed considerable spatial heterogeneity among reefs.
A better understanding of the environmental factors that are shaping the community of this intertidal ecosystem are required to understand species interactions. Sponge distribution and abundance relied on habitat features that affected sponge species composition among reefs. These features included, habitat complexity, the height of the rock pools on the shore, the volume of these pools, wave exposure and the season of the year. Manipulative experiments were used in situ to observe influencing factors for sponge distribution patterns, such as the increase of sedimentation loads on rock reefs, or predation.

A laboratory experiment assessed the impact of a storm on the east coast of New South Wales and its contribution to increased sediment loading and its effects on common sponge taxon. Different rates of sedimentation were used to test the effects on the survival of intertidal sponge adults and recruit-sized explants. High sediment deposition (200 mg cm\(^{-2}\)) proved to be an important factor in influencing the distribution patterns of some intertidal sponges but had disproportionate effects on small intertidal sponge individuals (recruits).

I used a field experiment to examine the effects of a biotic influence – predation – on sponge abundance; observations suggested that the major invertebrate spongivores on Illawarra rocky reefs may be the sea urchins - Centrostephanus rodgersii and Heliocidaris tuberculata. However, the predation treatments outcomes showed no effect on the sponge cover or survivorship from urchin grazing. Instead the experiment revealed a low level of predation by three species from the class Gastropoda, Dendrodoris nigra (Family Dendrodorididae) and two fissurellids - Diodora lineata and Montfortula rugosa. The importance of physical conditions was also highlighted as wave and tidal height were key factors that influenced sponge survivorship and cover. This outcome was surprising in that it conflicted with previous studies, which considered sea urchins the organisms with the most influence on community structure in shallow subtidal regions near Wollongong. Further studies could investigate, perhaps through laboratory experiments, whether sea urchins on intertidal reefs are feeding on sponges and thereby affecting their patterns of vertical distribution and abundance.

In conclusion, the outcomes of my thesis besides improving our understanding of a key and poorly understood taxon, build a baseline for effective future research programs and monitoring. My contribution includes information on: 1) the identification of the species present on reefs in the Illawarra region; 2) an estimate of the spatial and temporal patterns of distribution and abundance of the sponge assemblages; 3) the investigation of some of the key biotic and abiotic factors driving these patterns of abundance and distribution. The information presented in this thesis is important given threats such as ocean acidification, global warming and coastal disasters that may have effects on the population structure of intertidal sponges.
Therefore, my findings have important implications that will contribute to the establishment of adequate and representative intertidal protected areas in the Hawkesbury Shelf Marine Bioregion of NSW, along with conserving intertidal sponge biodiversity and community function.
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“Humans could reconcile themselves with the planet, finding a way to be useful and welcome in the system. We have disconnected ourselves from life on the planet, thinking that we are the intelligent ones. We cannot see that we are just part of an intelligent system”.
Ernst Gotsch
CHAPTER 1
General Introduction
1.1 Functional roles and importance of sponges to community structure and functioning.

Sponges (Porifera) are among the most diverse and important components of sessile benthic communities. They influence community dynamics and make an important contribution to ecosystem functioning (Hooper et al., 2002a; Bell, 2008a). The great variety of sponge species play a wide range of significant functional roles in marine systems, including nutrient cycling, bioerosion, consolidation of the reef framework, among others (Rützler, 1975; Corredor et al., 1988; Wulff, 2012). Sponges are sessile animals, exclusively aquatic that are filter feeding, varying to carnivorous sponges in deep-sea environments. They are characterized by a simple body plan built around a water system pumped by flagellated cells called choanocytes. These choanocytes efficiently filter the seawater retaining small plankton particles, including bacteria and viruses (Hoffmann et al., 2008). The structure of sponge community varies with environmental fluctuations such as substrate type (coral, igneous rock, limestone rock), substrate aspect (exposed, protected), substrate configuration (limestone platform, dissected reef) and depth (Fromont et al., 2006).

Sponges are the oldest metazoan group that still exists on our planet, with fossils dating from the Pre-Cambrian, 600 mya (Hooper & Van Soest, 2002; Yin et al., 2015). They are one of the most diverse groups of organisms with approximately 9,162 valid species described so far worldwide and with an estimated 12,000 left to be described by the end of this century (Fromont et al., 2016; Van Soest et al., 2019). Currently, the phylum Porifera has four different classes: Demospongiae Sollas, 1885, Calcarea Bowerbank, 1864, Hexactinellida Schmidt, 1870 and Homoscleromorpha Bergquist, 1978 (Hooper et al. 2002a; Van Soest et al., 2019). Documentation of regional sponge assemblages is still relatively rare. The number of undescribed species makes it difficult to improve our understanding of the distribution of these organisms (Fromont et al., 2016). Most sponge species are found in local or regional areas of endemism due their larvae swim ability limitations, and infrequent asexual propagation unless they are inadvertently spread globally or regionally by shipping traffic or ballast water (Hooper & Lévi, 1994). Sponge communities have a global range of distribution occupying a diverse array of aquatic habitats, from epifaunal rocky communities to mud bottoms and ephemeral freshwater habitats. They are distributed from intertidal zones to hadal depths as well as from tropical coral reefs to polar habitats (Hooper & Lévi, 1994; Van Soest et al., 2012). The evolutionary success of sponges and their importance to the environment can be related to an
array of adaptations; the totipotency of their cells, their ability to reproduce sexually and asexually, their positive and negative interactions with a variety of taxonomic groups, the production of secondary metabolites and even their morphological plasticity - which allows the survival of species of this group in different habitats (Hooper & Van Soest 2002; Fortunato, 2015)

Sponges have a simple level of organization, lacking tissues, but they have demonstrated a complex developmental and reproductive process (Kaye & Reiswig, 1991). For instance, versatility in feeding behaviour (Lopes et al., 2011); flow sensors (Ludeman et al., 2014); and production of the largest number of secondary metabolites among marine invertebrates that are of pharmacological interest and, in turn, considerable economic potential for biomedical research and public health (Leal et al., 2012).

The ecosystem services provided by the global sponge community in physical, chemical and biological environments are widely described in the literature and highlight the important contribution of those animals in maintaining biodiversity (Bell, 2008b). Sponges are also good ecological indicators. They have been suggested as monitors of organic or thermal pollution and contamination; as sessile organisms with susceptibility to variations in water quality (Alcolado & Herrera, 1987; Vilanova et al., 2004; DeMestre et al., 2012). Sponges’ functional roles have been categorized into three main areas (Bell, 2008b): (A) Impacts on the substratum including bioerosion (Rützler, 1975), reef creation, substrate stabilisation, consolidation and regeneration; (B) Bentho-pelagic coupling including oxygen depletion (Hoffmann, 2008), nutrient cycling, carbon cycling, silicon cycling (Maldonado et al., 2012) and nitrogen cycling (Corredor et al., 1988; Keesing et al., 2013). Bentho-pelagic coupling across habitats and bottom-up versus top-down processes are known to have an important impact on the assemblages structure of intertidal and shallow subtidal marine communities (Lesser, 2006). Sponges are important members of the benthic community and provide a crucial coupling between water-column productivity and the benthos due to their large biomass and high water filtering rates (Weisz et al., 2008); (C) Forming associations with other organisms including significantly contributing to primary production through microbial symbionts (Wilkinson 1983), facilitating secondary production (Goeij et al., 2013), provision of microhabitat (Webster & Taylor 2012), improved protection from predators (Goreau & Hartman, 1966) and range expansion and camouflage. Sponges are also recognized as a settlement substrate, agents of biological disturbance (Bell 2008a), producers of chemicals (Mehbub et al., 2014) and sponges as tools for other organisms, providing habitat and acting as food source (Wulff, 2006a; Sivadas et al., 2014).
Sponges interact with most other organisms in marine systems as competitors, consumers and prey (Wulff, 2006a). They also form a wide range of biological associations with organisms from microbial symbionts to vertebrates, which are important to their success (Webster & Taylor, 2012; Sivadas et al., 2014). Sponge symbionts play a decisive role in nutrient cycling. Some of those species have the ability to uptake dissolved organic nitrogen where nutrients in the water column are low, thereby contributing to organic production in oligotrophic habitats (Southwell et al., 2008). Their ability to facilitate secondary production makes the recycled of dissolved organic matter available to higher trophic levels (Goeij et al., 2013). Further investigation is necessary to understand the interaction between the pelagic environment and sponges, especially because change in sponge population are likely to induce cascading ecological effects (Butler et al., 1995; Bell, 2008b). Furthermore, specific species have the ability to bind unconsolidated substrate such as coral rubble into stable surfaces, reinforcing the reef frame and decreasing the loss of coral colonies by physical damage (e.g. wave action). They can also increase water clarity and facilitate reef regeneration. Nevertheless, sponges tend to be avoided in assessment and ecological monitoring (Bell, 2008b) principally because the difficulties in quantifying and identifying sponges combined with the limited number of specialists generate taxonomical uncertainties (Wulff, 2001).

Sponges are one of the top spatial competitors and are abundant in shallow and deep benthic habitats (Hooper et al., 2002a). They make an important contribution to ecosystem functioning through their functional roles. Therefore, as we gain more understanding of the roles of sponges and their ecological interactions in communities, the need to assess and monitor changes in sponges are becoming crucial (Wulff, 2001). Furthermore, to identify any future impact on sponge assemblages, it is important to quantify their temporal changes and spatial natural patterns, improving our understand in how such communities may respond to disturbance.

1.2 Hostile environment: Challenges for intertidal zone sponges.

Anthropogenic stresses are superimposed on the stress caused by a wide range of natural fluctuations on various temporal and spatial scales such as emersion in air due to the tides and wave action, making the intertidal zone a harsh environment for marine organisms (Crowe et al., 2000). The accessibility of rocky shores has rendered them susceptible to a variety of stresses caused by human activities, originating from both land and sea. Consequently, anthropogenic stress are often linked with effects which modify competition between species and affect indirectly their abundance and distribution (Thompson et al., 2002).
Intertidal biota must endure periods of emersion that can lead to physical stressors associated with alternating submersion and emersion in air (desiccation, temperature extremes, osmotic stress and exposure to UV radiation). Hence, organisms may be exposed to a range of physiologically unusual conditions simultaneously. Abiotic factors can be associated in the intertidal habitat; UVR and associated sunlight for instance can increase temperature, which can then increase evaporation rates in small pools and lead to increased salinity (Przeslawski et al., 2005). Therefore, most of the intertidal organisms must be tolerant of a variety of stressors. Organisms usually occur well within their range of tolerance of physical conditions and are not stressed except under unusual conditions (Crowe et al., 2000). To achieve this, they developed mechanisms to cope with those physical stresses which may often be effective for withstanding some anthropogenic stresses (Thompson et al., 2002). Consequently, rocky shore organisms may serve as models for understanding the impacts of climate change yet the impact of multiple stressors associated with climate change remains unclear and responses may be complex (Kelmo et al., 2014; Davis et al., 2013).

Despite the crucial ecological importance of sponges along with their high diversity and biomass in many intertidal and shallow subtidal benthic habitat (Bell, 2008a) how environmental variability affect reef organisms, other than corals and fish, remains studied (Kelmo, et al 2014). Studies on intertidal sponge fauna has rarely focused on community composition and abundance (see Barnes, 1999; Fromont et al., 2006). Furthermore, very few studies have examined the ecological interactions and unpredictable physical stresses on these communities. Moreover, natural environmental variables affecting intertidal sponges have been poorly studied.

Marine systems have proven to be a productive focus for understanding the processes that structure assemblages. A large number of studies attest to the importance of biotic and abiotic factors such as recruitment, predation, competition and physical variables in shaping ecological pattern in the rocky intertidal and sublittoral zones (Davis et al., 2013). Intertidal sponge assemblages are exposed to more stressful conditions than subtidal communities (Bell, 2008a). However, there is a clear need to understand how climate change will affect the processes that influence the intertidal community structure and identify strategies to mitigate harmful effects.

After corals, sponges are one of the most dominant taxa inhabiting sessile benthic communities. Changes in their interactions, distribution and abundance patterns have the potential to affect overall functioning of different marine ecosystems (Powell et al., 2014). However, identifying the variables that influence those patterns is important for our
understanding of the future effects that anthropogenic and climatic impacts may cause on intertidal rocky shores. Given the environmental variability intertidal reefs experience sponges may potentially be more resilient to climatic events and could provide important insights, serving as model for change in other ecosystems (Kelmo et al., 2014).

1.3 Sponges in future oceans.

Changes in global temperature and ocean chemistry correlated with high levels of greenhouse gas are pushing widespread shifts in biological systems. As consequence to warming, species ranges are moving toward the poles, up mountainsides, and deeper into the ocean (Harley et al., 2012). Factors, including warming and ocean acidification (OA), are causing the reorganization of local communities as species are added or deleted (via an increase in the mortality of marine benthic invertebrates) (Di Camilo et al., 2012), changed species distributional limits (Høgslund et al., 2014) and as interactions among species change in importance.

Uptake of CO₂ coexistence by the ocean is changing the seawater carbonate chemistry increasing the dissolved inorganic carbon availability while reducing the pH and carbonate saturation (Raven et al., 2005). Hence, the carbonate-accreting reef organisms have been affected as evidenced by reduced calcification of reef-building corals and crustose coralline algae (Jokiel et al., 2008; Anthony et al., 2008). Ocean acidification and elevated sea surface temperatures have also been shown to negatively affect reproduction and early developmental stages in calcifying marine intertidal invertebrates and can interfere with the settlement of coral larvae indirectly by modifying the inductive capacity of their preferred settlement substratum (Bell et al., 2013; Davis et al., 2013). Previous studies have shown that the high diversity and biomass of sponges in subtidal zones makes them a key taxon with important ecological roles in these communities (Fromont et al., 2016). For instance, in coral reefs they bind solid carbonate fragments together to make a stable surface for corals (Wulff, 1984; Díaz & Rützler, 2001). Wulff (2016) reports the relationship of sponges with corals and reef substrata through their accessory roles, such as improving survival of living corals by adhering them to the reef frame and protecting exposed solid carbonate from excavators. However, since any impact on sponges could affect a specific taxon such as corals or the whole benthic community structure (Díaz & Rützler, 2001). Sponges may serve as predictive model organisms to understand how environmental stress influences their subtidal counterparts and how they may respond to climate change impacts. Even though they are not the dominant species in the intertidal zones.
Effects of ocean acidification and global warming on sponges are mostly assessed in taxa from the subtidal zone (Wisshak et al., 2012; Stubler et al., 2014). Sponges are rarely included in research conducted on rocky shore habitats (Sarà et al., 2014) and the effects on sponge communities because there is a preference to include community dominants (Pitt et al., 2010; Poloczanska et al., 2011). Furthermore, currently there is no study that investigates how physical drivers, altered by climate change, act on intertidal sponge assemblages despite knowledge that species interactions also provide important information to understand changes in community structure (King & Sebens, 2018). Thus, increasing our understanding of how sponges respond to environment change may help to understand how multiple physical factors may impact the structure of intertidal communities. However, in the subtidal zone, studies have registered dramatic deleterious changes that have widespread effects worldwide as evidenced by increases in the incidence of coral and sponge disease, declines in live coral cover, concurrent with increases in algal and sponge cover (Di Camilo et al., 2012). The causes for these changes remain the subject of much debate and include a range of possible causes such as water quality degradation, climate change, diseases of generally unknown etiologies, physical impacts, and intensive fishing (Chaves-Fonnegra et al., 2015).

The condition and stability of coral reefs represents a balance between processes that contribute to calcium carbonate deposition and those forces that work to erode the reef framework (Wisshak et al., 2012). On healthy reefs, bioeroding organisms play a key role in facilitating carbonate cycling through the system by abrading or dissolving materials such as coral skeletons and oyster reef communities (Stubler et al., 2014). A variety of biological and physical factors influence carbonate erosion and accretion (Chiappone et al., 2007). Several vertebrate and invertebrate species are related in eroding carbonate substrates, including bivalves, sea urchins and sponges, particularly those in the genus Cliona (Wisshak et al., 2012). Clionid sponge interaction with stony coral plays a large role in shaping the physical and community structure on coral reefs (Stubler et al., 2014). This interaction becomes widely described since climate changes has modified the direct interaction between excavating sponges and corals, with broad implications for the balance between erosion of carbonate and biologically mediated deposition in reef communities. Moreover, the consequences on coral reefs are leading to long-term changes in community structure and physical stability due to the ability of sponges to increase the boring rates at lower pH and grow faster in warmer temperatures (Chaves-Fonnegra et al., 2015). However, while some sponges are eroders, others are known to bind reef fragments (Bell et al., 2013), possibly mitigating some of these impacts. On healthy reefs environment sponges play important functional roles such as
adhering corals securely to the reef and blocking further invasion by eroders by covering the coral skeletons where they lack living coral tissue (Goreau & Hartman, 1966; Wulff & Buss, 1979).

Bell et al., 2013 proposed that sponges will not respond uniformly to global warming and ocean acidification scenarios especially because their wide diversity of symbiotic microbes that reside within them. Specific species have the capacity to dominate sites where environmental quality has declined. Their low sensitivity to OA (Ocean acidification) and increases of sea temperatures combined with the predicted declines in coral cover suggest the possibility that sponges may benefit from future global warming (Bell et al 2013), or at least remain after corals have declined (Powell et al., 2014). However, sponges may not be the only potential competitors and other groups, such as soft corals and ascidians, will compete with sponges for the newly available space following declines in coral abundance.

It has been proposed that many coral reefs may shift to sponge-dominated systems in response to predicted climate change scenarios (Bell et al., 2013). Powell et al., 2014 provides support for this notion in that further reductions in herbivore abundance may also favour algal-dominated states. However, the sponge-dominated systems may likely be lower diversity systems than coral reefs due their overall complexity be considerably less than for most coral-dominated systems, which may reduce biodiversity as a result of reduced niche availability (Bell et al., 2013)

Despite the importance of sponges on reefs, research studies have focused on how stressors associated with OA and global warming will affect corals, however relatively little is known about the response of other reef invertebrates. Excavating sponges, for instance, have been proposed as environmental indicators that are sensitive to changes in coral reef communities (Wisshak et al., 2012). Currently understanding population dynamics of sponges is important because changes in sponge populations could have significant consequences in aquatic habitats. In rocky shores could affect their productivity, habitat biodiversity and its architectural complexity. However, my findings build baseline information about patterns of abundance and distribution of intertidal sponges assemblages that is essential to better understand the key drivers that may be influencing these patterns. The ecological processes investigated in this study also contribute important information about the factors that may be affecting these patterns. The information presented in this thesis is necessary especially in face of threats such as ocean acidification, global warming and coastal disasters (Duxbury & Dickinson, 2007; Bell et al., 2013; Long et al., 2015), that may have effects on intertidal sponge population structure.
1.4 Aims and structure of this Thesis

The sponge assemblages inhabiting intertidal zones has been scarcely studied worldwide and is currently unknown in south-eastern Australia, even though it is likely that intertidal organisms will be more exposed to disturbances than those in subtidal ecosystems. Although sponges have shown they can be important mechanisms in maintaining ecosystem function in marine benthic communities worldwide, their importance has been underestimated and there is an information gap about their current global conservation status. Therefore, further studies become evidently necessary. The aims of this study were to enhance our scientific understanding of the spatial distribution of the sponge assemblages from intertidal systems, considered vulnerable to natural fluctuations and human impacts, and investigate their potential environment impacts and ecological interactions.

The main aims of the present study were to:

1) Identify the sponge species inhabiting the intertidal rocky reefs of the Illawarra region,
2) Estimate the spatial distribution patterns and abundance of the sponge assemblages in this region,
3) Identify the key environmental factors that may determine the distribution of these assemblages.

Chapter 2 addresses the first two aims, developing an appropriate sampling design to identify the sponges species in the intertidal zones of the Illawarra region, NSW, Australia. Two different comparisons were made to examine their distributional patterns. The spatial and temporal distributional patterns of these assemblages were quantified for cross-site comparisons and to provide a detailed list of the intertidal sponge fauna (cumulative sampling). First, single inventories were conducted, using a timed, two-hour search design, to assess sponge abundance and diversity at 14 rocky intertidal reefs along the Illawarra coast. Summary information of the physical features of each intertidal reef were also provided. Second the same methodology was used to estimate temporal variation in the abundance and diversity of the sponge assemblages. I sampled six of the fourteen reefs, chosen to encopass a range of contrasting levels of wave exposure.

Based on the findings described on Chapter 2 the third aim was investigated in Chapters 3, 4 and 5. Chapter 3 focused on evaluating the relative importance of environmental factors that may determine the observed patterns of species distribution and abundance. The 14 sites were described using a range of criteria, including the topographic properties of the reef. Thus,
I evaluate each rocky reef and determined how two physical variables, habitat complexity and exposure to wave action, were influencing the distribution of sponges. Those two variables were classified as in Benkendorff & Davis (2002). Habitat complexity and the degree of wave action are well known as important factors influencing rocky shore community structure (Helmuth & Denny, 2003; Kostylev et al., 2005; Burrows et al., 2008). Therefore, six of the fourteen intertidal reefs were chosen according to their level of wave exposure and their degree of habitat complexity to investigate whether physical (abiotic) factors were correlated with these patterns. I investigated the attributes of rocky reefs (physical characteristics) haphazardly with a focus on the number of rock pools; the volume of each rock pool (m$^3$) and the total area of the reef containing pools (m$^2$). Surveys were also conducted to record the coordinates and tidal heights of each rock pool where a sponge individual was observed to assess how tidal heights were influencing the sponge survivorship. Finally, Chapter 3 also addressed seasonal variability in the diversity of intertidal zone sponges, as well as their abundance and cover through quantitative estimates of species over eighteen months.

Chapter 4 was based on field observations that sponge mortality was correlated with increased sedimentation loads on some Illawarra reefs. The aim of this chapter was to experimentally test whether the effects of different rates of sedimentation affected the survival of intertidal sponge adults and recruit-sized explants. In chapter 5 I experimentally investigated whether the spatial distribution of an intertidal sponge, Callyspongia (Callyspongia) sp. 6, was associated with the avoidance of predators. During the experiment we examined whether predation by common sea urchin species, Centrostephanus rodgersii and Heliocidaris tuberculata, play an important role in determining the lower limits of the vertical distribution of intertidal sponges in the Illawarra region.

Lastly, in the general discussion (chapter 6) I highlight the sampling challenges and suggest future directions built on baseline information generated by my findings. I propose a number of important considerations to establish adequate and representative intertidal protected areas in the Hawkesbury Shelf Marine Bioregion to conserve intertidal sponge biodiversity. Future research should focus in two directions 1) consider investigating the patterns of larval settlement and dispersal for intertidal sponges from the Illawarra region. 2) Conduct further manipulative experiments to validate my findings and confirm the major factors that are shaping the sponge community in this region.
CHAPTER 2

Spatial and temporal patterns of diversity and abundance of intertidal zone sponges in the Illawarra region, NSW, Australia.
2.1 INTRODUCTION

Sponges are receiving increasing attention in marine biodiversity research due to growing scientific and public awareness of their ecological and commercial importance (Przeslawski et al., 2014; Van Soest et al., 2018). Sponges are common and conspicuous members of shallow benthic community assemblages, where they compete for space with algae, sea grass, and corals (Wulff, 2006a; Wulff, 2006b; Wulff, 2008; Demers et al., 2015). Sponges will often dominate the diversity and biomass at the lower levels of the photic zone and deeper on many of the world’s continental margins; south western Australia for example (Keesing et al., 2013). In such environments, sponges can significantly influence water quality, substratum conditions, as well as provide nutrition and vital habitat for many other organisms (Fromont et al., 2006). Furthermore, sponges are efficient filter feeders, providing a crucial coupling between productivity in the pelagic environment and the benthos (Lesser, 2006) through nutrient cycling (Keesing et al., 2013) and are increasingly recognized as key contributors to ecosystem services (Bell, 2008a). In addition, secondary metabolites from sponges and their microbial symbionts have the potential to provide drugs to treat a range of microbial infections and cancers (Laport et al., 2009; Leal et al., 2012).

Australia has been consistently recognized as a global hotspot for sponge biodiversity (Przeslawski et al., 2014), along with high levels of sponge endemism and rarity in tropical regions (Hooper et al., 2002a; Fromont et al., 2006; Schönberg & Fromont, 2012; Fromont et al., 2016). Nevertheless, documentation of regional sponge assemblages is still relatively rare. Most studies have occurred outside Australia and have been undertaken in tropical regions, especially in the Caribbean region (Van Soest, 1993; Kelly et al., 2002; Burns et al., 2003; Bell & Smith, 2004; Wulff, 2006a). A few studies have examined sponge diversity in temperate environments (Roberts & Davis, 1996; Bell & Barnes, 2000) and dense sponge grounds from southern temperate regions have been reported (Sorokin et al., 2007). Despite sponges being frequently recorded in the intertidal temperate zone, this habitat exhibits a low number of sponges, even at sites with high sublittoral species richness (Barnes, 1999). Conversely, the sponges from the tropical intertidal zones are typically more diverse, abundant and morphologically varied (Barnes, 1999).

The majority of biodiversity studies on sponges within Australia have been species inventories; however, few have included quantitative estimates of species abundances.
(Fromont, 2004; Fromont et al., 2006; Hooper, 1994; Hooper et al., 1999, 2002a; Hooper & Kennedy, 2002; Przeslawski et al., 2014). Nevertheless, good management of marine resources ideally requires quantitative information (Benkendorff & Davis, 2004). Quantification of spatial patterns is also important for understanding which factors most influence the distribution and abundance of sponges (Fromont, 2006). For instance, the diversity of sponges has been shown to increase with increasing depth (Zea, 1993; Roberts and Davis, 1996; Bell & Barnes, 2000) and to be higher at sites with high structural complexity and high substratum availability (Diaz et al., 1990).

Marine conservation and management in the State of NSW includes a series of multi-use Marine Parks with interconnecting sanctuary zones to protect biodiversity and foster connectivity among bioregions (NSW Department of Primary Industries, 2018). In 2014 the NSW. However, the bioregion centred on the city of Sydney, the Hawkesbury Shelf Marine Bioregion (HSMB), currently lacks a Marine Park (NSW Marine Estate, 2016a). Although, Wollongong is a highly urbanized coastal city only an hour away from the major city of Sydney (Figure 2.1), there are currently no intertidal protected areas in this region besides a tiny reserve, ‘Bushranger's Bay’. This aquatic reserve with remnant vegetation lies at the eastern end of Bass Point (Benkendorff & Davis 2002; NSW Marine Estate, 2017). However, authority developed a project with options to choose representative system of marine protected areas for conservation and management of the biodiversity within the Hawkesbury Shelf marine bioregion (NSW Marine Estate, 2016a). “Traditional ocean resource management”, which uses a single sector or species as reference, has been proven to fail to protect marine ecosystems from the five major threats to the oceans (i.e. ocean disposal and spills; overfishing; climate change and anthropogenic pressures, such as pollution and degradation of coastal ecosystems) (Costanza et al., 1998; Long et al., 2015). The ineffective management of marine ecosystem services and the overuse of ocean resources has deeply affected ecosystem health and services (Long et al., 2015). Management options are being developed for this bioregion and will likely include a Marine Park. Therefore, it is important to reinforce the significance of improving conventional management practices and develop efficient management following the six Principles for Sustainable Governance of the oceans as a starting point (Costanza et al., 1998). Thus, investigating the patterns of abundance and distribution of a variety of key and poorly understood species, become essential to aid an understanding of the ecological processes affecting populations. This understanding is important especially in face of the threat of ocean acidification, global warming and coastal disasters (Duxbury & Dickinson, 2007; Bell et al., 2013; Long et al., 2015).
Marine reserves have become a highly recommended vehicle for marine conservation; although most of the literature concerning marine reserves is focused on their role in fisheries management (Long et al., 2015). To manage biodiversity loss in marine ecosystems, it is important to define priority areas for conservation including the full range of biodiversity present in the biogeographic region. This includes the identification of biodiversity hotspots, and the distribution of key organisms (May, 1994). In addition, the effective conservation of biological diversity will also benefit from greater understanding of the interactions between organisms and their habitat (Benkendorff & Davis, 2004).

In recent times, sponges have been recognised as a critical component of the marine benthos, but in many areas their species richness and abundance are largely unknown (Fromont, 2014). Moreover, the spatial patterns of species distribution and abundance of sponges in rocky intertidal reef ecosystems has rarely been investigated (see Barnes, 1999; Fromont, 2004; Fromont et al., 2006; 2016) even though intertidal sponges have been the subject of several manipulative experimental studies (Sivadas et al., 2014; Kelmo et al., 2014; Weigel & Erwin, 2016). In order to better understand the patterns of distribution and abundance of the intertidal sponge assemblages, the aims of this research were to (1) identify the sponge species inhabiting the intertidal rocky reefs of the Illawarra region and, (2) provide estimates of the spatial distribution patterns and abundance of the sponge assemblages in this region and (3) determine the likely reliance of each species on photosynthetic symbionts.

