Oxygen consumption rates of sponges and the effect of UV-B radiation and sediment

Heather Joanne Rose Murray

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VICTORIA UNIVERSITY OF WELLINGTON
Te Whare Wānanga o te Ūpoko o te Ika a Māui

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Abstract

Sponges are an important part of many benthic ecosystems, but little is known of their physiology and ecology, which is alarming given the predicted rise in global environmental stress and observed increases in mortality and disease of these organisms. The overall aim of this study was to further understand the physiological processes of sponges and the influence of environmental stress on these organisms. Oxygen consumption rates were investigated, as this is an important measure of the energy required for all physiological activities. The impact of ultraviolet-B (UV-B) radiation and sedimentation on sponges were selected because their input into the marine environment has been predicted to increase in the future, yet little is known about their affect on these organisms. Oxygen consumption rates were measured from a number of temperate and tropical sponges in New Zealand and Indonesia. Variability in oxygen consumption rates was found within and between species from their respective habitats. Interestingly, oxygen consumption rates in the temperate sponges appeared to increase with the proportion of inorganic material (spicule load). Ultraviolet-B radiation, at 60 μW cm^{-2}, was found to have no affect on the oxygen consumption of model temperate and tropical sponges. Sponge oxygen consumption, however, increased with repetitive exposure to 2.5 g L^{-1} of sediment, while rates decreased in specimens under higher levels at 8.5 and 16.5 g L^{-1}. Explanations for differences in oxygen consumption rates were constrained by the low level of information on sponges at a species-specific level, and highlighted the needed for future bioenergetic research. The results from the UV-B and sedimentation work suggest that some sponge species may be able to tolerate increasing environmental stress with the onset of global climate change, although interactions between factors could have the potential to negatively affect these organisms.

Keywords Sponges, respiration, oxygen consumption, spicules, ultraviolet-B radiation, sedimentation, New Zealand, Indonesia.

Acknowledgements

"I lift up my eyes to the hills, where does my help come from? My help comes from the Lord, the Maker of heaven and earth. He will not let your foot slip, he who watches over you will not slumber; indeed, he who watches over Israel will neither slumber nor sleep. The Lord watches over you, the Lord is your shade at your right hand; the sun will not harm you by day, nor the moon by night. The Lord will keep you from all harm, he will watch over your life; the Lord will watch over your coming and going both now and forevermore."

- Psalm 121

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General Introduction

Basic structure and function of sponges

Sponges are sessile aquatic multicellular organisms that live attached to benthic substrata in all depths of marine and freshwater environments. They occupy a significant amount of space in tropical areas (Rutzler 1970; Alvarez *et al.* 1990; Diaz *et al.* 1990; Schmahl 1990), polar regions (Dayton *et al.* 1974; Barthel & Gutt 1992; Sara *et al.* 1992), and temperate ecosystems (Lilly *et al.* 1953; Hiscock *et al.* 1983; Bell & Barnes 2000d). Their body consists of a thin outer layer called the pinacoderm, a central mass of cells and skeletal elements named the mesohyl, and the innermost choanoderm (Brusca & Brusca 2003). The choanoderm is composed of flagellated cells called choanocytes (Brusca & Brusca 2003). Sponges are suspension feeders; they draw water from the outside environment through pores (ostia) in the pinacoderm into the sponge matrix where oxygen and food particles are absorbed into the body cells by choanocyte flagella (Ruppert *et al.* 2004). The whip like action of choanocyte flagella circulate water through a unique system of canals within the sponge (Brusca & Brusca 2003). Wastes and unconsumed particles are then directed out of the sponge through controlled openings called oscula (Brusca & Brusca 2003).

The body form of a sponge can be divided into three basic types: asconoid (the simplest), syconoid, and leuconoid (the most complex) (Figure 1.1) (Ruppert *et al.* 2004). The choanoderm in the asconoid form is one cell thick; and can be simple and continuous or may become folded (the syconoid condition) (Figure 1.1) (Ruppert *et al.* 2004). The choanocyte

cells of the Leuconoid form are greatly subdivided comprising separate flagellated chambers (Figure 1.1) (Ruppert *et al.* 2004). Sponges have the unique ability to coordinate movement in all parts of the body, such as, the squeezing of water channels, or the contraction of oscula, without any form of nervous system (Nickel 2004). The mechanism of coordination is largely unknown, although movement may be controlled by chemical cues, electrical or mechanical stimuli (Pavans de Ceccatty 1971; Lawn *et al.* 1981; Mackie *et al.* 1983; Leys *et al.* 1999).

Asconoid   **Syconoid**   **Leuconoid**

↑ **Water flow**   ▨ **Pinacocytes**   ▩ **Mesohyl**   ■ **Choanocytes**
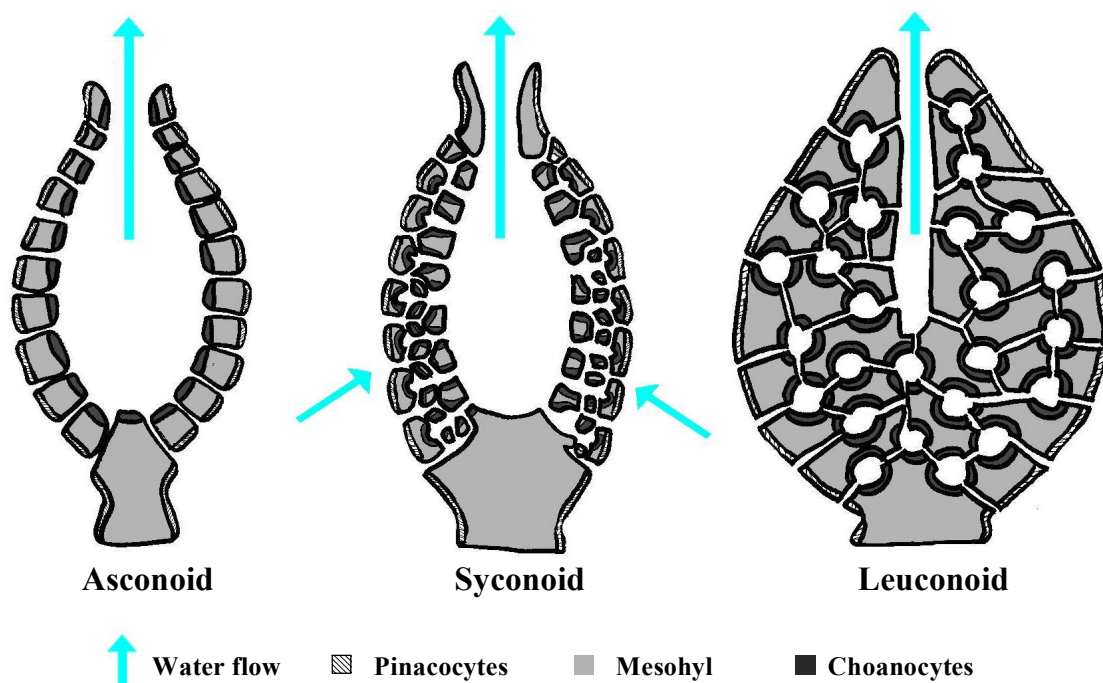
Figure 1.1   The three basic body types of sponges (Asconoid, Syconoid, and Leuconoid). The choanoderm in the asconoid form is one cell thick; this layer can remain simple and continuous, or may become folded (the Syconoid condition) (Ruppert *et al.* 2004). The choanocyte cells of the Leuconoid condition are greatly subdivided comprising separate flagellated chambers (Ruppert *et al.* 2004).

The skeleton in sponges consists of a soft mesohyl, which is stiffened by mineral spicules or spongin fibres (Bergquist 1978; Uriz *et al.* 2003a; Uriz *et al.* 2003b). Spicules are small silicon or calcium carbonate structures that come in a variety of shapes from rods to three-dimensional stars (Bergquist 1978). There are three main taxonomic divisions for sponges, within the phylum Porifera, calcareous (Calcarea), glass (Hexactinellida), and demosponges

(Demospongiae). Calcareous sponges consist of calcite spicules and can have an asconoid, syconoid or leuconoid body form (Bergquist 1998). Glass and demosponges, on the other hand, contain silica spicules and adopt only the leuconoid body form (Bergquist 1998). Many species of demosponge also contain spongin fibres and may not have spicules (Bergquist 1998).

The importance of sponges

Biochemical/Commercial significance

The marine environment has become a major source for new drug discovery (Mendola 2003; Blunt *et al.* 2004), ever since the first pharmaceutically important compound was isolated from a sponge (Bergmann & Feeney 1951). Sponges and their associated microbes can provide valuable natural resources, such as, cytotoxins, antifouling agents (e.g. anti-microbial compounds Cariello *et al.* 1982; Green *et al.* 1985; McCaffrey & Endean 1985), antibiotics, anti-tumour (Gunasekera *et al.* 1990; Litaudon *et al.* 1997), anti-inflammatory (Potts *et al.* 1992; Schmidt & Faulkner 1996) and antiviral compounds (Bergmann & Burke 1955; Perry *et al.* 1988) (see reviews by Lee *et al.* 2001; Taylor *et al.* 2007). Unfortunately the supply of natural compounds in wild sponges limits pharmaceutical development (e.g. Dumdei *et al.* 1998; Pomponi 2001; Sennet 2001), as harvesting is not always ecologically sustainable (Battershill & Page 1996). Sponge culture, however, is used for obtaining a reliable supply of bioactive products (Osinga *et al.* 1999; Donia & Hamann 2003).

Ecological significance

Sponges have a number of key functional roles within ecosystems including: impacting substrate, bentho-pelagic coupling, and associations with other organisms (see review by Bell 2008).

Sponges impact substrate via bio-erosion, mainly through the wearing away of coralline structures (Goreau & Hartman 1963; MacGeanchy 1977). It is a destructive process that creates reef sediment and impacts on the structural integrity of corals (Rutzler 1975). Sponges also impact substrate through reef creation, and substrate stabilisation, consolidation and regeneration by binding together fragments from the surrounding environment (Wulff & Buss 1979; Wulff 1984, 2001; Rasser & Riegl 2002).

Active suspension feeding in sponges link benthic and pelagic systems (bentho-pelagic coupling) through carbon, silicon and nitrogen cycling, and oxygen depletion (nitrogen cycling: Corredor *et al.* 1988; oxygen depletion: Richter *et al.* 2001; silicon cycling: Maldonado *et al.* 2005; Hadas *et al.* 2006; carbon cycling: Wulff 2006a; Jimenez & Ribes 2007). The high abundance of sponges in many environments (Barthel *et al.* 1990; Diaz *et al.* 1990; Bell & Barnes 2000d) and their ability to filter large quantities of water (Reiswig 1971b, 1974) increases their potential to significantly impact pelagic ecosystems (Bell 2008).

Sponges have many important associations with other organisms, such as, facilitating primary and secondary production (Bell 2008). Numerous marine sponges have been reported to contain unicellular cyanobacterial symbionts (Usher *et al.* 2005), which can comprise up to 60% of the sponge volume (Wilkinson 1992). Sponges with cyanobacterial symbionts occur frequently around the world (Wilkinson 1983; Roberts *et al.* 1998a), and these bacteria modify the physiology and morphology of these organisms (Sara *et al.* 1998). The symbionts may provide up to 80% of the carbon that sponges need (Wilkinson 1983; Cheshire *et al.* 1997), and they are thought to increase the growth of sponge hosts (Rutzler & Muzik 1993). It has been estimated that sponge symbiont relationships can contribute up to 10% of overall reef primary production in some areas (Wilkinson 1986). Primary and secondary production are linked due to the consumption of sponges by predators (Bell 2008). Sponge predators

include various species of crustaceans, opisthobranchs, molluscs, echinoderms and fish (Wulff 2006a).

Sponges also provide microhabitat and settlement substrate. Sponges support assorted microbial and macrofaunal communities (Rutzler 1976; Webster *et al.* 2004; Wulff 2006a; Taylor *et al.* 2007) and can provide habitat and protection for many benthic organisms, such as, juvenile crinoids (Barthel 1997) and fish eggs (Moreno 1980; Konecki & Targett 1989; Barthel 1997). Larger crinoids, ophiurids and holothurians are often observed on top or concealed inside Antarctic sponges (Gatti 2002).

Sponges disrupt near-boundary and reef level flow regimes (Hiscock 1983) and are also agents of biological disturbance due to the stability and variability in their assemblages (Pansini & Pronzato 1990; Bell *et al.* 2006; Roberts *et al.* 2006a; Wulff 2006a). Sponges also produce and release numerous chemicals that protect them against predation (Bakus & Green 1974; Pawlik *et al.* 1995; Becerro *et al.* 2003; Jones *et al.* 2005), aid in spatial competition (Engel & Pawlik 2005), and prevent overgrowth (Davis *et al.* 1991; Becerro *et al.* 1997; Lee *et al.* 2006).

Sponge physiology and ecology

Despite the vast ecological significance of sponges there is a lack of knowledge regarding their basic physiology (Wulff 2006b). This knowledge gap hinders the detection of factors responsible for the rapid decline of sponges in some marine habitats (Cerrano *et al.* 2000; Wulff 2006b; Garrabou *et al.* 2009). The overall aim of this thesis was, therefore, to better understand sponge physiology and the effect that environmental stressors may have on this physiology.

Physiology

Most publications on sponges have focused on ecology, taxonomy, and molecular biology (Becerro 2008). Publications on sponge physiology have accounted for only 0.7% of the literature on Porifera from 1945 to 2006 (Becerro 2008). The current study focuses on oxygen consumption as an indicator of the physiological response to stressful and non-stressful conditions. Oxygen consumption can be measured with relative ease and accuracy, compared to directly investigating other physiological aspects, such as, reproduction, assimilation, or growth. This also makes oxygen consumption measurements more favourable for studies investigating environmental effects on sponges. It is important, however, to first give a brief overview of the other energy-requiring physiological processes in sponges.

Growth and Development

Sponges are generally considered to be slow growing (Ayling 1983; Picton 1990; Fowler & Laffoley 1993; Turon *et al.* 1998), and the morphology, size, and colour of these organisms are highly varied, which makes taxonomic work difficult (Bell & Barnes 2001; Hentschel *et al.* 2006). A single sponge species can show a variety of different morphologies (Manconi & Pronzato 1991; Kaandorp & de Kluijver 1992), and changes to shape are mainly driven by environmental variation (Palumbi 1986; Kaandorp 1999; Hill & Hill 2002). The development of sponge morphology is important, therefore, as limitations in the body plan can influence the distribution patterns of these organisms (Bell & Barnes 2000b).

Growth can be affected by many factors, such as, sediment and light (Roberts *et al.* 2006b), nutrients from associated symbionts (Wilkinson & Cheshire 1988; Erwin & Thacker 2008), wave action (Wilkinson & Vacelet 1979; Bell 2002), and food availability (Trussell *et al.* 2006). When adverse conditions exist for growth, sponges often display fragmentation or

seasonal regression of their 'tissues' (Sara 1970; Elvin 1976; Barthel 1989; Bell & Smith 2004), fortunately they also possess fast regenerative capabilities (Ayling 1983). The energy needed for growth appears to vary between species, as several studies on different sponges have reported conflicting results (e.g. Riisgard *et al.* 1993; Thomassen & Riisgard 1995; Hadas *et al.* 2008). These authors showed that < 1 – 100% of the energy obtained by sponges from respiration was required for growth (Riisgard *et al.* 1993; Thomassen & Riisgard 1995; Hadas *et al.* 2008).

Reproduction

Reproduction in sponges is both asexual and sexual. Asexual reproduction occurs through fragmentation by budding or the production of gemmules (mainly in freshwater species) (Bergquist 1978; Brusca & Brusca 2003). Budding occurs when small sponge parts pull away from the parent and form new individuals, and has been associated with changes in water temperature in some cases (Corriero *et al.* 1998; Gaino *et al.* 2006). Gemmules are internal buds of sponge material, which can withstand freezing, desiccation, and anoxia due to a protective surface coating made from spicules and organic matter (Simpson & Fell 1974; Simpson & Gilbert 1974; Reiswig & Miller 1998). Most sponges are hermaphroditic; sperm are expelled into the water column and when they make contact with an individual of the same species are transported to the egg cells within the choanocytes (Elvin 1976; Fell 1976; Ayling 1980; Brusca & Brusca 2003). In some sponges eggs are expelled and fertilization occurs in the water column (Bergquist 1978). Fertilised larvae sink or crawl to a place of attachment where they transform into archeocytes and then miniature adult sponges (Bergquist 1978). To date no research has investigated the influence of reproduction on respiration rates in sponges, but it is assumed that this process is energetically costly as found in other suspension feeding organisms (Tankersley & Dimock 1993).

Assimilation, Excretion and the Pumping activity

The water pumping activity in sponges occurs as a result of beating choanocyte flagella (Bergquist 1978). The water current produced by pumping ensures food and oxygen can diffuse into the sponge, and is also used to exhale excretory and reproductive products (Bergquist 1978). Sponges are not selective in their particle uptake and therefore nutrients, regardless of their value, are filtered (Reiswig 1971b; Wolfrath & Barthel 1989). Particle uptake, however, is constrained by the maximum diameter of sponge ostia, generally 50 μm (Bergquist 1978; Kowalke 2000). Nutrient particles that enter the sponge body are unselectively phagocytosed by mobile archaeocytes (sponge cells) that move near the lining of inhalant canals, or captured by mucous nets or tentacles of choanocyte collars in the choanocyte chambers (Bergquist 1978). Phagosome vacuoles digest nutrients and once this process is completed they are expelled into the exhalent system or directly to the sponge exterior (Bergquist 1978).

In the past it was assumed that water pumping in sponges under normal activity was constant (Jorgensen 1966), but further research has found that sponges can reduce or stop pumping over several hours at irregular intervals (Reiswig 1971a; Vogel 1977; Pile *et al.* 1997; Tompkins-MacDonald & Leys 2008). Reproductive periods have also been correlated with a drop in pumping activity, as many choanocytes are transformed for gamete production (Bergquist 1978). Significant reductions in the water pumping activity of sponges can affect the oxygen consumption for respiration (Jorgensen *et al.* 1986). When pumping has ceased oxygen consumption rates are very low, but will rise with increased activity until a saturation point is reached (Hoffmann *et al.* 2008).

Respiration

At the organismal level, respiration is the transport of oxygen to cells (Raven & Johnson 1999). At the cellular level, respiration is the process of converting oxygen molecules and nutrients into usable energy (Lucas 1996), which then drives activities such as, biosynthesis, locomotion, digestion, assimilation, growth, and reproduction (McCue 2006). Oxygen consumption therefore indicates the total energy expenditure of an organism (Kleiber 1975). In sponges, oxygen diffuses into their 'tissues' along the outside cells of all inhalant canals, the general body exterior, and at the collar tentacles and cellular surfaces of the choanocytes (Bergquist 1978). The diffusion process is effective in sponges because the transmission path of cells is never more than 1.0 mm thick (Bergquist 1978).

Respiration rates have been used in a variety of studies of marine systems to measure:

1. Physiology and metabolic rates of a particular species (Ultsch 1973; Burlando *et al.* 1992; Thomassen & Riisgard 1995; Kowalke 2000; Gatti *et al.* 2002; Castellani *et al.* 2005; Hoffmann *et al.* 2005a; Hoffmann *et al.* 2005b; Schlappy *et al.* 2007; Hadas *et al.* 2008; Hoffmann *et al.* 2008).