Descriptive studies are a necessary pre-cursor to understanding the processes that underpin these patterns (Underwood et al., 2000). Furthermore, quantification of differences in the variability of assemblages is necessary to facilitate propositions to be made on which mechanisms could be responsible for the occurrence of distinct assemblages between sites of the same habitat, or between different habitats (Bulleri et al., 2005). This is the first study to comprehensively quantify the abundance and diversity of the intertidal sponge fauna of the Illawarra region, NSW, Australia. In sum, the data presented here, besides assisting in filling data gaps, is also valuable as it highlights the Illawarra reefs as a habitat for intertidal sponge distribution and enhances our understanding of sponge communities in the NSW region - building a baseline for effective future monitoring and research programs.

2.2 MATERIALS AND METHODS

2.2.1 Study area

Single inventories were conducted to determine the abundance and diversity of sponge assemblages at 14 rocky intertidal reefs along the Illawarra coast, NSW, Australia (Figure 2.1).
A summary of the physical features for each intertidal reef are provided in Table 2.1. These include the area of the reef, the degree of exposure to swell, the rock type, the number of microhabitats and the areal extent of rock pools and boulders in each reef. The following microhabitats were searched: flat rock platforms, boulders, rocky outcrops, crevices, caves, patches of sand, rock pools and shallow water-retaining hollows (Table 2.1).

Figure 2.1: Fourteen intertidal study sites in the Wollongong region of New South Wales (NSW), Australia.

The Illawarra coast experiences a tidal range of 2 m with approximately two low tides each 24h (Bennett 1992). The intertidal zone in this region is narrow and primarily vertical on a subset of these wave-cut rock platforms (Benkendorff, 2009). The intertidal reefs in this area are primarily composed of sandstone or basalt rock platforms and boulder fields, with most intertidal reefs exposed to the predominant SE swell (Table 2.1). Most of the exposed reefs are dominated by flat rock platforms with a large supra littoral belt above the high tide mark. The Illawarra reefs also vary in degree of habitat complexity, as judged by the numbers of rock pools and a variety of other habitat features (Table 2.1). Benkendorff (2009) observed that all
the exposed reefs along the Wollongong coast are periodically subject to natural impacts from extreme swell conditions and sand inundation.

It has long been known that biological communities on rocky shores are strongly influenced by wave exposure (Burrows et al., 2008). Consequently, I sought to sample across a full gradient of wave exposure in this region. Furthermore, heterogeneity of the environment has long been considered an important determinant of diversity and abundance of species present in marine communities (Carballo & Nava, 2007). Therefore, eight representative wave-exposed rock platforms were selected for sampling (Coalcliff, Scarborough, Wombarra, Coledale, Austinmer, Wanianora Point (South Bulli), Flat Rock (Woonona), and Towradgi; Table 2.1).

Relatively sheltered intertidal reefs can be found on the northern side of North Wollongong, Bellambi, Bulli and Bass Point. One site was selected on the north side of Bulli (Sandon Point) and two sites were selected on the northern side of Bass Point (North Shellharbour, South Shellharbour and Table 2.1). An additional site, on the northern side of Bass point was also sampled; this reef at Bass point represents a moderately exposed site (Table 2.1). These sheltered sites rarely experience swell greater than one metre. (Table 2.1). Sandon and Bass Point showed a high degree of habitat complexity.
Table 2.1: Summary of the intertidal habitats surveyed at 14 sites along the Illawarra Coast, NSW, Australia. The shaded cells represent the sites that were chosen for their differing levels of wave exposure for regular resampling.

<table>
<thead>
<tr>
<th>Site</th>
<th>Coordinates</th>
<th>Area of the reef (m²)</th>
<th>% of sponges found in pools</th>
<th>Wave Exposure</th>
<th>Substrate type</th>
<th>Natural habitat features</th>
<th>Area containing Pools</th>
<th>Area containing boulders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coalcliff</td>
<td>34°14′S, 150°58′E</td>
<td>64,538</td>
<td>100%</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Large rock platform with some boulder filled hollows, sandy patches, caves and crevices. Rocky pools were found in less than 10% of the whole rocky platform. Small and shallow pools more abundant and few large pools</td>
<td>&lt;10m²</td>
<td>&lt;50m²</td>
</tr>
<tr>
<td>Scarborough</td>
<td>34°16′14″S, 150°57′37″E</td>
<td>2,318</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Rock platform with sandy patches and several crevices.</td>
<td>0</td>
<td>&lt;2m²</td>
</tr>
<tr>
<td>Wombarra</td>
<td>34°16′30″S, 150°57′12″E</td>
<td>30,125</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Large rock platform and off-shore reef with caves, crevices and boulder filled hollows</td>
<td>0</td>
<td>&lt;50m²</td>
</tr>
<tr>
<td>Coledale</td>
<td>34°17′S, 150°57′E</td>
<td>93,000</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Large rock platform with shallow pools and crevices and small patch of submerged boulders</td>
<td>&lt;10m²</td>
<td>&lt;20m²</td>
</tr>
<tr>
<td>Austinner</td>
<td>34°18′23″S, 150°56′04″E</td>
<td>17.85</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Large rock platform with deep crevices and, few small shallow rocky pools and sandy patches</td>
<td>&lt;10m²</td>
<td>&lt;20m²</td>
</tr>
<tr>
<td>Bulli Point</td>
<td>34°20′03″S, 150°54′48″E</td>
<td>42,704</td>
<td>100%</td>
<td>North facing reef (Sheltered)</td>
<td>Sandstone</td>
<td>Rock platform interspersed with several large and small shallow rock pools, some boulder filled hollows, boulder filled crevices, sandy patches and caves</td>
<td>&gt;100m²</td>
<td>&lt;50m²</td>
</tr>
<tr>
<td>Waniora Point</td>
<td>34°20′03″S, 150°54′48″E</td>
<td>12.000</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Small rock platform with boulder filled hollows and crevices, deep rock pools, sandy patches, caves and rocky outcrops</td>
<td>&lt;5m³</td>
<td>50-100m³</td>
</tr>
<tr>
<td>Flat Rook</td>
<td>34°20′30″S, 150°54′22″E</td>
<td>21.697</td>
<td>NA</td>
<td>South facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Rock platform with shallow small and few large rock pools, sandy patches and caves</td>
<td>&lt;10m²</td>
<td>&lt;2m³</td>
</tr>
<tr>
<td>Bellambi</td>
<td>34°22′S, 150°55′E</td>
<td>12.446</td>
<td>NA</td>
<td>North facing reef (Sheltered)</td>
<td>Sandstone</td>
<td>Large boulder filled hollows and rock platform with caves, crevices and few small and large shallow rocky pools.</td>
<td>&lt;20m³</td>
<td>&gt;100m³</td>
</tr>
<tr>
<td>Towradgi</td>
<td>34°22′S, 150°55′E</td>
<td>19.014</td>
<td>NA</td>
<td>North facing reef (Highly exposed)</td>
<td>Sandstone</td>
<td>Large boulder field with small rock platform, caves, rocky outcrops and sandy patches and few rocky pools</td>
<td>&lt;5m³</td>
<td>&lt;50m³</td>
</tr>
<tr>
<td>North Wollongong</td>
<td>34°25′S, 150°53′E</td>
<td>28.521</td>
<td>100%</td>
<td>North facing reef (Sheltered)</td>
<td>Sandstone</td>
<td>Rock platform interspersed with boulder filled crevices, shallow and small rocky pools in more quantity than large and deep rocky pools and rocky outcrops with caves.</td>
<td>&lt;50m³</td>
<td>&lt;50m³</td>
</tr>
<tr>
<td>North Shellharbour</td>
<td>34°35′S, 150°52′E</td>
<td>67.904</td>
<td>NA</td>
<td>North facing reef (Sheltered)</td>
<td>Basalt</td>
<td>Rock platform interspersed with shallow boulder filled hollows and crevices</td>
<td>&lt;2m³</td>
<td>&gt;50m³</td>
</tr>
<tr>
<td>South Shellharbour</td>
<td>34°35′S, 150°52′E</td>
<td>30.936</td>
<td>NA</td>
<td>North facing reef (Sheltered)</td>
<td>Basalt</td>
<td>Rock platform interspersed with large boulder filled hollows, sandy patches, rocky outcrops, caves, crevices</td>
<td>0</td>
<td>&gt;&gt;100m³</td>
</tr>
<tr>
<td>Bass Point</td>
<td>34°35′50″S, 150°54′0″E</td>
<td>76.222</td>
<td>80%</td>
<td>North facing reef (Moderately exposed)</td>
<td>Basalt</td>
<td>Large rocky headland that extends approximately 3 km into the Tasman Sea with shallow boulder filled hollows, and a greater quantity of large deep than small shallow rock pools, caves and crevices.</td>
<td>&gt;100m³</td>
<td>50-100m³</td>
</tr>
</tbody>
</table>
2.2.2 Surveys and Species identification

Data are presented for a single inventory of each of the 14 sites. An additional sampling at 6 sites were repeated over a period of 18 months (February 2016 until August 2017). The single inventories were used to quantify the abundance and diversity of the intertidal sponge for cross-site comparisons, whereas the accumulated sampling records enable an assessment of temporal variation and provided a more comprehensive list of the intertidal sponge fauna of the Illawarra region. It is important to note that sponges were the only sessile fauna in many of the pools examined. Algae were present in some high shore pools and an examination of interactions between algae and sponges would have been interesting but in this study only sponges were examined. Furthermore, the temporal change may include some assessment of seasonal variation, but season were not formally incorporate into the sampling design. Intertidal surveys included reef walks at the 14 intertidal sites and were conducted in relatively calm sea conditions during low tide (maximum 0.5 m). After developing sufficient familiarity with the range of species found in the region, the surveys were conducted during a five-month period (from April 2015 to September 2015). Coalcliff (28.9.15); Scarborough (24.9.15); Wombarra (25.9.15); Coledale (14.6.15); Austinmer (15.6.15) Sandon Point (14.4.15); South Bulli (16.6.15); Wonoona (1.8.15); Bellambi (2.8.15); Towradgi (3.8.15); North Wollongong (21.5.15); Nort Shelharbour (2.7.15); South Shellharbour (3.7.15); Bass Point (3.7.15). A timed, two-hour search survey was used to produce a standardized inventory of the diversity and abundance of sponges at each study site. The two-hour search was determined considering the size, proportion of the intertidal zone and the complexity of the rock substratum of each reef. However, timed searches was based in field observations and after different attempts timed survey was chosen as the best approach to quantify the relative abundance and diversity of the sponge communities of intertidal zones in this region given the rarity of sponges and their patchy distribution over the rocky platforms assessed.

The timed search was conducted haphazardly at intertidal platforms across the entire range of habitats at all levels of the shore. In particular, attention was paid to two different topographic microhabitats: the underside of boulders and rock pools. The time when each survey started and the time that each sponge individual was found were recorded and the rock pools and boulders where individual sponges were found were measured (rock pools: maximum width, length and depth/ boulders: maximum width, length). Furthermore, information such as the geographic coordinates and the shore height
(low, mid or upper shore) where the sponges were found was also recorded. In this study, I use the term diversity when discussing species richness (number of species), and define abundance as density (i.e., number of individual sponges per site).

Six rocky reefs were chosen, for their different levels of wave exposure (Table 2.1) and regular sampling was conducted at these sites to estimate the temporal variation in the abundance and diversity of the sponge assemblages (Coalcliff, Austinmer, Bulli Point (Sandon Point), Bellambi, North Wollongong and Bass Point). The survey records were conducted over eighteen months, from February 2016 to August 2017. The surveys were all undertaken during the entire 2-4 hour period when the intertidal zone was exposed (i.e. the tide was low). All intertidal habitats were searched, as described above, and an abundance and species list of sponge was generated for each month.

Populations of sponges was quantified in three ways (1) by the number of individuals of each species; (2) by combined surface area covered by all individuals, pooled across species, at each site (3) by combined surface area covered by each species at each site. In addition, sponge biomass (cm$^3$) and abundance (number of individuals) recorded among the five rock reefs were plotted together to help understanding the ecological roles of sponges (Figure 2.2). For counting numbers of sponges, individuals were defined by physiological independence. However, it is important to note that depending on the species of sponge, physiologically-defined individuals may not correspond to genetically defined individuals (Wulff, 2001).

The sponge area was estimated by summing the estimates of cover by rendering them to assortments of two-dimensional geometric shapes. The surface area of each sponge was estimated using the image processing program, ImageJ (Rasband, 1997). Estimates of area were made by calculating the surface area of each sponge through the pinacoderm contour of each individual and by measurements using a metric tape or ruler to record the maximum width, length and thickness of each individual. For branching species, diameters as well as lengths were measured for each branch segment.
Figure 2.2: Comparison of sponge abundance and biomass (volume) at the five rock reefs sampled within Illawarra region. (A) mean (±SE) estimates of sponge abundance expressed as number of individuals per site. (C) mean (±SE) estimates of sponge volume expressed as cm³ per site.

Underwater photographs of each living specimen were taken (with a Canon power shot D20 camera or GoPro HERO3+ black edition with a known size scale in each photograph) to be used in Image J, as well as to assist in their identification. At all stations where sponges were found, a small piece of each specimen of each species was collected. Voucher specimens were also collected, if there were morphological or colour differences from previous vouchers. The specimens were labeled in the field (including information on color, location, date, ecological associations), fixed in 70% ethanol soon after collection and taken to the laboratory for identification. Spicule slide preparations, following traditional methods of nitric acid dissolution (Rützler, 1980), were used to identify the sponges to the lowest possible taxonomic level. The sponge skeleton was examined and the examination included sectioning of paraffin-embedded fragments, if necessary to assist with identification. Moreover, underwater pulse amplitude modulated (PAM) fluorometry was used in situ to measure the relative amount of photosynthetic chlorophyll of each
sponge species. The photosynthetic activity was measured with the assumption that the lower the intensity of the modulated measuring light (ML) then, the higher was the amount of Chlorophyll that the sponge contained. Thus, the greater the amount of chlorophyll, the higher the photosynthetic activity, evidence that these species may host photosymbionts (Appendix 1 Table A).

2.2.3 Analysis of data

Differences in the abundance and volume of each species among sites were tested using nested multivariate PERMANOVAs. These metrics were tested at five sites (Coalcliff, Sandon Point, North Wollongong, South Shellharbour and Bass Point). Orthogonal multivariate PERMANOVA was used (Anderson, 2001) on Bray-Curtis similarities calculated from untransformed data to analyse the differences in sponge abundance of each species among reefs. Sites were the random orthogonal factor analysed and rock pools at each site constituted the replicates, as most sponge species were found within rock pools. The Coalcliff site was not included in the PERMANOVA analysis, because it does not have enough replicates (a single pool) and the South Shellharbour site was not included because the sponge species were found on the underside of boulders. The analyses were also performed using both Fourth Root and Presence and Absence data to reduce the influence of abundant taxa (Clarke, 1993). Outcomes of the analyses with the three data transformations were graphically illustrated using a non-metric Multi-Dimensional Scaling (nMDS) plot and categorized by sites. The data were pooled for each site, to provide a centroid based on Bray–Curtis similarity measures. Similarity percentages (SIMPER) were used to determine which taxa most contributed to the difference of each assemblage within the group compared (Average dissimilarity). SIMPER analyses were based on a one-way design and Bray–Curtis similarity measures on untransformed data. Analysis of similarities (ANOSIM) was employed to test whether sponge assemblages differed statistically between selected sites. All multivariate analyses were carried out using the PRIMER package (Plymouth Routines In Multivariate Ecological Research, version 7).

A correlation was applied to test the relationship between cumulative species diversity with two factors; the cumulative abundance of intertidal sponges, and the number of species in a single inventory. The correlation was examined on the six intertidal reefs along the Illawarra Coast where intertidal zone sponges were observed (North Wollongong; Bass Point; Bellambi, Austinmer, Sandon Point, Coalcliff). A correlation was
also established between the total intertidal sponge diversity and the total molluscan species richness (see Benkendorff & Davis, 2002) across twelve intertidal reefs in the Illawarra region (Coalcliff, Scarborough, Wombarra, Coledale, Austinmer, Bulli Point (Sandon Point), Bellambi, Towradgi, North Wollongong, North Shellharbour, South Shellharbour and Bass Point).

### 2.3 RESULTS

Surveys of the shore platforms using quantitative methods recorded a total of 22 species restricted to just 5 of 14 intertidal reefs (Coalcliff, Sandon Point, North Wollongong, South Shellharbour and Bass Point). Twelve taxa were new occurrences for the Illawarra region and many of these were previously undescribed. A few species in South Shellharbour reef were only recorded on the underside of boulders and at Bass Point reef. Callyspongia (Callyspongia) sp. were also observed on rock substrata around and between pools; the majority of sponge species were recorded within rock pools. The most common morphology of sponges in all habitats was encrusting (66%), but massive forms were also present on 4 of 5 reefs (Appendix 1). The most common species Callyspongia sp. was more widely distributed among reefs than the other species, comprising 46% of the total of 65 individuals across four sites. In contrast, most species had a markedly low abundance recorded among the sites, with only one or two sponge individuals found within reefal habitat. At Bass Point three sponge species represented the majority of the total cover. These were Chondrilla sp., Chondrilla sp. 2 and Spheciospongia sp. The other five species were uncommon, constituting less than 5% of total sponge cover. The majority of the specie composition at North Wollongong reef were represented by two sponges Callyspongia sp. 4 and (Callyspongia) sp. 5. Both sponges species were the dominant and constituted more than half of total sponge coverage (72%) while Echinoclathria sp. contributed to 20% and the other two species (Chalinula sp. and Amorphinopsis sp.) were uncommon (less than 5%). Halichondria sp. 2 made up 52% of the total sponge cover in the South Shellharbour reef and was the dominant species on that reef. In contrast, for two of the five reefs on which sponges were recorded, only a single species was present. On Coalcliff reef, Tethya sp. was the only sponge species recorded while in Sandon Point only Callyspongia (Callyspongia) sp. 6 was the sole taxon observed.

During the initial inventory, 65 sponge individuals from 18 species, 11 families and 6 orders of demosponges were quantified (Table 2.3). The sponge specimens were identified to genus level, as this is the lowest taxonomic level that can be reliably obtained. Consequently, each taxon was simply recorded as “sp.” and given an equivalent number (Appendix 1).
majority of the intertidal Illawarra reefs were depauperate in sponge species, as sponge assemblages were sporadically distributed within sites. The poorest intertidal reefs for varieties of sponge species were Coalcliff and Sandon Point with only one species detected at each. South Shellharbour and North Wollongong reefs in total had moderate species richness, with three and four respectively. Bass Point was the only site with high species richness - a total of eight species (Figure 2.2B). After 18 months of surveys, the total number of species increased by 5, since one of the species (Echinoclathria sp.) found at Bass Point had already been observed in North Wollongong. Thereby, the total number of sponge families and orders increased with additional sampling, to 14 and 9 respectively (Table 2.3). Although, some species were not located when the photosynthetic chlorophyll was measured in situ, all the species analysed during the survey showed some photosynthetic activity. A list of the level of photosynthetic activity measured for each sponge species is given in Appendix 1, Table A.
Table 2.2: Maximum abundance of each species across sites. Species were organized in descending order based on their number of individuals pooled per site. Total number of sponges (N = 65).

<table>
<thead>
<tr>
<th>Sponge Species</th>
<th>Coalcliff</th>
<th>Scarborough</th>
<th>Wombarra</th>
<th>Coledale</th>
<th>Austinmer</th>
<th>Sandon Point (Bulli)</th>
<th>Waniora Point (Bulli)</th>
<th>Fat Rock (Woonona)</th>
<th>Bellambi</th>
<th>Towradgi</th>
<th>North Wollongong</th>
<th>South Shellharbour</th>
<th>North Shellharbour</th>
<th>Bass Point</th>
</tr>
</thead>
<tbody>
<tr>
<td>Callyspongia (Callyspongia) sp.4</td>
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<tr>
<td>Callyspongia (Callyspongia) sp.6</td>
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<tr>
<td>Callyspongia (Callyspongia) sp.2</td>
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<tr>
<td>Callyspongia (Callyspongia) sp.3</td>
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<td>Chondrilla sp.2</td>
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<td>Chondrilla sp.1</td>
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<tr>
<td>Amorphinopsis sp.</td>
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<tr>
<td>Halichondria sp.1</td>
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<tr>
<td>Pseudoceratina sp.</td>
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<tr>
<td>Sigmosceptrella sp.</td>
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<td>Spheciospongia sp.</td>
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<tr>
<td>Echinodictyum sp.</td>
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<tr>
<td>Halichondria sp.2</td>
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<tr>
<td>Myxilla sp.</td>
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<tr>
<td>Hyrtios sp.</td>
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Continued...
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<tr>
<th>Sponge Species</th>
<th>Coalcliff</th>
<th>Scarborough</th>
<th>Wombarra</th>
<th>Coledale</th>
<th>Austinmer</th>
<th>Sandon Point (Bulli)</th>
<th>Waniora Point (Bulli)</th>
<th>Fat Rock (Woonona)</th>
<th>Bellambi</th>
<th>Towradgi</th>
<th>North Wollongong</th>
<th>South Shellharbour</th>
<th>North Shellharbour</th>
<th>Bass Point</th>
</tr>
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<tr>
<td>Tethya sp.</td>
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</table>

=1, 2-5, 5-8, >8
Table 2.3: The number of species from different families of sponges recorded in a single inventory and cumulative surveys at 5 intertidal reefs along the Illawarra Coast, NSW, Australia. The total number of species in cumulative surveys is provided in parentheses.

<table>
<thead>
<tr>
<th>Families</th>
<th>Coalcliff</th>
<th>Sandon Point (Bulli)</th>
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<th>South Shelharbour</th>
<th>Bass Point</th>
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<td>Tethyidae</td>
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</tr>
<tr>
<td><strong>Total</strong></td>
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<td><strong>1 (1)</strong></td>
<td><strong>3 (5)</strong></td>
<td><strong>4 (4)</strong></td>
<td><strong>8 (11)</strong></td>
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</tbody>
</table>
The number of families and orders recorded at each site slightly increased, to a total of 14 and 8, respectively (Figure 2.2) following the repeated sampling of sites. The total number of species also increased only by two and three species with additional sampling at two sites; North Wollongong and Bass Point respectively (Figure 2.3B). In contrast to the diversity metrics, sponge abundance followed a different trend and varied considerably between 3 of 6 sites sampled. North Wollongong showed high variation in the number of individuals found during the survey time, as abundance decreased 48% in June 2016 and increased again to 26 individuals in February 2017 (Figure 2.3A). There was a strong correlation between the total species diversity from the cumulative sampling at each site and the number of species recorded in a single inventory (r = 0.9, P = 0.004, Figure 2.4B). Additionally, I recorded a strong correlation between the total of species richness and abundance at 6 of the 14 sites accessed (Coalcliff, Austinmer, Sandon Point, Bellambi, North Wollongong and Bass Point; Figure 2.4A). Thus, demonstrating that the sites with high species richness housed the highest abundances of sponge taxa (r = 0.9, P = 0.004, Figure 2.3A).

Figure 2.3: Sponges orders within Demospongiae on intertidal reefs of the Illawarra region. The values represent the percentage total numbers of individuals of each order.

Hadromerida (9%)
Verongida (4.5%)
Dendroceratida (4.5%)
Chondrosida (4.5%)
Poecilosclerida (18%)
Halichondrida (14%)
Haplosclerida (36%)
Dictyoceratida
Hadromerida (9%)
Figure 2.4: Temporal variation at 6 intertidal reefs along the Illawarra Coast, NSW., Australia (A) variation in the abundance of intertidal sponges; (B) variation in the diversity of intertidal sponges recorded. NW - North Wollongong, BP - Bass Point, Be – Bellambi, Au – Austinmer, SP – Sandon Point, Cc – Coalcliff.
Figure 2.5: The relationship between the cumulative species diversity of intertidal sponges at 6 intertidal reefs along Illawarra coast and (A) cumulative abundance; (B) the number of species in a single inventory. The reefs were North Wollongong; Bass Point; Bellambi, Austinmer, Sandon Point, Coalcliff.
Overall, species composition among reefs showed very high levels of dissimilarity. Only two species, *Callyspongia (Callyspongia)* sp. 4 and *Echinoclathria* sp., appeared at more than one reef (North Wollongong and South Shellharbour; North Wollongong and Bass Point respectively). PERMANOVA supported this pattern ($P < 0.001$; Table 2.4). The multivariate analysis confirmed that significant differences in sponge assemblage composition existed among reefs (Figure 2.5). The nMDS analysis was also performed using both Fourth Root and Presence and Absence data and were equivalent to outcomes with the untransformed data - thus these plots were excluded from the results. The first quantitative survey (first inventory; Figure 2.5A) showed dissimilarity in the assemblages within two reefs (Bass Point and South Shellharbour). North Wollongong and Sandon Point reefs differed from the others in the Illawarra region, showing a more homogeneous sponge community in relation to the number of species.

During the 18 months of monitoring, a slight increase of the sponge diversity at the two reefs was observed (North Wollongong and Bass Point) as well as an increase in the abundance across three reefs (Sandon Point, North Wollongong and Bass Point). Thus, the data were again pooled to compare the abundance patterns of each species recorded after 18 months of sampling (Figure 2.5B). However, the data on the cumulative survey plot also revealed similarity between the sponge assemblages observed in different rock pools within Bass Point reef (Figure 2.5B). The similarity in Bass Point reef after 18 months of monitoring occurred because *Callyspongia (Callyspongia)* sp. 2 was also documented in most of the rock pools, hence the nMDS plot showing a more homogeneous sponge community at Bass Point reef (Figure 2.5B; Appendix Table 2.6).
Figure 2.6: Non-metric multidimensional scaling (nMDS) plot of sponge abundance for each species in each rock pool among sites for (A) initial inventory and (B) cumulative survey. The data were pooled to provide a centroid for each site based on Bray-Curtis Similarity measures. ▲ North Wollongong, ▼ Bass Point, ■ Sandon Point, ◆ South Shellharbour, ● Coalcliff.
Table 2.4: Multivariate analysis of one factor nested PERMANOVA for sponge abundance of each species among four rocky intertidal reefs in Illawarra region. Factors were sites and the number of rock pools at each site served as replicates. Coalcliff site was removed because it has insufficient replicates. Analysis was based on Bray-Curtis similarity with permutation of the raw data. NS $P > 0.05$; *** $P < 0.001$.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>Pseudo $F$</th>
<th>P (perm)</th>
<th>d.f.</th>
<th>MS</th>
<th>Pseudo $F$</th>
<th>P (perm)</th>
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</thead>
<tbody>
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<td>Site</td>
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<td>31042</td>
<td>3.145</td>
<td>***</td>
<td>3</td>
<td>23024</td>
<td>8.3642</td>
<td>***</td>
</tr>
<tr>
<td>Residual</td>
<td>20</td>
<td>65803</td>
<td></td>
<td></td>
<td>37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
<td>40</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.5: Representation of Pairwise Similarity Analysis (ANOSIM) among sites. North Wollongong (Nw), Bass Point (BP), Sandon Point (SP), South Shellharbour (Ss), Coalcliff (Cc). Results including Coalcliff site are based on few permutations.