2. The effects of biotic and abiotic factors, such as, temperature (Vohmann *et al.* 2009), heat stress (Zocchi *et al.* 2003), pH (Herrera & Plaza 1981), interactions between organisms (Davy *et al.* 2002; Beach *et al.* 2003), size, composition and light (Cotter 1978), ultraviolet-B radiation stress (Thomson *et al.* 1980; Aguilera *et al.* 1999; Obermuller *et al.* 2007), and cyanide (Gallagher & Howland 1994).

3. Energy budgets for various benthic communities (Reiswig 1974; Jorgensen & Revsbech 1985; Klumpp *et al.* 1987; Hopkinson *et al.* 1991; Rasmussen & Jorgensen 1992; Witte & Graf 1996; Coma *et al.* 2002; Coma & Ribes 2003; Parra *et al.* 2003; Hargrave *et al.* 2004; Trussell *et al.* 2006; Cherbadgy & Propp 2008; de Goeij *et al.* 2008a; de Goeij *et al.* 2008b).

4. Photosynthetic production (Szuch *et al.* 1978; Kevin & Hudson 1979; Reiswig 1981; Wilkinson 1983; Cheshire & Wilkinson 1991; Sand-Jensen & Pedersen 1994; Cheshire *et al.* 1997; Schonberg *et al.* 2005; Erwin & Thacker 2008).

Influence of environmental factors on sponges

Understanding and identifying the environmental pressures that influence any organism is fundamental for ecological research and effective conservation (Williams *et al.* 2002; Tuomisto *et al.* 2003). Human activities, such as, unsustainable fishing, coral mining, and clearing for coastal shrimp ponds, threaten reef ecosystems where sponges exist (Gatson 2000; Roberts *et al.* 2002; Pandolfi *et al.* 2003). Some scientific literature has also related dramatic variation in sponge populations to ENSO events (El Nino Southern Oscillation) and climatic changes (Vicente 1989, 1990; Fromont & Garson 1999). Despite the importance of sponges and the globally changing nature of their environment, ecological information is lacking (Becerro 2008). A large number of abiotic and biotic factors are thought to affect sponge distribution, abundance, and diversity, e.g. substrate (Konnecker 1973; Barthel & Tendal 1993), depth (Wilkinson & Cheshire 1989; Alvarez *et al.* 1990; Bell & Barnes 2000d; de Voogd *et al.* 2006; de Voogd & Cleary 2007), light availability (Sara *et al.* 1979; Cheshire & Wilkinson 1991), water flow (Barnes 1999; Bell & Barnes 2000d), bathymetry (Alvarez *et al.* 1990; Witman & Sebens 1990), tidal amplitude (Barnes 1999), nutrient levels (Storr 1976), algal growth (Storr 1976), competition (Russ 1982), larval life span (Bergquist *et al.* 1970), and chemical defence (Wright *et al.* 1997). Two of these factors were chosen for the focus of this study: sediment and ultraviolet stress. Sediment deposition and the penetration of harmful ultraviolet wavelengths are increasing in the marine environment (Crutzen 1992; Harris *et al.* 1995; Schindler *et al.* 1996; Madronich *et al.* 1998; Takeuchi 2004; de Vente *et al.* 2008), which is likely to influence sponge assemblages, yet little is known about the interaction of these factors on these organisms.

Ultraviolet radiation

The solar spectrum consists of ultraviolet radiation (UV-C 200 - 280 nm, UV-B 280 - 320 nm, and UV-A 320 - 400 nm), photosynthetically active radiation (PAR 400 – 700 nm) and infrared radiation (IR > 700 nm) (Figure 1.2) (Whitehead *et al.* 2000). In the Earth's atmosphere, scattering and absorbance, which depends on the composition of gases and particles, reduces radiation from the sun by approximately 35% (Whitehead *et al.* 2000). Ozone in the atmosphere strongly absorbs all UV-C and some UV-B wavelengths (Inn & Tanaka 1953; Molina & Molina 1986). This means that the Earth's surface receives all wavelengths above 320 nm and occasionally small amounts of UV-B (mainly in the region of 300 - 320 nm) (as indicated in Figure 1.2 taken from Whitehead *et al.* 2000).
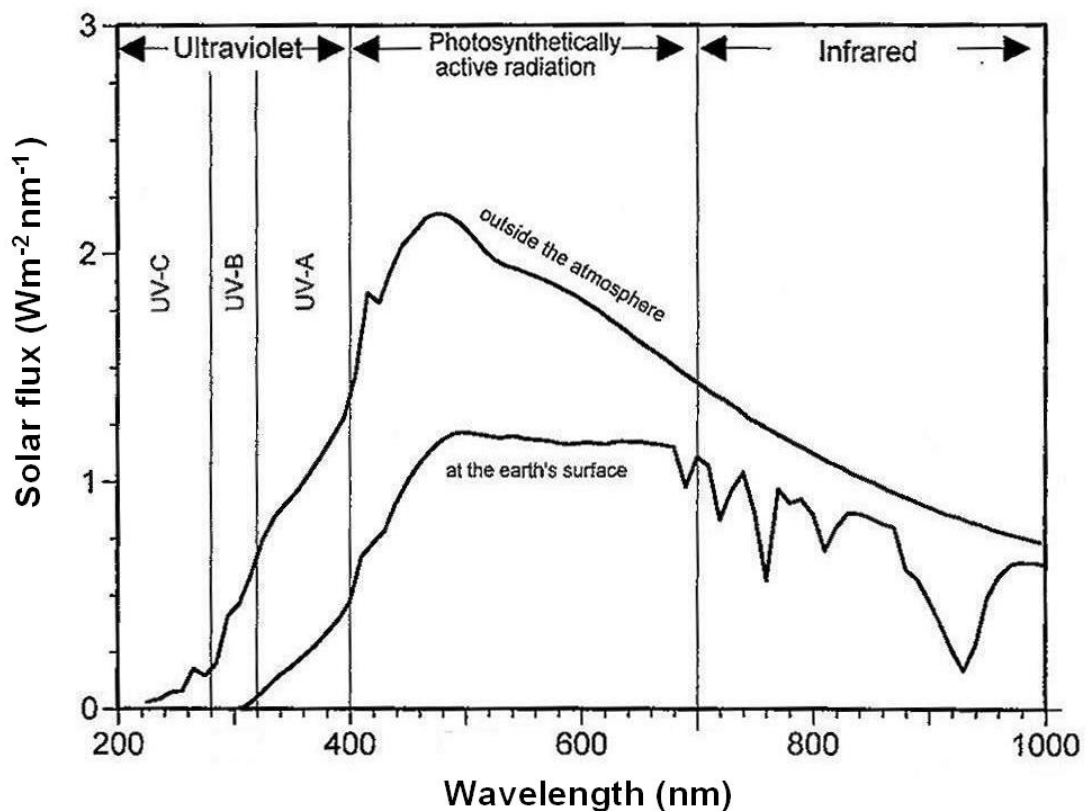
Figure 1.2 The solar spectrum outside the atmosphere and at the Earth's surface (figure from Whitehead *et al.* 2000). The spectrum consists of ultraviolet radiation (UV-C 200 - 280 nm, UV-B 280 - 320 nm, and UV-A 320 - 400 nm), photosynthetically active radiation (PAR 400 - 700 nm) and infrared radiation (IR > 700 nm) (Whitehead *et al.* 2000).

Stratospheric ozone depletion has increased substantially in the last 30 years at all latitudes due to atmospheric pollutants and interactions with climate change (Madronich *et al.* 1998; Salawitch 1998; Shindell *et al.* 1998), which has resulted in an increase in ultraviolet-B wavelengths reaching the Earth's surface (Madronich 1991; Crutzen 1992; Smith *et al.* 1992; Kerr & McElroy 1993). Global warming also acts to increase the penetration of ultraviolet radiation in aquatic ecosystems (Tedetti & Sempere 2006), due to the decrease in levels of dissolved organic matter in the water column (Hader *et al.* 2003). Photobleaching of particles in the water column due to ultraviolet-B radiation also enhances water clarity and increases the penetration depth of these wavelengths (Herndl *et al.* 1993; e.g. in open ocean surface waters: Sarpal *et al.* 1995; lakes: Williamson 1995; Lindell *et al.* 1996; Morris & Hargreaves 1997; and coastal regions Vodacek *et al.* 1997; Nelson *et al.* 1998).

Only 0.8% of the total energy reaching the Earth's surface is from ultraviolet-B radiation (UV-B radiation), yet this wavelength is responsible for half the photochemical effects in aquatic and marine ecosystems (Whitehead *et al.* 2000). The main effect of UV-B radiation in aquatic systems is to reduce productivity in freshwater and marine organisms, which includes bacteria and phytoplankton (Vincent & Roy 1993; Booth *et al.* 1997; Cullen & Neale 1997). The direct effects of UV-B radiation exposure can include damage to genetic constituents (Gorner 1994; Britt 1996; Buma *et al.* 1996a; Jeffrey *et al.* 1996; Malloy *et al.* 1997), proteins (Sinha *et al.* 1996; Wieinreb & Dovrat 1996), photosynthesis (Jones & Kok 1966; Post *et al.* 1996; Vass 1997), carbon allocation (Dohler & Bierman 1994; Goes *et al.* 1994; Wang & Chai 1994; Arts & Rai 1997), pigments (Hader & Worrest 1991; Dohler *et al.* 1995a; Buma *et al.* 1996b; Araoz & Hader 1997), respiration (Winckler & Fidhiany 1996; Beardall *et al.* 1997; Obermuller *et al.* 2007), nutrient uptake (Dohler & Kugel-Anders 1994; Dohler *et al.* 1995a; Goes *et al.* 1995; Hessen *et al.* 1997), nitrogen fixation (Sinha *et al.* 1996), and cell motility (Donkor *et al.* 1993; Elkelund 1994; Hessen *et al.* 1995; Hader 1997).

Prevention of damage by UV-B radiation occurs by avoidance, screening, photochemical quenching, repair, and acclimation (Vincent & Neale 2000). In marine organisms minimisation of ultraviolet damage occurs by (Roy 2000):

- Avoidance: repositioning away from light (Vincent & Quesada 1994), circadian rhythm (avoiding the surface at noon) (Tilzer 1973; Reynolds *et al.* 1987), and habitat choice (Ferreyra *et al.* 2006).

- Screening: outside the cell e.g. in skin (Lowe & Goodman-Lowe 1996), cell walls (e.g. in algae Xiong *et al.* 1996), cuticles (e.g. in zooplankton Hessen & Soerensen 1990), or sheaths (e.g. in cyanobacteria Garcia-Pichel & Castenholz 1991); inside the cell e.g. mycosporine-like amino acids (Karentz *et al.* 1991b; Dunlap & Shick 1998), lipid soluble vitamin D (Holick & Guillard 1982), water-soluble biopterin glucoside (Matsunaga *et al.* 1993), gadusol metabolite (Grant *et al.* 1980), inorganic (e.g. salt crystals) or organic (e.g. epiphytes) coverings (Trocine *et al.* 1981; Stochaj *et al.* 1994; Vincent & Quesada 1994).

- Repair of direct UV damage: DNA repair by photoreactivation or excision (Friedberg 1985; Pfeifer 1997), stress protein repair (i.e. heat-shock proteins: Shibata *et al.* 1991; Dohler *et al.* 1995b).

- Repair of indirect UV damage: antioxidant enzymes, lipid-soluble (e.g. carotenoids) and water-soluble (e.g. ascorbic acid) antioxidants (Dunlap & Yamamoto 1995).

- Acclimation: short (e.g. fluorescence Hall & Rao 1994) and long-term physiological changes (e.g. biosynthesis of screening compounds Carreto *et al.* 1989; Wood 1989; Lesser 1996), and community variations in ultraviolet sensitivity (Helbing *et al.* 1992; Karentz & Spero 1995; Davidson *et al.* 1996).

Harmful UV-B radiation, therefore, is likely to directly impact the surface layers (pinacoderm) of sponges, particularly as penetration of these wavelengths increase. The cells

in the pinacoderm, as mentioned previously, can harbour photosynthetic symbionts (Lee *et al.* 2001), are used for oxygen uptake (Bergquist 1978), can transfer electrical impulses to shut down pumping activity (Yahel *et al.* 2007), allow waste excretion (Bergquist 1978), produce buds in reproduction (Brusca & Brusca 2003), and form the pores for inhalant and exhalent current (Bergquist 1978). If surface layers are damaged by UV-B radiation, it seems likely that this will impair the aforementioned functions, and may ultimately limit growth, reproduction, and survival of sponges.

Sediment

Globally the discharge of sediment into oceans is estimated to be within the range of 15 - 20 billion tons per year (Milliman & Meade 1983; Milliman & Syvitski 1992; Walling & Webb 1996) and it is expected that this yield will continue to increase due to climate change and agriculture (Dunne 1979; Takeuchi 2004). Land-use and climate change accelerate the natural soil erosion process (de Vente *et al.* 2008), thereby elevating sedimentation levels in marine coastal environments (Rogers 1990). In the latter half of the 21st century rainfall intensity and volume increased (Folland *et al.* 2001), which has potentially caused a rise in global sediment production (Takeuchi 2004). Desertification is also another source of sediment increase, due to the loss of productive land, 60,000 km^2 since 1990, from over-cultivation, deforestation, and poor irrigation practise (Takeuchi 2004). Other research has found a decrease in sediment reaching the oceans in Europe, due to retention in reservoirs (Syvitski *et al.* 2005). Dam construction has been identified as a major cause for riverine sediment load decrease (Vorosmarty *et al.* 2003; Syvitski *et al.* 2005; Yang *et al.* 2005; Walling 2006). Changes to sediment discharge, therefore, will have a major impact on the global landscape and on water and nutrient circulation (Takeuchi 2004), which will have important ecological impacts on the marine environment, particularly in coastal waters.

The effect of sedimentation upon marine organisms has stirred much interest within the literature (Seapy & Littler 1982; Rogers 1990; Engledow & Bolton 1993; Shaffer & Parks 1994; Airoldi *et al.* 1995). The effects of sedimentation are varied. Sediment suspended in the water column can reduce light, which limits growth and survival of primary producers such as sea grasses (Fitzpatrick & Kirkman 1995), benthic algae (Vadas & Steneck 1988) and symbiotic micro-algae (Maldonado & Young 1998). High sediment and hydrodynamic forces can also have a deleterious abrasive effect on living organisms (Carballo & Garcia-Gomez 1994), whereas particles from sewage effluent and run-off can alter the chemical and physical properties of marine habitats (Baker *et al.* 1995). Sedimentation is also known to alter the dynamics and structure of subtidal assemblages (Rogers 1990; Airoldi & Cinelli 1997; Wulff 1997; Bell & Barnes 2000d), and changes often occur along a gradient (Naranjo *et al.* 1996; Bell & Barnes 2000d). High rates of sedimentation are expected to exclude less tolerant species, which will be detrimental to the richness and diversity of some marine communities (Daly & Mathieson 1977; Little & Smith 1980; Engledow & Bolton 1993; Salinas & Urdangarin 1994). Other papers, however, report that sediment disturbance can increase diversity by preventing competitively dominant species from monopolising space and maintaining patchiness within a habitat (Foster 1975; Taylor & Littler 1982; Littler *et al.* 1983; McQuaid & Dower 1990). Roberts *et al.* (1998b), for example, documented that sewage discharge into a temperate reef rapidly changed the biota from an assemblage of mainly sponge and algae, to an area dominated by silt and ascidians. Airoldi and Cinelli (1997), in contrast, found that a reduction in sediment resulted in a lower diversity and increased evenness of algal assemblages. It is clear that the distribution and abundance of organisms under sediment pressure is a careful balance between sensitivity to, and tolerance of stimuli produced by sedimentation (Tompkins-MacDonald & Leys 2008).

Sensitivity of invertebrates to high rates of sedimentation has been found in several studies (Wellington 1982; Rogers 1990; Riegl *et al.* 1996). High sedimentation suffocates corals, decreases their growth and calcification rates, and can alter branching morphology (Wellington 1982), consequently their abundance is significantly reduced in disturbed sites compared to more pristine reefs (Crabbe & Smith 2002). Sediment deposition has been found to be the most important factor controlling short-term sponge diversity (Carballo *et al.* 2008). Experimental studies have found that high rates of sedimentation, burial, or the smothering of sponges leads to the closure of their inhalant pores, and a shut-down of the normal pumping procedure (Gerrodette & Flechsig 1979; Cerrano *et al.* 1999; Tompkins-MacDonald & Leys 2008). Sponge assemblages, therefore, will be affected by increasing sediment yields in the marine environment, and more research is necessary to establish their tolerance levels.

Research objectives

Research into physiological processes within an organism and how these activities respond to specific stressors is important (Downs *et al.* 2005). The way in which key traits within an organism interact with changing environmental conditions will determine their survival, particularly characteristics that increase sensitivity to disturbance (Ribera *et al.* 2001; Charrette *et al.* 2006; Cleary & Mooers 2006).

The objectives for this study were to:

1. Measure and compare oxygen consumption rates between temperate and tropical sponges, and determine whether differences existed in the metabolic responses of these organisms to light.

2. Measure and compare the effect of ultraviolet-B radiation on the oxygen consumption rates of model temperate and tropical sponges.

3. Measure the effect of increasing levels of sediment on oxygen consumption rates of a model temperate sponge.

Metabolic rates in selected temperate and tropical sponges

Despite the importance of sponges in many benthic ecosystems, very little is known about their physiology. The aim of this study was to measure and compare oxygen consumption rates, an important indication of the energy required for all physiological processes, between temperate and tropical sponges and to establish whether their metabolic responses differed in response to light. It was hypothesised that dark respiration rates would be greater in tropical sponges due to higher temperatures and the need for increased pumping activity in food depleted waters, but net oxygen consumption would be lower in the light compared to temperate sponges due to oxygen production by photosymbionts. Oxygen consumption rates were measured for six temperate and six tropical sponge species from New Zealand and Indonesia, respectively. Dark respiration rates were approximately 60% higher for the tropical sponges than for temperate species, but in the light net oxygen consumption rates were the same. Oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) for the temperate sponges were found to increase with the amount of inorganic matter that they contained; this was not measured for tropical species. Of particular note, temperate calcareous sponges had a higher net oxygen consumption rate in the light and a greater proportion of inorganic matter compared to demosponges. The increase in inorganic material was linked to high wave-energy of the temperate habitat, and the need for a greater density of calcareous spicules than silica spicules to achieve an equivalent structural strength. The greater production of inorganic matter was thought to increase the energy demands for these sponges and hence account for their higher oxygen consumption.

Keywords Dark respiration, oxygen consumption, sponges, spicules, New Zealand, Indonesia.