<table>
<thead>
<tr>
<th>Groups</th>
<th>R</th>
<th>Significance $(P)$</th>
<th>Actual Permutations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nw, BP</td>
<td>0.616</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>Nw, SP</td>
<td>0.713</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>Nw, Ss</td>
<td>0.448</td>
<td>0.01</td>
<td>999</td>
</tr>
<tr>
<td>Nw, Cc</td>
<td>0.669</td>
<td>0.222</td>
<td>18</td>
</tr>
<tr>
<td>BP, SP</td>
<td>0.632</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>BP, Ss</td>
<td>0.461</td>
<td>0.001</td>
<td>999</td>
</tr>
<tr>
<td>BP, Cc</td>
<td>0.515</td>
<td>0.077</td>
<td>13</td>
</tr>
<tr>
<td>SP, Ss</td>
<td>0.71</td>
<td>0.001</td>
<td>792</td>
</tr>
<tr>
<td>SP, Cc</td>
<td>1</td>
<td>0.125</td>
<td>8</td>
</tr>
<tr>
<td>Ss, Cc</td>
<td>0.1</td>
<td>0.667</td>
<td>6</td>
</tr>
</tbody>
</table>
Additionally, ANOSIM confirmed dissimilarity between the assemblages among the selected sites (Global R = 0.604), which was significant, \( P = 0.001 \) (Table 2.5). However, data at Coalcliff are based on few permutations therefore the results that include Coalcliff must be regarded with caution. Furthermore, according to the Simper Analysis, species contribution to community composition reveals an average dissimilarity of 100% between most of the reefs, except for two groups which shows an average species dissimilarity of 85.72 and 99.82 (North Wollongong and South Shellharbour and North Wollongong and Bass Point, respectively) (Appendix Table 2.6). The species *Callyspongia (Callyspongia)* sp.4 was found in both reefs (North Wollongong and South Shellharbour) during the first inventories, whereas *Echinoclathria* sp. were recorded at North Wollongong during the first inventories and in Bass Point after a few months of sampling.

Lastly, patterns in sponge biodiversity were compared with those for the phylum Mollusca (Benkendorff & Davis, 2002) and a positive correlation between the total intertidal sponge diversity from cumulative surveys and the total of Mollusca species diversity across eleven sites was observed \( (r = 0.6; P < 0.05; \text{Figure 2.6}) \). It appears then, that the reefs of the Illawarra region with a high diversity of molluscs, also have high intertidal sponge richness.

![Figure 2.7: The relationship between the total intertidal sponge diversity from cumulative surveys and the total of Mollusca diversity across eleven sites (Benkendorff & Davis, 2002)](image)
2.4 DISCUSSION

2.4.1 Importance of intertidal sponge studies

Most studies that include intertidal sponges, focus on their seasonal growth (Elvin, 1976; Bell, 2008a), the impact of climate change (Sara et al., 2012; Kelmo et al., 2014) or adaptations to living in the intertidal zone (Maldonado et al., 2012; Weigel & Erwin, 2016). However, as shown in other marine systems, changes in sponge abundance could affect the habitat biodiversity, productivity and architectural complexity on rocky shores (Powell et al., 2015). For instance, sponges have the potential to influence other benthic community organisms (Bell & Smith., 2004), affecting the substratum availability for settlement (Bell et al., 2013) and altering the water column through their high water-filtering ability (Lesser, 2006). Therefore, quantitative information is essential to understand the factors that influence sponge abundance and distribution in a stressful environment such as intertidal reefs. Especially with the possible effects that global warming and ocean acidification may have on the abundance of sponges assemblages, as is already apparent for other marine systems, such as coral reefs (Bell et al., 2013).

Marine sponges are important group to be considered in the circumstances of a global biodiversity loss due their high diversity coupled with their ecological and commercial importance (Fromont et al., 2006). A review of the literature indicated that the analysis of spatial patterns has been limited to a narrow range of habitats and taxa. The most comprehensive biodiversity studies on sponges within Australia have been species inventories (Hooper, 1994; Hooper et al., 1999, 2002a; Hooper & Kennedy, 2002; Przeslawski et al., 2014). Most of these studies were undertaken in localities throughout subtropical and tropical Australian waters and very few studies have included quantitative estimates of species abundances (Hooper et al., 1999; Fromont, 1999; Fromont et al., 2006). Even fewer have assessed the biodiversity of sponge assemblages from rocky intertidal reefs, and most did not sample quantitatively in intertidal areas (Fromont, 2004; Fromont et al., 2006). Previous studies confirm that sponge species richness is much higher in tropical than temperate Australia waters (Roberts & Davis, 1996; Roberts et al., 2006; Hooper et al., 2002a; Hooper & Kennedy, 2002; Fromont et al., 2016). For instance, Przeslawski et al., (2014) collected 283 sponge species in northern Australia. Hooper & Kennedy, (2002) recorded 247 species of marine sponges in south-eastern Queensland. In north-western Australia Fromont, 2004; Fromont et al., (2006), reported a total of 275 species with most of the intertidal stations being depauperate in sponge species. Conversely, Roberts et al., (2006) identified a total of 82 species of sponge while Roberts & Davis, (1996) reported a lower species richness of around 50 sponge species in
south-eastern Australia. However, no study has reported the spatial distribution and abundance of sponges in intertidal ecosystems from south eastern Australia.

2.4.2 Illawarra intertidal sponges assemblages

The intertidal reefs of the Illawarra had only moderate abundances of intertidal sponges and were not very speciose. Surveys of the shore platforms recorded a total of 22 species in 5 of 14 intertidal reefs within a total combined surveyed area of ~ 516000 m² (0.516 km²). The assemblages were dominated by several patchily distributed species and included sparsely distributed, uncommon species at a few sites. These findings support earlier studies that have noted small-scale patchiness in sponge species distributions, which were attributed to a variety of physical and biotic factors such as: a low probability of long-distance dispersal, asexual propagation, lack of connectivity among populations, microhabitat requirements, and episodic disturbance (Hooper & Kennedy, 2002; Roberts & Davis, 1996; Demers, 2015), although none of these studies were in intertidal habitats.

Taxonomic similarities among the sponge assemblages of seagrass in Jervis Bay (Demers et al., 2015), estuarine lakes in NSW (Barnes et al., 2013) were observed with a few species that were recorded in deeper pools at the intertidal reefs of Illawarra. For instance, both habitat assemblages comprised one sponge taxon in common with the intertidal reef assemblages - *Halichondria* sp., although they may be different species. However, one intertidal species, *Callyspongia (Callyspongia)* sp., does not occur in these shallow subtidal habitats mentioned above, revealing that perhaps there are some species that are unique to these rocky reef habitats. Demers et al., 2015 encountered 20 sponge species in the seagrass habitat of Jervis Bay, NSW and Barnes et al., 2013 reported 18 sponge species in saline coastal lagoons in NSW, in a sampling area 30 and 20-fold smaller respectively than this study, which confirms that Illawarra reefs house a lower richness of sponge assemblages, if compared with other marine systems in NSW. Although, seagrass ecosystems of Jervis Bay show a relatively high species richness, it was surpassed by the subtidal temperate reefs of NSW (Roberts and Davis, 1996; Roberts et al., 1998; Roberts et al., 2006). In both studies, sponges were the most diverse and abundant taxon, which comprised more than double the sponge diversity I observed. Roberts and Davis, 1996 recorded a total of 50 species, whereas Roberts et al., 1998 and Roberts et al., 2006 identified over 100 and 82 species respectively.

Nevertheless, the species composition uncovered in this study was dissimilar across the sites. Of 22 species identified, only 2 (9%) in total were found to be present in more than one reef (site), which is an unusual pattern of distribution when compared to assemblages in other marine and terrestrial systems. As in my study, Wright et al., 1997 also observed considerable
spatial heterogeneity in sponge assemblages from shallow subtidal regions in temperate south-eastern Australia. None of the sponge species they recorded occurred in both habitats they sampled and only a few of the common species (<30%) were observed in both sites. Moreover, the percent cover of the common species was different at each site.

2.4.3 Unusual distributional pattern

It may be instructive to compare my findings on sponge assemblages with data for other biotic assemblages. Not surprisingly, due to their easy access, bird assemblages are a useful model to understand the relationship between species, locations and sampling time. Birds assemblages appear to show a similar distributional pattern as some subtidal sponges and fish communities in south east Australia (Gaston and Blackburn, 2000; Roberts & Davis, 1996). Biotic assemblages often show a different distribution pattern to the intertidal sponges from the Illawarra region. For example, bird assemblages in English woodlands are dominated by a small number of taxa, while most species are rare, being observed only once over the year (Gaston & Blackburn, 2000). This is the same pattern observed for fish communities sampled in rocky reefs from south eastern Australia as revealed by Baited Remote Underwater Video (BRUV) (Kelaher et al., 2014). Furthermore, if we return to sponges, on the Sunshine Coast, Queensland, ten subtidal reefs were sampled and in contrast to the Illawarra intertidal reefs habitat, 15 of the 247 sponge species identified co-occurred in 50% of the sites sampled (Hooper & Kennedy, 2002). Roberts & Davis, 1996 study also revealed that the sponge assemblages from reefs on south-eastern Australia show a different pattern than the intertidal Illawarra sponges community. The most common sponges species were found at most of the three locations and depths sampled. However, heterogeneity in sessile epifaunal invertebrate distribution at small spatial scales has been recorded in reef habitats (Roberts & Davis, 1996; Knott et al., 2004), coastal lakes (Barnes et al., 2013 as well as within kelp (Wright et al., 1997), seagrass habitat (Demers et al., 2015) and even on bare substratum in deep Antarctic waters (Barthel & Gutt, 1992).

2.4.4 Sponges adaptations

Organizational and morphological plasticity is undoubtedly important to help intertidal organisms to cope with stressful environments, particularly in the intertidal zone (Barnes 1999). Sponges show several adaptations that allow them to tolerate the drastic changes in the physical environment that mainly occur during low tides (Palumbi, 1984; Barnes, 1999). Intertidal sponges exhibit different morphologies, characteristics and variability in the timing of their responses when exposed to high or low wave force environments (Palumbi, 1984). Barnes (1999) identified that many tropical intertidal zone sponges had a low surface area to
volume ratio; encrusting species were rare. However, the most common morphology of sponges in all intertidal reefs in my study was encrusting (66%), but massive forms were also present on 4 of the 5 reefs (Appendix 1). Furthermore, the area in which sponges achieved greatest importance was the underside boulders and within rock pools. Barnes (1999) revealed that the caves and under-surfaces of boulders give some protection from wave and temperature extremes. In this study we found in total 4 species underside boulders and 19 in pools. Additionally, rock pools reduce evaporation, thus reducing salinity and desiccation changes (Barnes, 1999). In this study, it appears that the microhabitats may also help the intertidal sponges to minimize the environmental extremes experienced in this habitat mentioned above as well as disturbance from sand deposition, hydrodynamic forces, and predation.

2.4.5 Overall findings

Benkendorff and Davis, (2002) reported great variation in the species richness of molluscan fauna among the reefs in the Illawarra region. Hence, as Benkendorff and Davis, (2002) documented for intertidal molluscs, a single species inventory can likewise be used to accurately rank species richness and may be used to confidently set conservation priorities for intertidal sponges (Figure 2.5). However, the sampling methods must be standardized to facilitate the cross-comparison of sites. Comparison of biodiversity patterns with other intertidal phyla would provide a more comprehensive assessment of the bioregional invertebrate faunas in this region. As in my study, Benkendorff and Davis (2002) demonstrated that different intertidal reefs within a region are not equal in terms of the species richness, but the patterns of species richness were relatively consistent through time (Figure 2.3B). Furthermore, sponge species from this region were patchy in their distribution with most of the sponge species found inside of pools, making difficult the quantification using the two ecological tools (transects and quadrats). However, the sampling design chosen was based in field observations and after different attempts timed survey was chosen as the best approach to quantify the relative abundance and diversity of the sponge communities of intertidal zones in this region. Thus, my study establishes that 2 hour timed-search surveys, during low water spring tides, are appropriate for the rapid assessment of sponges on temperate Australian rocky reefs. It would be worthwhile to establish whether this method is useful for other regions.
2.5 CONCLUSIONS

The intertidal sponge communities in the Illawarra region are comparatively depauperate, which supports previous studies in temperate waters that have recorded sponges in the intertidal zone (Fromont, 2004, 2006).

Sponge species from this region were patchy in their distribution, showing high levels of heterogeneity of sponge assemblages among sites with only 2 species (9%) in total present in more than one location (*Callyspongia (Callyspongia)* sp.4; *Echinoclathria* sp.). However, a few species including *Callyspongia (Callyspongia)* sp. 4 have not previously been observed in other marine ecosystems in NSW Australia (Roberts & Davis, 1996; Wright et al., 1997; Ferguson & Davis, 2008; Demers et al., 2015; Barnes et al., 2013), revealing that perhaps there are some species that are unique to this rocky reef habitat. Furthermore, *Callyspongia (Callyspongia)* was the most common genus, which showed great spatial variation in their presence and abundance across intertidal reefs - with 46% of the total of 65 individuals at 4 sites. In contrast, most genus showed a markedly low pattern of abundance recorded among the reefs with species being represented by only one or two sponge individuals within each reef. This likely has important implications for sponge reproduction and recruitment.

Despite the great commercial and ecological importance of sponges along with their high diversity, the documentation of regional sponge assemblages is still relatively rare with most of the studies undertaken in subtidal tropical areas (van Soest, 1993; Hooper et al., 2002a; Hooper & Kennedy, 2002; Kelly et al., 2002; Bell & Smith, 2004; Fromont et al., 2006; Fromont et al., 2016). Furthermore, the majority of biodiversity studies within Australia have been species inventories (Hooper, 1994; Hooper et al., 1999, 2002a; Hooper & Kennedy, 2002; Przeslawski et al., 2014), with higher sponge species richness being found in tropical Australia waters than in temperate ecosystems (Roberts & Davis, 1996; Roberts et al., 2006; Hooper et al., 2002a; Hooper & Kennedy, 2002; Fromont et al., 2016). There is a lack of studies sampling intertidal localities quantitatively (Fromont, 2004; Fromont et al., 2006; Fromont & Sampey, 2014; Fromont et al., 2016). However, similarly to what was found in my study, Benkendorff & Davis, 2002 observed that different intertidal reefs in the Illawarra region were not equal in terms of species richness and for low diversity sites their patterns of diversity were consistent through time. In contrast, they reported that rare molluscan species continued to be recorded at sites supporting high levels of diversity (Benkendorff & Davis, 2002). The total number of sponge species recorded at each site only increased by one or two species with additional
sampling - thus a total of 22 sponge species were encountered, where 12 were new occurrences for the Illawarra Region and many of these were previously undescribed.

To my knowledge, no other studies have provided estimates of the spatial distribution patterns and abundance of these assemblages in south east Australia. Further studies need to adopt an experimental approach in order to disentangle the key processes and factors responsible for the distribution patterns observed (see Chapter 3). Further studies will then also benefit from greater understanding of the drivers of high levels of heterogeneity among reefs. Examining the response of intertidal sponges to a stressful environment remains a key challenge.
2.6 APPENDIX

Table 2.6: Percentage similarity analysis (SIMPER) for sponge abundance of each species among sites in rocky intertidal reefs of Illawarra region. Global R clearly showed dissimilarity in the assemblages among sites (R = 0.604), which was significant, \( P < 0.001 \).

**Sites: NW, BP**

Number of species: 16  
Average dissimilarity = 99.82

<table>
<thead>
<tr>
<th>Species</th>
<th>NW Average of Abundance</th>
<th>NW Average of Abundance</th>
<th>NW Dissimilarity</th>
<th>NW Diss/SD</th>
<th>Percentage of contribution</th>
<th>Cumulative contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Callyspongia (Callyspongia) sp.4</td>
<td>1.02</td>
<td>0</td>
<td>31.44</td>
<td>1.64</td>
<td>31.49</td>
<td>31.49</td>
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<tr>
<td>Callyspongia (Callyspongia) sp.2</td>
<td>0</td>
<td>0.87</td>
<td>23.58</td>
<td>1.17</td>
<td>23.62</td>
<td>55.11</td>
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<tr>
<td>Chondrilla sp.1</td>
<td>0</td>
<td>0.27</td>
<td>5.41</td>
<td>0.54</td>
<td>5.42</td>
<td>60.53</td>
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<tr>
<td>Echinoclathria sp.</td>
<td>0.06</td>
<td>0.08</td>
<td>3.25</td>
<td>0.35</td>
<td>3.25</td>
<td>83.51</td>
</tr>
<tr>
<td>Hyrtios sp.</td>
<td>0</td>
<td>0.17</td>
<td>5.15</td>
<td>0.4</td>
<td>5.15</td>
<td>71.01</td>
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</tbody>
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**Sites: NW, SP**

Number of species: 6  
Average dissimilarity = 100.00

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<th>Species</th>
<th>NW Average of Abundance</th>
<th>NW Average of Abundance</th>
<th>NW Dissimilarity</th>
<th>NW Diss/SD</th>
<th>Percentage of contribution</th>
<th>Cumulative contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Callyspongia (Callyspongia) sp.6</td>
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<td>Callyspongia (Callyspongia) sp.4</td>
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<td>0</td>
<td>40.79</td>
<td>2.03</td>
<td>40.79</td>
<td>87.89</td>
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## Sites BP, SP

Number of species: 12  
Average dissimilarity = 100.00

<table>
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<th>SP</th>
<th>Dissimilarity</th>
<th>Diss/SD</th>
<th>Percentage of contribution</th>
<th>Cumulative contribution</th>
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<tr>
<td>Callyspongia (Callyspongia) sp.6</td>
<td>0</td>
<td>1.14</td>
<td>38.1</td>
<td>2.82</td>
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<tr>
<td>Callyspongia (Callyspongia) sp.2</td>
<td>0.87</td>
<td>0</td>
<td>24.7</td>
<td>1.17</td>
<td>24.7</td>
<td>62.8</td>
</tr>
<tr>
<td>Chondrilla sp.1</td>
<td>0.27</td>
<td>0</td>
<td>5.6</td>
<td>0.54</td>
<td>5.6</td>
<td>68.4</td>
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<tr>
<td>Halichondria sp.1</td>
<td>0.18</td>
<td>0</td>
<td>5.6</td>
<td>0.41</td>
<td>5.6</td>
<td>74</td>
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</table>

## Sites NW, Ss

Number of species: 10  
Average dissimilarity = 85.72

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<th>Species</th>
<th>NW</th>
<th>Ss</th>
<th>Dissimilarity</th>
<th>Diss/SD</th>
<th>Percentage of contribution</th>
<th>Cumulative contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Callyspongia (Callyspongia) sp.4</td>
<td>1.02</td>
<td>0.2</td>
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<td>0.79</td>
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<tr>
<td>Myxilla sp.</td>
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### Sites BP, Ss

Number of species: 16  
Average dissimilarity = 100

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<th>Ss</th>
<th>Dissimilarity</th>
<th>Diss/SD</th>
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<tr>
<td>Callyspongia (Callyspongia) sp.3</td>
<td>0</td>
<td>0.51</td>
<td>16.16</td>
<td>0.74</td>
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### Sites SP, Ss

Number of species: 6  
Average dissimilarity = 100.00

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CHAPTER 3

Independent effects of environmental factors: what drives the distribution of intertidal sponges
3.1 INTRODUCTION

Sponges (Porifera) are a major component of hard-substratum benthos, where a number of factors, including habitat type, control species distribution and assemblage structure (Carballo & Nava, 2007). The wide range of significant functional roles that sponges play, means they have the potential to exert major control on overall ecosystem functioning and likely have stronger effects on marine systems in light of current environmental change (Bell, 2008a). Any exclusion of sponges from monitoring programmes is of considerable concern, as their distribution can be an indicator of overall biodiversity (Hooper et al., 2002b; Przeslawski et al., 2014) and they often dominate the benthos.

Understanding the factors that influence community structure of a region, and thus ecosystem function remains the central aim of ecological research (Leonard et al., 1998; Davidson et al., 2004). The past two decades have witnessed increasing interest in understanding how the abundance and distribution of species vary and how the interplay between species interactions and abiotic factors influence their ecological patterns (Kordas et al., 2011). In part, the interest has grown because the climate continues to warm, due to anthropogenic influence, causing changes in species range limits and abundance-distributions (Lathlean et al., 2015). Rocky shores occur at the interface of the land and sea (Tomanek & Helmuth, 2002), thus, animals and algae in this ecosystem must contend with the physical conditions of both environments (Helmuth et al., 2006a). Hence, there is a strong possibility that these habitats may serve as a model for change in other ecosystems (Helmuth, 2002), as climate change seems likely to have a more pronounced impact on the intertidal communities (Sara et al., 2014). Thus, these systems could be an ideal habitat to provide understanding of the role of biological and physical factors in influencing the distribution and abundance of organisms (Tomanek & Helmuth, 2002).

Rapid changes can occur in the distribution, abundance and range limits of intertidal species. As an example, the poleward-range edges of marine species have shifted by as much as 50 km per decade (Helmuth et al., 2006a). Although, the majority of studies still focus on species-range limits, some studies have highlighted how changing parameters, such as the amount of time that an organism spends emergent during low tide, can lead to multiple environmental stresses (Helmuth et al., 2006a). For example, Petes et al., 2007 performed transplants on New Zealand rocky shores, suggesting that the abundance of the competitive
dominant mussel species may decrease due to increases in aerial temperatures, predicted from climate change scenarios. Changes in the community-dominant species could drastically alter the community structure of the New Zealand intertidal rocky shores (Petes et al., 2007). In addition, recent findings have supported the concept that altered species interactions are anticipated to have stronger effects on the structure of assemblages than the direct impacts of physical factors such as warming (Lathlean et al., 2017).

The structure of communities is determined by processes attributed to a variety of factors, including primary productivity and recruitment (Leonard et al., 1998), environment factors such as chemical (i.e. variations in temperature, oxygen, salinity) physical (i.e. topography) and biological (i.e. competition, predation and disease) interactions (White et al., 2015). However, intertidal ecosystems are characterized by patterns of vertical distribution (zonation) which are determined by species’ physiological adaptations to a variety of factors, including: wave exposure, temperature and desiccation stress (Tomanek & Helmuth, 2002). In addition, on intertidal reefs, species’ interactions among organisms and with their environment may also exert a major influence on community dynamics and vertical zonation (Connell, 1972; Harley & Helmuth, 2003). Although, many studies have sought to determine which biological and physical factors are controlling intertidal distribution, their combined effects have been poorly investigated (Leonard et al., 1998). Furthermore, Menge (2000) suggested that top-down processes (control by consumers) are in fact tightly associated to bottom-up effects (productivity and nutrients) in marine rocky intertidal habitats. Hence, both processes may have important effects, playing a determining role in the structure of rocky intertidal ecosystems.

The upper vertical range limits of a species in the intertidal zone are frequently driven by physical factors, such as temperature, irradiance and desiccation (Stickle et al., 2017). In contrast, at the lower vertical range, biotic interactions play an overarching structuring role, but this process is influenced by the underlying environmental gradient (Helmuth et al., 2006a). The position of the organisms between the low shore and the stressful high-intertidal zone can be positively correlated with the organisms vertical lethal limits (Tomanek & Helmuth, 2002). This positive relationship may occur especially if the variation in the degree of exposure to the wave and the microhabitat complexity were taken into account (Tomanek & Helmuth, 2002).

Intertidal organisms experience noticeably different environments to those of their subtidal counterparts, due their exposure to aerial conditions. (Lathlean et al., 2015). During low tide, drastic changes in the physical environment occur (i.e. variation in temperature and irradiance conditions, including UV exposure) and the intertidal environment becomes physiologically stressful, particularly for sessile filter feeding organisms that are not able to
filter feed due the periodic aerial exposure (Davidson, 2005; Weigel & Erwin, 2016). However, sponges show several adaptations that allow them to tolerate the harsh environment (see below). Sponge morphological and organizational plasticity play a decisive role, especially in intertidal habitats (Gaino et al., 1995; Barnes, 1999; Hill & Hill, 2002), as they provide adaptive responses to ensure their survival and support their ecological success in the community (Gaino et al., 1995).

A small number of studies have assessed the adaptations sponges possess to survive in the intertidal habitat (Bergquist & Sinclair, 1968; Barnes et al., 1999; Steindler et al., 2002; Gaino et al., 2010). Barnes et al., 1999 investigate the intertidal zone sponge assemblages of the Quirimba Archipelago, Africa. They identified that many tropical intertidal zone sponges, had a low surface-area-to-volume ratio, are peripherally toughened or pocketed to trap water. Moreover, sponges recorded in non-shaded soft substrata showed adaptations to be able to trap greater volumes of water, such as partial burial or becoming more highly porous. Additionally, some intertidal species, which also occur in the subtidal zone, showed a great deal of bathymetric morphological plasticity. Davidson et al., 2004 and Davidson, 2005) investigated the intertidal community in southwest Ireland and revealed that sessile filter feeding organisms, including sponges, were more abundant at low-mid shore than the mobile taxa. The reason for this spatial pattern may reflect their dependency on water movement to provide food and their poor desiccation tolerance. However, intertidal sponges were found to contain a higher percentage of photosymbionts than subtidal species (Steindler et al., 2002). The photosynthetic activity was also measured in periodically exposed sponges in situ suggesting that the association with photosymbionts may be an alternative important food source, during their interrupted filtering capacity. He also suggested that the photosymbionts product antioxidant substances as a UV radiation protection (Steindler et al., 2002).

The intertidal ecosystems are harsh environments that can affect their communities causing different adaptations in animals’ colonization (Bergquist & Sinclair, 1968; Gaino et al., 2010). Additional evidence for reproductive adaptions in the intertidal zone sponges has revealed that First, larvae released at an advanced stage only demanded a short time frame to complete its free life cycle (Bergquist & Sinclair, 1968). Second, a demosponge species, *Hymeniacidon perlevis*, presented female gamete differentiation during its reproductive cycle, which anticipate the presence of sperm cysts by one month (Gaino et al., 2010). However, the sponges plasticity capacity also reflects in their reproductive pattern, as a strategy of these phyla to survive and spread in the unpredictable intertidal environment (Gaino et al., 1995; Gaino et al., 2010).
Diversity in intertidal sponge communities has barely been investigated (see, Barnes, 1999; Fromont et al., 2006, 2016). Although, there are numerous previous studies that have assessed the impacts of environment changes on other intertidal organisms (Lathlean et al., 2017; Stickle et al., 2017; King & Sebens, 2018), is important to mention that no study has vigorously investigated the processes that regulate patterns in intertidal sponge communities. Indeed, very little is known about the drivers of intertidal sponge distribution and abundance (Davidson et al., 2004; Davidson, 2005). Most of the studies focused on intertidal sponges are about their microbial symbiont communities (Steindler et al., 2002; Weigel & Erwin., 2016) or related to their patterns of reproduction (Bergquist & Sinclair 1973; Gaino et al., 2010). Therefore, to address this important knowledge gap, the purpose of this research was to focus on evaluating the relative importance of key environmental factors that may determine the observed patterns of species distribution and abundance of intertidal sponges with a focus on the Illawarra region, NSW, Australia.

3.2 MATERIAL AND METHODS

3.2.1 Study sites and sampling methods

As explored in the previous chapter an inventory of sponges was conducted at 14 intertidal reef habitats along the coast of the Illawarra region, NSW, Australia (Table 2.2). Estimates of diversity and abundance were drawn from a timed search (2hr) at each of 14 intertidal reefs. Sponge diversity and abundance were quantified by counting the number of individuals (abundance) and species at each rocky reef. The information about all the species recorded in each reef can be found on the "Sponge Identification Guide" (Appendix 2.6). Furthermore, the surface area of each sponge was estimated using the image processing program, ImageJ (Rasband, 1997) by tracing the pinacoderm contour of each individual (Figure 3.1). For branching species, diameters as well as lengths were measured for each branch segment.
Figure 3.1: Methodology for calculating the surface area of each sponge through the pinacoderm contour of each specimen using the image processing program, ImageJ. Note the ruler for scale (cm) and the number, above the image, is the size in the photo in pixels.

Sample sites were described using a range of criteria, including the topographic properties of the reef. Thus, each rocky reef was ranked according to two physical variables: habitat complexity and exposure to wave action (Table 3.1). Those two variables were classified as in Benkendorff & Davis, 2002. The majority of intertidal reefs of the Illawarra region (NSW) are predominantly exposed to a south-easterly swell (Bennett, 1992). Thus, the sites were classified as either wave exposed or sheltered, according to the orientation of each reef (Table 3.1; Figure 3.2).

The Illawarra coast contains eight highly wave-exposed rock platforms; Coalcliff, Scarborough, Wombarra, Coledale, Austinmer, Waniora Point (South Bulli), Flat Rock (Woonona) and Towradgi. In contrast, the sheltered reefs found along this region rarely experience swell greater than one meter and are represented by six reefs; North Wollongong, Bellambi, Bulli Point, North Shelharbour, South Shelharbour and Bass Point. These north-facing reefs are afforded protection by headlands to their south. The intertidal reefs in this area are primarily composed of wave-cut rock platforms and boulder fields (Bennett 1992). Reefs
were also classified according to their habitat diversity (Table 3.1; Figure 3.2; Figure 3.3). Four
natural microhabitat types were investigated. These habitat groupings were also used by NSW
Fisheries (2001) in their assessment of intertidal reefs: (1) rock platforms; (2) caves and
crevices; (3) rock pools; and (4) areas containing boulders. In this study, boulders refer to any
loose rocks with a diameter less than 1m (NSW Fisheries 2001; Benkendorff & Davis 2004).
It is important to note the difference in the level of structural complexity between reefs. The
microhabitats, particularly boulders and rock pools, vary in their quantity depending on the reef
(Figure 3.2; Figure 3.3).