2.1 **INTRODUCTION**

Despite the significance of sponges in many benthic environments there is a lack of information regarding their basic physiology, which may hinder the detection of factors responsible for their rapid decline in some marine habitats (Cerrano *et al.* 2000; Wulff 2006b; Garrabou *et al.* 2009). Oxygen consumption, or respiration, is one particular aspect of sponge physiology in which investigations have been limited to a few species (e.g. Kowalke 2000; Gatti *et al.* 2002; Hoffmann *et al.* 2005a; Hadas *et al.* 2008; Hoffmann *et al.* 2008). At the organismal level, respiration is the transport of oxygen to cells (Raven & Johnson 1999). At the cellular level, respiration is the process of converting oxygen molecules and nutrients into usable energy (Lucas 1996), which can then drive activities such as, biosynthesis, locomotion, digestion, assimilation, growth, and reproduction (McCue 2006). Information on respiration, or oxygen consumption, is important therefore, as oxygen uptake is required for all energetic processes, and indicates the total energy expenditure of an individual (Kleiber 1975). Understanding the energetic needs and constraints that influence sponges and their growth is of considerable interest for understanding natural sponge assemblages and aquaculture systems (Hadas *et al.* 2008), and indicates how an organism's physiology responds to its environment (Coma *et al.* 2002).

Most sponges contain a large number of associated microbes, some of which are photosynthetic (Wilkinson 1983; Wilkinson 1992; Roberts *et al.* 1998a; Usher *et al.* 2005). The oxygen consumption rates of sponges will therefore reflect the combined activity of the sponge and these microbes, and it is difficult to separate the two (Cheshire *et al.* 1997). Measurements made in the dark, therefore, will indicate respiratory oxygen consumption of the sponge and microbes. Measurements in the light, however, will indicate net oxygen flux (i.e. the balance between respiratory oxygen consumption of the sponge and photosynthetic oxygen production of symbionts, if present). For phototrophic sponges measurement of net

oxygen flux in the light can indicate the level of photosynthetic activity from associated microbes, and such data are important for determining the combined production exhibited in these sponges (Cheshire & Wilkinson 1991).

Sponges living in temperate and tropical latitudes experience significantly different environmental pressures and this may have an impact on their oxygen consumption rates. High light, low nutrient tropical waters often favour sponges with high numbers of photosynthetic symbionts (Reiswig 1973; Wilkinson 1979; Wilkinson & Vacelet 1979; Bak & Luckhurst 1980; Wilkinson 1983). Higher irradiance levels in these tropical areas increases the photosynthetic oxygen production in sponges with symbionts (Cheshire & Wilkinson 1991), while warmer temperatures are associated with higher respiration rates, potentially due to increased growth (Schmidt-Nielsen 1975). Low food concentrations in tropical waters also increase the need for suspension feeders to filter water, which elevates their energetic expenditure (Willows 1992; Trussell *et al.* 2006). Particular characteristics of sponge species within temperate and tropical latitudes may also have an influence on oxygen consumption rates. Demosponges, for example, are the most common sponge class and adopt the leuconoid body form, which consists of complex folded mesohyl tissue with a greater surface area for oxygen diffusion (Bergquist 1978). This means that such sponges are likely to have higher oxygen consumption rates per unit of body mass. Reiswig (1981) also suggested that respiration rates may differ between asconoid, syconoid and leuconoid sponges due to the varying nature of their aquiferous systems. Demosponges are also thought to contain a greater abundance of associated microbes (some being phototrophic) than do calcareous or hexactinellid sponges (Vacelet & Donadey 1977; Hentschel *et al.* 2002; Hentschel *et al.* 2003) elevating the level of photosynthetic oxygen production.

Aim and hypotheses

A number of studies have investigated photosynthetic oxygen production and consumption in tropical species (Wilkinson 1983; Cheshire & Wilkinson 1991; Seddon *et al.* 1992; Schonberg *et al.* 2005; Erwin & Thacker 2008), but little is known about the oxygen consumption and respiration rates of temperate species (Coma *et al.* 2002). The aim of this study was therefore, to measure and compare oxygen consumption rates between temperate and tropical sponges and to establish whether metabolic responses differed in response to light. This was accomplished by measuring oxygen consumption rates in the light (net oxygen consumption rates) and dark (dark respiration rates) for selected temperate and tropical sponges. It was hypothesised that:

1. Dark respiration rates would be greater in tropical sponges due to higher temperatures and the need for increased pumping activity in food depleted waters (Schmidt-Nielsen 1975; Willows 1992), but net oxygen consumption rates in the light would be lower than temperate sponges due to oxygen production by photosymbionts (Cheshire & Wilkinson 1991; Schonberg *et al.* 2005).

2. Oxygen consumption rates would be different between sponge species within their respective habitats (as observed by Hadas *et al.* 2008).

3. Dark respiration rates would be higher for demosponges than calcareous sponges due to greater aquiferous system complexity (Bergquist 1978), but net oxygen consumption rates in the light would be lower as a result of abundant photosymbionts (Hentschel *et al.* 2003).

4. Oxygen consumption rates would be lower in the light than in the dark for individual species due to the influence of abundant associated microbes (Cheshire & Wilkinson 1991; Schonberg *et al.* 2005).

2.2 **METHODS**

Sponges and collection sites (temperate and tropical)

The sponges for this study were chosen based on abundance, ease of collection, and the ability to identify them to genus level.

Temperate sponges

The temperate sponge specimens were collected from the Wellington South Coast of New Zealand, at Princess Bay, Breaker Bay and Barretts reef (Figure 2.1). *Mycale* sp. were collected from the piles at Queens Wharf, inside Wellington Harbour (41°17'S 174°46'E). Four demosponges (*Tethya bergquistae* Hooper 1994, *Strongylacidon conulosa*, *Mycale* sp., and *Stellata* sp.) and two calcareous sponges were chosen (*Leucosolenia echinata* and *Leucetta* sp.) (Figure 2.2). These sponges were identified from spicule preparations and photos with the taxonomic assistance of Jade Berman (VUW) and Dr. Michelle Kelly (NIWA).

Tropical sponges

The tropical sponges were collected from the reefs around Hoga Island, in the Wakatobi Marine National Park off the Southeast coast of Sulawesi, Indonesia (Figure 2.3). All the species investigated were demosponges (*Cribochalina* sp., *Dysidea herbacea*, *Aaptos* sp., *Hyrtios* sp., Unidentified sp., and *Liosina* sp.) (Figure 2.4). These sponges were identified from Colin and Arneson (1995).
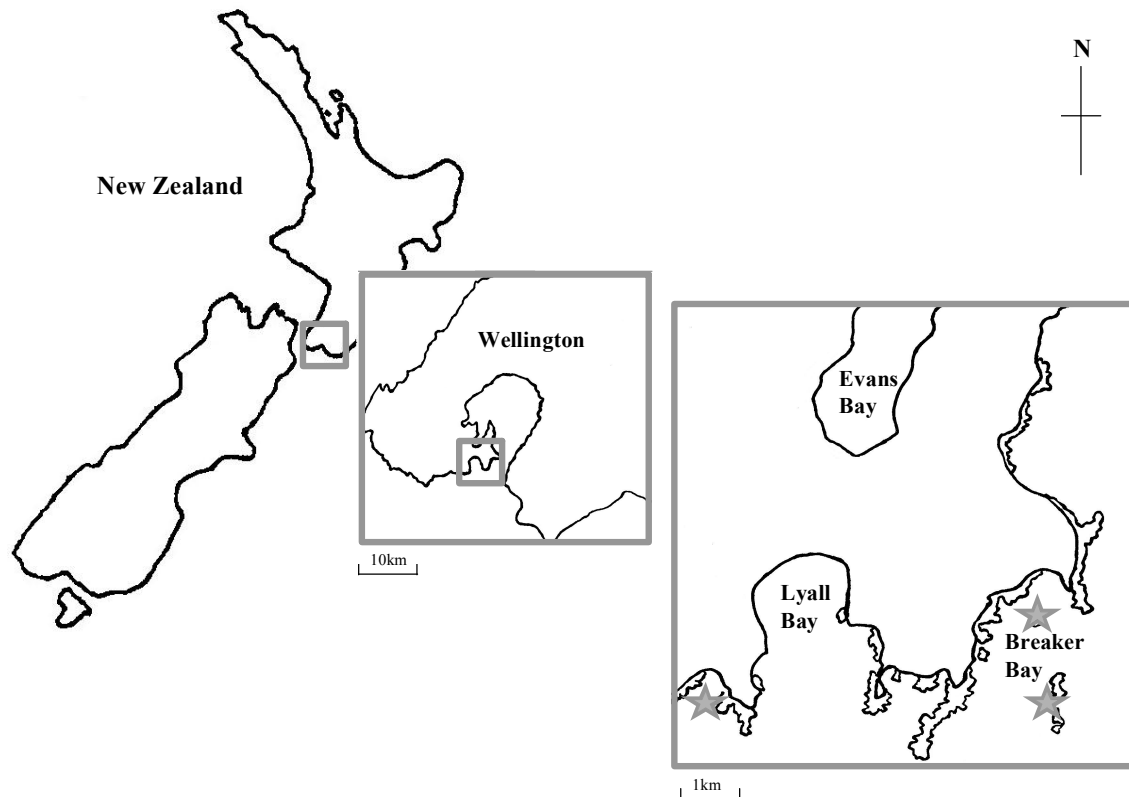
Figure 2.1 Collection site of the temperate sponges at Princess Bay, Breaker Bay, and Barretts reefs (stars in order left to right), Wellington South Coast, New Zealand. Collection site within Wellington Harbour (Queen's Wharf) not shown.

Figure 2.2 Temperate sponge species collected for this study (each approximately 4 cm^3). Column A includes pictures of the sponges alive in the aquaria, while column B shows the specimens removed from the water.
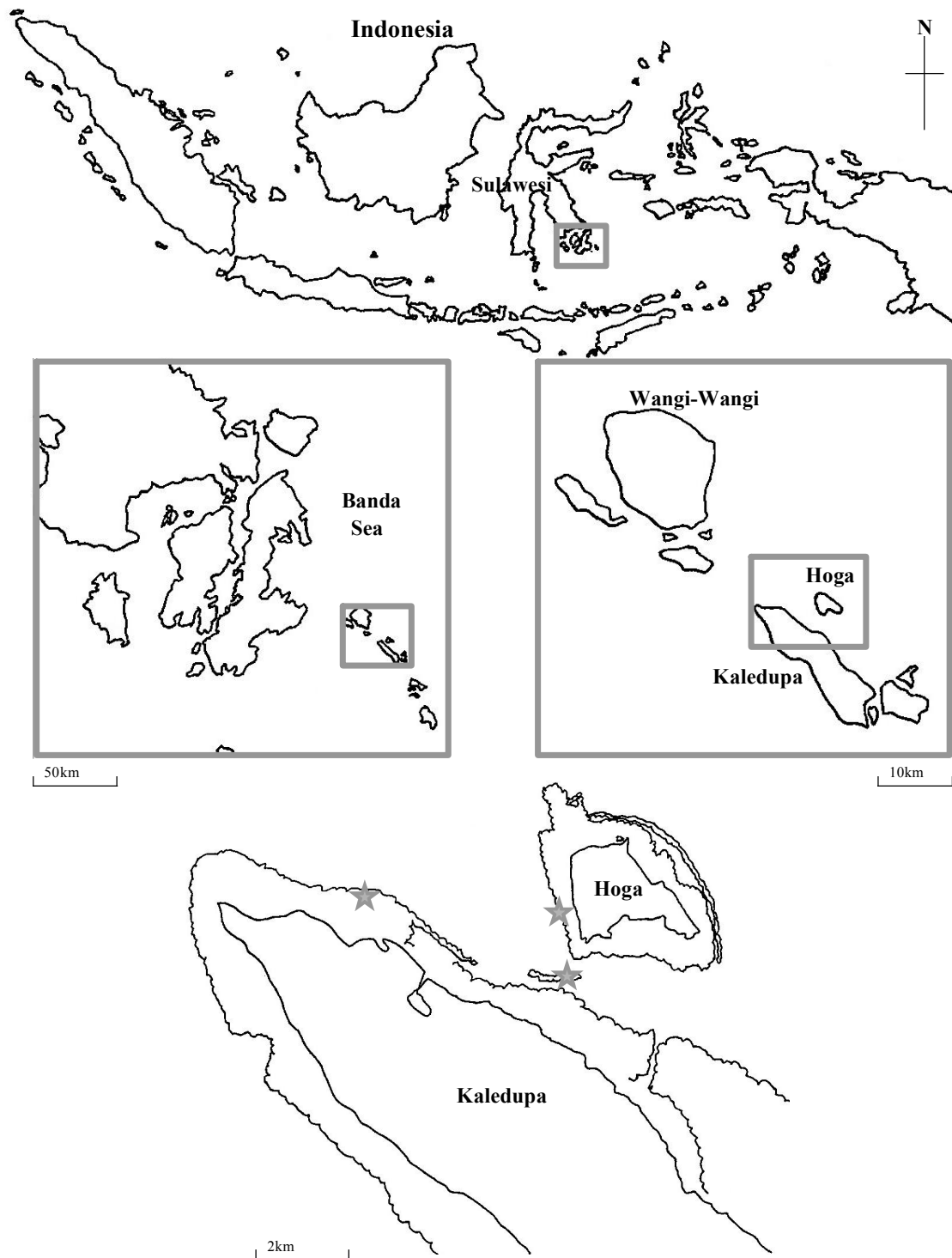
Figure 2.3 Collection sites (stars) of the tropical sponges, Hoga Island, Wakatobi Marine National Park off the Southeast coast of Sulawesi, Indonesia.

Cribochalina sp.

Dysidea herbacea

Aaptos sp.

Hyrtios sp.

Unidentified sp.

Liosina sp.

Figure 2.4 Tropical sponge species collected for this study (each approximately 4 cm^3). All the pictures are of specimens that have been removed from the water.

Collection method and housing prior to measurement

<u>Temperate</u>

Temperate sponges were collected in June – September 2008 from the Wellington South Coast by SCUBA or snorkelling. Sponge specimens of approximately 4 cm^3 were carefully removed with a knife by cutting close to the substrate, minimising cut surface area, and avoiding slicing through oscula. In some cases part of a larger sponge was used, but it was ensured that each specimen piece had its own central osculum and represented a complete entity (i.e. with inner and outer 'tissue'). Parts of large sponges are commonly used to make oxygen measurements more manageable without negative effects occurring (Cotter 1978; Burlando *et al.* 1992). Sponges were transported in seawater to an aquarium and housed in glass tanks of approximately 100 L when not in experimental use. Fresh unfiltered seawater was constantly supplied to each tank at approximately 13.4 L min^{-1}, creating an open flow system, which is important for sponges (Vogel 1974, 1977, 1978). The seawater temperature remained at approximately 13 ± 1ºC for the duration of the experiment. Each sponge was attached with cotton to a circular plate used to anchor the sponges and employed in the chamber to measure oxygen consumption. The sponges were acclimated for 24 hours prior to experimentation, consistent with other sponge physiology studies (Zocchi *et al.* 2003; Nickel 2004; Hadas *et al.* 2008). It is noted, however, that much shorter acclimation periods with no negative effects have also been used (Riisgard *et al.* 1993; Kowalke 2000).

<u>Tropical</u>

The tropical sponges from around Hoga Island were collected in July – August 2008 by SCUBA or snorkelling. Only four specimens could be collected at a time due to limited aquarium space. The sponges were transported as described above, to the laboratory on the island. The specimens were acclimated in the experimental aquarium (explained below), as large-scale holding tanks were not available. The sponges were acclimated for approximately two hours prior to measurement (rather than 24 hours in the temperate sponges), as electrical

power was unavailable over night to run aquarium pumps and aeration stones. The potential effects of different acclimation periods are considered in the discussion. Seawater was sourced from the shore by bucket every 20 minutes and fed into a header tank that supplied the experimental aquarium, as pumps providing unfiltered seawater were not available. The seawater temperature remained at approximately $28 \pm 1°C$ for the duration of the experiment.

Sampling design (temperate and tropical)

Oxygen consumption was measured over 15 minutes in both the light and the dark for 10 - 20 replicates of each sponge species, depending on the number of specimens that could be collected. Fewer replicates were used for the tropical sponges due to the limited sampling time on the Island.

Experimental set up (temperate and tropical)

The experimental aquarium (approximately 20 L) was an open flow system with seawater being replaced at a rate of 4 L min^{-1} (see Figure 6.1, 6.2 in Appendix for set-up details). Two aquarium pumps were used to increase the current within the experimental tank, each device circulating the water at 4 L min^{-1}. Four halogen lamps fitted with neutral density filters provided photosynthetically active radiation (PAR) at 20 μmol photons m^{-2} s^{-1}. Photosynthetic compensation in sponges can occur within the range of 10 - 30 μmol photons m^{-2} s^{-1} (Cheshire *et al.* 1995; Schonberg *et al.* 2005) and therefore, the irradiance chosen was expected to be sufficient to produce net production of oxygen in the light, if photosymbionts were present.

Measuring oxygen consumption (temperate and tropical)

In the experimental tank, a clear plastic closed-system cylinder (300 ml) was used to measure oxygen consumption, similar to that employed by Gatti *et al.* (2002). The cylinder was placed over a sponge and a fibre-optic oxygen mini-sensor and temperature electrode was fitted into

a rubber bung that was secured in the top of the chamber (FIBOX 3, 505 nm, combined with

$_{FIBOX}$ 5.20 Software for data logging; Precision Sensing GmbH, Regensburg, Germany). The

rubber bung prevented air bubbles or new water entering the cylinder; a magnetic spin bar

rotating at 130 rpm kept water flow constant and well mixed within the chamber. The oxygen

electrode was calibrated at the beginning of each working day in 100 ml of water either

containing 1 g of sodium sulphite (Na_2SO_3) for 0% oxygen saturation, or with air bubbled

through it for 10 minutes beforehand for 100% oxygen saturation. The salinity level in the

experimental aquarium was measured every working day with a refractometer.

After the acclimation period each temperate sponge was moved into the experimental tank 15

minutes prior to measurement. Tropical sponges did not need to be moved as they were

acclimated in the experimental tank. Oxygen consumption of each sponge was recorded

every five seconds for 15 minutes in the light (net oxygen consumption), and in the dark (dark

respiration) after a two-hour dark acclimation period. Only sponges that had their oscula fully

expanded, indicating normal pumping activity, were used for measurements of oxygen

consumption. Once measurements were completed, each specimen was photographed for

identification, blotted with a paper towel and wet weighed. Net oxygen consumption rates

were calculated from the decrease in oxygen concentration (% saturation) over 15 minutes,

taking into account temperature, salinity, and water volume (i.e. chamber volume minus

sponge volume). These measurements were standardised for the dry weight of each specimen

and multiplied by four to represent the hourly oxygen consumption rate (units mg O_2 g^{-1} DW

h^{-1}). At the completion of the oxygen measurements each sponge was transferred into a

drying oven at 60°C for three days to reach a stable weight, and its dry weight recorded.

Percentage of inorganic matter in sponges

<u>Ash weight</u> (temperate sponges only)

As there were unexpected patterns in the oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) of the temperate sponges ash weight measurements were collected. Ash weight is the inorganic fraction of the sponge dry weight and is commonly used to describe the spicule content (e.g. Stone 1970; Palumbi 1986; Barthel 1991). Unfortunately, many of the previously measured sponges had already been disposed of (*Strongylacidon conulosa*, *Stellata* sp., *Leucetta* sp., most of the *Tethya bergquistae* and *Leucosolenia echinata*), so new specimens of the same size were collected for those species. Ash weight was obtained by heating the sponges in a muffle furnace at 500°C for five hours to remove all organic matter. The sponges were allowed to cool in the muffle furnace overnight, and then the ash weight of each was recorded. The proportion of inorganic matter in each temperate sponge was calculated from the ash weight divided by the dry weight. There were no facilities at the tropical site to ash sponges.

Analysis of data

In all cases where the assumption of normality or equal variances was not satisfied ($p < 0.05$) data were log transformed or, failing that, a non-parametric test was used. Means and 95% confidence intervals were reported for the original untransformed data set. Independent *t*-tests or the associated Mann Whitney analysis was used to test differences between oxygen consumption rates of temperate and tropical sponges, demosponges and calcareous sponges, and light and dark rates within a species. The Kruskall Wallis analysis and the non-parametric *post-hoc* test (see Field 2005) analysed differences in oxygen consumption rates between species, and were also used to test differences in the percentage of inorganic matter between temperate sponge species. A Mann Whitney analysis was used to test differences in the percentage of inorganic matter between temperate calcareous sponges and demosponges. A regression equation was used to establish whether a relationship existed between the

average percent of inorganic matter and average oxygen consumption rates between temperate sponges. Effect sizes (r) were also calculated to indicate the strength of the relationship between light and dark oxygen consumption rates of tropical and temperate sponges, calcareous sponges and demosponges, within a species, and between the amount of inorganic matter of calcareous sponges and demosponges (large effect size $\geq$ 0.50, medium $\geq$ 0.30, and small $\leq$ 0.10, which account for over 25%, 9%, or 1% of the total variance respectively) (see Field 2005). *Liosina* sp. and Unidentified sp., two of the tropical sponges, were not included in the analyses as there were not enough replicates collected for these species ($N = 2$).

2.3 **RESULTS**

Oxygen consumption

Temperate vs. tropical

There was no difference in the net oxygen consumption rates between tropical and temperate sponges in the light (t_{119} = -0.719, p = 0.473, r = 0.066) (Figure 2.5). In the dark, however, tropical sponges had a 60% higher respiration rate than the temperate species (U = 501.000, p = 0.007, r = -0.297) (Figure 2.5).
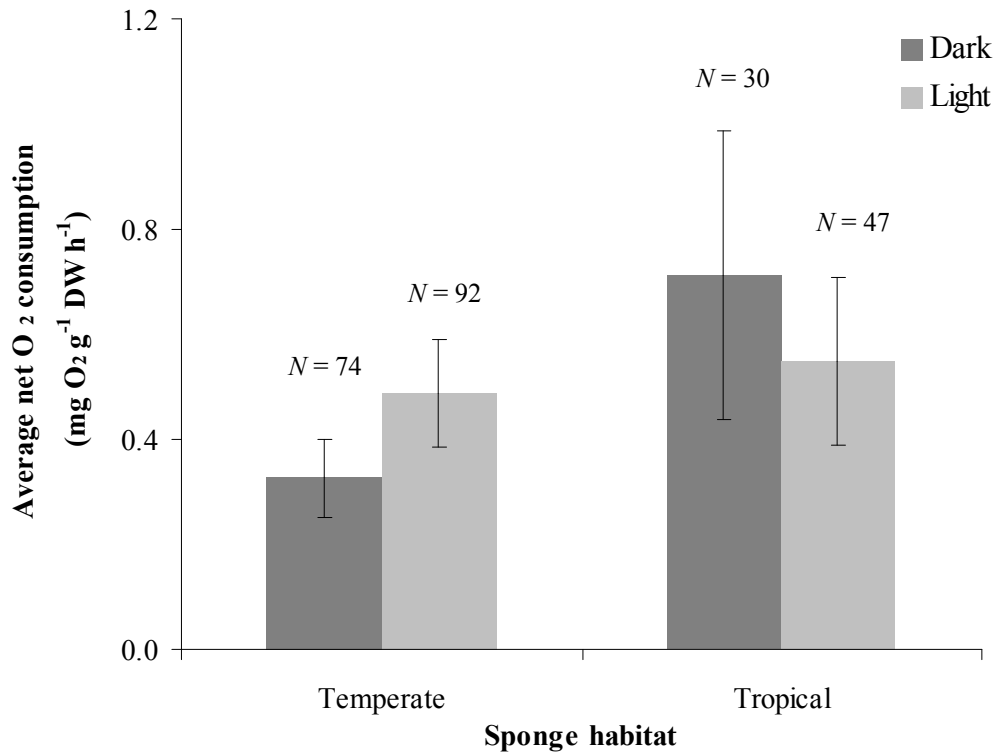
Figure 2.5 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) for temperate and tropical sponges in the light (20 μmol photons m^{-2} s^{-1}) and the dark, ± 95% confidence intervals. The temperate sponges consisted of four species of demosponge (*Tethya bergquistae, Strongylacidon conulosa, Mycale* sp., and *Stellata* sp.) and two calcareous sponges (*Leucosolenia echinata*, and *Leucetta* sp.). The tropical specimens consisted of six demosponges (*Aaptos* sp., *Dysidea herbacea, Hyrtios* sp., Unidentified sp., *Liosina* sp., and *Cribochalina* sp.).

Temperate

Oxygen consumption rates between species

Net oxygen consumption rates measured for six temperate sponges in the light and the dark varied considerably, and two species demonstrated large variability (Figure 2.6). In both the light and dark there were differences in the net oxygen consumption rates between species (H_5 = 51.165, $p < 0.001$; H_5 = 35.821, $p < 0.001$, respectively). The *post-hoc* analysis showed that oxygen consumption rates in *Strongylacidon conulosa* did not differ from any of the other species in the light or dark ($p > 0.05$). In the dark, respiration rates in *Leucosolenia echinata*

did not differ from any of the other species ($p > 0.05$). In the light, however, *L. echinata* had a higher net oxygen consumption rate than did *Tethya bergquistae* and *Stellata* sp. ($p < 0.05$). In the light and dark *Leucetta* sp. and *Mycale* sp. had a higher net oxygen consumption rate than did *T. bergquistae* and *Stellata* sp. ($p < 0.05$).
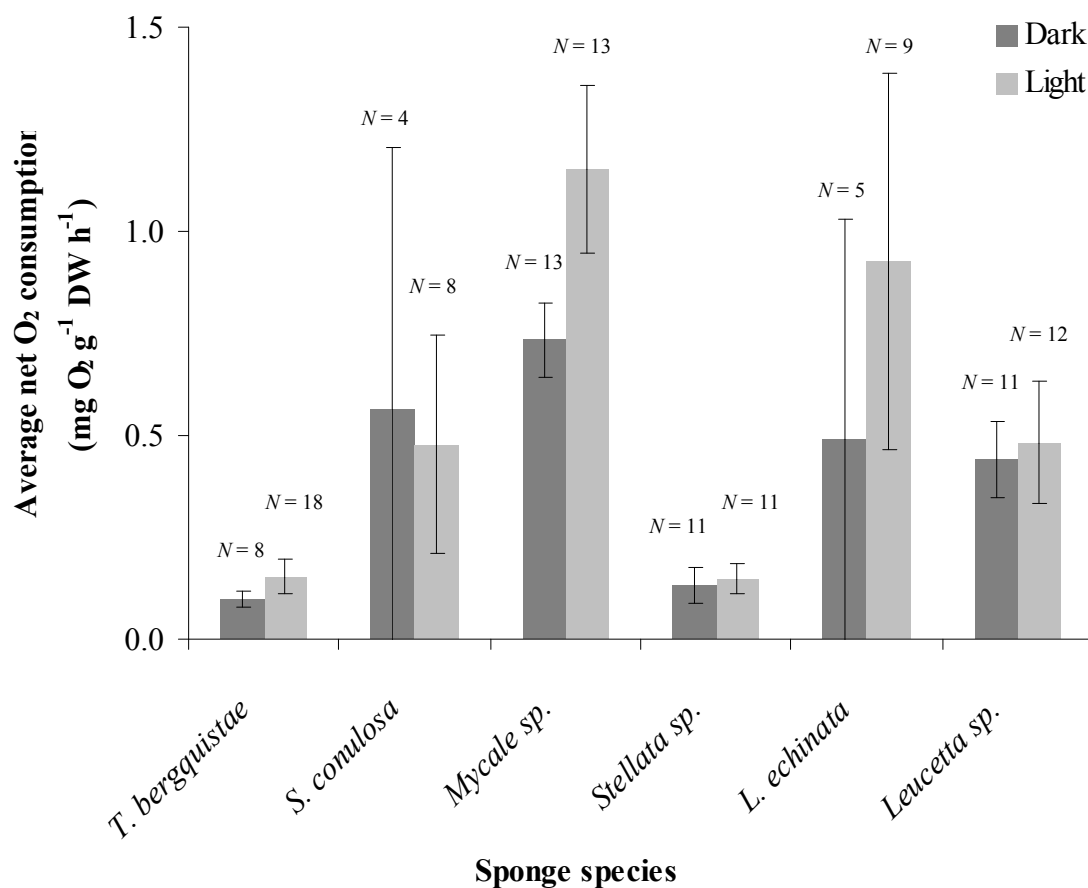
Figure 2.6 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) in the light (20 μmol photons m^{-2} s^{-1}) and the dark, ± 95% confidence intervals, for six temperate sponge species. Four species of demosponge (*Tethya bergquistae, Strongylacidon conulosa, Mycale* sp., and *Stellata* sp.) and two calcareous sponges (*Leucosolenia echinata*, and *Leucetta* sp.) were investigated.

Calcareous sponges vs. demosponges

Net oxygen consumption rates for temperate calcareous sponges were approximately 30% higher than demosponges ($U = 305.000$, $p < 0.01$, $r = -0.329$), while in the dark respiration rates were the same ($U = 230.000$, $p = 0.250$, $r = -0.159$) (Figure 2.7).
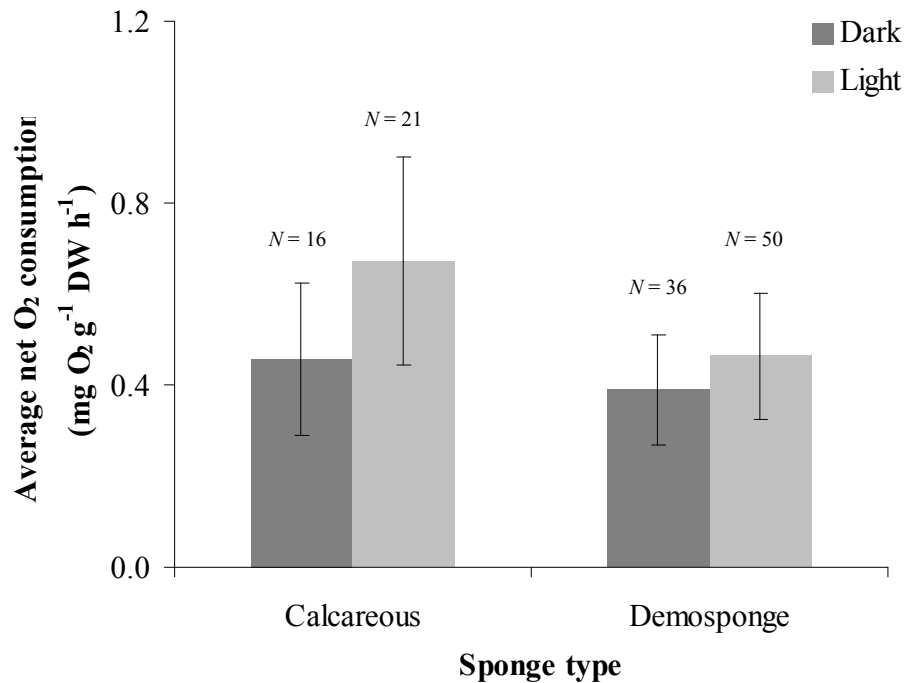
Figure 2.7 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) in the light (20 μmol photons m^{-2} s^{-1}) and the dark, ± 95% confidence intervals, for calcareous sponges and demosponges. Two calcareous sponges (*Leucosolenia echinata* and *Leucetta* sp.) and four species of demosponge (*Tethya bergquistae*, *Strongylacidon conulosa*, *Stellata* sp. and *Mycale* sp.) were used.

Net oxygen consumption in the light vs. dark respiration in each species

Of the temperate sponges, only *Mycale* sp. had a significantly higher rate of oxygen consumption in the light than in the dark (Table 2.1). In the other temperate sponges (*T. bergquistae, S. conulosa, Stellata* sp., *L. echinata*, and *Leucetta* sp.) there were no differences between their light and dark rates (see Table 2.1).

Table 2.1 Analysis of the net rates of oxygen consumption between light and dark for each temperate species (*** $p < 0.001$).

Sponge species	Net oxygen consumption rates		Test statistic (t / U)	P	Effect size (r)
	Light	Dark			
T. bergquistae	0.153 ± 0.021	0.100 ± 0.010	$t_{24} = 1.255$	0.221	0.248
S. conulosa	0.477 ± 0.136	0.563 ± 0.328	$U = 11.000$	0.396	-0.245
Mycale sp.	1.152 ± 0.105	0.733 ± 0.047	$t_{24} = 4.196$	***	0.651
Stellata sp.	0.149 ± 0.020	0.131 ± 0.022	$t_{20} = 0.767$	0.452	0.169
L. echinata	0.926 ± 0.235	0.491 ± 0.274	$t_{12} = 1.565$	0.144	0.412
Leucetta sp.	0.482 ± 0.076	0.442 ± 0.049	$t_{21} = 0.437$	0.666	0.095

Tropical

Oxygen consumption rates between species

Net oxygen consumption rates measured for six tropical sponges in the light and dark also varied considerably, and a number of the species demonstrated large variability (Figure 2.8). In both the light and dark there were differences in net oxygen consumption rates between species ($H_3 = 22.389$, $p < 0.01$; $H_3 = 9.035$, $p < 0.05$, respectively). The *post-hoc* analysis showed that in the light *Cribochalina* sp., *Hyrtios* sp. and *Dysidea herbacea* had higher net oxygen consumption rates than did *Aaptos* sp. ($p < 0.05$). In the dark, however, only *Dysidea*

herbacea had a higher respiration rate than did *Aaptos* sp. ($p < 0.05$), whereas *Cribochalina* sp. and *Hyrtios* sp. did not differ from any of the other species ($p > 0.05$).
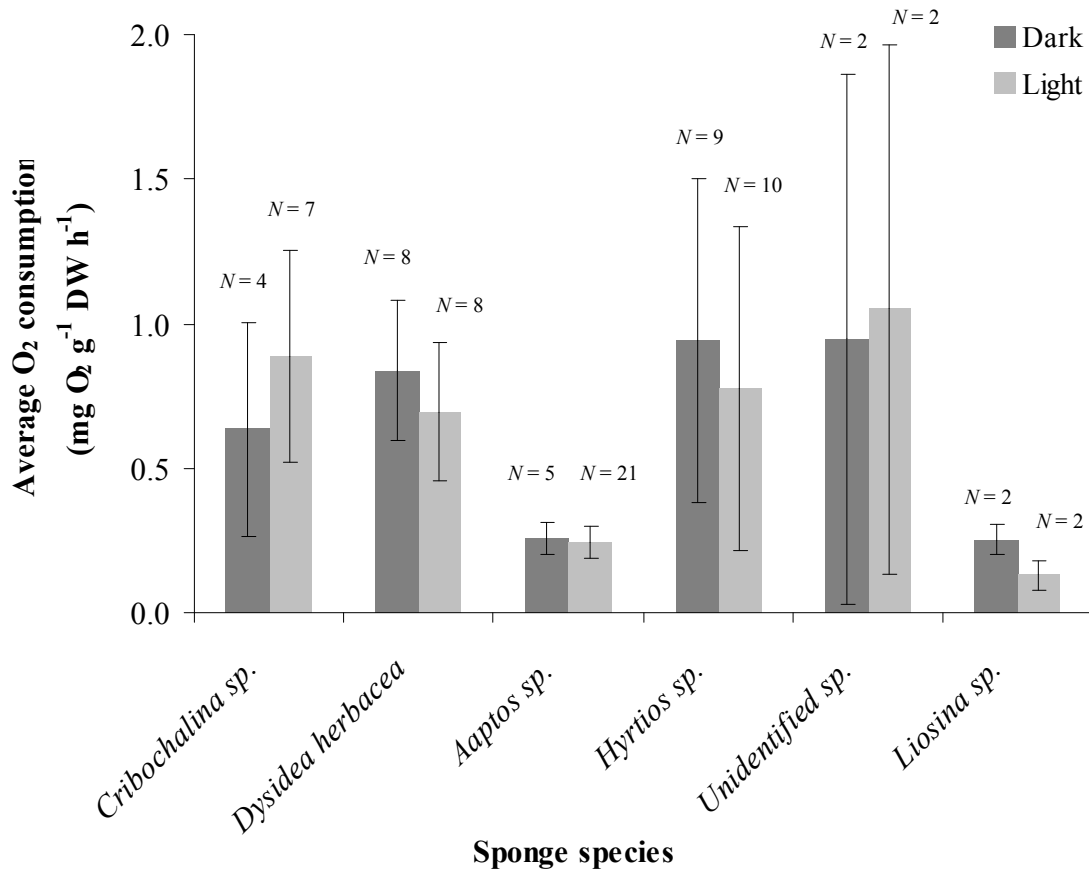
Figure 2.8 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) in the light (20 μmol photons m^{-2} s^{-1}) and the dark, $\pm$ 95% confidence intervals, for six tropical sponges. All the species investigated were demosponges (*Cribochalina* sp., *Dysidea herbacea*, *Aaptos* sp., *Hyrtios* sp., Unidentified sp., and *Liosina* sp.).

Net oxygen consumption in the light vs. dark respiration in each species

There were no differences between light and dark rates in the tropical sponges (*Cribochalina* sp., *Dysidea herbacea*, *Aaptos* sp., *Hyrtios* sp.) (see Table 2.2).

Table 2.2 Analysis of the net rates of oxygen consumption between light and dark for each species.