Habitat complexity and the degree of wave action are well known as important factors
influencing rocky shore community structure (Helmuth & Denny, 2003; Kostylev et al., 2005;
Burrows et al., 2008). Thereby, six of the fourteen intertidal reefs were chosen according to
their level of wave exposure and their degree of habitat complexity; Coalcliff, Austinmer and
Bass Point (Highly exposed); Sandon Point, Bellambi and North Wollongong (Sheltered);
(Table 3.1). Most of the sponge species I recorded have been found within rock pools (see
Chapter 2), thus surveys were conducted on these six reefs in September 2017 to estimate and
assess whether physical (abiotic) factors were correlated with the patterns of abundance and
distribution of sponge species. The three factors examined were: the number of rock pools; the
volume of each rock pool (m³) and the total area of the reef containing pools (m²). The total
area of each rocky reef was measured using geospatial tools in ‘Google Earth Pro’. The volume
and the number of rock pools were measured, for each of the six reefs, during the survey
conducted in September 2017. I haphazardly sampled each reef using five transects of 20 m in
length. The number of each pool and volume were estimated by counting and measuring the
volume of all rock pools, respectively, that each transect made contact with.
Table 3.1: Habitat ranking for fourteen intertidal reefs along the Illawarra coast. Each site has been ranked for two physical features; wave exposure and habitat complexity. The rankings were assigned completely independently of the diversity and abundance data. A ranking of 5 indicates the site is highly exposed to wave action or has high habitat complexity, whereas, a ranking of 1 indicates the site is sheltered from strong swell or has low habitat complexity.

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<tr>
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<td>5</td>
</tr>
<tr>
<td>Austinmer</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Bulli Point (Sandon Point)</td>
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<td>1</td>
</tr>
<tr>
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<td>5</td>
</tr>
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<td>Flat Rook (Woonona)</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Bellambi</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Towradgi</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>North Wollongong North Shellharbour</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Bass Point</td>
<td>5</td>
<td>1</td>
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Figure 3.2: Reefs with contrasting structural complexity: Examples of three intertidal reefs on the Illawarra coast, NSW, Australia according to the degree of habitat complexity; (A) a wave exposed reef in Coalcliff with low level of habitat complexity and rock pools found in less than 10% of the whole reef; (B) Sandon Point, a large area of complex intertidal habitat with numerous pools protected from strong swell; (C) moderate level of habitat complexity and north facing (sheltered) reef at North Wollongong with numerous pools across the shore.
Figure 3.3: Examples of two reefs with contrasting densities of boulders on the Illawarra coast, NSW, Australia; (A) North Shellharbour reef with the area containing relatively few boulders (<50m² of the total reef); (B) South Shellharbour reef with a large area of complex intertidal habitat including a large area of boulders (> 100m² of the total reef).
As noted in Chapter 2, the genus *Callyspongia* (*Callyspongia*) was more widely distributed than the other genera among reefs, with 46% of the total of 65 individuals across four of 14 reefs. In contrast, the species from the other genus had a markedly lower abundance recorded among the sites, with only one or two sponge individuals found within reefal habitat reef. A distinct zonation pattern of sponges was observed in most of the rocky intertidal reefs of Illawarra region, with a clearly restricted vertical distribution. Most of the species were limited either to the low or mid shore. No species were present at all intertidal reefs, or at all shore heights - although, *Callyspongia* sp.4 and sp.2 were the two species found in high shore pools in North Wollongong and Bass Point reef, respectively. Furthermore, unlike the other species, *Callyspongia* sp. showed a marked zonation pattern during the quantitative monitoring showing a decrease in abundance and cover area during autumn and winter. These observations prompted me to test the hypothesis that sponges found in rock pools, lower on the shore enjoy higher survivorship than sponges recorded in high shore pools.

Surveys were conducted to record the coordinates and tidal heights of each rock pool where individual sponges was observed. The intertidal sponge survivorship were assessed and compared at different tidal heights. The global positioning system (GPS) surveys were conducted in November 2017 using a Real time kinematic (RTK-Trimble R8s GNSS) and an integrated TSC3 controller to record the relative coordinates of each rock pool in four intertidal reefs in the Illawarra region (Coalcliff; Sandon Point; North Wollongong and Bass Point). A base station was set up at a point close to each rock pool. The Trimble R8s GNSS receiver of the RTK- GPS system was fixed on top of a 2m high stake (Figure 3.4). A cm-level accuracy of the position (0.8 cm H/ 1.5 cm V Max. Precision) was then obtained in real-time according to the phase measurements transmitted by radio link to the roving GPS receiver. Thus, the geographic coordinates along with the tide height of each rock pool was obtained. Subsequently, the coordinates acquired from the RTK-GPS system were used to estimate the distance from the beach for each rock pool using ArcMap 10.4.1.

Quantitative estimates of species’ abundance were conducted over eighteen months, from February 2016 to August 2017. The six reefs (Coalcliff; Austinmer; Sandon Point; Bellambi; North Wollongong and Bass Point) were assessed once per month to investigate seasonal variability in the diversity of intertidal zone sponges, as well as their abundance and cover. The surveys were all undertaken during the entire 2-4 hr period when the intertidal zone was exposed, as described in Chapter 2. The change in the sponge assemblage at each site were
recorded and a diversity and abundance list of the intertidal sponge fauna was generated for each month, in order to assess the effects of seasonal variation in the Illawarra reefs.

Water quality within rock pools was measured using a Hydrolab quanta (Temperature (°C), Salinity (‰), Dissolved Oxygen (mg/L) and pH (mmHg)). The measurements were done in rock pools containing sponges along with rock pools that did not contain sponges, but which were chosen for similarity in volume and vertical height. However, it was not impossible to measure the quality of water in the pools at the six different reefs at the same day. Thus, the data collected were used to compare the pools at the same reef with the intention to check whether the physical factors were reaching unusual levels.

Figure 3.4: The Real time kinematic (Trimble R8s GNSS) GPS system being placed close to one of the rock pools in Sandon Point, NSW, Australia. An integrated TSC3 controller was also used to record the relative coordinates of each rocky reef.
3.2.2 Statistical analyses

The composition of the intertidal sponge community was compared between sites and analyzed using the major environmental factors that may be responsible for structuring these assemblages. Statistical tests were performed to assess the relationship between the number of intertidal sponge species and abundance within the habitat rankings of all intertidal reefs along the Illawarra Coast, NSW. A correlation was applied to investigate the hypothesis that habitat complexity influences the diversity and abundance of the sponge assemblage among all reefs. Additionally, as the most structurally complex habitats also exhibited the highest number of rock pools and most of the sponges individuals from Illawarra reefs were found inside of this topographic microhabitat, a correlation between habitat complexity and the number of rock pools was also investigated to confirm this hypothesis. The last correlation was performed among six reefs, which were chosen because they were already being monitored to estimate the temporal variation in the diversity and abundance of sponge assemblages. Furthermore, A Mann-Whitney U test was performed to test the hypothesis that sheltered reefs are higher in species richness and abundance than wave exposed reefs.

A correlation was performed to test whether the size of each of the 14 rock platforms (m²) was influencing the patterns of sponge species distribution and abundance. The correlation was also applied to test the relationship between the sponge diversity and abundance, in six reefs (Coalcliff, Sandon Point, North Wollongong and Bass Point) with three factors: The number of rock pools on each reef; the volume of each rock pool (m³) and the total area of each reef that contained pools (m²). The total area of each reef that contained boulders (m²) was not included because sponge species recorded underside boulders were only found in one Illawarra intertidal reef. The cover of the dominant sponge in this assemblage, *Callyspongia* (*Callyspongia*) sp. (Chapter 2) was compared with the patterns of cover for all other sponge taxa combined, as the other taxa demonstrated low abundance. Therefore, the relationship between the coverage area of *Callyspongia* (*Callyspongia*) sp. and the other sponge species was compared for two sites (North Wollongong and Bass Point) to assess whether they show similar changes in their coverage during the 18 months that they were monitored. Finally, a student’s t-test was employed to compare how the mean tidal height of pools affected sponge survivorship at the end of the monitoring period (18 months). All correlations and the t-test were completed using R Studio (version 3.4.2) while the non-parametric test was performed on SPSS Statistics 24 (SPSS Inc.). I set α at 0.05 in all analyses.
3.3 RESULTS

Both habitat rankings (habitat complexity and degree of exposure to wave action) were correlated with the number of sponge species and sponge abundance on rocky reefs in the Illawarra (Figure 3.5; Figure 3.6). Habitat complexity demonstrated a significant influence on both species richness (\(r = 0.7, P = 0.003\); Figure 3.5B) and abundance (\(r = 0.6, P = 0.015\); Figure 3.5A). Additionally, a strong positive correlation (\(r = 0.9, P = 0.01\)) was observed between habitat complexity and the number of rock pools for the six rocky reefs (Coalcliff; Austinmer; Sandon Point; Bellambi; North Wollongong and Bass Point). This correlation confirmed that habitat complexity was correlated with sponge diversity and abundance, as most of the reefs with structurally complex habitat also had the highest number of pools. With regard to the degree of wave exposure of the reef, north facing reefs clearly showed a higher abundance and diversity than wave-exposed reefs (Figure 3.6). Sheltered reefs contributed with 95% of the total species and had six times more abundance than wave exposed reefs. A non-parametric test confirmed the hypothesis that sheltered exposed reefs were higher in the number of sponge species and individuals; Abundance (\(U = 9, P = 0.024\)) and Diversity (\(U = 9.5, P = 0.029\)).
Figure 3.5: The relationship between the habitat complexity of 14 intertidal reefs along the Illawarra Coast, NSW, Australia. (A) Abundance (number of individual sponges) and (B) Sponge diversity (number of species). Diversity ($r = 0.7, P = 0.003$); Abundance ($r = 0.6, P = 0.015$). Note that some sites overlap on this plot, hence only 8 points are visible.
Figure 3.6: Sponge species diversity and abundance at two degrees of exposure to wave action – low and high. Each bar represents a mean (±SE) of: (A) sponge abundance represented as number of individuals and (B) sponge richness expressed as number of species per site. Estimates of diversity and abundance were drawn using timed search (2 hr) at each of 14 intertidal reefs. Low wave exposure (N = 5) and high wave exposure (N = 9). A Mann-Whitney U test revealed significant differences at the 5% level as denoted by the asterisk (see text for details of the analysis).
Comparison of the survivorship of sponges in rock pools at different tidal heights revealed that sponges found in rock pools, lower on the shore enjoy higher survivorship than sponges individuals recorded in high shore pools on all the three different periods of monitoring (six, twelve and eighteen months; Figure 3.7). The great contrast in the sponge survivorship between the two different vertical heights was particularly evident at the end of the experiment (18 months) with a 50% increase in mortality in high shore over low shore pools. Thus, pool height appears to be an important predictor of the survival of intertidal sponge assemblages. A t- test confirmed this hypothesis, after eighteen months of monitoring, demonstrating that the tidal heights of pools has a significant influence on sponge survivorship t (18) = 2.79, P = 0.01.

I sought to assess three features of reefs on sponge diversity and abundance. Although, the only feature of rock pools which correlated with species diversity and abundance across the six reefs, was the volume of rock pools (m$^3$) (Abundance: $r = 0.6$, $P = 0.0001$ and Diversity: $r = 0.6$, $P = 0.0002$; Figure 3.8), it is important to highlight that the outcome needs to be interpreted with caution. When the outliers were removed, the interpretation of the relationship changed showing that rocky pool volumes have no significant effect on sponge diversity and abundance. However, a high sponge abundance of a single species was recorded in small rock pools (< 2m$^3$) at North Wollongong reef, while large pools at Bass Point reef was observed housing not only a high sponge abundance but also a greater diversity than other reefs. For instance, small pools on North Wollongong reef supported a great number of sponge individuals of Callyspongia (Callyspongia) sp.4, then pools four to ten times larger (Figure 3.8A). The maximum number of species observed in any one pool, among the six reefs, were five. However, Bass Point reef was the only site where a high sponge diversity (four species) was recorded (Figure 3.8B). Conversely, several features of rock platforms were not correlated with sponge diversity and abundance; the number of rock pools and the area containing pools, along with the size of the rock platforms has shown no statistically significant influence on sponge richness and abundance (P > 0.05). Consequently, I have not presented these figures.
Figure 3.7: Comparison of the survivorship of sponges in rock pools at different tidal heights at four intertidal reefs in the Illawarra region (Coalcliff; Sandon Point; North Wollongong and Bass Point – data pooled from the four sites). Each bar represents a mean (±SE) of the tidal height of rock pools in which associated sponges did not survive (0%) and those that did (100%). (A) survivorship was recorded after six months, (B) twelve months; and (C) eighteen months (N = 30). A t-test was used to compare tidal heights of pools at the end of the experiment (18 months), t (18) = 2.79, P = 0.01. Tidal height was assessed with a differential GPS see text for details.
Figure 3.8: The relationship between the volume of rock pools (m$^3$) recorded on six intertidal reefs in the Illawarra region, NSW, Australia (Coalcliff; Austinmer; Sandon Point; Bellambi; North Wollongong; Bass Point – data presented are pooled from these sites): (A) abundance as number of individual sponges ($r = 0.6$, df = 32, $P = 0.0001$); (B) diversity as number of species ($r = 0.6$, df = 32, $P = 0.0002$).
Finally, *Callyspongia (Callyspongia)* sp.4, in North Wollongong, was the only species that revealed notable seasonal variability on its coverage area, with positive growth rates often being observed during warmer months and higher mortality rate and shrinkage of their surface area during winter (Figure 3.9). Thus, a correlation was applied to test whether *Callyspongia (Callyspongia)* sp. and other species on two rocky reefs (North Wollongong and Bass Point) show similar changes in the coverage area during 18 months of monitoring. A significantly positive correlation was observed only in North Wollongong (NW: $r = 0.6, P = 0.03$). In June 2016, an intense storm with damaging winds, heavy rainfall and huge waves, of up to eight metres, hit the coast of New South Wales. During the storm, an increase in the movement or resuspension of sediment was observed on the majority of the six reefs monitored.

Figure 3.9: Percentage cover of *Callyspongia (Callyspongia)* and all other species combined during 18 months of monitoring: (A) North Wollongong (NW) reef and (B) Bass Point (BP) reef. A correlation confirmed that these taxa showed similar changes in cover over the 18 months of monitoring for each site (NW: $r = 0.6, P = 0.03$ and BP $r = 0.7, P = 0.14$). The arrow indicates the severe storm that occurred in June that pounded the NSW coast. Summer (Su), Autumn (A), Winter (W), Spring (Spr).
3.4 DISCUSSION

3.4.1 Unpredictable environment

The rocky intertidal zone is known to be a harsh environment with often extreme environmental conditions (Helmuth, 1998; Tomanek & Helmuth, 2002). Marine invertebrates and algae living in this habitat must deal with the highly variable conditions. Hence, intertidal organisms are subject to a variety of physical stressors, such as repeated disturbance from sand deposition and hydrodynamic forces (Benkendorff & Davis, 2004). Furthermore, they are also exposed to thermal stress during low tide periods (Tomanek & Helmuth, 2002). Although, we still do not totally understand the reasons that zonation patterns are variable in space and time (Harley & Helmuth, 2003). Earlier researchers have revealed that the upper limits of the species range in the rocky intertidal zone is commonly related to the species tolerance of desiccation and emersion temperature and by biotic interactions at the lower limits (Molina-Montenegro et al., 2005; Petes et al., 2007; Stickle et al., 2017).

3.4.2 Factors driving assemblages’ structure

It has long been recognized that although there are other factors responsible for determining the distribution of intertidal assemblages of the NSW coast, the nature of the animal communities on NSW rocky reefs depend on their tidal height as well as the degree of wave exposure (Dakin et al., 1948). The data in this chapter gives a preliminary insight into the factors that are shaping the sponge assemblages. The outcomes address an important knowledge gap and expand our understanding of the importance of the structuring agents on rocky intertidal shores. The data described in this study revealed that intertidal reefs might differ in their suitability for sponge species composition according to their habitat complexity, the height of the rock pools on the shore, the volume of these pools, wave exposure and the season of the year. Each habitat feature was assessed separately, but there is some likelihood that these features interact to influence species diversity and abundance.

Spatial heterogeneity and habitat complexity (e.g. rock pools; boulders) are crucial factors that affect the structure of rocky shore assemblages (Kostylev et al., 2005). Habitat type has a strong effect on the distribution and composition of sponge assemblages. Increases in the surface area available for settlement of marine organisms (Bartol et al., 1998) is known to provide refuge against harsh physical and biotic conditions (Jackson et al., 2013). In turn, habitat type influences important factors such as light, smothering, or abrasion by sediment and water movement (Carballo & Nava, 2007). Moreover, studies have revealed that heterogeneity of the environment provides intra-habitat diversity and enables species to co-exist in a given area (White et al., 2015). However, the effects of area and surface complexity on species
diversity and abundance have rarely been addressed (Beck, 2000). Hence, more investigation is necessary to clarify the relationship between habitat complexity and sponge diversity and abundance, especially in intertidal habitats (Kostylev et al., 2005).

As in previous studies with other intertidal fauna (Bartol et al., 1998; Beck, 2000), species richness and abundance of intertidal sponge assemblages was positively correlated with habitat heterogeneity. The intertidal sponge species richness and abundance across Illawarra reefs also appears to be influenced by habitat structure, including the degree of complexity of the habitat, the rock pool volume, and degrees of exposure to wave action (sheltered or exposed). As the study by Benkendorff & Davis, 2002 demonstrated, by identifying hot spots of molluscan species richness in the intertidal reefs of Illawarra, they also suggested that habitat heterogeneity should be used as a potentially useful abiotic surrogate for the identification of biologically important intertidal sponge habitat. Conversely, other components, such as the size of each reef, along with number of rock pools and the total area covered by the pools, did not show a statistically significant influence on sponge species richness and abundance.

Some environment variables, such as wave exposure, have such an impressive local effect on zonation patterns, that it is often difficult to determine the impacts of other variables (Harley & Helmuth, 2003). However, hydrodynamic forces generated by breaking waves is thought to be among the most important causes of mortality in this habitat (Helmuth & Denny, 2003). Breaking waves have been hypothesized to act as one of the main physical mechanisms that inhibit growth, and act to break or remove organisms once they exceed a critical size (Blanchette, 1997). Not surprisingly, Benkendorff & Davis (2004) observed similar outcomes, although their focus was on molluscan species along the NSW coast. My data also reveal that higher abundance and the majority of sponge species were recorded at north-facing (sheltered) reefs, particularly those with high habitat complexity. The lower number of species and individuals found on exposed reefs may be related to two hypotheses. First, due to the reef be regularly subjected to natural impacts from extreme swell conditions. Second, as a result of the difficulty in conducting surveys in extreme environmental conditions. I contend that my surveys were undertaken when swell conditions were relatively benign and argue that the destructive effects of wave exposure are responsible for the patterns I have observed.

The height of intertidal shores is correlated with a diversity of biological and physical factors that are applicable to littoral species (Harley & Helmuth, 2003). The higher positions on the shore expose the intertidal organisms to a prolonged time of emersion, thus resulting in a diversity of potential stressors, including desiccation, lower oxygen availability, osmotic stress, as well as high temperature (Harley & Helmuth, 2003). Furthermore, potential thermal
stress has long been associated with patterns within and among species’ biological zonation on the shoreline (Harley, 2008). Previous studies have noted that high shore environments are physically more stressful than those on low-shore, due to extended periods of emersion (McQuaid et al., 2000), suggesting that some biological and physical factors associated with tidal height strongly influences growth and mortality processes of intertidal organisms (Underwood & Jernakoff, 1984; Bartol et al., 1998; Helmuth et al., 2006b; Petes et al., 2007). My study emphasizes early studies findings when compare the survivorship of sponges in rock pools at different tidal heights. My outcome reinforces that long periods of exposure to air may play an important role in structuring the community mostly because at the conclusion of the experiment the survival of sponge assemblages recorded inside of low shore pools were greater than individuals in high shore pools. How such variability, in both ocean and terrestrial condition, influences large-scale patterns of intertidal communities remains poorly understood (Lathlean et al., 2015).

Volume of rock pools (m$^3$) showed an important influence on sponge species richness and abundance across the six reefs I sampled. Although the result should be interpreted with caution, as revealed in previous studies for intertidal fish species (Godinho & Lotufo, 2010; White et al., 2015). My study also suggests that a higher sponge abundance and diversity was more likely to be found in pools with greater volumes. Earlier studies have shown that organisms found at higher intertidal levels are exposed to more stressful physical conditions than those found lower on the shore (Bartol et al, 1998; Davenport & Davenport, 2005; White et al., 2015). Small intertidal pools (<0.05m$^3$) containing sponges, high in the intertidal zone of the North Wollongong reef were shown to reach temperatures of up to 32 °C, dissolved oxygen levels as low as 0.1 mg$l$ and salinity of 39 o/o. However, the interesting point shown by these data is that despite the presence of a single species, Callyspongia (Callyspongia) sp. these small pools surprisingly revealed a high sponge abundance.

The sponge specimens found in small high shore pools in North Wollongong did not appear to demonstrate stress caused by the fluctuation changes in the temperature, salinity and oxygen levels during most months. The degree to which a species is able to occupy and survive in the upper inter-tidal zone may be also related to its capacity to withstand the extreme changes in the chemical characteristics of the pool’s sea water, as most of the species were found in rock pools at low-mid shore - likely minimizing mortality risk. However, to analyze how the volume of the rock pools will affect the species richness and abundance, it is important to
consider that the volume is linked to the variability of the physicochemical factors observed within rock pools and its vertical location on the rocky shore. The vertical location of a rock pool is, in turn, associated with the amount of time for which they are isolated from the sea during the low tide period (White et al., 2015). Thus, the volume of pools and their position on shore may influence sponge richness and abundance as most of the intertidal sponge species were recorded at low-mid shore pools and smaller pools at high shore are preferred by *Callyspongia (Callyspongia)* sp.4. Moreover, large pools at Bass Point shown to house not only a high abundance but also a great diversity of sponges when compared with the total species richness observed among the six reefs in this region.

The seasonal fluctuations in the spatial patterns of common temperate intertidal sponges has been investigated by a few authors (Tanaka, 2002; Barnes & Bell, 2002; Bell, 2008a). The study conducted by Bell, 2008a, suggested that sponge growth patterns were correlated with season. He observed the expansion of occupied space during spring and summer, with subsequent reductions during autumn and winter. Conversely, Underwood & Jernakoff, 1984 found that the early colonists of an intertidal macroalgae on a NSW shore, demonstrated that the number of species of macroalgae was not different from season to season. This lack of seasonality was also apparent in this study, where sponges showed a slight increase in the number of species present in only two of the five reefs, during the 18 months of monitoring (see Chapter 2). Further, on all shores *Callyspongia (Callyspongia)* sp. 4 was the only species that revealed a marked seasonal pattern on its coverage, with growth rates often being observed during warmer months and regression in winter. However, it remains unknown whether less favorable environmental conditions are an important determinant of reductions in sponge cover (Bell, 2008a).

*Callyspongia (Callyspongia)* sp., unlike the other species, were also found in small pools at high shore and was observed on rock substrata around or between rock pools with six-hour emersion in a 12 hour period on Bass Point reef. However, *Callyspongia (Callyspongia)* sp. seems to have the capacity to cope with a wide variety of unusual physical conditions, such as prolonged periods of emersion, and its capability of living in higher pools in the intertidal zone, which may be a strategy to escape negative biological interactions such as predation. Furthermore, atterns of abundance and cover of *Callyspongia* sp. changed more frequently than the other species during the 18 months of my monitoring. The seasonal variability may be altered by physical disturbances over relatively short time frames.

To minimize mortality risk and maximize growth, plants and animals regularly face trade-offs between their demands (Halpin, 2000). Not surprisingly, most of the intertidal
sponge species, from the Illawarra region, are restricted to the low-mid shore, with the exception of *Callyspongia* (*Callyspongia*) sp.4 and sp.6 species. The observed sponge distribution pattern is probably a response to avoid being exposed to a physically harsh environment, thus minimizing mortality risk. However, the understanding of the role of additional parameters, such as thermal history and desiccation, remain unaccounted for. Therefore, the foundations of my study point to relevant questions for further studies. A complex interaction between these physical factors, along with biological factors such as predation, may be setting the upper and lower limits of the vertical range of sponges in most of the reefs - and may have a significant influence in sponge assemblage survivorship in the Illawarra region. This may explain the higher chance of survivorship of sponges found inside of rock pools at lower tidal heights. Furthermore, future studies will need to conduct an experiment - preferably in the field and measure the quality of water in pools over an extended period. This should be done monthly over a minimum of two years using perhaps sensors and data loggers. The information would help to better understand the variation over yearly time scales allowing a detailed investigation of the effects of physicochemical factors on the distribution of intertidal sponge assemblages.

### 3.5 CONCLUSION

The data provided in this chapter not only enhances our knowledge of how environmental factors are driving the patterns of intertidal sponge species distribution and abundance, but also helps to understand which mechanisms could be responsible for the occurrence of distinct assemblages among reefs. This study considers that the intertidal reefs from the Illawarra region may differ in their sponge species assemblage according to five physical parameters that may interact to regulate species abundance and diversity (Habitat complexity, the vertical position of rock pools on the shore, the volume of the pools, wave exposure and the season of the year). These parameters play a key role, favoring or acting to restrict the structure of the sponge community.

The degree of complexity of the habitat showed a positive influence on the abundance and diversity of the sponge communities found in the intertidal reefs of Illawarra. This finding lends support to the patterns of distribution of molluscan species reported by Benkendorff & Davis (2002) for the same habitat and suggests that heterogeneity can be used as a potentially useful abiotic surrogate for the identification of biologically important intertidal sponge habitat. However, it is noteworthy that the effect of the degree of exposure to wave action and the rock pool volume on the intertidal sponge community are important contributing factors. My data
also revealed similar outcomes to the study of Benkendorff & Davis (2002) regarding the impact of wave exposure. The highest abundance and the majority of the sponge species were recorded at north-facing (sheltered) reefs, particularly those with high habitat complexity. Although the outcome of the relationship between the volume of rock pools and sponge richness and abundance needs further attention given that it is correlative, this study demonstrate that sponge diversity and abundance was more likely to be found in pools of large volume.

Previous studies have noted that high shore environments are physically more stressful than those on low-shore, due to extended periods of emersion (McQuaid et al., 2000). My other key finding is the contrast in sponge survivorship in rock pools at different tidal heights. At the end of the 18 months, monitoring there was a 50% increase in mortality in high shore over low shore pools. Conversely, *Callyspongia (Callyspongia)* sp. unlike the other species, was the only species observed in small high shore pools at North Wollongong reef. Therefore, sponge species recorded in this region might have particular microhabitat requirements for recruit settlement, as most of them were found in rock pools limited to either the low or mid shore whereas *Callyspongia (Callyspongia)* sp.4 preferred smaller pools in the high shore.

Lastly, on all reefs monitored, *Callyspongia* sp. 4, recorded at North Wollongong reef, was the only species that revealed a marked seasonal pattern. Their abundance and cover changed more frequently over relative short time frames than the other species. During warmer months, I observed rapid growth while higher mortality was observed during winter. In conclusion, multi-stressor studies conducted in intertidal habitats have focused on the effects of biotic and abiotic factors on organisms other than sponges (Bartol et al., 1998; Van Katwijk & Hermus 2000; Davenport & Davenport, 2005; Lathlean et al., 2013). Furthermore, climate change and ocean acidification have a potential impact on intertidal species populations (Helmuth et al 2006a; Findlay et al., 2010; Lathlean et al 2013; Paganini et al., 2014), through association with multiple physical factors (Kelmo et al., 2014) and influence on species interactions (Lathlean et al., 2017; King & Sebens, 2018). Nevertheless, this is the first study to address the potential physical factors that influence the distribution and abundance of the intertidal sponge fauna of the Illawarra region, NSW, Australia. The understanding of the relative importance of both interactions among species (see Chapter 5) and the influence of the major assemblages disturbances, especially for those key and poorly understood species, provide a crucial information of the environmental factors that are shaping the community of this ecosystem.
CHAPTER 4

Impacts of sediment smothering on large and small explants of the intertidal reef sponge *Callyspongia (Callyspongia)* sp.
4.1 INTRODUCTION

Sponges (Porifera) are highly diverse and are an important component of sessile benthic ecosystems, across temperate, tropical and polar habitats (Dayton et al., 1994; Maldonado et al., 2008; Fromont et al., 2012; Bell et al., 2015). They are also the major space occupiers in different regions such as deep-water environments and coral reefs (Pineda et al., 2015). This diverse phylum makes important contributions to marine ecosystem functioning (Bell, 2008b) through their functional roles, for instance, affecting the substrate as bioerosion agents or consolidating the reef framework (Rützler, 1975; Wulff & Buss, 1979; Diaz & Rützler, 2001). Furthermore, as sessile filter-feeding organisms, they have the potential to alter the water column through their high water-filtering capabilities, removing nutrients (i.e. nitrogen, oxygen and silicon) and food particles (carbon cycling) from the water (Bell, 2008b). The high-water filtering rates of sponges act as a major link between pelagic and benthic environments. However, with the increase of sediment resuspension and loading in the water column (Lohrer et al., 2006) the direct ingestion of resuspended particles could clog or block their water system (Bell et al., 2015).