Sponge species	Net oxygen consumption rates		Test statistic (t / U)	P	Effect size (r)
	Light	Dark			
Cribochalina sp.	0.885 ± 0.188	0.635 ± 0.215	$U = 9.000$	0.345	-0.285
Dysidea herbacea	0.695 ± 0.123	0.837 ± 0.082	$t_{14} = -1.384$	0.188	0.347
Aaptos sp.	0.241 ± 0.029	0.258 ± 0.058	$t_{24} = -.352$	0.728	0.072
Hyrtios sp.	0.778 ± 0.286	0.944 ± 0.432	$U = 43.000$	0.905	-0.037

Inorganic content

<u>Patterns in the percent of inorganic matter between species</u>

The proportion of inorganic material was different between temperate sponge species ($H_5 = 45.497$, $p < 0.001$) (Figure 2.9). The *post-hoc* analysis showed that *L. echinata*, *Leucetta* sp., and *Mycale* sp. had a higher proportion of inorganic material than did *T. bergquistae* ($p < 0.05$). Only *L. echinata* and *Leucetta* sp. had higher proportions of inorganic material than *Stellata* sp. ($p < 0.05$). *S. conulosa* did not differ from any of the species apart from *L. echinata* ($p < 0.05$).
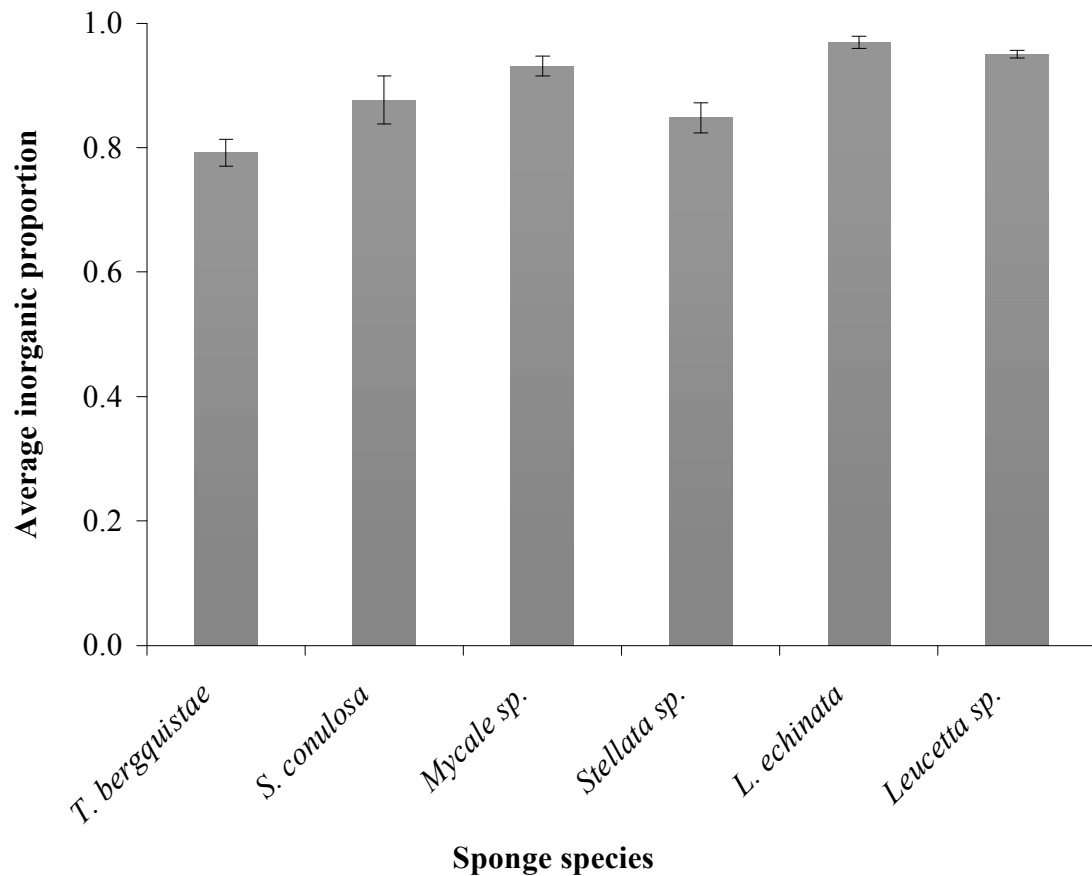
Figure 2.9 Average proportion of inorganic matter, ± 95% confidence intervals, for several temperate sponge species. Four species of demosponge (*Tethya bergquistae* $N = 22$, *Strongylacidon conulosa* $N = 4$, *Mycale* sp. $N = 13$, and *Stellata* sp. $N = 5$) and two calcareous sponges (*Leucosolenia echinata* $N = 7$, and *Leucetta* sp. $N = 7$) were used.

Calcareous sponges vs. demosponges

The proportion of inorganic matter in temperate calcareous sponges was approximately 11% higher than in demosponges ($U = 34.000$, $p < 0.001$, $r = -0.654$) (Figure 2.10).
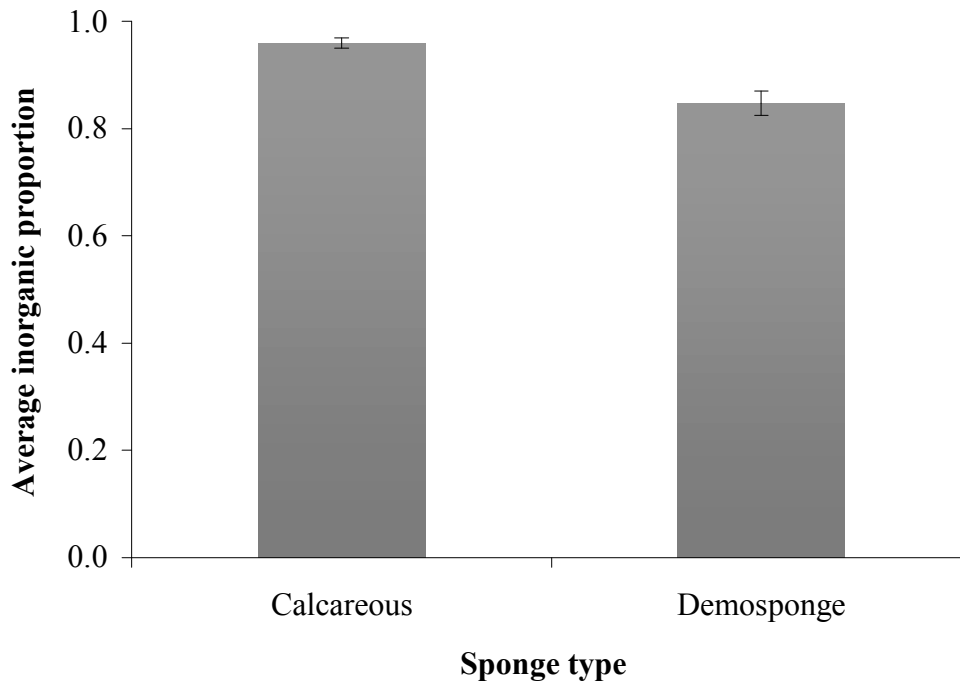
Figure 2.10   Average proportion of inorganic matter, $\pm$ 95% confidence intervals, for temperate calcareous sponges ($N = 14$) and demosponges ($N = 31$). Two calcareous sponges (*Leucosolenia echinata* and *Leucetta* sp.) and four demosponges (*Tethya bergquistae*, *Mycale* sp., *Strongylacidon conulosa*, and *Stellata* sp.) were used.

Correlation between net oxygen consumption rates and the inorganic proportion

The proportion of inorganic matter in temperate sponges explained approximately 60% of the variance in their net oxygen consumption rates ($R^2 = 0.599$) (Figure 2.11).   A positive relationship existed between the proportion of inorganic matter and net oxygen consumption rates, and for every one-unit rise in the proportion of inorganic matter, net oxygen consumption rates will increase by 4.650 mg O_2 g^{-1} DW h^{-1} ($b = 4.650$).
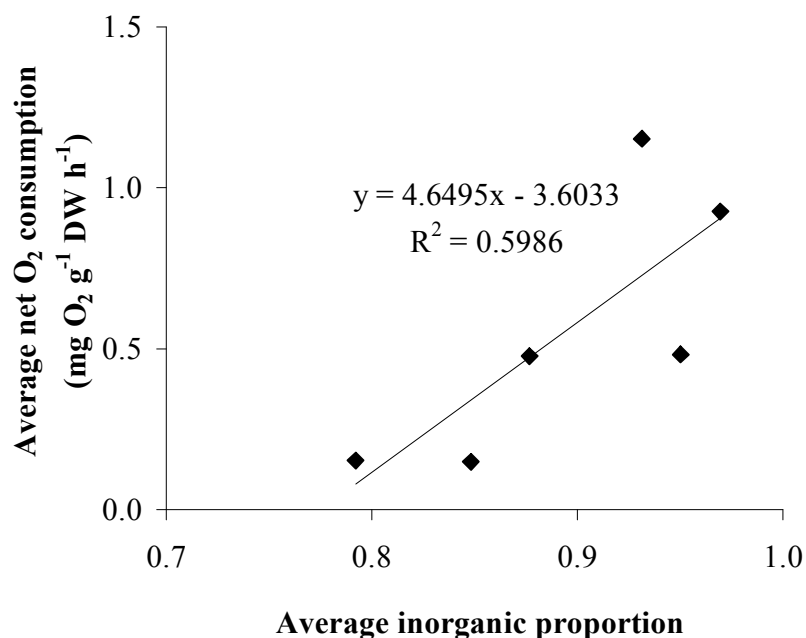
Figure 2.11 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) in the light (20 μmol photons m^{-2} s^{-1}), for six temperate sponges (*Tethya bergquistae*, *Strongylacidon conulosa*, *Mycale* sp., *Stellata* sp., *Leucosolenia echinata*, and *Leucetta* sp.) graphed against the corresponding proportion of inorganic matter.

2.4 DISCUSSION

Oxygen consumption rates are important as they provide valuable information on the energetic processes of an organism (Kleiber 1975). The aim of this study was to measure and compare oxygen consumption rates between temperate and tropical sponges and to establish whether their metabolic responses differed in response to light. Dark respiration rates were 60% higher for the tropical sponges than for temperate species, but in the light net oxygen consumption rates were the same. Within the temperate and tropical habitats, oxygen consumption rates were not the same between sponge species. Net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) for the temperate sponges were found to increase with the amount of

inorganic matter that they contained; this was not measured for tropical species. Of particular note, temperate calcareous sponges had a higher net oxygen consumption rate in the light (0.7 mg O_2 g^{-1} DW h^{-1}) and a greater proportion of inorganic matter (96%) compared to demosponges (0.5 mg O_2 g^{-1} DW h^{-1} and 84%). Lastly, the only difference in light and dark net oxygen consumption rates was found in the temperate sponge, *Mycale* sp., which had a 36% higher oxygen uptake in the light than in the dark.

Temperate vs. tropical oxygen consumption

Dark respiration rates of the tropical sponges were 60% higher than the temperate sponges. Food depleted waters of tropical areas often increase the need for higher water filtration and energetic expenditure in suspension feeders (Willows 1992) and it has also been found that warmer water temperatures increase sponge respiration rates due to increased growth (Schmidt-Nielsen 1975) potentially explaining these results. In the light, however, net oxygen consumption rates for the temperate and tropical sponges were the same. High light, food depleted tropical areas often favour sponges with abundant photosynthetic microbes (Wilkinson & Vacelet 1979; Wilkinson 1983). It is likely, therefore, that net oxygen consumption rates for the tropical sponges were lower in the light due to the influence of photosynthetic oxygen production from abundant associated microbes (e.g. Cheshire & Wilkinson 1991; Schonberg *et al.* 2005). It is unlikely that the differences in response could have been an artefact of the acclimation period used prior to oxygen consumption measurements between the two habitats, as dark respiration rates from this study compared to those reported in the literature are similar, validating these results (see Table 2.3).

When data from the literature and this study were combined, dark respiration rates (standardized against wet weight) for temperate and tropical sponges were found to be the same, in contrast to the current study (Figure 2.12). This was surprising, although many

factors may have influenced the respiration rates of these sponges, such as, ambient oxygen concentrations, salinity, water flow, and food concentrations (Jorgensen *et al.* 1986; Sebens 1987; Patterson & Olson 1991; Lucas 1996; Riisgard & Larsen 2001). Temperate regions often experience dramatic fluctuations in environmental factors, which perhaps causes large variability in temperate sponge respiration rates compared to tropical species (Coma & Ribes 2003). More respiration work is needed for temperate sponges, however, as to date only 16 species have been sampled, compared to 37 from tropical regions (Table 2.3). Sponge respiration rates from polar areas are also reported in the literature but it was difficult to compare these values with the other data as they are mostly standardized to ash free dry weight, while wet weight is used for almost all tropical species (Table 2.3). Polar sponge respiration rates do seem to be lower than temperate species, however, which indicates that their rates of oxygen consumption are lower than tropical sponges (Table 2.3).

Table 2.3 Dark respiration rates for marine sponges from all ecosystems

Ecosystem	Species	mg O_2 g^{-1} WW h^{-1}	mg O_2 g^{-1} DW h^{-1}	mg O_2 g^{-1} AFDW h^{-1}	Reference
Polar	*Cinachyra antarctica*			0.337	Gatti et al.(2002)
	Crella guemei	7.579 x 10^{-9}			Hargrave et al. (2004)
	Geodia barretti	3.459 x 10^{-5}			Hoffmann et al. (2005a)
	Isodictya kerguelensis			0.050	Kowalke (2000)
	Mycale acerata			0.126	Kowalke (2000)
	Scypha ciliata	1.015 x 10^{-8}			Hargrave et al. (2004)
	Stylocordyla borealis			0.203	Gatti et al. (2002)
	Tetilla cranium			0.602	Witte & Graffe (1996)
	Thenea abyssorum			0.707	Witte & Graffe (1996)
	Thenea muricata			0.624	Witte & Graffe (1996)
Temperate	*Aplysina aerophoba*	1.144 x 10^{-4}			Hoffmann et al. (2008)
	Dysidea avara		0.310	0.930	Coma et al. (2002)
	Grantia sp.	0.179			Hyman (1925)
	Halichondria panicea		0.901	2.631	Thomassen & Riisgard (1995)
	Halichondria panicea			0.266, 0.787*	Barthel (1988)
	Halichondria panicea	1.194 x 10^{-4}			Osinga et al. (1999)
	Hippospongia equina	0.008			Von Putter (1914)
	Leucetta sp.	0.072	0.442		This study
	Leucosolenia echinata	0.137	0.491	2.114	This study
	Mycale sp.	0.080	0.733		This study
	Stellata sp.	0.021	0.131	3.379	This study

Table 2.3 *Continued*

				Reference
Strongylacidon conulosa	0.024	0.563		This study
Strongylacidon sp.	0.065	0.279	1.018	This study
Suberites carnosus	0.068	1.130		Cotter (1978)
Suberites domuncula	0.011			Von Putter (1914)
Suberites massa	0.034			Nicol (1970)
Sycon ciliatum	0.790	1.130		Cotter (1978)
Tethya aurantium	0.011			Von Putter (1914)
Tethya bergquistae	0.023	0.100	0.483	This study
Tropical				
Aaptos sp.	0.052	0.258		This study
Axinella polycapella	0.019			Osinga et al.(1998)
Axinella waltonsmithi	3.294×10^{-5}			Osinga et al.(1998)
Carteriospongia flabellifera	0.033			Cheshire & Wilkinson (1991)
Carteriospongia foliascens	0.059			Cheshire & Wilkinson (1991)
Carteriospongia sp. fp	0.075			Wilkinson (1983)
Carteriospongia sp. fr	0.075			Wilkinson (1983)
Cinachyrella apion	0.018			Osinga et al. (1998)
Cribochalina sp.	0.064	0.635		This study
Cymbastela concentrica	0.081			Seddon et al. (1992)
Dysidea herbacea	0.171	0.837		This study
Dysidea herbacea	0.111			Cheshire & Wilkinson (1991)
Haliclona – Ceratodictyon	5.76×10^{-7}			Davy et al. (2002)
Haliclona rubens	0.001			De Laubenfels (1932)
Hyrtios sp.	0.091	0.944		This study
Ianthella basta	0.108			Cheshire & Wilkinson (1991)

Table 2.3 *Continued*

Iotrochota birotulata	2.258×10^{-4}			De Laubenfels (1932)
Ircinia ramosa	0.025			Wilkinson (1983)
Ircinia sp.	0.077			Cheshire et al. (1991)
Jaspis stellifera	0.079			Cheshire & Wilkinson (1991)
Liosina sp.	0.054	0.252		This study
Mycale sp.		2.131		Reiswig (1974)
Negombata magnifica	0.072	0.476	0.595	Hadas *et al.* (2008)
Neofibularia irata	0.067			Cheshire & Wilkinson (1991)
Pericharax heteroraphis	0.037			Cheshire & Wilkinson (1991)
Phyllospongia lamellose	0.097			Cheshire & Wilkinson (1991)
Phyllospongia papyracea	0.111			Cheshire & Wilkinson (1991)
Pseudaxinyssa sp.	0.035			Cheshire & Wilkinson (1991)
Pseudosuberites andrewsi	7.322×10^{-5}			Osinga *et al.* (1998)
Spongia sp.	0.032			Wilkinson (1983)
Strepsichordaia lendenfeldi	0.044			Cheshire & Wilkinson (1991)
Tethya cyrpta		0.629		Reiswig (1974)
Unidentified sp.	0.054	0.945		This study
Verongia fistularis	0.152			Reiswig (1981)
Verongia gigantean		1.544		Reiswig (1974)
Freshwater *Ephydatia muelleri*			0.250	Vohmann *et al.* (2009)
Spongilla lacustris		0.972		Karchenko & Lyashenko (1986)

* Two measurements taken at different temperatures, 1.4 - 4.6°C and 10 - 16°C respectively.

Values from the literature were standardised using volume-to-weight conversions into the unit mg O$_2$ g^{-1} h^{-1}.
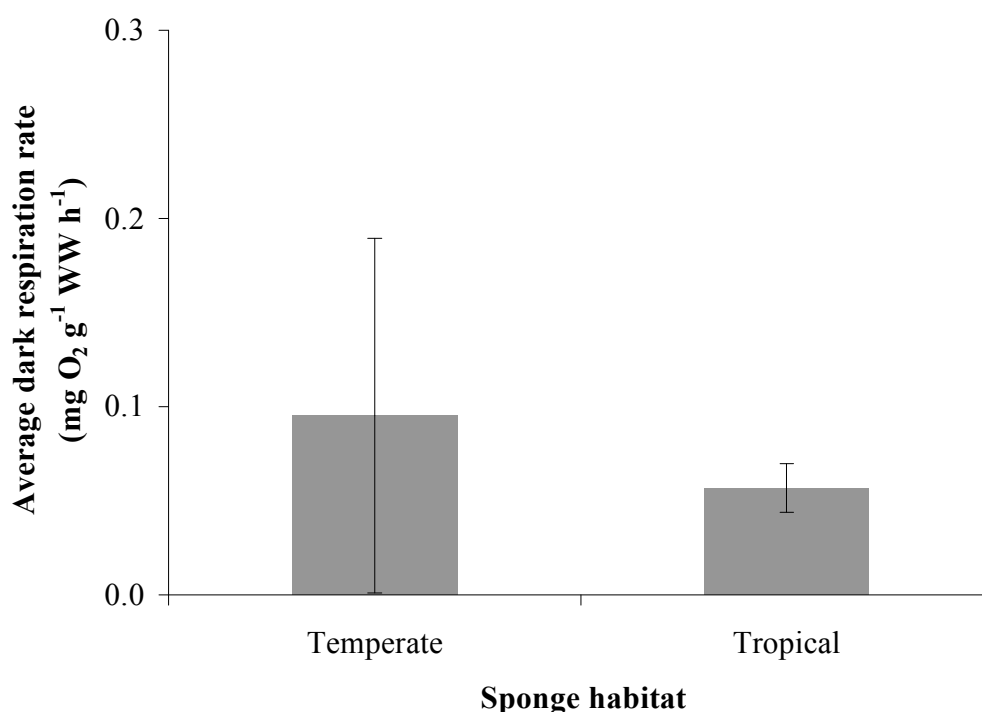
Figure 2.12 Average dark respiration rate (mg O_2 g^{-1} WW h^{-1}) for temperate and tropical sponges, ± 95% confidence intervals (N = 16 and 37, respectively). This data includes respiration rates from this study and those reported in the literature (see Table 2.3).