Marine systems often receive sediment load as natural sediment deposition (Carballo, 2006) or derived from anthropogenic activity (Roberts et al., 2006; Pineda et al., 2017a, b). Sedimentation events, from the intertidal zone to the subtidal, are continually affected by the action of tidal resuspension, wind-wave and currents - where the wind and weather play a role in controlling temporal fluctuations in the rates of sediment movement in coastal ecosystems (Miller et al., 2002; Carballo, 2006). Furthermore, storm events can also increase the suspended sediment levels in surface waters of an estuary (Ellis et al., 2002). Consequently, marine organisms experience natural sedimentation processes such as settling and suspended sediment (Miller et al., 2002). However, the impacts of natural sedimentation on the benthic community has been poorly investigated (Carballo, 2006).

Human activities are also recognized as agents that influence changes in patterns of sedimentation (Miller et al., 2002). The movement of sediment to coastal waters from land-based sources has increased worldwide, becoming a potentially crucial factor in the function of coastal marine ecosystems - altering the natural patterns of erosion and sediment deposition (Miller et al., 2002; Carballo, 2006; Bell et al., 2015). There are different reasons for these increases, but most are terrestrially derived sediment inputs related to changes in land use, especially deforestation, coastal development and agricultural intensification (Bell et al., 2015).
Additionally, the increase in the amount of suspended sediment in the water column is a common consequence of many anthropogenic disturbances in the ocean, such as maintenance dredging, drilling, seabed mining and trawling (Carballo, 2006). Modification of the volume of sediment has a strong capacity to influence marine productivity and biodiversity, especially for the benthic community (Bell et al., 2015). For instance, soil erosion resulted from human activities can increase the sediment load in coastal catchments (coastal and estuaries waters) (Raffaelli & Hawkins, 1999). Gradually the sediments sink, clearing the surface water, but turbidity may remain on the nearbed because of the resuspension processes by tides and waves (Lohrer et al., 2006). Therefore, sedimentation can interfere with the availability of surfaces for settlement, photosynthetic activity and growth of benthic organisms, whereas elevated suspended particles could affect primary production decreasing the filter feeding efficiency of benthic invertebrates, clogging their filtration systems (Schiel et al., 2006; Lohrer et al., 2006; Maldonado et al., 2008). A further facet of sedimentation includes the continuous sand inundation of either shallow subtidal or rocky intertidal reefs. Research has shown that it can regulate community composition by keeping the balance between sand intolerant and sand tolerant competitors for space (McQuaid & Dower, 1990). Moreover, Maldonado et al., 2008 revealed that sediment deposition affects the survival of small, individual sponges found in sublittoral rocky communities. The field experiment they conducted confirmed that sediment deposition is the major mortality factor among sponge recruits, causing smothering of the small individuals.

Rocky shore assemblages may potentially be affected by suspended sediment in the water column (Crowe et al., 2000). In rocky shore habitat, for instance, sand inundation is recognized as a major natural catastrophe, causing periodic alteration in the intertidal ecosystems across the world (McQuaid & Dower, 1990). Sand smothering and sand scour play an important role in eliminating intolerant organisms, thus decreasing species richness, which results in the impoverishment of the biota (McQuaid & Dower, 1990). Any increase of sedimentation rates in an environment could result in two kinds of threats. The first consequence of inundation, resulted from deposition of sediment, is the complete burial and smothering of the benthic organisms (Ilan & Abelson, 1995; Pineda et al., 2015; Pineda et al., 2017b). The second effect is a consequence of the erosive force of moving particles. The combination of the increase of the suspended sediment concentration with water movement can result in the dislodgement of an organism from the substratum and scouring of the organism’s external tissue (Ilan & Abelson, 1995; Bell, 2015; Pineda et al., 2017a). Furthermore, sediment may influence assemblages indirectly; the distribution of intertidal
organisms can be affected by sand movements if they are involved in biological interactions that have critical influences on the structure and function of communities such as predator/prey interactions (Littler et al., 1983; Bell et al., 2015).

The sensitivity to siltation and sediment movement differs considerably among species (Miller et al., 2002), the increase of sedimentation, through both suspension and deposition, can negatively influence sponges through different mechanisms (Bell et al., 2015). The sediment effects on sponges include: i) Clogging of the aquiferous (filtration) system. Studies recognize the ingestion of suspended sediments as the most important direct impact affecting physiological processes (Bell et al., 2015); ii) Abrasion by sediment particles, combined with high water movement can scour external tissue or the entire sponge; iii) Impacts on photosynthetic symbionts within sponge tissue. The increase of turbidity by suspended sediment can alter irradiance levels thus reducing light availability; iv) Reduced settlement success. A veneer of sediment over a surface can also limit access of larvae to suitable substrate on which to settle (Bell et al., 2015). Thus, a high level of sediment deposition can significantly influence the abundance, diversity and structure of sponge communities (Pineda et al., 2015). For instance, Pineda et al., 2015 tested the effects of elevated sedimentation on coral reef sponges. Their laboratory experiment revealed that the morphology of sponges influenced significantly the percentage of necrosis and sponge surface covered by sediments. Sponges with cup morphologies showed the highest percentage of necrosis whereas wide cup, encrusting and massive species accumulated more sediment than erect morphologies. The specific impact of this physical process on some key organisms has rarely been understood and investigated (Maldonado et al., 2008). Furthermore, the response of sponges to changes in sediment rates has been poorly studied (see Roberts et al., 2006).

Sponges have shown specific abilities, not only to survive in this stressful condition, but also to turn exposure to sediment into an advantage (Cerrano et al., 2007; Hanna & Schönberg, 2016). Some sponge species are usually observed in an environment with high levels of settled and suspended sediment. Soft bottom specialist sponges, *Biomia ehrenberghi* and *Oceanapia oleracea*, are known to be very resilient to sedimentation (Werding & Sánchez 1991; Ilan & Abelson 1995; Maldonado et al., 2008; Bell et al., 2015). Thus, researchers believe that these organisms may have developed adaptive capabilities and even strategies to turn this supposed stressful condition into a favorable habitat (Bell et al., 2015). Furthermore, this abiotic stress may also influence a long-term genetic change in the structure of this sponge population - giving them the ability to adjust to high levels of sediment (Maldonado et al., 2008).
The deposition of sediments, however, has been considered a determinant ecological factor of the benthic environment (Bell & Smith., 2004). The admission of the importance of sponge conservation has increased (Bell et al., 2015), especially because these organisms represent one of the significant habitat-forming taxa on the seafloor and play a vital role in the ecology of benthic marine ecosystems (Rützler et al., 2007). Moreover, as sedimentation has a negative impact in some intertidal and subtidal organisms (Littler et al., 1983; Carballo, 2006; Pineda et al., 2017a), global interest to gain an understanding of the influences of sand scour and settled sediment on marine organisms has increased. There is a lack of research into the impacts of sediment on the physiological activity of sponges, especially how different sediment grain composition, concentration and size affect sponges (Bell et al., 2015). Furthermore, sponges’ adaptive responses have been poorly understood and rarely investigated (Miller et al., 2002; Bell et al., 2015). Thus, further research would help to understand the indirect and direct physiological effects of sedimentation on sponges, their tolerance limits, their adaptive capabilities to unpredictable high sediment levels and lastly the specific impact of sediment on early life stages (Bell et al., 2015).

In winter of 2016, the east coast of New South Wales was affected by a massive storm which increased sedimentation loads on many Illawarra reefs. After the storm, most of the *Callyspongia* (*Callyspongia*) sp. specimens I was sampling showed high mortality or shrinkage of their surface area. *Callyspongia* sp. specimens were found mostly in small rock pools, in only three of the six sites monitored (North Wollongong, Sandon Point and Bass Point reef). Some five months after the drastic decrease in abundance, the species seemed to recover, and sponge recruits were found in different spots in the same rock pools affected by the high sediment load. This resulted in a slight increase in its abundance a few months after the storm. Consequently, to better understand how the increase in the natural levels of sedimentation affected the intertidal sponge assemblages, an aquarium-based experiment with the most affected sponge species, *Callyspongia* sp., was performed. I hypothesized the high mortality I observed, particularly at North Wollongong (Chapter 3), was driven by the increased sediment load associated with this storm. Therefore, the principal aim of this study was to examine whether the observed general models of increased siltation may be an explanation for the increase in the mortality of sponges at intertidal reefs in south eastern Australia, while also influencing their within-habitat abundance. I sought to examine this hypothesis experimentally, testing whether the effects of different rates of sedimentation affected the survival of intertidal sponge adults and recruit-sized explants.
4.2 MATERIALS AND METHODS

4.2.1 Study sites and study species

Impacts of sedimentation were examined for four species of *Callyspongia* (*Callyspongia*) in the Illawarra region. I tested the hypothesis that sponge assemblages were affected by smothering. Due to the reduction of sponge area and high mortality observed in some reefs after the severe storm in the winter of 2016. Individuals of *Callyspongia* (*Callyspongia*) sp. 6 were collected for this experiment at Sandon Point (34.3306° S, 150.9274° E). This taxon presents a massive, irregular morphology and is found on rock substrata inside rock pools. Two different body fragments (explants) were removed from each of the 15 different non-clonal adult sponges with a dive knife. A total of 30 explants, representing recruits (~2cm²) and adult (~6cm²) were created from each of 15 adult sponges and used in the experiment. Fragments of e specimen were separated in small plastic bags, which were filled with sea water, sealed, and stored on ice in coolers during transportation (Davis et al., 2014) to the Ecological Research Centre (ERC) at the University of Wollongong, NSW (Figure 4.1). The sponges were acclimated in 50 liter tanks for two days with seawater at ambient seawater temperature (20°C) and 35 ppt salinity, environmental conditions that were comparable to the collection site.

![Figure 4.1: Marine Aquaria Recirculating system at the Ecological Research Centre (ERC). Each unit includes 8 x 50-litre glass tanks on a multi-level rack unit. Each individual aquariums has a small air bubbler to oxygenate the tank](image-url)
4.2.2 Experimental design

The amount of silt to be applied was estimated from field rates of deposition in rock pools from six different rocky reefs sites (Coalcliff, Austinmer, Bellambi, Sandon Point, North Wollongong, and Bass Point). These sites were chosen due to the different composition of the sponge community, the degree of exposure of the reef (sheltered or exposed to wave action) and habitat complexity. To measure the sediment level for each reef site, duplicate benthic sediment samples were collected using a syringe (60 ml) from each rock pool, chosen randomly at each of four different distances from nearby sandy beaches: 5; 12; 25; 35 meters. The sediment level was measured by filtering each sediment sample through previously weighed (90mm) polycarbonate filters (Advantec MFS, Inc.). The dry sediment weights were recorded the next morning after being dried overnight at 45°C.

Sponges were cut into two different body fragments (explants) represented by recruits (~2 cm²) and adult (~6 cm²) sizes. The sponge explants were attached with super glue to a ceramic tile (9 cm x 9 cm) and randomly placed in each aquarium (15 aquarium in total). To prevent antagonistic interaction, all sponges were separated by > 15 cm. Sponges were exposed to three different sediment treatments. Each treatment comprised five replicate aquaria containing one of each size of explant (i.e. one adult and one recruit from the same sponge individual in each aquarium). The exposure of sponges to sediments lasted for 20 days.

The aquarium experiment was carried out in fifteen 50 l tanks at the ERC, where three different sediment levels were applied to five tanks each. The sediment used was collected from Sandon Point reef, where the sponge individuals were also collected. Sponges were exposed to three sediment treatments; control tanks that did not receive any sediment 0 g l⁻¹ (control) and two treatments where the sponge explants were exposed to a medium (100 mg cm⁻²) and high (200 mg cm⁻²) level of sediment as determined from field measurements of sediment load. The levels of sediment of each treatment was applied as a pulse disturbance every two days. For the high and medium treatment, the sediment was blended with seawater, forming a slurry and with a syringe it was poured carefully onto each sponge explant.

Prior to the addition of the sediment, and every two days after, underwater photographs of each sponge explant were taken with a Canon PowerShot D20 digital camera, to determine the sponge surface area covered by sediment. At the conclusion of the experiment, all sediment was removed along with any attached algae. Additional pictures were then taken of all
individuals, to assess the percentage of the area change (growth or tissue loss), the percentage of necrotic tissue and lastly to confirm sponge mortality. All assessments of area were performed using the image analysis software (Image J).

**4.2.3 Statistical analyses**

Each of the sponges provided two explants of different sizes represented by recruits (~2cm²) and adults (~6cm²). Changes in the percentage of necrotic tissue, surface area (i.e., growth), and percentage of area covered by sediments at the end of the experiment were analysed separately. For each variable, I performed a general linear model (GLM) ANOVA, with explant size and sediment treatment as fixed factors and aquaria as a random factor. The aquaria were a random factor with five levels, whereas size and treatment were both fixed orthogonal factors, with two and three levels respectively. Size with Adult and Recruit and Treatment with three sediment levels: control, medium, and high. The ANOVA analyses were followed by post-hoc pairwise comparisons Tukey's Honestly Significant Difference (HSD) to compare all fixed factor levels with one another. Additionally, a two-way ANCOVA was used to determine whether treatments had a significant effect on the percentage of necrotic tissue, as a function of the percentage of area covered by sediments (the covariate). Ultimately, to test whether the sponge size influenced their response to sediment, a correlation was applied to test the relationship between the percentage of tissue affected by necrosis with the percentage of area covered by sediments for the two levels of the factor size (Adult and Recruit). Statistical analysis was performed using the software IBM SPSS statistics 25.

**4.3 RESULTS**

The sediment load in the field was measured to estimate the sediment level dosed for each treatment. The average sedimentation at most of the sites was (100 mg/cm²). The highest sediment level was registered in Sandon Point reef (200 mg/cm²), and Bass Point reef revealed the lowest level of sediment (50 mg/cm²). Sediment deposition events were created every two days during 20 days of experiment, with the smothering treatment keeping a permanent layer of sediment over sponges. All specimens of *Callyspongia (Callyspongia)* sp. 6 survived in the control treatment until the end of the experiment, suggesting that this species may be suitable for further aquarium-based experimentation and that the glue was not toxic to this sponge in the experiment. A lack of toxic effects of superglue has been observed with sessile invertebrates previously (Davis, pers. comm.). Apart from recruit-sized explants that were exposed to the high sedimentation treatment, all sponges survived until the end of the experiment in both
sediment treatments, however necrosis and bleaching were observed on individuals in both treatments. In contrast, 40% of the recruits in the high sediment treatment died, whereas all recruits in the medium treatment survived, indicating the vulnerability of the recruit-sized individuals to elevated sediment levels (Figure 4.2).

![Figure 4.2: Sponge explants prior the addition of sediment (before), during the experiment (during) and after sediments removal (after): (A) adult exposed to medium level of sedimentation; (B) adult exposed to high level of sediment; (C) recruit exposed to medium level of sediment; (D) recruit exposed to high level of sediment. Scale bars: 1 cm.]

At the end of the experiment, an analysis of growth rate based on surface area measurements showed positive growth in the control treatment, and attrition in all sponge explants that were covered by sediments within the smothering treatments (Figure 4.3). Statistically significant differences in growth were only observed when comparing among treatments (Table 4.1). Although differences in growth between explants of different sizes were
not statistically significant (Table 4.1; ANOVA: P > 0.05), recruit-sized explants showed significantly higher growth than adult explants in the control treatment. Adults in the medium sediment treatment exhibited a slightly more marked reduction of their surface area comparing to the recruits, whereas recruits exposed to the high sediment treatment showed a significantly larger decrease than the adults sized explants (Figure 4.3). Sponges exposed to control treatments grew significantly more than sponges in the medium and high sediment treatments (Figure 4.3; Table 4.1). Recruit-sized individuals in the high sediment treatment showing a more significant reduction in growth than individuals in the medium treatment, whereas adult sponges had a more marked decrease in growth in the medium than high sediment treatments.

![Figure 4.3: Percentage of growth or tissue loss at the completion of the experiment for all sponge explants, grouped by size, at the three sediment treatments (control, medium and high), N = 5.](image-url)
Table 4.1: ANOVA investigating the effects of treatment and tanks on growth among the sponge explants of two sizes after 20 days. Tanks were included as a random factor. * NS P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

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Significant Pairwise Multiple Comparisons (Tukey HSD).
C > M (P = 0.007) > H (P = 0.008).

Table 4.2: ANOVA investigating the effects of tanks and treatment on the percentage of necrosed tissue between the two sizes of explants after 20 days. * NS P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

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<td>Error</td>
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</table>

Significant Pairwise Multiple Comparisons (Tukey HSD).
H (P = 0.0001) > M (P = 0.005), C (P = 0.094).

Table 4.3: ANOVA investigating the differences in the surface area covered by sediment treatment for the two sizes of sponge explants after 20 days. NS P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

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Significant Pairwise Multiple Comparisons (Tukey HSD).
The majority of individuals in the medium and high treatments developed tissue areas affected by necrosis (Figure 4.4). I detected a significant size x treatment interaction, with a tripling in necrosis for recruit-sized explants under the high sediment treatment. (Table 4.2). Individuals in the high sediment treatment developed the highest percentage of necrosis. All sponge explants in the high sediment treatment showed signs of necrosed tissue, with 40% mortality of recruits compared with the medium treatment where 40% of adults and 65% of recruits showed areas of necrosed tissue. I did not detect mortality among individuals in the medium sediment treatment. In contrast, tissue necrosis was not observed in any individual in the control treatment. Although the sponge individual responses were size-specific and notable differences were observed between controls and sediment treatments, mortality of sponge explants was only observed in recruit-sized explants in the high sediment treatment.

Figure 4.4: Percentage of tissue affected by necrosis at the completion of the experiment for all sponge explants placed by size, with the two smothering treatments (medium and high). Note: as controls showed no sign of necrosis, they were not plotted. (N = 5).
The percentage of sediment covering the surface of sponges at the end of the experiment (after 20 days) differed significantly between both explant size and sediment treatments and again I detected a significant interaction between these two factors (Figure 4.5; Table 4.3). Unlike previous studies, I saw no evidence that *Callyspongia* sp. was able to reduce sediment on its surface over time (Figure 4.6). Adult explants revealed lower amounts of deposited sediment than recruits. Furthermore, total sediment on recruit-sized explants was significantly lower in the medium treatments than the high (Figure 4.5). However, the percentage of sponge surface covered by sediment increased significantly on the recruits over time, whereas the adults had a slight increase -reaching just 3% more sediment deposit in the high treatment after 20 days. Additionally, the different sediment treatments had no statistically significant effect on the percentage of necrosis once controlled for the percentage of area covered by sediments (ANCOVA: $P > 0.05$). No correlation was observed between the percentage of tissue affected by necrosis and the percentage of area covered by sediments in a bivariate plot of each level of the factor size; Recruits ($r = 0.3$, $P = 0.2$) and Adults ($r = 0.1$, $P = 0.6$) (Figure 4.7). However, the correlation became statistically significant when the data was pooled ($r = 0.5$, $P = 0.03$).

![Figure 4.5: Mean percentage of sponge surface covered by sediments (± SE) at the completion of the experiment (20 days) for all sponge explants grouped by size, with the two sediment treatments (medium and high). Note: As controls lacked sediment, they were not plotted. (N = 5).](image)
Figure 4.6: The percentage of sponge surface covered by sediments (± SE) at day 2, 10 and 20 following sediment addition, for both explant sizes in the high sediment treatment. (N = 5).

Figure 4.7: The relationship between the percentage of tissue affected by necrosis and the percentage sponge surface area covered by sediment. Recruits (r = 0.3, P = 0.2) and Adults (r = 0.1, P = 0.6).
4.4 Discussion

The effects of sedimentation are an increasingly important and widespread physiological factor that influence hard bottom organisms on most rocky coasts (Carballo, 2006). Furthermore, sedimentation has been considered a key driver of sponge diversity and abundance patterns (Bell et al., 2015) and identified along with water flow, as one of the major factors regulating local sponge populations in the temperate region (Bell & Smith, 2004). Investigations in a number of sub-tidal communities have generally shown sediments to be detrimental to the benthic biota (Littler et al., 1983), including macroalgal (Airoldi & Cinelli, 1997); sponges (Roberts et al., 2006; Carballo, 2006) and coral assemblages (Bannister et al., 2011; Pollock et al., 2014). Likewise, rocky shore communities across the world are subject to fluctuations in the level of sand that could directly affect inter-tidal organisms by eliminating individuals that are intolerant to smothering by sand or sand scour (Littler et al., 1983; McQuaid & Dower, 1990). However, more studies are needed to provide information about the effects of increasing sediment level on rocky inter-tidal communities (Thompson et al., 2002).

For any habitat, a species shows tolerances and adaptations to changes in its environment. Thus, the dimension of the organism's distribution will be restricted when its capacity for adaptation and tolerance to change is limited (Miller et al., 2002). Although some benthic assemblages show adaptation to continuous sediment burial and erosion (Miller et al., 2002), siltation and suspended sediment in the water column will continue to increase due to the artificial replenishment of coastlines as a consequence of both natural (i.e., storms), and anthropogenic impacts such as urbanization and changes in land use (Thompson et al., 2002). The increase of coastal sediment deposition may show considerable changes at regional and local scales, which may favor the dispersion of more sediment-tolerant organisms, such as anemones and turfing algae (Thompson et al., 2002). Thereby, it is essential to understand the magnitude of the perturbations and how far off those natural boundaries organisms begin to exceed their capacity of adaptation and show negative responses (Miller et al., 2002).

It appears likely that sediment and sedimentation also affect benthic organisms other than filter feeders such as sponges. Small-scale variability in sediment deposition may influence algal assemblages through direct effects, smothering and scouring, and indirect effects as a consequence of modified competitive interactions (Airoldi & Cinelli, 1997). The distribution of algae is also influenced through the elimination of less tolerant species (Littler et al., 1983). A similar story is emerging for corals as Pollock et al., 2014 demonstrated that turbidity and sedimentation result in elevated levels of coral disease. Among sponges, earlier
studies recognized sedimentation as a key factor affecting the composition and structure of sponge assemblages (Carballo, 2006). Carballo (2006) suggests different sediment impacts on the communities, such as a decrease in diversity, substitution or loss of sediment intolerant species and reductions in morphological diversity; all resulting in a more unstable community. Pineda et al. (2017b) revealed that sediment smothering can restrict the distribution of more vulnerable morphologies such as massive, encrusting, plate and cups. The physiological response of a sponge species found in reef environments across the Great Barrier Reef (GBR), also supports the notion that sediment is a key factor affecting the abundance and distribution of these organisms, revealing an increase (up to 40%) on its respiration demand (Bannister et al., 2011). Changes in the reproductive status and growth of the sponge *Cymbastela concentrica* were also documented by Roberts et al., 2006 as a consequence of the increase in siltation.

Environmental data from June 2016, showed variation of local patterns of sediment deposition after a strong storm hit the coast of New South Wales. During the months prior, little variation in sponge diversity and abundance was observed. After the storm, the increase in the movement of or re-suspension of sediment were observed on the majority of the six intertidal reefs that were being monitored. A few weeks after the storm (July 2016), all species found at North Wollongong reef - including 90% of the *Callyspongia (Callyspongia)* sp. individuals, stood out - owing to the presence of light brown, superficial patches which spread across the sponge’s pigmented purple surface (Figure 4.8). The brown patches appeared to be a consequence of sediment burial causing partial tissue necrosis followed by algal recruitment to the sponge tissue, compromising the sponge individuals. The population structure of this species was the most affected, showing high mortality and a decrease in their surface area. Surveys documented that this phenomenon lasted less than one month from the first record, until the complete mortality of most sponge individuals (authors’ observations – Chapter 3). A similar pattern was observed in previous studies which indicated that high sediment deposition affected the diversity of tropical rocky sponge assemblages, in this case, facilitating the monopolization of space by the most tolerant species and excluding less tolerant taxa (Carballo, 2006). The difference in my study was that only one species showed a high mortality rate.
In high sediment environments, different sponge species have demonstrated specific strategies and adaptations, as a mechanism to reject sediment and to tolerate this unpredictable stress (Roberts et al., 2006; Pineda et al., 2017b). Sponges use several passive strategies to cope with increased sedimentation, including mechanisms to prevent the sediment settling on the sponge surface, morphological adaptation and plasticity (Carballo, 2006; Roberts et al., 2006). Some sponges are effective in removing the sediment from their surfaces by utilizing strategies including: reversal of feeding current flow, mucous production (Pineda et al., 2015) and forming associations with other in-faunal organisms. These associations avoid sediment accumulation, thereby enhancing the sponge filtration capacity and increasing sponge survival (Hendler, 1984; Burns & Bingham., 2002; Bell et al., 2015; Pineda et al., 2015). Another strategy used by sponges is the closing of their pores in order to help prevent the clogging of the aquiferous canals by sediment particles (Roberts et al., 2006). Sponges can also reduce the number of oscula and change the arrangements of their spicules. The spicule adaptation to sedimentation includes projecting the spicules through the surface, thereby preventing sediment particles from adhering to the sponge. Additionally, some sponge larvae demonstrate...
capacity for habitat selection by moving away from sediment prior to settlement (Bell et al., 2015). However, the metabolic demand on sponges in order to survive with this stressful environment is considerable. Differences in growth rates and decrease of the reproductive potential are some examples of this metabolic cost (Bell et al., 2015).

Pineda et al., (2015, 2017b) revealed that sponges found on the Great Barrier Reef often show a reduction in the percentage of sediment covering during their experiments and that the capacity for self-cleaning varied noticeably between species. However, the decrease of these sponge surfaces covered by sediment was a result of different mechanisms - such as the production of mucus, pumping activity and removal of sediment by other in-fauna organisms. Conversely, *Callyspongia* sp. did not show a reduction in sediment on its surface over time (Figure 4.6) perhaps because these sponge explants received higher doses of sediment, more often, than sponges in the studies mentioned above. However, most of the *Callyspongia* sp. individuals were able to survive, even showing no direct connection to the water column after complete burial. Although the mechanisms used by intertidal sponges to cope with sedimentation has not been explored in this thesis, the only sediment adaptation demonstrated by *Callyspongia* sp. was pores contraction, closing their entrances - possibly to prevent clogging of the aquiferous system (authors’ observations).

Sediment burial may also have broader effects. High levels of inundation by sediment may directly influence sponge recruitment by scouring or burying early settlers and decreasing the chances of the settling larvae finding available rocky surfaces (Maldonado et al., 2008). Maldonado et al., 2008 revealed that high sediment rates are the major cause of mortality and growth limitation among small sponge individuals in sublittoral rocky communities. Likewise, the results suggested that high sediment deposition levels also might have a greater impact on small intertidal sponge individuals. All sponge explants of the high treatment developed necrosed tissue, with 40% mortality of recruit explants, whereas in the medium treatment, the sponges showed a lower percentage of explants exhibiting tissue necrosis (40% and 65% adults and recruits respectively) but with no apparent mortality of the explants. The outcomes of this study indicate an important difference in the percentage of necrosis when comparing the explants sizes, showing the sensitivity of the recruit individuals to elevated sediment levels.

### 4.5 CONCLUSION

My experiment provided credence to my suggestion that a large storm had driven patterns of sponge mortality – although it would have been interesting to examine more
sediment tolerant taxa. Species whose abundance was not affected by the storm event helped to understand the changes in the distribution and abundance patterns observed *in situ* - especially after a severe storm where the intertidal sponge community was exposed to a higher level of sediment. The main conclusion was that high sediment deposition is an important factor that may influence the distribution patterns of some intertidal sponges by have disproportionate effects on small intertidal sponge individuals (recruits) and may disturb settling larvae to reach a suitable substrate. The experimental data also suggests that the capacity of intertidal sponges to ‘self-clean’ may be varied between species and may depend on the quantity of sediment to which sponges are exposed. My findings enhance our understanding of how patterns of sedimentation affect intertidal sponge assemblage structure and how the sponge community may respond to sediment burial. The outcomes will also contribute to further biodiversity research to evaluate risk to the intertidal sponge assemblages, helping to produce better conservation outcomes for this region.
CHAPTER 5
The effects of spongivory on the survivorship of the intertidal sponge *Callyspongia (Callyspongia)* sp. in New South Wales, Australia.
Chapter 5

5.1 Introduction

Ecological interactions play an important role in contributing to the biodiversity and resilience of ecosystems. The predominant biotic and physical conditions in a specific habitat can affect the nature of the interaction between two species – ensuring that this interaction will likely vary over time and space (Bertness et al., 1999; Stachowicz, 2001; Molina-Montenegro et al., 2005; Alberti et al., 2008 Loh & Pawlik et al., 2009; Gilman et al., 2010). An example is the indirect effects that trophic cascades can cause, when a component of the system is disturbed (Schmitz et al., 1997; Mumby et al., 2006; Loh & Pawlik et al., 2009). In intertidal ecosystems for example, patterns of zonation reflect the enormous importance of biotic and abiotic factors in influencing the lower and upper limits of that an organism occupies (Harley & Helmuth, 2003). The species tolerance to physiological stresses, such as temperature, irradiance and desiccation, frequently set an organisms upper limits (McQuaid & Lindsay 2000; Somero, 2002; Stickle et al., 2017) while the lower limits on the shore are commonly related to species biotic interactions (Lathlean et al., 2017; King & Sebens, 2018). Furthermore, Connell (1972) suggested that species interactions, such as competition, force intertidal species to live in a less physiologically favourable region at high levels on the shore. Field experiments demonstrated that predation or grazing play an important role in limiting the downward spread of intertidal species (Connell, 1972).

The explanation of ecological processes and natural phenomena are the primary objective of ecological investigations - thus resultant patterns of abundance, distribution and interactions of species can be better understood (Underwood et al., 2000). Furthermore, understanding the interactions among species along with quantitative information on their abundance and distribution is important to explain the spatial and temporal population dynamics from a specific region (Underwood et al., 2000). The physical habitat features can, in some cases, be sufficient to determine the patterns of species distribution and abundance at different spatial scales (Underwood et al., 2000). However, the complex behavioural interaction between individuals can also provide relevant information to understand the community responses to environment change (Underwood et al., 2000; King & Sebens, 2018).

The importance of abiotic and biotic factors in controlling sponge communities has been the focus of debate among researchers (Lesser & Slattery, 2013; Pawlik et al., 2013; Powell et al., 2015). Although, numerous studies have investigated the environmental factors influencing a variety of intertidal organisms (e.g. Stickle et al., 2017; Lathlean et al., 2017;
King & Sebens, 2018) only a few studies have focussed primarily on sponge community composition and abundance (Barnes, 1999; Fromont et al., 2006, 2016). No studies have assessed the variety of physical stressors or investigated the ecological interactions that regulate the intertidal sponge assemblages in south eastern Australia. Intertidal sponge assemblages are exposed to more stressful conditions than subtidal communities (Bell, 2008a). Organisms on the rocky shore are usually adapted well and can tolerate change in physical conditions except under unusually stressful circumstances (Crowe et al., 2000). Consequently, intertidal-zone sponges may provide an excellent opportunity to explore the relative roles of abiotic and biotic factors on subsequent patterns of distribution and abundance in response to stressful scenarios.

Sponges are one of the most abundant and top spatial competitors of shallow benthic community assemblages across temperate, tropical and polar environments (Hooper et al. 2002a; Bell & Smith, 2004; Carballo & Nava, 2007). They can influence community dynamics and other benthic community organisms through their important functional roles (Bell & Smith, 2004; Bell, 2008 b). Sponges interact with a huge range of organisms in marine systems (Wulff, 2006a). Although it is difficult to identify the functional role that sponges play in these relationships, the development in the field of chemical ecology has considerably helped to enhance the understanding of the association between other organisms and sponges (Bell, 2008b). The interactions between sponges and other organisms include symbiotic associations, sponge-associated microorganisms, consumers, sponges as a food source, spatial competitors and sponges as microhabitats (Wulff, 2006a; Bell, 2008b).

Coral-sponge interactions are influenced by spongivores (Hill, 1998). However, most of the information on spongivory, for instance, comes from studies conducted on tropical coral reefs - especially in the Caribbean (Meylan, 1988; Chanas & Pawlik, 1995; Pawlik, 1998; Hill, 1998; Wulff, 2000 ; Hill & Hill, 2002; Loh & Pawlik et al., 2009; Pawlik et al., 2013; Loh and Pawlik, 2014), see Wright et al., 1997; Ferguson & Davis 2008. The predator-sponge interaction observed in tropical waters differs from those in temperate systems, since vertebrate animals also join the ranks of spongivores (Wulff, 2006a). In temperate waters, invertebrate predators, such as asteroid and echinoid echinoderms, opisthobranch molluscs and a range of small crustaceans are the main consumers of sponges (Wulff, 2006a). However, spongivory in tropical systems also include some fish and sea turtle species (Burns et al., 2003; Goude et al., 2013). Predation can cause both indirect and direct effects, by influencing other processes such as competition or affecting prey densities, respectively (Powell et al., 2015). Furthermore, some studies suggest that spongivory may play a role in affecting the patterns of sponge species.
diversity indirectly, while also restricting their dominance in different tropical coral reef communities (Hill, 1998; Hill & Hill., 2002).

Plants and animals regularly face trade-offs that are vital to maximising their growth and survival (Halpin, 2000). These trade-offs are of particular importance to intertidal organisms such as algae and molluscs (Hobday, 1995; Hunt & Denny, 2008). Intertidal zones are susceptible to highly variable conditions. Thus, intertidal algae and animals are often exposed to dry and hot conditions during low tide on a daily basis (Helmuth & Denny, 2003). For instance, Hunt & Denny, 2008 demonstrated through laboratory experiments that intertidal marine algae show ecological trade-offs, due to the concomitantly disruptive and protective influence of desiccation. Conversely, animals often need to make decisions on a variety of feeding options with a high energetic gain - based on balancing the risk of predation and starvation (Houston et al., 1993). Halpin (2000), revealed that a fish species, *Fundulus heteroclitus*, found in the intertidal zones frequently face trade-offs between growth and predation risk. This species preferentially uses habitat refugia where growth rate is low in order to avoid predators. Unlike sessile organisms, mobile animals react quickly to environmental changes and may have low mortality rates because of their ability to recolonise habitats through seasonal, tidal and diel periods (Halpin, 2000). Hence, regulatory processes and population dynamics of mobile and sessile organisms could show high dissimilarity (Halpin, 2000).

Sponge assemblages of Caribbean mangroves and coral reefs revealed variation in growth rate that was inversely associated to different defences against predators and resistance to competition (Wulff, 2005). More than half of the coral reef sponge individuals that survived after a storm in the San Blas Province of Panama were recorded dead or still deteriorating after one month had elapsed. These sponge communities also showed a trade-off between their capacity to recover, and morphological strategies that promote resistance to damage (Wulff, 2006b).

Shallow subtidal reefs in temperate Australia, particularly in central and southern areas of New South Wales, are characterized by a mosaic of habitats that are associated to wave exposure, depth and different biological factors, especially herbivory (Underwood et al., 1991). Furthermore, in sheltered or deeper water in these areas, the abundance of invertebrate grazers, including sea urchins, decline. In contrast, ascidians, red algae and sponges show greater abundance (Underwood et al., 1991). Sea urchins in tropical reefs may dramatically affect sponge populations due to periodically reducing their coverage and diversity (Burns et al., 2003). One of the sea urchin species observed in the low intertidal zone of the Illawarra region, *Centrostephanus rodgersii*, is considered to have the most influence on habitat structure in the
region, as it removes practically all macroalgae in shallow subtidal regions near Wollongong (Ferguson & Davis, 2008). In addition, studies conducted at two sites at the same region also observed spicules within the guts of *C. rodgersii*, confirming that sea urchin species consume sponges in this region (Wright et al., 1997; see also Ferguson & Davis, 2008).

The aim of this chapter was to establish a transplant experiment to gauge whether the survivorship of sponge explants into rock pools at the lower tidal zone was depressed when compared with those transplanted to higher pools, due the presence of predators. The common sponge *Callyspongia (Callyspongia)* was the only sponge species that was observed in pools high on the shore in the Illawarra region. Therefore, sponge explants of this species were used in this experiment. This represents the first study conducted in south-eastern Australia with the purpose to experimentally investigate whether the spatial distribution of an intertidal sponge, *Callyspongia (Callyspongia)*, was associated with the avoidance of predation. The study examined whether predation by common sea urchin species (*Centrostephanus rodgersii* and *Heliocidaris tuberculata* Figure 5.1) play an important role in determining the lower limits of the vertical distribution of intertidal sponges in the Illawarra region, NSW, Australia.

5.2 Methods

5.2.1 Study location and Experimental design

Experimental caging transplants were conducted at Bass Point reef (34°35’S 150°54’E). Bass Point is north facing and the second largest reef that was monitored, (see Chapter 2) with 80% of sponges found in rock pools. Using a combination of caging and transplantation, individuals of 30 *Callyspongia (Callyspongia)* sp. 2 were transplanted to two different heights on the rock platform. This site was chosen because it had a significant population of sea urchin species (*Centrostephanus rodgersii* and *Heliocidaris tuberculata*) (Figure 5.1). *Callyspongia* sp. individuals were also observed on shallow rock substrate during the low tide during prolonged periods of emersion. Two sponges fragments (~ 5cm²) were removed from each sponge with a dive knife. Thus, a total of thirty fragments were taken from 15 different specimens of *Callyspongia* sp. 2. To minimise the possibility of collecting genetically identical individuals, an effort was made to collect sponges that were separated from one another by at least 1 metre. Each sponge explant was attached with super glue to PVC tiles (9 cm x 9 cm) which were then attached to a brick (23.5 cm x 6 cm x 6 cm; Figure 5.2). The thirty sponge explants were translocated with predator exclosures, to a large rock pool high on the shore - with a low concentration of urchins. Only three *H. tuberculata* individuals were observed in
the high shore rock pool chosen to place the sponge explants (< 1 urchin/m²). Sponge explants remained in this rock pool for ten days to allow explants to recover from their excision.

Sponges are likely consumed by a suite of predators, but an initial set of observations suggested that the major invertebrate spongivores on Bass Point may be the sea urchins (*Centrostephanus rodgersii* and *Heliocidaris tuberculata*; Figure 5.1). Both sea urchin species occur along the NSW coast (Jones & Andrew, 1990; Andrew & Underwood, 1993; Edgar, 2008), however, *H. tuberculata* appears to be the dominant sea urchin in the intertidal zone in the Illawarra region, as it was found in greater abundance in most of the mid to high shore rock pools (Figure 5.1B;C). Once sponges had demonstrated signs of recovery, half of the bricks (N = 15) were subsequently relocated to a rock pool that was frequented by urchins, on the low shore of the reef (density >6 urchins/m²). Five sponge explants remained with predator enclosures (Figure 5.2A), five explants were changed to a half cage (cage controls, N= 5; Figure 5.2C) and the other replicates were exposed to predators by removing the cages (N = 5; Figure 5.2B). The same treatments were applied to the replicates in the high tidal pool. Predator exclusion cages consisted of a net of 16 x 20 cm mesh, supported by two pieces of PVC pipe (8 cm) on each end of the brick. The mesh was secured to the bricks using small cable ties. As for the cage controls, half of the bricks were covered by the mesh (8 cm x 20 cm) and supported by one piece of PVC pipe on one end of the brick (Figure 5.2C).

Underwater pictures of each sponge explant were taken with a Canon power shot D20 digital camera prior to the experiment and were repeated every week during the 30 day experiment. The bricks were always approached cautiously to identify the presence of potential predators. I then assessed each explant for signs of any predator activity and whether the sponges remained healthy. The sponges pictures were analyzed to determine the percentage of remaining sponge surface area, survivorship, the percentage of tissue affected by necrosis, the percentage of the area of sponge eaten and finally the area of the sponge covered by algae. The measurements were performed using the image analysis software (Image J) as outlined in Chapter 2.
Figure 5.1: Photographs of the low shore rock-pool habitat found at Bass Point (A) note the concentration of the largely nocturnal sea urchins; (B) and (C) shows the two sea urchin species *Centrostephanus rodgersii* and *Heliocidaris tuberculata*. *Centrostephanus rodgersii* is the larger (12 cm test diameter), dark-purple sea urchin, with long slender spines.

Figure 5.2: Field experimental setups. All cages and cage controls were fabricated in Vexar to create these enclosures. (A) Predator exclusion cages explants recovering prior to initiating the experiment; (B) Sponges in predator exclusion cages and uncaged controls and (C) Sponge in the cage control treatment.
5.2.2 Statistical analyses

The changes in the survivorship, coverage area, percentage of necrotic tissue and percentage of the area of sponge eaten were each analysed separately. Percentage of the area of sponge eaten was not included in the general linear model (GLM) ANOVA analysis, because of the very low levels of predation observed during the monitoring. For the other three data variables, an ANOVA was performed with tide height and predation as fixed factors and blocks as a random factor. Blocks were a random factor with three levels, whereas tide height and predation were both a fixed orthogonal factor with two and three levels respectively. The factor ‘tidal height’ had two levels; low and high shore areas. The factor ‘predation’ had three treatment levels: cage control, uncaged sponges and predator exclusion cages. Each predation treatment was replicated five times (N = 5). In addition, a two-way analysis of covariance (ANCOVA) was conducted to determine whether tidal height had a significant effect on the percentage of necrotic tissue on explants with the cover of algae prior to the experiment as a covariate.

The correlation was completed using R Studio running platform version 3.4.2 with α set at 0.05, while the Analyses of variance (ANOVA) and covariance (ANCOVA) was performed on IBM SPSS Statistics 25 (SPSS Inc.).

5.3 Results

Significant differences in percentage of sponge survivorship, sponge coverage area and the percentage of necrosed tissue that were measured at the completion of the experiment were only found when comparing among tide heights (Table 5.1). Explants transplanted to the low shore demonstrated the highest percentage of survivorship (Figure 5.3) and three fold lower necrosis (as a percentage) than high shore pool explants (Figure 5.4). The low shore pool showed stable survival of explants up to the third week of the experiment with only 20% of the individuals exhibiting necrotic tissue and sponge area covered by algae. At the end of the experiment, 40 % of the low tidal pools explants survived with the uncaged individuals presenting a great level of mortality (90%) (Figure 5.3A) and with 25% of the live explants showing necrosed tissue (Figure 5.4). Conversely, high shore specimens showed decrease in their survivorship after the second week followed by a surprisingly large decrease in the survivorship of the predator exclusion explants in the third week. A total mortality rate of 80% of high-shore explants was observed at the completion of the experiment with only cage control individuals surviving (Figure 5.3B). However, the amount of algae in the tissue prior to the
experiment was not shown to influence the percentage of necrotic tissue at the end of the experiment.

Table 5.1: Analyses of variance (ANOVA) comparing variation among Treatments, Blocks and Tidal height for sponge Survivorship at the conclusion of the experiment and the percentage of tissue affected by necrosis. NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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<th>Source</th>
<th>d.f</th>
<th>Sponge Survivorship</th>
<th>Necrotic tissue</th>
<th>Sponge Coverage area</th>
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<td></td>
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<td>MS</td>
<td>$F$</td>
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<tr>
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<td>10.156</td>
<td>6.534</td>
<td>**</td>
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<tr>
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<td>2.798</td>
<td>1.800</td>
<td>NS</td>
</tr>
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<td>2</td>
<td>1.430</td>
<td>0.920</td>
<td>NS</td>
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<tr>
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<tr>
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<td>1.554</td>
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Figure 5.3: The relationship between sponge survivorship (%) and weeks after the initiation of the caging experiment. Mean (±SE) estimated survivorship for each level of predation factor (predator exclusion, cage control, uncaged) with each bar representing a mean of the percentage of remaining sponges cover from five sponges in each treatment (N= 5).
Figure 5.4: Mean percentage (±SE) of sponge tissue with algae (☐) before the experiment and the percentage of tissue affected by necrosis ( ) at the end of the experiment at the two tidal heights (Low and High shore). Data has been pooled across levels of the factor “Predation”, and each bar represents a mean of fifteen sponges at each tidal height (N= 15).

After 30 days of the experiment, despite observing a significant decrease in the percent cover of the sponge explants, low shore individuals showed a great percentage of their remaining cover (66%) than high shore individuals (34%) (Figure 5.5). In addition, during the experiment a marked difference in the overall sponge surface area was documented between the sponge explants placed on high versus those low on the shore (Figure 5.6). The explants in the high shore pool exhibited a constant decline in their mean surface area following the second week of the experiment, whereas sponge explants at low shore revealed a slight increase on their surface area during the second week, followed by a marked decrease at the fourth week. The low shore individuals also revealed a five times greater difference in their surface area than the sponges placed in high tidal pools at the end of the experiment (Figure 5.6).
Figure 5.5: Changes in the percent cover of sponges (cm²), at the two tidal heights in Bass Point, one month after the experiment was initiated. Bars are mean (±SE) estimates of the percentage of the remaining sponge cover. Data has been pooled across levels of the factor “Predation” as there was no evidence of an effect due to predation, not an interaction among the factors of interest. Each bar represents a mean of fifteen sponges at each tidal height (N= 15).

Figure 5.6: Comparison of changes in sponge surface area (cm²) before the experiment (week 1), and for each following week, for a period of one month at the two tidal heights (High and Low shore). Mean (±SE) estimates of sponge surface area. Data has been pooled across levels of the factor “Predation” and each bar represents a mean of fifteen sponges at each tidal height (N= 15).
The experiment revealed that there was no statistically significant difference between percentage survivorship, necrotic tissue and sponge surface area between the predation treatments (Table 5.1). Nevertheless, the uncaged explants were the only individuals at low shore that showed a decreased of 5% on their surface area by the first week. The explants in the other treatments (predator exclusion and cage control) revealed a slight increase on their coverage area, which then decreased after the second week (Figure 5.7A). Although, the sponge surface drastically decreased in all predation treatments after the third week of experiment, none of the three levels at low shore showed a total sponge surface loss at the conclusion of the experiment. Additionally, the explants at low shore presented a three times greater percentage of the remaining cover than the high shore explants after the four weeks of the experiment (Figure 5.7A). Conversely, at the high shore, the sponge area had a continuous decline, but only uncaged and predator exclusion explants revealed a total loss of the surface area, while caged control explants had 15% cover remaining at the end of the experiment (Figure 5.7B). Finally, the ANCOVA analysis did not reveal a statistically significant effect of the sponge area covered by algae on the percentage of necrotic tissue at the two tidal heights.
Figure 5.7: Changes in the sponge area (cm$^2$) since the initiation of the caging experiment. Mean (±SE) estimated sponge surface area for each level of predation factor (predator exclusion, cage control, uncaged) with each bar representing a mean of five sponges in each treatment. (N= 5).
During the cage exclusion experiment, species from two different Phyla (Mollusca and Echinodermata; Figure 5.8) were found associated with the bricks supporting the sponge explants, but only three species from the class Gastropoda were observed consuming individuals of *Callyspongia* (*Callyspongia*) sp.2 (Figure 5.9). These three species include the nudibranch, *Dendrodoris nigra* (Family Dendrodorididae) and two fissurellids - *Diodora lineata* and *Montfortula rugosa* (Family Fissurellidae) (Figure 5.9B; C). A low level of predation was recorded in only two (13%) of the 30 explants placed on the rocky shore. None of the explants in low shore pool showed evidence of consumption. The two explants at high shore showed 16% and 8% of sponge tissue eaten by a predator, thus the response variable “Percentage of predation” could not be included in the statistical analysis.

Figure 5.8: Total number of species found associated with the bricks during the cage exclusion experiment. One species of nudibranch (*Dendoris nigra*) and 2 species from the family Fissurellidae (*Montfortula rugosa* and *Diodora lineata*) were observed consuming the sponge *Callyspongia* (*Callyspongia*) sp.2.
Figure 5.9: Photographs of the variety of species (A) found near the sponge explants but without signs of predation: *Dolabrifera brazieri*; *Nassarius pauperatus*; *Notoacmea flammea* and *Astralium tentoriiformis*. Evidence of consumption of the sponge explants (B) *Diodora lineata* and (C) *Dendrodoris nigra* and *Montfortula rugosa*. Scale bars: 1 cm.
5.4 Discussion

5.4.1 General findings

_Callyspongia_ sp. species showed a distinct distribution in one of the Illawarra reefs (North Wollongong reef). My experimental prediction was following the notion that these specimens were occupying the high shore to avoid predation by the two sea urchin species observed in the intertidal reefs in Illawarra region. However, during the monitoring of my experiment, predator activity was only observed on the high shore and then was inconsequential. Gastropod predators were the dominant consumers. Three species including the nudibranch, _Dendrodoris nigra_ (Family Dendrodorididae) and two fissurellids - _Diodora lineata_ and _Montfortula rugosa_ (Family Fissurellidae) were observing eating sponges but only affected 13% of the explants.

5.4.2 Community Structure

Intertidal communities are structured by a wide range of abiotic and biotic factors that interact with growth and mortality of intertidal organisms (Bertness et al., 1999; McQuaid & Lindsay, 2000; Van Katwijk & Hermus, 2000; Thompson et al., 2002; Helmuth & Denny, 2003). The degree of wave exposure and height on the shore are among the most important physical factors affecting intertidal organisms (McQuaid et al., 2000). In terms of emersion, high shore environments are physically more stressful than low shore due to desiccation and high temperature (McQuaid et al., 2000). Hydrodynamic forces are also thought to be among the most important determinants of mortality in the rock intertidal zone, as intertidal invertebrates are at risk of dislodgment and damage from breaking waves (Helmuth & Denny, 2003). However, species interactions also provide important information to understand changes in the community structure due to environmental stress (King and Sebens, 2018).

Most of the intertidal sponge species from the Illawarra region were found in rock pools at the low to mid tide. _Callyspongia Callyspongia_ was the only species observed in rock pools high on the shore and found emergent during the low tide, with small individuals varying between 2 cm$^2$ to 8 cm$^2$. Specimens of this species were observed on rocky substrate inside of rock pools on three rocky reefs - Sandon Point, North Wollongong and Bass Point. The natural habitat features in North Wollongong and Sandon Point reef, included a greater quantity of smaller and shallow rock pools than Bass Point reef, where larger pools predominated. At North Wollongong and Sandon Point reefs, _C. Callyspongia_ individuals were found predominantly in small pools, but in North Wollongong this species was also registered in pools higher on the shore than other species. Conversely, Bass Point reef was dominated by a large number of much larger and deeper pools, but _Callyspongia (Callyspongia)_ specimens
were found in smaller pools at the low/mid-shore. Individuals were also observed on rocky substrata on the low shore exposed to air during the low tide, usually among canopy-forming algae (Figure 5.10).

Figure 5.10: Photograph of a *Callyspongia Callyspongia* sp. 2 individual observed on rocky substrata at Bass Point reef. Some individuals were found at low shore exposed to air during low tide, usually among canopy-forming algae. Scale bar: 1 cm.
5.4.3 Factors driving sponge distribution

One of the key purposes of ecological research is to understand how trade-offs influence the distribution and abundance of species (Werner & Anholt, 1993). My field experiment sought to test whether the apparent preference of Callyspongia (Callyspongia) for high shore pools was due to the risk of predation, balancing their survivorship in a more physically stressful environment to avoid being attacked by predators. Previous studies have shown trade-offs between the growth rate of organisms or their survivorship and negative biological or physiological interactions (Hobday, 1995; Halpin, 2000; Wulff, 2005; Wulff, 2006b). How trade-offs influence community structure and function has been the focus of several studies conducted in intertidal habitats (Hobday 1995; Halpin 2000; Tanaka, 2002). Intertidal organisms living in more wave protected areas or higher on the shore are more likely to exhibit physiological changes, as trade-offs, than individuals located in less stressful conditions (Fitzgerald-Dehoof et al., 2012). Stress caused by this unpredictable environment can cause slower growth, decrease levels of metabolism and lower reproductive effort of individuals (Fitzgerald-Dehoof et al., 2012). The intertidal fish Fundulus heteroclitus, for instance, faced trade-off between growth and predation (Halpin, 2000). The specimens were observed using refugia from predation, even if this affected their subsequent growth. In a further example, drawn from rocky shores, acclamatory responses to heat and food stress were identified affecting Californian mussels, reducing their tissue mass and shell growth (Fitzgerald-Dehoof et al., 2012). Petes et al., (2007) investigated the costs related with repairing thermal harm caused by the increase of aerial temperatures at the upper limit of two intertidal mussel species from the east coast of New Zealand. They demonstrated that the mussels transplanted to high shore environments had their ability to reproduce and grow affected. Finally, Underwood & Jernakoff (1984) described the importance of grazing by molluscs on rock-platforms in New South Wales. They demonstrated that on the low shore grazers were relatively ineffective as algae grew rapidly due to reduced physical stresses, such as temperature and emersion. However, the algae species were restricted from colonising the higher parts of the shore by grazing activity, which was identified as being the major influence on the upper limits of vertical abundance and distribution of different species of macroalgae.

Guida, (1976) documented spongivory by different generalist and specialist invertebrates from two major classes (Gastropoda and Echinoidea) on oyster beds of North Carolina. The ability to eat sponges was tested with a laboratory experiment and was attributed to different invertebrates predators, including the generalist limpet Diodora cuyenensis and the
specialist cerithid snail *Seila udamsi*. Furthermore, a sea urchin, *Arbacia punctulata*, was numerous and the most voracious spongivore, completely consuming the sponges during the experiment and were observed controlling the abundance of sponges at one of their sites. In contrast, my experiment revealed very low levels of predation and brings into question whether the top down action of predators might drive sponge diversity and abundance on shores of south eastern Australia.

It is important to mention that many of the “potential predatory” species found under/above the bricks were simply associated with the bricks as a 'refuge', or a spot to lay egg masses and were not interacting with sponges as predators (Figure 5.11). Additionally, sea urchins are nocturnal animals that do most of their grazing at night (Andrew & Underwood, 1993), and I conducted monitoring at low tide during daylight hours. Therefore, grazing activities by the sea urchins could be missing, restricting my observations of spongivory.
Figure 5.11: Photographs of different species found associated with bricks. A greater variety of species of the Phylum Mollusca was found under/above the bricks (A) nudibranch specimen of *Discodoris confuse* found near egg masses, (B) *Discodoris lilacina* (C) *Umbraculum umbraculum*. (D) One of the three starfish species also observed associated with the bricks *Astrostole scaber*. Scale bar: 1 cm.

The need to conduct more transplantation experiments could be crucial in order to confirm whether the species of molluscs observed consuming sponges were indeed the main predators responsible for determining the upper limits of these organisms in the Illawarra region. It seems there is a need to better understand the role of specialist vs generalist predators and their influence of sponge cover and survivorship. Furthermore, as previous studies in the same region have observed spicules within the guts of *C. rodgersii* (Wright et al., 1997; Davis et al., 2003) and Ferguson & Davis, (2008) considered this sea urchin species the organism with the most influence on community structure in shallow subtidal regions near Wollongong. I also suggest that further studies investigate, perhaps through laboratory experiments, whether
sea urchins on intertidal reefs are feeding on sponges and thereby affecting their patterns of vertical abundance and distribution.

Previous studies have found that sponge growth and survivorship are also influenced by water flow, depth and seasonal variation in water temperature (Duckworth et al., 2004). Corriero et al. (2000) revealed water movement as a major factor of mechanical stress affecting a semi-submerged cave sponge fauna, and that the decrease in diversity and abundance of the sponge fauna in this habitat might be related to potential food depletion due to a low water turn-over in some parts of the cave. As sponges are filter-feeding organisms, they may be better adapted in environments with high water movement. Rock pools can retain water at high tide and may be used as a refuge and aid sponges to not only tolerate unpredictable physical changes, but also enable them to escape from some of their predators. However, the rock pools on the high shore where I placed the intertidal sponge explants, was a static environment with hydrodynamic movement being observed only during large swell conditions. These conditions may also represent an important stressor, which influences food availability in this rock pool environment. Therefore, low water movement and food depletion at the high shore pool may explain the increase cases of necrosis and the decreased survival of these individuals, as high shore pools have a restricted tidal exchange. Consequently, the spatial distribution of *Callyspongia* (*Callyspongia*) in the Illawarra region may not only be related to substratum availability but also to the structure of the reef. Microhabitats as rock pools and their position on the shore may influence sponge richness and abundance. Rock pools may be the best option for larval settlement to avoid stressful conditions in the high shore environment, such as desiccation and high temperature but also biological factors such as predation.