Patterns in oxygen consumption rates between species

<u>Temperate</u>

In both the light and the dark there were significant differences in net oxygen consumption rates between species. These differences appeared to be correlated with the percent of inorganic material; net oxygen consumption rates increased for sponges with higher proportions of inorganic material. This correlation was surprising, with the reverse expected, as only organic matter can be used for oxygen uptake. Other factors could have affected oxygen consumption rates within the experiment. If some of the assayed species were engaged in physiological processes, such as, gametogenesis or embryo production, oxygen consumption rates would be expected to be higher (Barthel & Theede 1986; Tankersley &

Dimock 1993; Whalan *et al.* 2007). These factors could have caused the variability within *Strongylacidon conulosa* and *Leucosolenia echinata*. Unfortunately, factors such as reproductive state and symbiont abundance were not measured. The strong correlation with the proportion of inorganic matter, however, suggests that other physiological factors, such as, reproduction, did not influence oxygen consumption rates.

Published values were graphed with the values from this study to find out if the pattern of higher inorganic matter and oxygen consumption rates was also present elsewhere (Figure 2.13). Interestingly, the opposite trend was discovered, respiration was found to decrease with the proportion of inorganic matter (Figure 2.13). The sponges with the lowest proportion of inorganic matter had the highest respiration in Reiswig (1974). Reiswig (1981), meanwhile, found that the sponge *Verongia fistularis* had a high respiration rate, similar to *Mycale* sp. from this study, yet the proportion of inorganic matter was substantially different (27% versus 93%, respectively). The respiration rate of *Halichondria panicea* was also similar to a sponge from this study (*Leucosolenia echinata*), yet the proportion of inorganic matter was much lower (77% versus 97%, respectively) (Palumbi 1986). These results illustrate how concentrated studies on only a few species do not necessarily identify trends at a larger-scale.

The spicule proportions reported for this study, however, are notably higher than others in the literature (Table 2.4) and this suggested that perhaps unique environmental pressures influence sponges occurring along the Wellington South Coast. A number of studies have found that the proportion of spicules in sponges is greater at sites with high wave energy (Palumbi 1984; Schonberg & Barthel 1997; McDonald *et al.* 2002; Meroz-Fine *et al.* 2005). Transplant studies have shown a significant increase in spicule abundance at high wave energy sites (21% over six months, Meroz-Fine *et al.* 2005) and individual spicules were

found to have greater mass, volume, surface area, and number per tissue (Palumbi 1984). The increase in spicule size and abundance has been found to enhance colony stiffness and strength (Palumbi 1984) as sponges in high wave force environments often need a robust inorganic frame to prevent significant loss of biomass (Vicente 1978; Meroz & Ilan 1995; Bell *et al.* 2002b). The Wellington South Coast site is well known as a high wave energy environment and it is likely that this could cause an increase in spicule density. Research from the literature suggests that high spicule composition will influence the pumping activity of sponges and increase their energy expenditure. Spicule production requires complex organization of specialized cells (Ledger & Jones 1977; Sethmann & Worheide 2008) and several studies have suggested that an increase in spicule content with high water flow will require additional energetic costs at the expense of organic material (McDonald *et al.* 2002; Carballo *et al.* 2006). Palumbi (1986) concluded that high inorganic contents will be expensive to sustain, as there will be increased energetic costs to pumping water through narrow spaces. Small pores will have higher resistance to water flow and require greater energy expenditure for pumping activity (Vogel 1981). It is likely, therefore, that the higher wave force conditions of the Wellington South Coast increasing the production or growth of spicules in the sponges creates higher resistance for water pumping activity and increases the demands for energy and subsequently oxygen uptake.
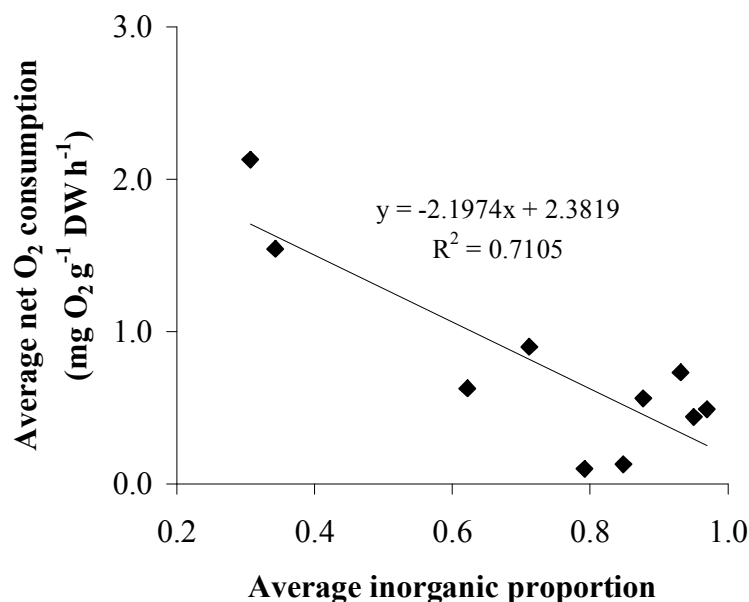
Figure 2.13 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) graphed against the corresponding proportion of inorganic matter for sponges from the literature and this study. Sponges added from the literature were *Halichondria panicea*, *Tethya crypta*, *Verongia gigantea*, and *Mycale* sp. Respiration rates were taken from Thomassen & Riisgard (1995) and Reiswig (1974), and the proportion of inorganic material from Palumbi (1986) and Reiswig (1981).

Despite the discussion above, it is unclear why the spicule concentrations in the current study were so much greater than those reported in the literature, even for high-energy environments. The differences in spicule content could suggest that concentrations of silica and calcite in the water column around the Wellington South Coast may be particularly high. High concentrations of silica or calcite activate spicule formation genes in sponges - increasing spicule size and content (Stone 1970; Frohlich & Barthel 1997; Schonberg & Barthel 1997; Mercurio *et al.* 2000; Le Pennec *et al.* 2001; Mercurio *et al.* 2006). Unfortunately, there are no recorded values for silica or calcite concentrations around the Wellington South Coast, but perhaps high levels are present.

Table 2.4 The proportion of inorganic matter for some marine sponges

Ecosystem	Species	Inorganic matter (%)	Reference
Temperate	*Leucosolenia echinata*	96.9	This study
	Leucetta sp.	95.0	This study
	Mycale sp.	93.1	This study
	Strongylacidon sp.	86.8	This study
	Stellata sp.	84.8	This study
	Tethya bergquistae	79.2	This study
	Strongylacidon conulosa	77.2	This study
	Halichondria panicea	65.2 - 77.1	Palumbi (1986)
Tropical	*Cinachyrella australiensis*	62.0 - 78.0	McDonald *et al.* (2002)
	Tethya crypta	62.2	Reiswig (1971a)
	Geodia cydonium	55.0 - 77.0	Mercurio *et al.* (2006)
Temperate	*Cliona celata*	50.0	Bell *et al.* (2002b)
	Haliclona caerulea	46.0	Enriquez *et al.* (2009)
	Cacospongia sp.	38.0	Ferguson & Davis (2008)
Tropical	*Verongia gigantean*	34.3	Reiswig (1971a)
	Mycale sp.	30.7	Reiswig (1971a)
	Verongia fistularis	27.0	Reiswig (1981)
	Tetilla sp.	16.0 - 34.0	Meroz-Fine *et al.* (2005)
Temperate	*Tedania anhelans*	13.0	Ferguson & Davis (2008)
	Callyspongia sp.	11.7	Ferguson & Davis (2008)
	Clathria pyramida	9.4	Ferguson & Davis (2008)
	Chondrilla sp.	7.3	Ferguson & Davis (2008)
	Chondrilla australiensis	5.8	Ferguson & Davis (2008)

Calcareous sponges vs. demosponge respiration

Demosponges have a much more complex aquiferous system (Bergquist 1978) and contain a greater abundance of associated microbes than do calcareous species (Vacelet & Donadey 1977; Hentschel *et al.* 2002; Hentschel *et al.* 2003). These factors were expected to elevate the dark respiration rates of demosponges over calcareous species, however, this was not found. In the dark, respiration rates in temperate calcareous sponges and demosponges were the same. In the light, however, the net oxygen consumption rates of the calcareous sponges were 30% higher than in demosponges. It was expected that net oxygen consumption rates in the light would be lower in demosponges than in calcareous sponges as a result of abundant

photosymbionts (Hentschel *et al.* 2003). Looking more closely at the results, however, the oxygen consumption rates within the demosponges do not show a difference between light and dark, but rather it is a shift in higher oxygen consumption rates of the calcareous sponges in the light that produce the significant result. To help understand these results, respiration rates were combined from the literature and this study (standardised for wet weight) to compare calcareous sponges and demosponges (Figure 2.14). These data show that respiration rates were the same between calcareous sponges and demosponges, but the sample size of the former was low compared to demosponges ($N = 7$ versus $N = 49$, respectively). More research is necessary on oxygen consumption rates from calcareous sponges to provide conclusions regarding the results found here.
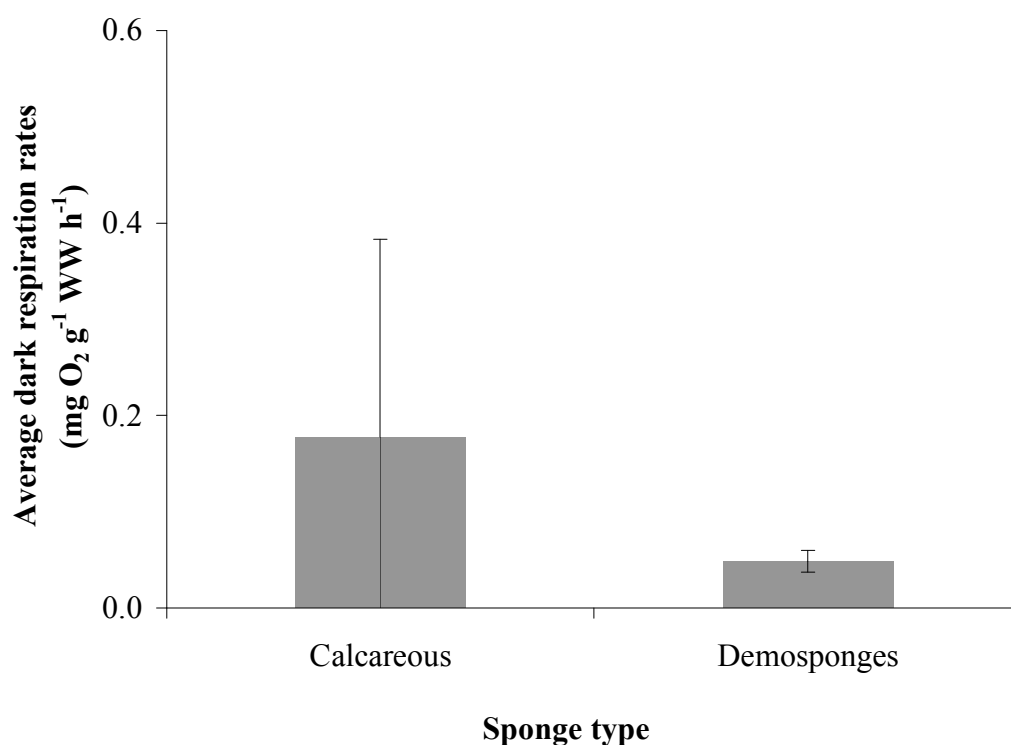
Figure 2.14 Average dark respiration rates (mg O_2 g^{-1} WW h^{-1}) for calcareous and demosponges, ± 95% confidence intervals ($N = 7$ and 49 respectively). This data includes respiration rates from this study and those reported in the literature (see Table 2.3).

The results from the current study also found that temperate calcareous sponges had a greater proportion of inorganic matter compared to demosponges. Calcareous spicules are generally more fragile with a tendency to break easily, compared to silica spicules, which are much tougher and resistant to fracture (Sethmann & Worheide 2008). The temperate calcareous sponges, therefore, may need higher proportions of inorganic matter compared to the demosponges, to combat the wave force conditions of the Wellington South Coast due to the fragile nature of their spicules. This idea does not explain why *Mycale* sp., a demosponge, had a similar inorganic content to the calcareous sponges. Spicule content, however, has also been suggested to be higher with sediment in areas with low water flow to trap silt, potentially keeping it away from important water pumping cavities (Mercurio *et al.* 2006). *Mycale* sp. were collected from the Wellington Harbour, which does have a higher amount of suspended sediment due to input from storm water drains and the Hutt River. The harbour environment experiences lower wave energy than the Wellington South Coast, which could mean that sediment has a larger influence on sponges in the harbour, and hence they produce more spicules.

Tropical

Phototrophic sponges can contribute up to 50% of the biomass on tropical reef ecosystems (e.g. Cheshire & Wilkinson 1991) and it is possible that all the tropical sponges investigated in this study contained photosynthetic symbionts, although the abundance and activity of microbes may differ between species. Interestingly, the only difference in oxygen consumption rates between tropical species was recognised for *Aaptos* sp.. *Aaptos* sp. had a lower net oxygen rate in both the light and dark compared to the other tropical species. Low numbers of replicates did not appear to have caused variability in oxygen consumption rates between species. *Hyrtios* sp. with 9-10 replicates, for example, was found to have large variability almost as much as Unidentified sp., which had a sample size of just two sponges,

yet variability in the respiration rates for *Liosina* sp. ($N = 2$) was small. Unfortunately, without knowing anything more about reproductive cycles, growth rates, inorganic content, or symbiont activity in these species it is hard draw conclusions about these respiratory patterns.

Net oxygen consumption in the light vs. dark respiration

Oxygen consumption rates within the sponge species were expected to be lower in the light than in the dark, due to the influence of photosynthetic oxygen production by symbionts (Cheshire & Wilkinson 1991; Schonberg *et al.* 2005). Only one of the studied sponges (*Mycale* sp.), however, was found to have different oxygen consumption rates between light and dark. The results for *Mycale* sp. were counterintuitive, as this temperate sponge displayed a higher net oxygen consumption rate in the light than in the dark. This species' oxygen consumption rate may have been influenced by diurnal filtration activity. Wilkinson *et al.* (1988) found that both phototrophic and heterotrophic sponges could have higher filtration rates during the day than at night.

It is possible that the light level used in the experiments was not high enough to elucidate a strong difference between dark and light oxygen consumption rates. Phototrophic sponges will be net producers of oxygen in the light at all but the lowest irradiances (Cheshire & Wilkinson 1991; Seddon *et al.* 1992; Erwin & Thacker 2008). Light compensation in phototrophic sponges, where photosynthetic production of oxygen is equal to respiratory consumption of oxygen, however, can occur at low irradiances ranging from 10 - 67 μmol photons m^{-2} s^{-1} (Seddon *et al.* 1992; Cheshire *et al.* 1995; Cheshire *et al.* 1997; Schonberg *et al.* 2005), which includes the level used for this study (i.e. 20 μmol photons m^{-2} s^{-1}). This level was expected to be sufficient to produce net production of oxygen in the light if photosymbionts were present, but in light of the results it appears that the tropical sponges may have needed a higher level of irradiance to induce a greater response in photosynthetic

oxygen production from associated microbes. The temperate sponges from this study, however, which would normally experience much lower light levels than tropical sponges, should have demonstrated reduced rates of net oxygen consumption, or even net oxygen production in the light if they contained high levels of photosymbionts, but this was not observed.

Conclusions and future study

This study showed that more variability existed in oxygen consumption rates among sponge species than between temperate and tropical sponges in general. This study also found an unexpected impact of wave-energy on inorganic matter and oxygen consumption rates of the temperate sponges. Temperate and tropical sponges in this study were found to have different metabolic responses in the dark, potentially a result of higher temperatures and the need for increased pumping activity in food depleted waters (Schmidt-Nielsen 1975; Willows 1992). This difference was not observed at a broader scale, however, as combining oxygen consumption rates from this study and those in the literature showed temperate and tropical sponges to have similar rates. More research is needed to specifically relate variation in oxygen consumption rates to other physiological processes, such as, growth or reproduction, which may explain why differences were not apparent between temperate and tropical sponges within the literature.

The effect of UV-B radiation on the oxygen consumption of a model temperate and tropical sponge

The predicted rise in harmful ultraviolet-B radiation and deeper penetration depths of these wavelengths in the marine environment are concerning, as the effects on important marine benthic taxa, such as sponges, are not well known. The aim of this study was to investigate the influence of ultraviolet-B radiation on the physiological functioning of model temperate and tropical sponges, *Tethya bergquistae* and *Aaptos* sp., respectively. Oxygen consumption, a measure of the energy needed for all physiological processes, was determined for sponges exposed to ultraviolet-B radiation over 7 hours. It was expected that sponge oxygen consumption rates would increase with the exposure to radiation, due to the energy cost for repair processes caused by direct DNA damage. It was found, however, that ultraviolet-B radiation, at 60 μW cm^{-2}, had no effect on the oxygen consumption rate of either sponge species over the experimental period. The results indicate that long-term survival and distribution patterns in *T. bergquistae* and *Aaptos* sp., and perhaps other sponges, may not be influenced by exposure to ultraviolet-B radiation levels up to 60 μW cm^{-2}.

Keywords Ultraviolet-B radiation, oxygen consumption, respiration, sponges, New Zealand, Indonesia.

3.1 INTRODUCTION

Ultraviolet-B (UV-B) radiation is increasing at the Earth's surface due to the reduction of stratospheric ozone (Crutzen 1992; Harris *et al.* 1995; Madronich *et al.* 1998). Climate

change is closely linked to the loss of ozone as it affects stratospheric temperature (Salawitch 1998; Shindell *et al.* 1998). Colder, more stable vortex circulations in the stratosphere are predicted to accelerate the chemical removal of ozone at high latitudes resulting in increased ultraviolet radiation penetrating through the atmosphere (e.g. in Polar regions Salawitch 1998; Shindell *et al.* 1998). Penetration of UV-B wavelengths into the water column is also increasing with acidification and global climate change (Schindler *et al.* 1996; Williamson & Zagarese 2003; Zepp *et al.* 2007). The increase in global UV-B radiation is concerning, as this wavelength is responsible for half of the damaging photochemical effects in aquatic and marine ecosystems, even though it makes up only 0.8% of the total energy reaching the Earth's surface (Whitehead *et al.* 2000).

The effects of UV-B

The detrimental influence of UV-B radiation (280 - 320 nm) has been widely demonstrated (e.g. Holm-Hansen *et al.* 1993; Vincent & Roy 1993; Baker & Allen 1994; Allen *et al.* 1998; Mitchell *et al.* 2009) and is known to damage DNA, tissues, cells, and physiological and metabolic processes (Jokiel 1980; Karentz *et al.* 1991a; Smith *et al.* 1992; Buma *et al.* 1995; Davidson *et al.* 1996). Toxic effects of ultraviolet radiation occur through two pathways: at the chromaphores of biomolecules, and indirectly through the production of intermediate compounds (Vincent & Neale 2000). Chromaphores exist on biomolecules within an organism such as, proteins and nucleic acids, and absorb radiation in the ultraviolet spectrum (Vincent & Neale 2000). The direct effects of UV-B wavelengths are therefore on DNA and RNA, as they have the highest absorbance coefficients for short wavelength radiation among all cellular components (Karentz *et al.* 1991a; Quaite *et al.* 1992; Vincent & Neale 2000). In extreme cases of ultraviolet radiation exposure, these systems (DNA and RNA) become over saturated, resulting in impairment or complete loss of biological function (Dunlap & Shick 1998; Vincent & Neale 2000). Ultraviolet-B radiation can also induce indirect effects on the

tissues of an organism (Abele & Puntarulo 2004; Lesser 2006). The absorption of UV-B radiation, within or outside the cell, can cause the proliferation of reactive oxygen species (ROS) (Abele & Puntarulo 2004; Lesser 2006). These toxic radicals cause damage to biomembranes and other cellular components, such as DNA (Halliwell & Gutteridge 1999; Abele & Puntarulo 2004). Functional changes can also occur, including alterations to an animals metabolic performance, growth or reproduction, and may ultimately limit survival (Boveris 1998; Abele & Puntarulo 2004).