Ultimately, tidal height was an important driver of sponge cover and survivorship. Despite the decrease in survival of all explants in low tidal pools, none of the individuals suffered total mortality at the conclusion of the experiment. Conversely, only the cage control explants in the high shore pool survived at the end of the experiment. Whereas explants in the predator exclusion treatment and the uncaged explants was 100% by the fourth week. The complete mortality in the explants from which predators were excluded is consistent with my sponge transplants stressing these animals, thereby making interpretation of my experiment problematic. I speculate that limited water movement in the pools is the underlying factor driving mortality rather than the presence of predators in this region. Survivorship was higher on the low shore – indicating high shore conditions stressed the sponges.
5.5 Conclusion

Predation treatments showed no effect on the sponge cover or survivorship. Conversely, tidal height was a key factor influencing sponge survivorship and cover. The high shore explants developed a 55% greater percentage of necrosis in their tissue than low shore explants. In addition, only the cage control individuals showed a level of survivorship (20%) whereas the other two-predation levels showed a total mortality of their explants at the completion of the experiment. Nevertheless, the total remaining sponge cover was three times higher at the low shore pool where none of the explants suffered total mortality after the 30 days of the experiment. The experiment revealed a different outcome than was predicted; a low level of predation by three species from the class Gastropoda. However, there was recognition that some physical conditions, such as tidal height and water movement, may be the key factors that influence sponge survivorship, rather than the presence of predators in this region. These abiotic factors could limit the high-shore distribution of Callyspongia sp. on some reefs. It was noteworthy that healthy specimens of the same genus were observed in high tidal pools at North Wollongong. Clearly, further studies need to be conducted to confirm whether species of molluscs are indeed the main predators responsible for determining the upper limits of the distribution of this sponge. This study has generated important information to elucidate and expand our understanding of the environmental factors that may act as structuring agents in this ecosystem.
CHAPTER 6

Discussion and conclusions
6.1 GENERAL FINDINGS

The data presented in this study, besides assisting in filling biodiversity gaps, also addresses the importance of taxonomic expertise in reporting natural patterns of species abundance and distribution. To the best of my knowledge, this is the first study to conduct a comprehensively quantification of the abundance of sponges species in intertidal reefs from southeastern Australia. Earlier studies of sponges in these ecosystems were very limited and quantitative surveys have rarely been undertaken. In Australia, for instance, most of the information provided from studies conducted in intertidal systems are based on species inventories and some are only qualitative surveys seeking to record additional numbers of species (Fromont, 2004, Fromont et al., 2006). The primary basis to develop a general ecological understanding of the importance of habitat, which has not been previously studied, is to investigate its impact on population dynamics (Underwood et al., 2000). Therefore, firstly it is crucial to understand the patterns of species abundance, distribution and interaction between organisms in their habitat (Underwood et al., 2000). Given the taxonomic uncertainty surrounding sponges I adopted a slightly different set of priorities. I sought to identify the sponges to the lowest possible taxonomic level, quantify their spatial and temporal patterns of abundance and diversity among reefs, with an investigation of the environmental factors responsible for structuring the sponge community in this ecosystem. Species abundance was sampled using a combination of two different kind of surveys. The single inventories were used to comprehensively quantify the species abundance for cross-site comparisons, whereas the accumulated sampling records allowed an assessment of temporal variation and provided a more detailed list of the intertidal sponge fauna of the Illawarra region (Chapter 2). The measure of natural patterns of spatial differences and understanding temporal changes were important to identify baseline information against which to assess any future impacts. I then sought to examine biotic and abiotic factors as determinants of the structure of intertidal sponge assemblages (Chapter 3). Importantly, after a storm most of *Callyspongia* (*Callyspongia*) sp. specimens showed a significant mortality and the shrinkage of their surface area. I then hypothesised that an increase in sediment was an important driver of the high mortality of these individuals, particularly at North Wollongong and Sandon Point reef. The impact of different rates of sedimentation on the survival of intertidal sponge adults and recruit-sized explants were experimentally tested (Chapter 4). Ultimately, based on the observation that *Callyspongia* (*Callyspongia*) sp. was the only species found in high shore pools in the Illawarra region. I
used manipulative field experiments to investigate whether the spatial distribution of *Callyspongia* (*Callyspongia*) on Illawarra reefs was associated with the avoidance of predation (Chapter 5). This data chapter assessed whether feeding by the sea urchin species, *Centrostephanus rodgersii* and *Heliocidaris tuberculata*, play an important role in determining the lower limits of the vertical distribution of intertidal sponges on reefs in the Illawarra region.

### 6.2 PATTERNS OF DISTRIBUTION

Sponges have great ecological and commercial importance, but their patterns of biodiversity have rarely been investigated and understood compared to other benthic taxa, such as corals (Fromont et al., 2016). Australian waters revealed high sponge biodiversity (Heyward et al., 2010; Schönberg & Fromont, 2012), showing a number of regions as sponge biodiversity hotspots (Hooper et al., 2002b; Schönberg & Fromont, 2012; Fromont et al., 2016) with high levels of sponge endemism and rarity in tropical regions (Fromont et al., 2006; Hooper et al 2002b). However, little is known about sponge patterns of occurrence in the Indo-Pacific region and Australia still have understudied geographical areas for sponges (Schönberg & Fromont, 2012). Most of studies that estimate sponge species abundance and distribution have been undertaken outside Australia, particularly in subtidal tropical areas in the Caribbean region (Fromont et al., 2016). However, a few studies have assessed sponge richness in temperate environments (Roberts & Davis, 1996; Bell & Barnes, 2000; Fromont et al., 2012). The majority of comprehensive biodiversity studies on sponges in Australia have been species inventories (Hooper & Lévi, 1994; Hooper et al., 1999, 2002a; Hooper & Kennedy, 2002; Przeslawski et al., 2014) and there is a clear lack of studies sampling intertidal localities quantitatively (Fromont, 2004; Fromont et al., 2006; Fromont & Sampey, 2014; Fromont et al., 2016).

Intertidal sponges have been the subject of several manipulative experimental studies. Earlier studies have reported the reproductive cycle of intertidal sponge species (Gaino et al., 2010), their organizational plasticity (Palumbi, 1984; Gaino et al., 1995), investigated their capacity as bioindicators (Mahaut et al., 2013) and characterized their microbial symbiont communities (Steindler et al., 2002; Weigel & Erwin, 2016). However, few studies focus in understand their distributional patterns and any process that may influence these patterns. The majority of studies conducted in the intertidal zone are species inventories (Barnes & Bell, 2002) or examine the entire intertidal community structure but do not generate specific information about the sponge assemblages (Davidson et al., 2004; Davidson, 2005). Davidson,
2005, for instance, investigate the taxonomic, horizontal, and vertical gradients in intertidal biodiversity in southwest Ireland and only mentioned sponges as one of the most species-rich sessile taxa on the lower shore. Intertidal sponge assemblages were also sampled in coastal regions of Mozambique (Barnes & Bell, 2002). Although their study revealed that sponges represent a major taxon in all the habitats they sampled, but with lower diversity of species in the intertidal reefs, the sponges ecology in this region is still unknown. Barnes (1999), on the other hand, sampled quantitatively the sponge community of eight different intertidal habitats but in tropical zones. Among all sessile intertidal zone communities, sponges were the only organism that revealed a ubiquitous and commonly occurred in all intertidal habitats he sampled, a finding that differed from that in the Illawarra region where most of the reefs were depauperate in sponge species.

Not surprisingly, Australia is no different; only a few studies have evaluated the diversity of the intertidal sponge community in Western Australia (Fromont, 2004; Fromont et al., 2006, 2016; Fromont & Sampey, 2014). However, intertidal reef habitats were not sampled quantitatively (Fromont, 2004; Fromont et al., 2006) or the species recorded were not coded for habitat (Fromont & Sampey, 2014). Fromont et al., 2006, for instance, estimate the total sponges richness in subtidal and intertidal habitats using non-parametric methods. However, due the lack of information about intertidal sponges assemblages within Australia, the sponge diversity quantified in my study cannot be strictly compared to other intertidal regions where survey effort did not generate specific information about the intertidal sponge communities.

The ecological process of intertidal marine sponges has scarcely been studied, not only in Australia but worldwide. Therefore, a combined area of the Illawarra region coastline, 516000 m$^2$ (0.516 km$^2$), was surveyed and my study recorded previously unknown intertidal sponge species in five of the 14 intertidal reefs I sampled in the region. It is important to highlight that twelve of the total 22 species recorded were new occurrences for the region and many of these were previously undescribed. Overall, the key finding was that sponge species was patchy in their distribution in this region, with high levels of dissimilarity of sponge assemblages among reefs (Appendix 2.6). Earlier studies, conducted in different marine ecosystems, also recorded small-scale patchiness in sponge species distributions (Roberts & Davis, 1996; Hooper & Kennedy, 2002; Fromont et al., 2006; Fromont et al., 2012; Demers, 2015). The assemblages showed a sparsely distribution and revealed a low number in the abundance of species, with most of the species been represented by only one or two sponge individuals, including. My findings supported previous studies in shallow Australian habitats (Hooper & Kennedy 2002; Fromont, 2003; Fromont et al., 2006; Sorokin et al., 2007; Fromont
& Vanderklift, 2009). The patchy distribution of sponge species was mentioned in previous studies and linked to a variety of physical and biotic factors such as limited dispersal ability, asexual propagation, episodic disturbance, lack of connectivity among populations and microhabitat requirements (Roberts & Davis, 1996; Hooper & Kennedy, 2002; Demers, 2015).

The intertidal reefs of the Illawarra revealed only moderate abundance of sponges and were less speciose than other marine ecosystems of New South Wales, Australia (Roberts and Davis, 1996; Roberts et al., 1998; Roberts et al., 2006; Barnes et al., 2006, 2013; Demers et al., 2015). For instance, Barnes et al., (2013) encountered 18 sponge species in saline coastal lagoons in a sampling area 20 fold smaller than this study. However, Demers and co-workers (2015) revealed that seagrass in Jervis Bay has a more speciose sponge community than saline coastal lagoons in NSW, even in a sampling area 10 folder smaller. Despite their quite higher specie richness, the seagrass ecosystem appears to comprise a smaller diversity than the subtidal reefs of NSW, with more than double the sponge diversity I recorded on the intertidal reefs (Roberts and Davis, 1996; Roberts et al., 1998). Roberts and Davis, (1996) quantified over 50 species of sponges on rocky reefs of NSW coastline, whereas Roberts et al., 1998 recorded, using photo-quadrats, over 100 sponge species.

Many environmental factors have been shown to influence sponge community structure, regulating their species abundance and morphology (Barnes, 1999; Bell & Barnes, 2000; Carballo et al., 2008; Przeslawski et al., 2014). Although, such interactions are rarely common across all regions and sites (Przeslawski et al., 2014) sponge richness is known to increase with increasing depth (Zea, 1993; Roberts and Davis, 1996; Bell & Barnes, 2000) and to be higher at sites with high structural complexity and high substratum availability (Diaz et al., 1990). Cleary & Voogd, (2007) revealed that reef sponge assemblages structure in Indonesia was governed by the interaction of a number of environmental factors such as water velocity, suspended sediment, salinity and temperature. Furthermore, a study conducted in coastal regions of Mozambique revealed that the most important variable affecting the diversity of species was the type of substratum (habitat) (Barnes & Bell, 2002). However, the diversity of sponges was affected differently in this region depending of the habitat. For example, in the intertidal zone, a negative correlation between species diversity and light intensity was observed and may explain the lower species richness in this habitat.

Vertical species distribution in intertidal habitats is influenced by the tolerance of organisms to physiological stresses caused by the periods of emersion, such as a decrease in the food supply, irradiance, leading to an increased risk of desiccation and thermal stress (Petes et al., 2007). Furthermore, sessile intertidal invertebrates must also adapt to temperature
extremes as they are exposed to temperature fluctuation in both marine and terrestrial environments (Harley & Helmuth, 2003; Davenport & Davenport, 2005; Lathlean et al., 2011). Although there are other mechanisms responsible to determine the species spatial distribution in intertidal ecosystems of the NSW coast, such as habitat complexity (Beck, 2000), grazing activity (Underwood & Jernakoff, 1984).

Some key factors were investigated to uncover their role in the intertidal ecosystem structure from Illawarra region. The data described in this study provided a primary investigation of the environmental factors driving this community generating crucial information to understand why the intertidal reefs of this region differ in their suitability for sponge species. In terms of emersion, high shore environments are physically more stressful than low shore due to desiccation and high temperature (McQuaid et al., 2000). During the low tide the intertidal environment becomes physiologically stressful, particularly for sessile filter feeding organisms that are not able to filter feed due the periodic aerial exposure (Davidson, 2005; Weigel & Erwin, 2016). The abundance of sessile filter feeding organisms, including sponges, found in intertidal ecosystems in southwest Ireland showed more abundance at low-mid shore than the mobile taxa (Davidson et al., 2004; Davidson, 2005). Barnes, (1999) assessed the sponge assemblages in eight different intertidal habitats in Mozambique. The results showed tubular and encrusting morphologies restrict to the lower shore and that sponges dominate the diversity and biomass in cryptic communities probably to avoid high levels of irradiance. In contrast, the most common morphology of sponges in all habitats of the Illawarra region were encrusting (66%) and the majority of sponge species were recorded within rock pools at low-mid shore - likely minimizing mortality risk (see Chapter 2). The outcomes of Chapter 3 evidenced a higher chance of survivorship of sponges inside of rock pools at lower tidal heights, where the survival were five times greater than individuals recorded in high shore pools. This finding supports earlier studies (Barnes, 1999; Davidson et al., 2004; 2005), reinforcing that microhabitat requirements, position on shore and episodic disturbance, such as long periods of exposure to air may play an important role influencing sponge species distributions in the Illawarra region. Conversely, *Callyspongia (Callyspongia)* sp. was the only species found in small pools at high shore in North Wollongong reef or on rock substrata around rock pools in Bass Point reef. This species seems to have the capacity to deal with stressful conditions such as long periods of emersion.

Habitat type has been recognized as a crucial factor controlling the structure of rocky shore communities (Kostylev et al., 2005). Topographic heterogeneity has been shown to increase the surface area available for settlement of marine organisms, as well as provide refuge
against harsh physical and biotic conditions (Jackson et al., 2013). Thus intra-habitat diversity may enable species to co-exist in a given area (White et al., 2015). Barnes, 1999 showed that the diversity and morphology of sponge communities in the intertidal zones of Mozambique are influenced by the habitat complexity. This complexity protects some sponge species from environmental extremes, allowing a high number of distinct sponge morphologies and species to occur in habitats exposed to salinity and thermal stress. My work on the reefs of the Illawarra region also points to the importance of habitat, as evident from the positive correlation with habitat complexity and rock pool volume. My data supports the suggestion of Benkendorff & Davis, (2002) that habitat heterogeneity was a useful abiotic surrogate for the diversity and abundance of intertidal zone taxa.

Hydrodynamic forces generate by breaking waves is one of the most important physical mechanisms that determine local zonation patterns (Harley & Helmuth, 2003), causing mortality and inhibiting the growth of organisms in this habitat (Blanchette, 1997; Helmuth & Denny, 2003). As earlier studies conducted along the NSW coast, but with focus on molluscan diversity (Benkendorff & Davis, 2004), my data also showed a higher abundance and number of sponge species found on sheltered reefs, especially those with high habitat complexity. Thus, my data also indicate the degree of exposure to the wave and habitat complexity as important factors regulating the structure of the intertidal sponge communities.

Furthermore, as mentioned above the common sponge Callyspongia (Callyspongia) was the only species that was observed in small pools high on the shore in the Illawarra region. Therefore, I used manipulative experiments to investigate whether predation pressure was determining the spatial distribution of rocky intertidal sponges. The complex interaction between individuals can also provide relevant information to understand the community responses to environment change (Underwood et al., 2000; King & Sebens, 2018). The survivorship of sponge explants was investigated using a transplant experiment to uncover whether the presence of predators was depressing the survivorship of sponges in rock pools at the lower tidal level when compared with those transplanted to higher pools. Ferguson & Davis, 2008 revealed the sea urchin, Centrostephanus rodgersii, had a significant impact on the benthos in shallow subtidal regions near Wollongong. Furthermore, earlier studies conducted at two sites at the same region also observed spicules within the guts of C. rodgersii, confirming that sea urchin species consume sponges (Wright et al., 1997; see also Ferguson & Davis., 2008). Therefore, two common sea urchin species (Centrostephanus rodgersii and Heliocidaris tuberculata), observed in large quantities in the intertidal reefs of the Illawarra region, were chosen to assess whether predation plays an important role in determining the lower limits of
vertical distribution of intertidal sponges. However, I found very low levels of predation, with just three species of gastropods only affecting 13% of the explants placed in the high shore pool and none of the explants placed on low shore pools showed signs of predation.

Tidal height was a key driver of sponge cover and survivorship. My experimental manipulation revealed that despite the decrease in survival of all low tidal pools explants, none of the individuals suffered total mortality at the competition of the experiment. Conversely, only the cage control explants in the high shore pool survived at the end of the experiment. A decrease in the percent cover of the sponge explants was also observed. However, low shore individuals showed a two times great percentage of their remaining cover area (66%) than high shore individuals (34%). The high shore where I placed the intertidal sponge explants, was a static environment with hydrodynamic movement being observed only during large swell conditions. I concluded that limited water movement in the pools might be the underlying factor driving mortality rather than the presence of predators in this region. However, the monitoring was conducted only at low tide during daylight hours thus grazing activities by the sea urchins could be missed, restricting my observations of spongivory. Therefore, further field experimentation would be necessary to investigate whether sea urchins play a key role in influence the intertidal sponge assemblage structure.

6.2.1 Sampling challenges

There were some challenges that should be considered for future effective sampling and monitoring of sponges in rocky intertidal reef habitats. Sponges tend to be ignored in assessment and ecological monitoring mainly because they are difficult to identify sponges given the lack of taxonomic expertise available (Bell & Smith, 2004). Disturbingly, several taxa were very similar and could only be distinguished by a taxonomic expert.

As related in previous studies sponge species may show dissimiliar morphologies as well as similar physical characteristics such as form, texture and colour (Demers et al., 2015). Moreover, depending on the species of sponge, physiologically-defined individuals may not correspond to genetically defined individuals (Wulff, 2001). During the quantitative surveys I observed an encrusting purple sponge species at four of five reefs where sponges were recorded (Appendix 1). In total four different purple species were identified (Chalinula sp; Callyspongi sp.4; Callyspongia sp.5 and Callyspongia sp.2, Appendix 1). In North Wollongong, there were three purple sponge species, representing two different orders and only North Wollongong and Shellharbour reef shared the same purple sponge species (Callyspongia sp.4). Therefore, the use of conventional taxonomic methods, such as spicule and skeleton preparations are critical, and it is important to
highlight the value of a taxonomic expert to ensure the correct identification of sponge specimens. Without the spicule mounts and careful attention to the sponge characteristics, these four species could be identified as a single common species. Furthermore, incorrect identification of sponges could limit the understanding of species biogeography presenting difficulties in conducting future biodiversity research (May, 1995; Fromont et al., 2006). An identification mistake could also affect the access of information on the functional roles of specific sponge taxa. For instance, some members of the order Hadromerida are excavating species, which can have a strong impact on reef-building corals (Wulff, 2001; Bell et al., 2013). Future studies that aim to better understand the importance of intertidal habitats for these sponge assemblages may need to adopt genetic techniques along with taxonomic expertise to ensure adequate identification of the sponges to the level of species.

Invertebrate taxa within rocky intertidal habitats have shown unusually high levels of spatial variability and some earlier studies have noted difficulties in estimating patterns of abundance in this ecosystem (Miller & Ambrose, 2000). I found it difficult to design an accurate and representative method to quantify the sponge communities of intertidal zones in this region. Mostly because the majority of the individuals were recorded inside rock pools and because of their highly patchy distribution; rendering quadrats or transects unusable. Therefore, a timed, two-hour search survey was the sampling design chosen to quantify the diversity and abundance of the sponge assemblages for cross-site comparisons (single inventories) and assessment of their temporal variation (cumulative sampling). The sampling procedure was established to ensure adequate estimation of the intertidal sponge assemblages and their spatial variability. A similar design was used to sample sessile epifaunal invertebrates in different marine habitats in NSW, Australia. Barnes et al., 2006, 2013 used timed searches and transects methodology to sample coastal saline lakes while Demers et al., 2015 combined timed searches and transects to sample seagrass meadows in south-eastern Australian coast.

6.3 CONSERVATION AND MANAGEMENT

Intertidal environments are receiving increasing attention due the crucial socio-economic and ecological services provided by these systems (Sarà et al., 2014), but particularly as a consequence of the threat of climate change and anthropogenic pressures (Long et al., 2015). Rocky shore habitats are the transition zone between marine and terrestrial biomes (Tomanek & Helmuth, 2002). Therefore, intertidal organisms, such as sponges, are exposed to more stressful conditions to those in the subtidal zone, due their exposure to aerial conditions.
(Bell, 2008a; Lathlean et al., 2015). The intertidal ecosystems are characterized by patterns of vertical distribution (zonation) which reflects the species’ physiological adaptations to a variety of environmental factors (Tomanek & Helmuth, 2002).

Intertidal organisms usually occur well within their range of tolerance of physical conditions and are not stressed except under unusual conditions (Crowe et al., 2000). However, is expected that climate change will have a potential impact, in the next few decades, on intertidal species distribution and survival (Helmuth et al 2006a; Findlay et al., 2010; Lathlean et al 2013; Paganini et al., 2014), through association with multiple physical factors (Kelmo et al., 2014) and the influence on species interactions. Therefore, the ecosystem services provided by these systems could be affected due to changes in ecological community dynamics (Sarà et al., 2014). Changes in the biological patterns and process are already being observed to a wide range of taxa worldwide (Sarà et al., 2014; Richards et al., 2016). The loss of at least 150 species associated with macroalgal beds in Southern Australia, for instance, was associated with the poleward expansion of the sea urchin, Centrostephanus rodgersii, from NSW south to eastern Tasmania (Richards et al. 2016).

Climate is not, however, the only threat to intertidal marine assemblages (Long et al., 2015). Human activities, such as overfishing, pollution, degradation of coastal ecosystems and shipping (Long et al., 2015; Richards et al., 2016; Davis et al., 2016) are superimposed on the stress caused by natural fluctuations, thus influencing the community structure on various temporal and spatial scales (Crowe et al 2000). Sponges are negatively impacted by a range of stressors caused by anthropogenic activities, specially dredging and trawling (Wassenberg et al., 2002; Pineda et al., 2017a, b). However, the combined effects of natural factors and human activities have been poorly investigated (Leonard et al., 1998) and despite that numerous previous studies have assessed the impacts of environment changes on intertidal organisms (Stickle et al., 2017; Lathlean et al., 2017; King & Sebens, 2018) no study has vigorously investigated the effects on sponge communities.

Marine ecologists have developed a great deal of study on rocky shore habitats to understand how natural systems work (Thompson et al 2002). Years of experimental research within ecology provided descriptions of abundance and distribution patterns of diverse animal and algal population (Dayton, 1971). Intertidal research has also investigated the relationships between physical processes and these species patterns (Griffiths, 2003). The rocky intertidal zone in New South Wales, for instance, is relatively well studied (Underwood 1991). These
environments have been extensively studied because of their unique physical disturbances impacting organisms (Weigel & Erwin, 2016), including desiccation and temperature stress, exposure to wave action and competition for space (Paine, 1994; Helmuth & Denny, 2003; Stickle et al., 2017). Therefore, intertidal habitats could serve as predictive model systems to investigate the role of environmental stress on species and to understand the community response to climate change impacts (Judge et al., 2018). However, our understanding of the socio-economic consequences from the impacts listed above remains limited, and there is a lack of knowledge of the value of these ecosystems among stakeholders and local residents (Sarà et al., 2014).

Although sponges are recognized as the most diverse and important components of sessile benthic assemblages they are not usually the most common or the major space occupiers in rocky intertidal reef ecosystems. Previous research has demonstrated that barnacles, mussels and in some instances ascidians are the dominant space occupiers across temperate and tropical environments (Dayton, 1971; Underwood, 1984; Castilla et al., 2004; Mayakun et al., 2010). For instance, rocky intertidal zones of the northeast Pacific show competition for primary space between barnacles and algae, with a mussel dominance in some of the locations sampled (Dayton, 1971). Underwood et al., 1983 revealed that grazing gastropods occupy most of the space in sheltered areas on rocky shores in New South Wales whereas barnacles are the dominant species in wave-exposure areas. Furthermore, earlier studies conducted on rocky intertidal shores along the coast of New South Wales investigated spatial variation in community structure of organisms other than sponges (Underwood et al., 1983; Underwood, 1984; Underwood & Jernakoff, 1984; Benkendorf & Davis, 2002; Griffiths, 2003). Intertidal macroalgae seasonal abundance and vertical distribution were examined in sheltered shore areas in Botany Bay (Underwood, 1984.) Benkendorf & Davis, 2002 assessed hotspots of molluscan species diversity along the Illawarra coast. However, environmental stress affecting individual organisms may influence their abundance at population and ecosystem levels, inducing quantitative and qualitative changes in the structure of communities (Carballo et al., 1996), but as the patterns of occurrence of sponges are still poorly known, loss of taxonomic diversity in this phylum would be difficult to identify and monitor (Fromont et al., 2006).

6.3.1 Ecological value

Additionally, sponges have been scarcely studied in rocky intertidal systems. Although sponges are not a conspicuous organism in these habitats, it is important to better understand the fauna of this ecosystem before passing comment on its conservation and management. Sponges cover more space in the subtidal zone, representing one of the top spatially abundant
taxa and representing effective competitors on hard substratum in benthic marine habitats (Dayton et al., 1974; Bell & Smith, 2004; Carballo & Nava, 2007). Therefore, sponges likely perform more important ecological roles in subtidal communities because of their high diversity and biomass (Fromont et al., 2016). Sponges play a range of functional roles (Bell, 2008), showing their potential to influence other benthic community organisms (Bell & Smith., 2004). They can influence substrate conditions and water quality, affecting the substratum availability for settlement (Bell et al., 2013) and altering the water column through their high water filtering ability (Weisz et al., 2008). The ability of sponges to link the pelagic zone to the benthos through nutrient cycling is also recognized as an on the community structure of intertidal and shallow subtidal marine communities (Lesser, 2006; Southwell et al., 2008; Goeij et al., 2013; Keesing et al. 2013).

Sponges can affect substrate conditions, influencing other benthic organisms positively (Wulff & Buss, 1979; Wulff, 1984; Rasser & Riegl 2002). Some studies experimentally demonstrate that sponges play a key role on coral reefs, increasing the rates of carbonate accretion and providing suitable substrata for settlement and growth of corals in deep and shallow reef zones (Wulff & Buss, 1979; Wulff, 1984; Diaz & Rützler, 2001). Sponges have been recognized as binding agents “gluing together” coral colonies (Rasser & Riegl, 2002). Non-burrowing sponges, from Caribbean reef environments, are found to reinforce the reef frame, decreasing the probability of coral loss by natural events (fish predation and wave action) thus helping considerably the consolidation of coral colonies in the Caribbean region (Wulff & Buss, 1979).

Sponges are very sensitive to changes in the environment due their strong association with abiotic components (Carballo et al., 1996). Therefore, the inclusion of locally abundant filter feeders and particularly sponges into environmental assessment and management have been recognized as an important tool by monitoring and environmental protection agencies (Hanna & Schönberg, 2016). Some intertidal sponge species can endure highly unusual physical conditions and ecological impacts associated with climate change (Kelmo et al., 2014; Weigel & Erwin, 2016). *Callyspongia* (*Callyspongia*) sp, unlike the other species restricted to the low-mid shore, was the only species found in high shore pools in the Illawarra region. Small intertidal pools high in the intertidal zone of the North Wollongong reef were shown to reach temperatures of at least 32 °C, dissolved oxygen levels as low as 0.1 mg l and salinity of 39 °/oo. Nevertheless, *C. Callyspongia* sp. was in surprisingly high abundance in these small pools. In addition, *Callyspongia* sp. were observed on rock substrata around or between rock pools with six-hour emersion in a 12 hour period at Bass Point reef. Therefore, *C.
(Callyspongia) sp seems to have the capacity to cope with a wide variety of unusual physical conditions, such as prolonged periods of emersion, while its capacity to live in higher pools in the intertidal zone, may be a strategy to escape negative biological interactions. Hence, intertidal sponge population may serve as a model to understand how unpredictable stress changes their community structure relative to their subtidal counterparts.