Marine systems and ultraviolet radiation

Ultraviolet-B radiation not only influences the surface layers of marine systems (Larkum & Wood 1993; Hader 2001; Marcoval *et al.* 2007; Yuan *et al.* 2007; Wangberg *et al.* 2008), but can also penetrate deeply into the water column. In productive lakes and coastal areas, for example, ultraviolet radiation can penetrate 20 – 30 m (Jerlov 1976; Smith & Baker 1979; Kirk 1994; Scully & Lean 1994). A recent review by Tedetti and Sempere (2006), described how UV-B can penetrate up to 17 m in the open ocean but doses for effective DNA damage have only been recorded down to 12 m. For coastal areas UV-B penetration varied from 0.1 – 6 m and doses for effective DNA damage were recorded down to 5 m (Tedetti & Sempere 2006).

Despite the increasing penetration of UV-B radiation in the marine environment, little research has looked at the effects of these wavelengths on important benthic taxa, particularly sponges. The widespread nature of sponges on reefs across the world, and their important functional roles (review by Bell 2008) highlight the need for research in this area. Many papers suggest that ultraviolet radiation explains sponge distributions (Wilkinson & Vacelet 1979; Jokiel 1980; Wilkinson & Evans 1989; Cheshire & Wilkinson 1991; Seddon *et al.* 1992; Steindler *et al.* 2002), yet experimental evidence is scarce. Some research has also

suggested that sponges may screen UV-B radiation with pigmentation, melanin, symbiotic bacteria, or organic coverings of microalgae to prevent damage (Bergquist 1978; Corriero *et al.* 1989; Duckworth *et al.* 1997; Mercurio *et al.* 2006). Yet low levels of mycosporine-like amino acids (MAAs), which act as screening particles, have been found in a number of Antarctic sponge species (McClintock & Karentz 1997).

Stronger evidence exists to support the presence of protective repair mechanisms within sponges. Sponges have been found to contain two DNA repair systems, SOS-response and photolyase, which can be used to manage the toxic effects of ultraviolet radiation as well as other environmental stressors (Krasko *et al.* 1998; Schroder *et al.* 2003). Schroder *et al.* (2003) found that the hexactinellid sponge *Aphrocalliestes vastus* possessed a DNA repair photolyase protein that was expressed in regions most exposed to ultraviolet radiation. They found that *Esherichia coli* hosting the photolyase-related sponge protein DNA experienced almost complete repair of ultraviolet damage and only a small reduction in survival, while cells without the protein were sensitive to UV-B radiation (Schroder *et al.* 2003). Batel *et al.* (1998) demonstrated that ultraviolet radiation induced effective enzymatic DNA excision repair systems in the sponge *Geodia cydonium*. The antioxidant enzymes catalase and superoxide dismutase (SOD) that prevent the proliferation of damaging reactive oxygen species (ROS) induced by ultraviolet radiation have also been recognised in a freshwater sponge and marine sponge (Gordeeva *et al.* 2006; Kultz *et al.* 2007). A large number of stress repair proteins have also been identified in various marine and freshwater sponges, and are induced by environmental factors, such as heat, hyperosmotic, oxidative, and ultraviolet radiation stress (e.g. Koziol *et al.* 1996; Koziol *et al.* 1997; Schroder *et al.* 2000; Bohm *et al.* 2001; Kultz *et al.* 2007). These studies suggest that repair systems are present and very efficient in sponges, yet there remains little evidence for how sponges, at the organismal level, are influenced by UV-B radiation.

Aim and hypotheses

The aim of this study was to investigate whether UV-B radiation (280 – 320 nm) affects the physiological functioning of sponges. This was accomplished by measuring oxygen consumption of two model sponges exposed to UV-B radiation over 7 hours. Oxygen consumption is required for energetic processes, and therefore indicates total energy expenditure of an organism (Kleiber 1975). Obermuller *et al.* (2007) suggested that higher oxygen consumption rates in response to strong ultraviolet radiation are needed to offset the costs of repair processes caused by direct DNA damage. Direct exposure to UV-B radiation has been found to increase the oxygen consumption of microorganisms, bacteria, and amphipods (Thomson *et al.* 1980; Moran & Zepp 1997; Pakulski *et al.* 1998; Rusch *et al.* 2006; Obermuller *et al.* 2007). It was hypothesised, therefore, that over time oxygen consumption would increase significantly for those sponges exposed to UV-B radiation but not for those under a control treatment. It was also determined whether temperate and tropical sponges respond differently to UV-B radiation stress. Clear nutrient poor tropical water enables relatively deep penetration of ultraviolet radiation (Jerlov 1976). Ecological systems at high latitudes, however, have developed under lower levels of ultraviolet radiation and may not adapt well to large shifts or increases in the spectrum (Weiler & Penhale 1994). It was hypothesised, therefore, that a temperate sponge species would have a significantly higher net change in oxygen consumption in response to UV-B radiation exposure than a tropical sponge species.

3.2 **METHODS**

Sponges and collection sites (temperate and tropical)

The sponges chosen for this study were *Tethya bergquistae* (Hooper 1994) and *Aaptos* sp., from a temperate and tropical region, respectively. They are both good models for other demosponges in their environments as they are abundant and found in a range of habitats. *T. bergquistae* were collected by SCUBA or snorkelling from the Wellington South Coast of New Zealand at Breaker Bay (Figure 3.1). *Aaptos* sp. were collected by SCUBA from the reefs around Hoga Island, situated in the Wakatobi Marine National Park off the South-East coast of Sulawesi, Indonesia (Figure 3.2).
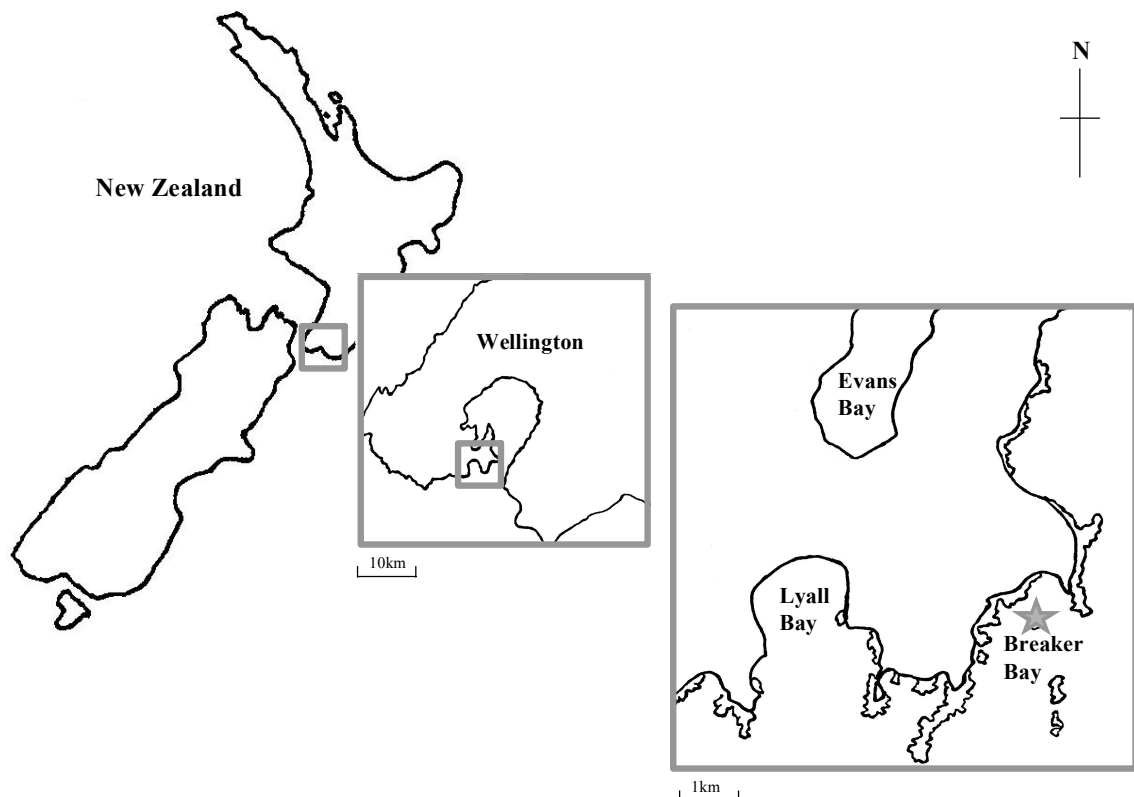
Figure 3.1 *Tethya bergquistae* collection site at Breaker Bay (star), Wellington South Coast, New Zealand.
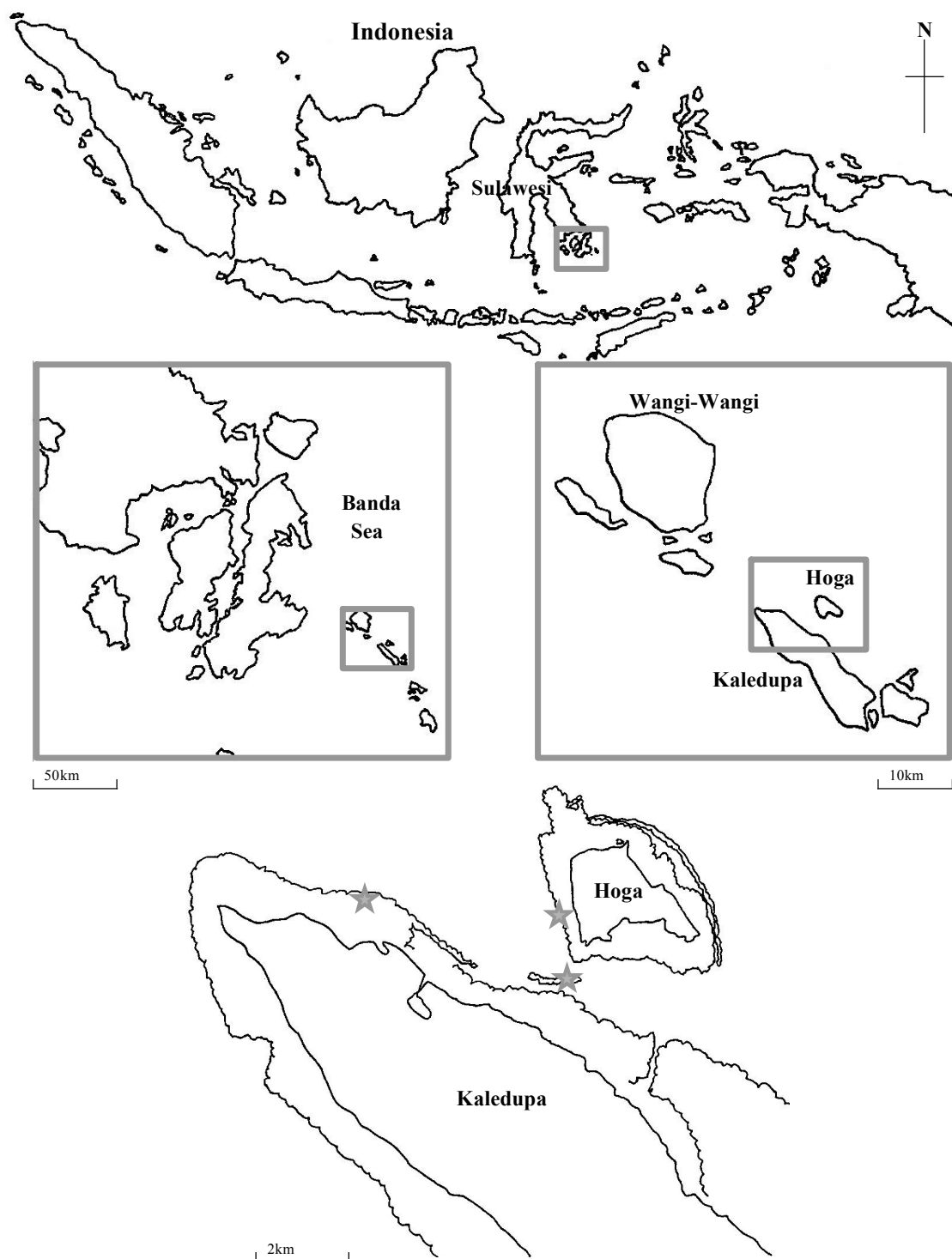
Figure 3.2 Collection sites (stars) of *Aaptos* sp., Hoga Island, Wakatobi Marine National Park off the South-East coast of Sulawesi, Indonesia.

Collection method and housing prior to the experiment

Temperate

Collected specimens of *T. bergquistae*, approximately 4 cm^3, were transported in seawater to an aquarium and housed in glass tanks of approximately 100 L when not in experimental use. Fresh unfiltered seawater was constantly supplied to each tank at approximately 13.4 L min^{-1}, creating an open flow system, which is important for sponges (Vogel 1974, 1977, 1978). Each sponge was attached with cotton to a circular plate used to anchor the sponges and employed in the chamber to measure oxygen consumption. The sponges were allowed to acclimate for 24 hours prior to experimentation, consistent with other sponge studies (Zocchi *et al.* 2003; Nickel 2004; Hadas *et al.* 2008).

Tropical

Specimens of *Aaptos* sp., approximately 4 cm^3, were transported in seawater to the laboratory on the island and placed in a holding tank (approximately 20 L) for not more than 45 minutes in preparation for the experiment. A 24-hour acclimation period was not possible as electrical power was unavailable over night. A pump circulated water in the holding tank (at 4 L min^{-1}) and lost oxygen was replaced using an aeration stone. Seawater was replenished every 20 minutes by bucket from the shore, as pumps providing unfiltered seawater were not available.

Sampling design

Temperate

Oxygen consumption was measured at 0, 1, 2, 4, 6, and 7 hours for 12 specimens of *T. bergquistae* per ultraviolet radiation treatment (High UV-B, 58.5 μW cm^{-2}; Control, no UV-B bulb). Each treatment was carried out on four sponges at a time, to make oxygen measurements more manageable, and the whole process was repeated three times with different specimens. Natural levels of UV-B penetrating into the water column fluctuate

around 35 μW cm^{-2}, and therefore the level used in the experiment was much higher than the sponges would normally experience (Diaz *et al.* 2000).

Tropical

The tropical experiment was carried out in the same manner but with only eight specimens of *Aaptos* sp. per ultraviolet radiation treatment, due to time constraints and electrical power limitations.

Experimental set up (temperate and tropical)

The experimental aquarium (approximately 20 L) was an open flow system with seawater being replaced at a rate of 4 L min^{-1}. Two aquarium pumps were used to increase the current within the experimental tank, each device circulating the water at 4 L min^{-1}. Four halogen lamps fitted with neutral density filters provided photosynthetically active radiation (PAR), at an irradiance of 20 μmol photons m^{-2} s^{-1}. An ultraviolet bulb (Phillips TL12 100 W which emits 285 - 350 nm with a maximum between 310 - 315 nm) was fitted lengthwise across the middle of the experimental aquarium 350 mm above the base. The bulb was wrapped with a single layer of PVC filter to block all UV-C emissions, and Mylar sheets enclosed the experimental tank to protect the surroundings from UV-B radiation (Cullen & Neale 1997; Neale 2000). The bulb provided UV-B radiation (280 - 320 nm) at 58.5 μW cm^{2}. Wavelength emission was measured with a Kratos spectroradiometer (Kratos Monochromator GM200-2).

Measuring oxygen consumption under UV-B radiation (temperate and tropical)

In the experimental tank, a closed-system cylinder (300 ml) was used to measure net oxygen consumption rates, similar to that employed by Gatti *et al.* (2002). The clear plastic cylinder was placed over a sponge and a fibre-optic oxygen mini-sensor and temperature electrode was fitted into a rubber bung that was secured in the top of the chamber (FIBOX 3, 505 nm,

combined with ₍FIBOX₎ 5.20 Software for data logging; Precision Sensing GmbH, Regensburg, Germany). A magnetic spin bar rotating at 130 rpm kept water flow constant within the chamber.

After the acclimation period a sponge was moved into the experimental aquarium and the '0 hour' oxygen consumption measurement began. Oxygen concentration in the chamber was then recorded every five seconds for 15 minutes. This sponge was then moved from the chamber in the tank, and after the next sponge was placed in the cylinder the UV-B bulb was switched on. The cylinder was not transparent to ultraviolet radiation so sponges within the chamber received no UV-B wavelengths. This process was repeated until four sponges had been transferred into the experimental tank. At the completion of the fourth sponge, oxygen measurements were repeated sequentially on the specimens for each time point (1, 2, 4, 6, and 7 hours). The four individuals were rotated clockwise around the experimental tank after each oxygen measurement. This ensured that no bias existed between positions within the tank and the amount of UV-B radiation received. It was expected that the sponges would respond rapidly to the stress of UV-B radiation and therefore more measurements were taken in the first couple of hours (0, 1, 2, 4, 6, and 7 hours). Net oxygen consumption rates were calculated from the decrease in oxygen concentration (% saturation) over 15 minutes, taking into account temperature, salinity, and water volume (i.e. chamber volume minus sponge volume). These measurements were standardised for sponge dry weight and multiplied by four to represent the hourly net oxygen consumption rate (units mg O_2 g^{-1} DW h^{-1}). Sponge dry weight was obtained at the completion of the experiment by drying specimens in an oven at 60°C for three days to reach a stable weight.

Analysis of data (temperate and tropical)

Two-way mixed model ANOVAs were used to analyse whether the net oxygen consumption rate of each sponge species differed with exposure to UV-B over 7 hours. The independent variable 'Time' used the same individuals over seven sampling hours (a repeated measure). Each 'Treatment' (Control or UV-B) used different sponges (a fixed factor). A Bonferroni multiple comparison was used for *post-hoc* analysis. Equal variance was satisfied in all time treatments ($p > 0.05$). Sphericity was not satisfied ($p < 0.05$), therefore, values were corrected using the *Green-house-Geisser* estimates of sphericity ($\varepsilon = 0.607$) (Field 2005). Means and 95% confidence intervals were reported. There was no significant effect of UV-B on net oxygen consumption rates of *Aaptos* sp. or *T. bergquistae*, therefore, statistical analysis was not carried out to compare between the two sponges.