6.3.2 Hawkesbury Shelf Marine Bioregion

The most important factors that influence the distribution of species are the occurrence of microhabitats for successful reproduction, and access to suitable habitat (Hubbell and Foster, 1986). Thus, the intertidal species that breed and live on rocky shores could be influenced by the availability of different microhabitats (Benkendorff & Davis, 2004). The “Habitat Diversity Hypothesis” predicts that habitat diversity should be a better predictor of species richness than area (Gaston & Blackburn 2000). Large areas may contain more species because they simply contain more habitats. This hypothesis has not been directly tested at the scale of intertidal reefs. Nevertheless, NSW Fisheries (2001) used habitat diversity as a surrogate for species diversity, in their preliminary assessment of rocky shores in New South Wales (NSW) for the identification of candidate sites for marine protected areas (Benkendorff & Davis, 2004).

In 2013, the Marine Estate Management Authority (MEMA) was established in response to the recommendation from the Scientific Audit of NSW Marine Parks (NSW Marine Estate, 2013). The Audit also mentioned that the existing system of marine protected areas in NSW was incomplete because it lacked a marine park in two bioregions, the Hawkesbury Shelf and Twofold Shelf (NSW Marine Estate, 2013). In 2014 the NSW Authority developed a project with options to choose representative system of marine protected areas for conservation and management of the biodiversity within the Hawkesbury Shelf marine bioregion (NSW Marine Estate, 2016a). State authorities in NSW have moved from a system where marine parks are establishing to a system where an assessment of risk is being used to manage resources. The NSW Authority outlined a new approach to manage the NSW marine estate that include five steps (NSW Marine Estate, 2013). The second step includes the Threat and Risk Assessment process (TARA). This new approach comprises a risk assessment process in order to identify the activities that may cause environmental, economic and social impact to the community benefits of the marine estate (NSW Marine Estate, 2016b). Currently, the State of NSW includes a series of multi-use Marine Parks with interconnecting sanctuary zones as key strategy to protect biodiversity. However, the Hawkesbury Shelf Marine Bioregion (HSMB) still lacks marine protection. The submission of the public proposal for a new marine park in
the HSMB occurred in the end of 2018. The feedback contributed to the final considerations by the NSW Authority and generated a “discussion paper”, divided into two parts, addressing the Authority’s priority to enhancing the conservation of marine biodiversity in the bioregion (NSW Marine Estate, 2016a). In the second part of the document, about the intertidal protected areas, the community feedback calls attention to the lack of baseline data and that these areas are not being actively managed.

Spatial heterogeneity is usually the way that species are dispersed in nature (Miller & Ambrose, 2000). Therefore, monitoring programs and quantitative surveys should be designed accordingly. Intertidal reef sponges from the Illawarra region shows a different pattern of community assembly than other biotic assemblages, including subtidal sponges communities from the same region. My results show an unusual level of spatial heterogeneity in sponge assemblages among reefs. Accordingly, I support previous studies concluding the importance to establish large conservation areas as a strategy to properly encompass these elements of biodiversity (Hooper et al., 2002b; Fromont et al., 2006). However, the data presented in this thesis suggests that sponge assemblages on Illawarra reefs are too patchy to be used as useful surrogates, and that mollusc assemblages recorded at the same region (Benkendorff & Davis, 2002) represent a better proxy for developing intertidal biodiversity conservation priorities.

The establishment of a marine park may not be the best approach to manage the conservation of the intertidal sponge biodiversity in this region. For instance, the major threats identified by the Threat and Risk Assessment (TARA) in intertidal reefs were trapping and harvest of invertebrate species, which associated with fishing activities, became a major impact reducing biodiversity in these habitats (NSW Marine Estate, 2016b). However, based on my findings (see Chapter 4) and previous studies (Roberts et al., 2006; Pineda et al., 2017a, b; Batista et al., 2018), the threats affecting the sponge communities on rocky shores may be more related to the catchments feeding these areas and anthropogenic impacts, such as pollution and increase of sedimentation, than the presence of people on the shore.

Sponges have been shown to be affected by human activities (Roberts et al., 2006; Pineda et al., 2017a; Batista et al., 2018). Discharge of sewage effluent into the ocean can not only alter the physical and chemical nature of the receiving water but also change the distribution and structure of multiple biological communities (Roberts et al., 2006). Discharge of sewage in a south-eastern region of Brazil affected some sponge species microbial and metabolites communities and antifouling activity (Batista et al., 2018). In addition, sewage has the potential to increase suspended sediments, limiting the light availability and influencing the rates of siltation that may result in the smothering or burial of encrusting species (Roberts
et al., 2006). Roberts et al., (2006) found that the sponge species \textit{Cymbastela concentrica} showed a decline in growth, lower reproductive activity and had their photosynthetic symbionts affected by siltation. Sediment deposition and resuspension of particulate material are key factors in the functioning of coastal ecosystems (Carballo, 2006) and the negative effects of sedimentation on sponges has been reported previously (Carballo, 2006; Roberts et al., 2006; Pineda et al., 2015, 2016 and 2017). Sand inundation in rocky shore habitats, for instance, is known to cause periodic alterations in this ecosystem across the world, affecting intertidal organisms by eliminating individuals that are intolerant to smothering by sand or sand scour (Littler et al., 1983; McQuaid & Dower, 1990). Not surprisingly, I found evidence that high sediment deposition is an important factor that may influence the distribution patterns of some intertidal sponges by affecting small intertidal sponge individuals (recruits) and may reduce the likelihood of settling larvae reaching a suitable substratum (see Chapter 4).

The designation and management of a representative system of marine protected areas is widely regarded as one of the most effective mechanisms for conserving biodiversity and helping to support ecologically sustainable uses, including fishing and tourism (NSW Marine Estate, 2017). However, marine protected areas in Kenya showed little or no ability to protect coral reefs against pollution (Kaimba et al., 2019). Kaimba et al., (2019) investigated whether the level of marine protection reduced human-derived pollution, such as nutrient and \textit{E. coli} concentrations on Kenya coral reefs. The results revealed that the level of protection did not avoid the increase of orthophosphate concentrations and that nitrate concentrations showed no correlation with protection. Therefore, I suggest the adoption of a catchment perspective to sustainably manage intertidal habitats and enhance the conservation of sponges diversity from the Illawarra region based on the principles of Total Catchment Management (TCM), defined in the New South Wales Catchment Management Act 1989 (Wells & Huntingdon, 1999). Although, more data are required on patterns of recruitment and to understand interactions between intertidal sponges and their habitat. My findings reveal important information that will allow future studies to assess risk to intertidal sponge assemblages, helping to conserve rocky shores in this region. Thus, contributing to the establishment of comprehensive and representative intertidal protected areas in the Hawkesbury Shelf Marine Bioregion of NSW, Australia (NSW Marine Estate, 2013).

6.3.3 Conclusion and Future directions: great model system to explore

Pattern of larval dispersal have been investigated for other marine organisms along the New South Wales (NSW) coast and showed no evidence of population subdivision (Hunt,
1993; Murray-Jones & Ayre, 1997; Ayre, 1997). These studies investigated the biological significance of the East Australian Current (EAC) affecting population connectivity, comparing the size of the coastline surveyed and the number of effective migrants per generation. The high levels of dissimilarity in the species composition among reefs shows how unique the intertidal sponge population of the Illawarra region are, suggesting that these populations may be poorly connected. Restricted population connectivity is often observed among sponge communities (Hooper et al., 2002b; Hooper & Kennedy, 2002; Blanquer & Uriz, 2010) and can also result in unusual sponge aggregations, with the majority of the species (61%) being recorded at only one or two stations (Fromont et al., 2006). It is important to mention that dispersal capabilities of sponges vary among species, relying on their reproductive output, larval lifespan and the swimming ability of their larvae (Uriz et al., 1998). For example, Davis et al., 1996 examined sponge species from south-eastern Australia that showed a genetic diverse population with wide larval dispersal. Some of the intertidal reefs that I monitored were inundated by sand after a storm that hit the NSW coast, which caused a huge effect on their sponge assemblages, with sponge individuals disappearing completely. This impact has implications for conservation and management in the sense that intertidal sponge assemblages from this region may have limit ability to reinvade this location based on poor population connectivity. I suggest that a limited larval dispersal range could be an important determinant explaining the patchy patterns of distribution of the sponge taxa I examined. However, future research probably will need a population genetics approach and should consider investigating the patterns of larval settlement and dispersal for sponges inhabiting intertidal reefs of this region. This would broaden our knowledge about the reproductive strategy of these assemblages, identifying effective management for the recovery of these populations.

Although, a variety of studies have investigated how environmental factors drive intertidal species distribution, very few studies have included sponges assemblages to understand the key roles of physical and biological factors in influence community structure in these ecosystems. Additionally, the effects of a combination of physical and biological disturbances remain scarcely understood (Leonard et al., 1998). Nevertheless, good management of marine resource requires quantitative information to access the variation in the abundance and distribution of the species, but it must also include an understanding of how ecological patterns are determined by the interplay between species interactions and major abiotic disturbances (Kordas et al., 2011). This urgent need for quantitative estimates of species is due the possible effects caused by climate change and ocean acidification that in part is influenced by anthropogenic activity. Most of the intertidal sponge species were recorded in
rock pools limited to either the low or mid shore whereas *Callyspongia (Callyspongia)* sp.4 were observed to prefer smaller pools in the high shore. Therefore, sponge species might have particular microhabitat requirements for recruit settlement and their distribution pattern may be influenced by environmental factors investigated in this study, such as sedimentation, wave exposure and microhabitat complexity. Future research should consider conducting more manipulative experiments to validate my findings and confirm the factors that are shaping the sponge community in this region, generating specific information to compare my results with other intertidal habitats within Australia or worldwide. For instance, transplant experiment could be conducted in which of the five rocky reefs where sponge species were recorded. The sponges individuals from each reef community could be relocated to different levels on its own shore to test whether their growth or survivorship are differently affected by environment factors depending on the natural habitat features of each rocky reef.

It is important to emphasise that the data present in this study besides assisting in filling biodiversity gaps of a rarely studied taxon also seeks to improve our understanding of the biodiversity on the rocky intertidal zone of south-eastern Australia. This is the first study to assess the distribution and abundance patterns of sponge assemblages in this habitat, along with the investigation to understand some of the processes responsible for influencing these patterns. There is an increase in the awareness that such studies are urgently need, particularly to record patterns in sponge richness, as sponges assemblages are threatened by anthropogenic activities, such as dredging operations and fishing activity (Pineda et al., 2017b; Dayton et al., 1995). This study recognises a number of important considerations and enhances our understanding of sponge communities in the NSW region that will likely contribute to the improved management of biodiversity in the Hawkesbury Shelf Marine Bioregion.
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References


APPENDIX 1

Intertidal Sponge Identification Guide for Illawarra Region
Table A: Summary of Sponge ID: code, Order, Family, Genus, presence of spicule, specimen, Photosynthetic activity (PA) and Australian Museum voucher availability. All species belong to the Demospongiae class and have photos available. The species identification was confirmed by the expert Lisa Goudie. (NA) species not found when the amount of photosynthetic chlorophyll was measured. (L) Low; (M) Medium; (H) High photosynthetic activity.

<table>
<thead>
<tr>
<th>Code</th>
<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Spicule</th>
<th>Specimen</th>
<th>PA</th>
<th>Voucher #</th>
</tr>
</thead>
<tbody>
<tr>
<td>COAL1</td>
<td>Hadromerida</td>
<td>Tethyidae</td>
<td>Tethya sp.</td>
<td>Megascleres: Styles 175 μm</td>
<td>Available</td>
<td>M</td>
<td>Z.7403</td>
</tr>
<tr>
<td>NWPUR</td>
<td>Haplosclerida</td>
<td>Chalinidae</td>
<td>Chaetos sp.</td>
<td>Megascleres: Oxeas 80-100 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>NWRP16</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.4</td>
<td>Megascleres: Oxeas 50-75 μm</td>
<td>Available</td>
<td>M</td>
<td>Z.7401</td>
</tr>
<tr>
<td>NWRP4</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.5</td>
<td>Megascleres: Oxeas 50-65 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>NWYEL</td>
<td>Halichondrida</td>
<td>Halichondridae</td>
<td>Amorphopon sp.</td>
<td>Megascleres: Thin Oxeas 100-400 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>NWORA1</td>
<td>Poecilosclerida</td>
<td>Microcionidae</td>
<td>Echinoclathria sp.</td>
<td>Megascleres: Styles (165 μm), Subtylosyles (140-175 μm) Acanthostyles (85-100 μm)</td>
<td>Not Available</td>
<td>M</td>
<td>-</td>
</tr>
<tr>
<td>NW7 (1)</td>
<td>Dictycoceratida</td>
<td>Dysideidae</td>
<td>Euryspongia sp.</td>
<td>None</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>SYYEL1</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.3</td>
<td>Megascleres: Curved Oxeas 75 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>SSYP5</td>
<td>Halichondrida</td>
<td>Halichondridae</td>
<td>Halichondria sp.2</td>
<td>Megascleres: Oxeas 60-200 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>SSY5</td>
<td>Poecilosclerida</td>
<td>Raspaulliidae</td>
<td>Echinodictyum sp.</td>
<td>Megascleres: Oxeas 40-75 μm, Styles 75 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>SSY6</td>
<td>Poecilosclerida</td>
<td>Myxillidae</td>
<td>Myxilla sp.</td>
<td>Megascleres: Subtylosyles 200 μm and Subtylosyles 170 μm, Microscleres: C-sigma 30 μm and Islandes 30 μm</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>BPPurple</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.2</td>
<td>Megascleres: Small Oxeas 65-80 μm</td>
<td>Available</td>
<td>M</td>
<td>Z.7394</td>
</tr>
<tr>
<td>BPDB1</td>
<td>C. hondrosida</td>
<td>Chondrillidae</td>
<td>Chondrilla sp.2</td>
<td>Microscleres: Spherasters (20-25 μm), Tyasters spined (15-18μm)</td>
<td>Available</td>
<td>L</td>
<td>Z.7262</td>
</tr>
<tr>
<td>BPLB1</td>
<td>Haplosclerida</td>
<td>Chondrillidae</td>
<td>Chondrilla sp.1</td>
<td>Microscleres: Spherasters (12-15 μm), Tyasters spined (15-18μm)</td>
<td>Available</td>
<td>L</td>
<td>Z.7261</td>
</tr>
<tr>
<td>BPO1</td>
<td>Hadromerida</td>
<td>Clionaidae</td>
<td>Speciesponga sp.</td>
<td>Megascleres: Subtylosstrongyles of two sizes 250μm-300 μm, Microscleres: Sprasters of two sizes 30μm-40 μm</td>
<td>Available</td>
<td>M</td>
<td>Z.7396</td>
</tr>
<tr>
<td>BPLP1</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.</td>
<td>Megascleres: Small Oxeas small 75-80 μm</td>
<td>Available</td>
<td>NA</td>
<td>Z.7395</td>
</tr>
<tr>
<td>BPP3</td>
<td>Dendroceratida</td>
<td>Darwinellidae</td>
<td>Darwinella sp.</td>
<td>None</td>
<td>Not Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>BPLBLU6</td>
<td>Halichondrida</td>
<td>Halichondridae</td>
<td>Halichondria sp.1</td>
<td>Megascleres: Curved thin Oxeas 210-500 μm</td>
<td>Available</td>
<td>M</td>
<td>Z.7398</td>
</tr>
<tr>
<td>BPY9/2</td>
<td>Verongida</td>
<td>Pseudoceratinidae</td>
<td>Pseudoceratina sp.</td>
<td>None</td>
<td>Available</td>
<td>H</td>
<td>Z.7400</td>
</tr>
<tr>
<td>BPDP10</td>
<td>Dictycoceratida</td>
<td>Thoreciidae</td>
<td>Hyrion sp.</td>
<td>None</td>
<td>Available</td>
<td>NA</td>
<td>-</td>
</tr>
<tr>
<td>BP011</td>
<td>Poecilosclerida</td>
<td>Podospongidae</td>
<td>Sigmosceptrella sp.</td>
<td>Megascleres: Anisostyles 300-350 μm, Microscleres: Asymmetrical spinorhabds 30μm</td>
<td>Available</td>
<td>L</td>
<td>Z.7399</td>
</tr>
<tr>
<td>SPRP1</td>
<td>Haplosclerida</td>
<td>Calyspongiidae</td>
<td>Calyxsponga (Calyspongea) sp.6</td>
<td>Megascleres: Oxeas 50-75 μm</td>
<td>Available</td>
<td>L</td>
<td>Z.7402</td>
</tr>
</tbody>
</table>
**Family:**
Tethyidae

**Scientific name:**
*Tethya* sp.

**Temporary name:**
Coalcliff 1 (Coal1)

**Spicule Morphology:**
- **Megascleres:**
  - Styles (monactical monaxons) of 175 μm
- **Microscleeres:**
  - Micrasters of 10 μm and Megasters of 25 μm

**Morphology Category:**
Roughly spherical massive sponge with smooth surface, texture firm and slightly compressible with no visible oscules.

**Size Information**
- 0.5cm - 1cm

**Colour**
Reddish orange alive and light pink in ethanol.

**Habitat Information**
Found under rock substrates - usually shaded environments.

**Location**
Coalcliff
Family: 
Callyspongiidae

Scientific name: 
*Callyspongia (Callyspongia)* sp.6

Temporary name: 
Sandon Point RP1 (SPRP1)

Spicule Morphology: 
**Megascleres:** 
Oxeas (diactinal monaxons) of 50-75 μm

Morphology Category: 
Irregular massive sponge. Smooth surface with a firm, soft and elastic texture. Scattered small circular oscules over surface.

Size Information
- Varying between 4 cm to 8 cm

Colour
Light purple alive and sandy beige in ethanol.

Habitat Information
Found on rock substrata inside of rock pools with a few specimens found out of water during low tide.

Location
Sandon Point rocky platform (South Bulli beach).
Family: Chalinidae

Scientific name: Chalinula sp.

Temporary name: North Wollongong purple (NWPUR)

Spicule Morphology:
Megascleres:
Oxeas (diactinal monaxons) of 80-100 μm

Morphology Category:
Irregular massive sponge. Smooth surface with a firm, soft and elastic texture. Scattered small circular oscules over surface.

Size Information
- 23cm

Colour
Light purple alive and sandy beige in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
North Wollongong.
Family: Callyspongiidae

Scientific name: Callyspongia (Callyspongia) sp.4

Temporary name: North Wollongong RP16 (NWRP16)

Spicule Morphology:
Megascleres: Oxeas (diactinal monaxons) of 50-75 μm

Morphology Category:
Irregular massive sponge. Smooth surface with a firm, soft and elastic texture. Scattered small circular oscules over surface.

Size Information
- Varying between 1 cm to 5 cm

Colour
Light purple alive and sandy beige in ethanol.

Habitat Information
Rock substrata inside of rock pools with most of the specimens found out of water during low tide.

Location
North Wollongong.
Family: Callyspongiidae

Scientific name: *Callyspongia (Callyspongia)* sp.5

Temporary name: North Wollongong RP4 (NWRP4).

Spicule Morphology:
Megascleres:
Oxeas (diactinal monaxons) of 50-65 μm

Morphology Category:
Lobed encrusting sponge.
Smooth surface with a firm, soft and elastic texture. Scattered small circular oscules over surface.

Size Information
- 32 cm

Colour
Light purple alive and sandy beige in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
North Wollongong.
Family:
Halichondriidae

Scientific name:
Amorphinopsis sp.

Temporary name:
North Wollongong yellow (NWYEL)

Spicule Morphology:
Megascleres:
Thin Oxes (diactinal monaxons) of 100-400 μm

Morphology Category:
Encrusting irregular sponge. Texture firm, compressible and easily torn. Surface translucent, smooth with long, tapering fistules. Oscules not visible.

Size Information
- 10cm

Colour
Yellow alive and light grey in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
North Wollongong.
**Family:**
Microcionidae

**Scientific name:**
*Echinoclathria* sp.

**Temporary name:**
North Wollongong orange 1 (NWORA1)

**Spicule Morphology:**

**Megascleres:**
Abundant Styles of 165 μm

Subtylostyles thin (140-175 μm)

Acanthostyles (85-100μm)

**Morphology Category:**
Thinly encrusting sponge with smooth surface and tiny oscules.

**Size Information**
- 10cm

**Colour**
Orange alive and beige in ethanol.

**Habitat Information**
Rock substrata inside of rock pools.

**Location**
North Wollongong.
Family:  
Dysideidae  

Scientific name:  
*Euryspongia* sp.  

Temporary name:  
North Wollongong 7(1) (NW7 1)  

Spicule Morphology:  
NA  

Morphology Category:  
Thick encrusting sponge. Texture firm and compressible. Surface uneven, with conulose areas, porous patches and few circular, dispersed oscules  

Size Information  
- 5 cm  

Colour  
Brown with lighter brown shading and dark brown in ethanol.  

Habitat Information  
Rock substrata inside of rock pools.  

Location  
North Wollongong
Family: Callyspongiidae

Scientific name: Callyspongia (Callyspongia) sp.2

Temporary name: Bass Point Purple (BPPurple)

Spicule Morphology: Megascleres: Small Oxeas (diactinal monaxons) of 65-80 μm


Size Information
- 2 cm

Colour
Light purple alive and sandy beige in ethanol.

Habitat Information
Rock substrata around rocky pools.

Location
North Wollongong.
Family:
Clionaidae

Scientific name:
Spheciospongia sp.

Temporary name:
Bass Point orange 11 (BPO1)

Spicule Morphology:
Megascleres:
Subtylostrongyles of two sizes 250μm-300 μm

Microscleres:
Spirasters of two sizes 30μm-40 μm

Morphology Category:
Solid massive sponge. Surface opaque, optically uneven with regularly dispersed conules. Texture firm and rubbery with not visible oscules.

Size information
- 60 cm

Colour
Bright orange alive and beige in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
Bass Point.
Family: Callyspongiidae

Scientific name: Callyspongia (Callyspongia) sp.1

Temporary name: Bass Point Light Pink 1 (BPLP1)

Spicule Morphology:
Megascleres: Small oxeas 75-80 μm

Morphology Category:
Massive sponge with vertically irregular shape. Smooth and uneven surface. Texture soft and elastic. Apical and circular/oval oscules usually about 3-6 mm in diameter.

Size information
- 10 cm

Colour
Light Pink alive and pale pink in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
Bass Point.
Family: Halichondriidae

Scientific name: Halichondria sp.1

Temporary name: Bass Point Blue 6 (BPBLU6)

Spicule Morphology:
Megascleres:
Curved thin oxeas (diactinal monaxons) of 210-500 μm

Morphology Category:
Encrusting irregular sponge. Texture soft and elastic. Uneven surface with smooth patches between the circular raised oscules scattered over surface. Oscules usually about 2-5 mm in diameter.

Size information:
- 1 m

Colour
Light Blue with yellow shading and tips. Beige in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
Bass Point.
Family:  
Chondrillidae

Scientific name:  
*Chondrilla sp.1*

Temporary name:  
Bass Point light brown (BPLB1)

Spicule Morphology:  
Microscleres  
Spherasters (12-15 μm)

Spined Tylasters spined (15-18μm)

Morphology Category:  
Thick encrusting sponge. Surface opaque, membranous, optically smooth, uneven with regularly dispersed microconules. Texture firm, rubbery and mucusy with raised scattered oscules over surface.

Size Information
- 60cm -1 m

Colour  
Orange brown sometimes with irregular dark brown spots alive and beige with darker brown shades in ethanol.

Habitat Information  
Rock substrata inside of rock pools.

Location  
Bass Point.
Family: Chondrillidae

Scientific name: Chondrilla sp.2

Temporary name: Bass Point dark brown (BPDB1)

Spicule Morphology: Microscleres
Spherasters (20-25 μm)

Spined Tylasters spined (15-18μm)

Morphology Category: Thick encrusting sponge. Surface opaque, membranous, optically smooth, uneven with regularly dispersed microconules. Texture firm, rubbery and mucusy with raised scattered oscules over surface.

Size information
- 70cm -1 m

Colour
Mostly dark brown with some lighter brown exterior unpigmented alive and beige with dark brown shades in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
Bass Point.
Family:
Darwinellidae

Scientific name:
Darwinella sp.

Temporary name:
Bass Point Pink 3 (BPP3)

Spicule Morphology:
NA

Morphology Category:
Encrusting sponge with a firm and soft texture. Spiny, uneven surface with few tiny oscules randomly scattered.

Size Information
- 6cm

Colour
Bright Pink in life and brown with pink shades in ethanol.

Habitat Information
Rock substrata inside of rock pools.

Location
Bass Point.
Family:
Pseudoceratinidae

Scientific name:
Pseudoceratina sp.

Temporary name:
Bass Point yellow 9 (BPY9)

Spicule Morphology:
NA

Morphology Category:
Solid massive sponge. Texture firm and compressible. Surface uneven, some areas are conulose with smooth and porous patches between and few circular, dispersed oscules.

Size information
- 24cm

Colour
Dark yellow in life light yellow in ethanol.

Habitat Information
Rock substrata inside of rocky pools.

Location
Bass Point.
Family: Thorectidae

Scientific name: *Hyrtios* sp.

Temporary name: Bass Point Dark Purple 10 (BPDP10)

Spicule Morphology: NA


Size Information
- 12 cm

Colour
Dark purple alive and in ethanol.

Habitat Information
Rock substrata inside of rocky pools.

Location
Bass Point.
Family: Podospongiiidae

Scientific name: Sigmosceptrella sp.

Temporary name: Bass Point Orange 11 (BP010)

Spicule Morphology:
Megascleres:
Anisostyles (Styles with unequal ends) of 300-350 μm

Microscleres:
Asymmetrical spinorhabds of 30 μm

Morphology Category:
Thick encrusting sponge. Surface opaque with regularly dispersed conules. Texture firm and rubbery with few small visible oscules.

Size Information
• 15 cm

Colour
Dark orange alive and light orange with sand colour patches in ethanol.

Habitat Information
Rock substrata inside of rocky pools.

Location
Bass Point.
Callyspongiidae

**Scientific name:**
*Callyspongia (Callyspongia) sp.3*

**Temporary name:**
South Shellharbour yellow 1 (SSYEL1)

**Spicule Morphology:**
Megascleres:
Curved Oxeas of 75 μm.

**Morphology Category:**
Thinline encrusting to irregular massive sponge. Texture soft not elastic. Smooth surface with few small circular oscules.

**Size Information**
- 2-4 cm

**Colour**
Light yellow alive and light beige in ethanol.

**Habitat Information**
Underside of boulders.

**Location**
South Shellharbour.
Family:
Halichondriidae

Scientific name:
*Halichondria* sp.2

Temporary name:
South Shellharbour yellow purple 5 (SSYP5)

Spicule Morphology:
Megascleres:
Oxeas of 60-200 μm.

Morphology Category:
Thinline encrusting to irregular massive sponge with soft texture. Smooth surface with few circular oscules.

Size Information
- 3-5 cm

Colour
Light yellow with purple shading alive and light beige in ethanol.

Habitat Information
Underside of boulders.

Location
South Shellharbour.
Family: Raspailiidae

Scientific name: Echinodictyum sp.

Temporary name: South Shellharbour yellow 5 (SSY5)

Spicule Morphology:
Megascleres:
Abundant oxeas of 40-70 μm

Less abundant styles of 75 μm

Morphology Category:
Thinline encrusting to irregular massive. Texture soft and easily torn. Smooth surface with circular oscules.

Size Information
• 1-5 cm

Colour
Light yellow alive and light beige in ethanol.

Habitat Information
Underside of boulders.

Location
South Shellharbour.
Family: Myxillidae

Scientific name: Myxilla sp.

Temporary name: South Shellharbour yellow 6 (SSY6)

Spicule Morphology:
Megascleres:
Subtylostyles of 200 μm

Subtylotes of 170 μm

C-sigmas of 30 μm

Isochelae of 30 μm

Morphology Category:
Encrusting sponge. Texture firm easily torn. Surface uneven, with poral channels and oscules not visible.

Size Information
- 2 cm - 5 cm

Colour
Dark yellow alive and light beige in ethanol.

Habitat Information
Underside of boulders.

Location
South Shellharbour.