3.3 **RESULTS**

The effect of UV-B exposure on net oxygen consumption in *Tethya bergquistae*

The net oxygen consumption rate of *Tethya bergquistae* in both the control and UV-B treatment followed the same pattern, dropping by approximately 40% after the first hour and then staying relatively constant for the following 7 hours (Figure 3.3). Statistical analysis revealed that there was no difference between the control and UV-B treatment on the net oxygen consumption rates of *T. bergquistae* (Table 3.1). There was an effect of time (irrespective of UV-B treatment) on the net oxygen consumption rates of *T. bergquistae* (Table 3.1). The *post-hoc* analysis indicated that net oxygen consumption rates for both the control and UV-B treatment were higher at the 0 h (hour) measurement (0.114 ± 0.020 mg O_2 g^{-1} DW h^{-1}) compared to 1 h (0.076 ± 0.016 mg O_2 g^{-1} DW h^{-1}), 2 h (0.066 ± 0.013 mg O_2 g^{-1} DW h^{-1}), and 7 h (0.074 ± 0.013 mg O_2 g^{-1} DW h^{-1}) ($p < 0.05$), but no other comparisons differed ($p > 0.05$).

Table 3.1 Results of the two-way mixed model ANOVA for the effects of UV-B treatment over time on the oxygen consumption rates of *Tethya bergquistae* (** $p < 0.01$).

Variable	*df*	*F*	*P*
Time	3, 67	6.393	**
Treatment	1, 21	7.169×10^{-6}	0.916
Time x Treatment	3, 67	1.812	0.153
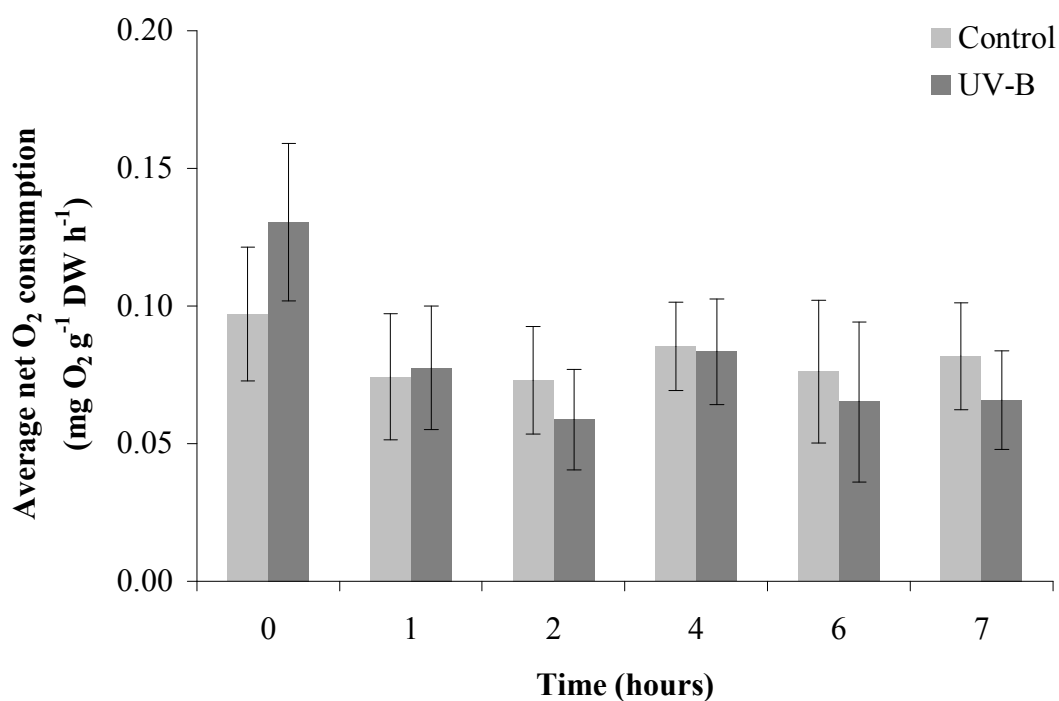
Figure 3.3 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) of *Tethya bergquistae*, ± 95% confidence intervals, over 7 hours with and without ultraviolet radiation (UV-B and Control) ($N = 12$).

The effect of UV-B exposure on net oxygen consumption in *Aaptos* sp.

The net oxygen consumption rate of *Aaptos* sp. in both the control and UV-B treatment followed the same pattern, slowly increasing over the 7-hour measurement period (Figure 3.4). Statistical analysis revealed that there was no difference between the control and UV-B treatment on the net oxygen consumption rates of *Aaptos* sp. (Table 3.2). There was an effect of time (irrespective of UV-B treatment) on the net oxygen consumption rates of *Aaptos* sp. (Table 3.2). The *post-hoc* analysis indicated that in both the control and UV-B treatment net oxygen consumption rates at the 0 h (hour) measurement (0.270 ± 0.066 mg O_2 g^{-1} DW h^{-1}) were lower than at 4 h (0.492 ± 0.089 mg O_2 g^{-1} DW h^{-1}), 6 h (0.558 ± 0.091 mg O_2 g^{-1} DW h^{-1}), and 7 h (0.508 ± 0.081 mg O_2 g^{-1} DW h^{-1}) ($p < 0.05$). Net oxygen consumption rates at 2 h (0.378 ± 0.057 mg O_2 g^{-1} DW h^{-1}) were also lower than at 6 h ($p < 0.05$), but no other comparisons differed ($p > 0.05$).

Table 3.2 Results of the two-way mixed model ANOVA for the effects of UV-B treatment over time on the oxygen consumption rates of *Aaptos* sp. (*** $p < 0.001$).

Variable	*df*	*F*	*P*
Time	5, 70	7.857	***
Treatment	1, 14	0.232	0.637
Time x Treatment	5, 70	1.113	0.362
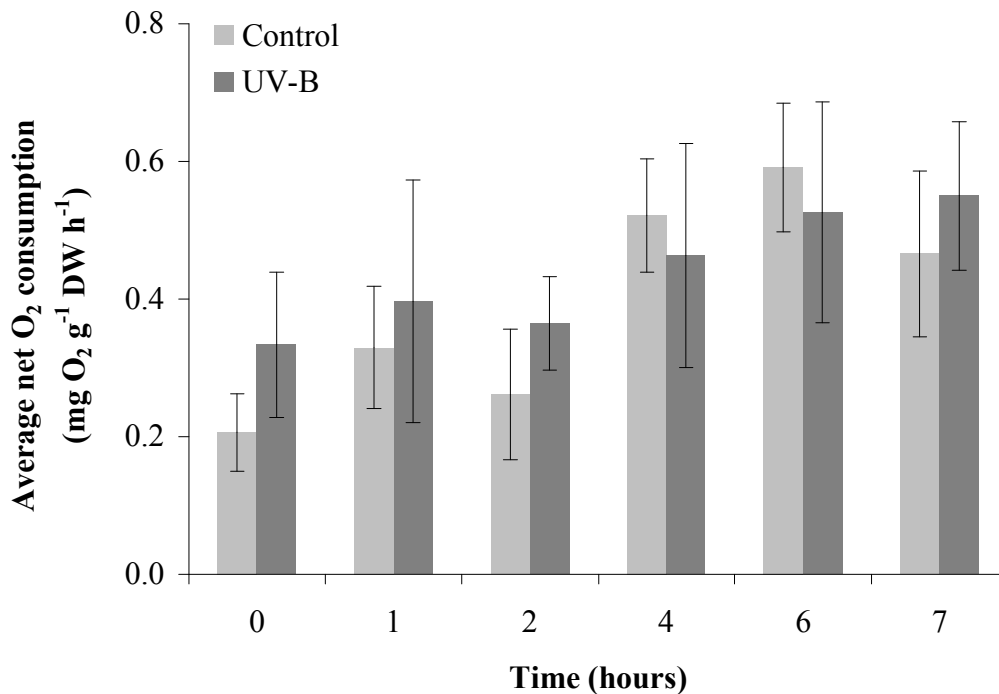
Figure 3.4   Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}) of *Aaptos* sp., ± 95% confidence intervals, over seven hours with and without ultraviolet radiation (UV-B and Control).

3.4 DISCUSSION

Harmful UV-B wavelengths are increasing at the Earth's surface and penetrating deeper into the water-column of marine ecosystems, due to ozone depletion and interactions with climate change (Crutzen 1992; Harris *et al.* 1995; Schindler *et al.* 1996; Madronich *et al.* 1998). The deeper penetration depths of harmful UV-B radiation in the marine environment are concerning, as the effects on important marine benthic taxa, such as sponges, are not well known. This study investigated the influence of UV-B radiation on the oxygen consumption rates of model temperate and tropical sponges, *Tethya bergquistae* and *Aaptos* sp., respectively. It was found that UV-B radiation, at 60 μW cm^{-2}, had no effect on the oxygen consumption rates of either sponge species over 7 hours.

Explaining no effect of UV-B

It was surprising that no effect of UV-B radiation was observed on the oxygen consumption rates of *T. bergquistae* and *Aaptos* sp., as these wavelengths have been found to significantly affect the respiratory activity of microorganisms, bacteria, plankton, and amphipods (Thomson *et al.* 1980; Gerber & Hader 1992; Moran & Zepp 1997; Pakulski *et al.* 1998; Rusch *et al.* 2006; Martinez 2007; Obermuller *et al.* 2007). Most of these authors suggested that respiration rates were increased in response to stressful environmental conditions for cellular maintenance, growth, and repair of damaged DNA, all of which needed excess oxygen to compensate for these energy requirements (Thomson *et al.* 1980; Pakulski *et al.* 1998; Gustavson *et al.* 2000; Pakulski *et al.* 2008). Variability in response to ultraviolet radiation exposure, however, can differ due to the following: duration of exposure, pre-acclimation state of the cell, spectral irradiance, interactions with other variables, delayed effects and recovery, intensity of exposure, and efficiency of protection and repair strategies (Vincent & Neale 2000).

Duration of exposure and pre-acclimation state of cell

Ultraviolet-B radiation may have altered the oxygen consumption rates of *T. bergquistae* and *Aaptos* sp. if the sponges had been exposed to these wavelengths for a longer period of time, as the effect of UV-B is often cumulative (Behrenfeld *et al.* 1993; Buma *et al.* 1996a). Pre-acclimation to UV-B radiation can also reduce the harmful effects of this wavelength. Martinez (2007) suggested that acclimation to UV-B radiation can occur in the respiratory electron transport systems of plankton, with these systems being less inhibited if they had been previously exposed to higher doses of UV-B radiation. None of the sponges were pre-acclimated to UV-B wavelengths as high as 60 μW cm^{-2}, as the level used in the experiment was much higher than would be received *in situ*, e.g. 35 μW cm^{-2} (Diaz *et al.* 2000).

Delayed response

It is possible that the increased oxygen consumption needed for repair may not be induced immediately, and significant effects of UV-B radiation on *T. bergquistae* and *Aaptos* sp. may have been observed if measurements had continued past 7 hours. Respiration rates of other aquatic organisms, however, have been shown to respond within 3 hours to harmful UV-B radiation exposure (Gerber & Hader 1992; Martinez 2007; Obermuller *et al.* 2007). Other authors investigating stress responses in sponges have also shown a relatively fast response time (within 12 hours) to environmental factors (Krasko *et al.* 1998; Schroder *et al.* 1999a; Schroder *et al.* 1999b; Fafandel *et al.* 2003). Fafandel *et al.* (2003), for example, found that the sponge *Suberites domuncula* had significantly higher levels of the stress-responsive KRS_SD protein kinase after only 2 hours of treatment with tributyl-tin. Schroder *et al.* (1999a) found that DNA strand breakage and heat shock protein accumulation occurred in sponges after 12 hours of exposure to PCB pollutants, which are known to induce oxidative stress and free-radical DNA damage, similar to that caused by ultraviolet radiation (Stohs 1990; Mantyla & Ahotupa 1993; Oakley *et al.* 1996). Unfortunately there is little known of the response times for repair processes and oxygen consumption rates in sponges to ultraviolet radiation, or other environmental stress.

Spectral irradiance

Some authors have suggested that UV-A and PAR play a role in photoenzymatic repair of damage caused by UV-B (Hanawalt & Setlow 1975; Friedberg 1985; Malloy *et al.* 1997; Williamson *et al.* 2001; Goncalves *et al.* 2002). Martinez (2007), for example, showed that UV-A prevented inhibition of respiratory electron transport systems in plankton. It is unlikely that UV-A radiation could have induced fast repair mechanisms in *T. bergquistae* and *Aaptos* sp., however, as the lights used in this experiment emitted only a small quantity of UV-A, incomparable to the large amounts that occur naturally. It is acknowledged that laboratory

experiments can never accurately simulate natural solar conditions and the ratios of ultraviolet wavelengths to PAR and IR, but they are useful in determining crude effects (Neale *et al.* 1994; Neale 2000).

Interactions with other variables

A micro-layer of algae covering the surface of *T. bergquistae* or *Aaptos* sp., may have inhibited UV-B wavelengths from damaging the sponges. Other marine organisms can be protected from ultraviolet exposure by organic or inorganic coverings (Stochaj *et al.* 1994; Vincent & Quesada 1994). Some sea anemones, for example, attach debris to their surface to shield them from increased irradiance (Stochaj *et al.* 1994) while salt crystals can attenuate solar radiation received by floating cyanobacterial mats (Vincent & Quesada 1994). Corriero *et al.* (1989) hypothesised that thick microalgae covering *Tethya aurantium* were protecting the sponge from light radiation. If a layer of microalgae protected *T. bergquistae* and *Aaptos* sp., long term-exposure to ultraviolet radiation may deplete this covering and leave the sponge surface open to damage. No visible layer of algae, however, was observed on any of the *T. bergquistae* or *Aaptos* sp. specimens used in the experiment.

Insufficient energy

The level of UV-B radiation used in the experiment, approximately twice as much as natural intensities e.g. 35 μW cm^{-2} (Diaz *et al.* 2000), may not have been high enough to elucidate a response in the sponges. The depth of water in the experimental tray was only 10 cm and it seems unlikely that this would have significantly lowered the UV-B radiation experienced by the sponges (Jerlov 1976; Kirk 1994). Previous research has indicated that ultraviolet radiation must be absorbed, and have a high enough energy level to influence molecules within an organism (Whitehead *et al.* 2000). The most likely scenario, therefore, is that the amount of ultraviolet radiation in the experiment was not at a high enough energy level to

produce a reaction in the cellular constituents of the sponges, and an effect on oxygen consumption rates. This suggests that long-term survival of these sponges may not be affected by exposure to UV-B radiation of up to 60 μW cm^{-2}. Distribution patterns for *T. bergquistae* and *Aaptos* sp. within benthic areas, therefore, should not be affected by UV-B penetration of up to 60 μW cm^{-2}, approximately twice the level experienced *in situ*. Further study, however, is needed to establish how much UV-B radiation these sponges withstand before negative effects are observed.

Efficient protection and repair strategies

The UV-B radiation emitted in the experiment was roughly twice as much as *T. bergquistae* and *Aaptos* sp. would naturally be exposed to (Diaz *et al.* 2000), therefore if the energy was not enough to damage cellular constituents within the sponges this suggests that they have a high tolerance to these wavelengths. It has been recognized that sponges have effective repair systems for DNA damage (Krasko *et al.* 1998; Schroder *et al.* 2003), but the induction of these mechanisms should have affected oxygen consumption rates. The production of heat shock stress proteins, for example, is considered energetically expensive (Fargestrom *et al.* 1987; Feder *et al.* 1992). This suggests that alternative mechanisms, such as screening compounds, may have prevented the UV-B radiation from having a high enough energy level to affect oxygen consumption rates in these sponges.

A large number of caratenoids have been isolated from many different sponges (Liaaen-Jensen *et al.* 1982; Tanaka *et al.* 1982a; Tanaka *et al.* 1982b; Yagamuchi 1982; Matsuno *et al.* 1984; Tanaka & Ito 1985; Mercadante 1999). These red and yellow pigments play a role in photo-protection as they can deactivate toxic reactive oxygen species (ROS) and free radicals, but only absorb light between 400 - 500 nm, but not the UV-B spectrum of 280 - 320 nm (Matsuno 2001). Mycosporine-like amino acids (MAAs), however, do absorb light in the

UV-B spectrum within 305 - 360 nm (Bandaranayake 1998). Only bacteria, fungi, and algae produce mycosporine-like amino acids, but other organisms acquire this compound through diet transfer, or symbiotic associations (Stochaj *et al.* 1994; Carroll & Shick 1996). Bandaranayake *et al.* (1996) was the first to report the presence of UV-B absorbing MAAs in the tropical sponge *Dysidea herbacea*. Only one other paper has investigated MAAs in sponges but reported low levels of these screening compounds in species from Antarctica (McClintock & Karentz 1997). Mycosporine-like amino acids absorb ultraviolet radiation and dissipate the energy as heat, but they can also act as antioxidants scavenging reactive oxygen species (ROS) (de la Coba *et al.* 2009). These processes are important for absorbing ultraviolet radiation and for preventing ROS formation, but it is also vital that the energy dissipation does not cause photodynamic oxidative stress (de la Coba *et al.* 2009). *Tethya bergquistae* and *Aaptos* sp. could contain protective mycosporine-like compounds in high levels that prevent UV-B radiation stress from affecting oxygen consumption, but limited research makes it difficult to draw a strong conclusion.

Measurement tools

Other measurements, such as, chlorophyll *a* concentrations, symbiotic bacteria counts, stress protein expression, or expression of the SOS response might have been a better indicator for the effects of UV-B radiation, by identifying changes on a finer scale (e.g. Wilson & Greenberg 1993; Krasko *et al.* 1998; Schroder *et al.* 1999a; Schroder *et al.* 1999b; Webster *et al.* 2001; Fafandel *et al.* 2003). Oxygen consumption rates, however, have an advantage in that they reflect internal processes that change in response to stress, giving support for its use as an indicator of ultraviolet damage. Other studies have shown that using photosynthetic systems to indicate effects of ultraviolet radiation were masked due to repair and protective mechanisms (Wilson & Greenberg 1993). Repair processes cannot mask the effects of ultraviolet radiation on oxygen consumption, rather oxygen consumption rates should indicate

increased energy uptake to carry out protective mechanisms. It would be valuable, however, to conduct further work using oxygen consumption rates and some other internal measure, such as, stress protein expression, to give a clearer picture of UV-B radiation effects and to corroborate the respiratory trends seen.

Temperate - tropical comparison

The results indicated that the tropical and temperate sponges responded differently to the environmental conditions set up in the experiment, but this was unrelated to UV-B radiation. The difference in response may be the result of variation in the acclimation period prior to measurement. *Tethya bergquistae* had a 24-hour acclimation period, but *Aaptos* sp. only received approximately 45 minutes prior to experimentation, due to the electrical supply constraints. Oxygen consumption rates in *Aaptos* sp. could have been lowered in the collection period and regained normal metabolic speed during the experiment, as shown by the increase in oxygen consumption over time. Hoffmann et al. (2008) found that sponges, after a non-pumping period, slowly increased their oxygen consumption rates to an optimal level, although, this occurred over a short time period (30 - 40 minutes) compared to the elevation of oxygen consumption over 7 hours in *Aaptos* sp.. *Tethya bergquistae*, on the other hand, showed a 40% drop in oxygen consumption after the first hour. Activity could have decreased due to factors such as, insufficient food, or water flow or volume (e.g. Hummel *et al.* 1988; Leichter & Witman 1997; Osinga *et al.* 1999; Hadas *et al.* 2008). Sponges are known to be difficult to maintain in aquaria (e.g. Reiswig 1981; Osinga *et al.* 1999).

Conclusions, implications, and future study

The results from this study seem to indicate that long-term survival and distribution patterns in *Tethya bergquistae* and *Aaptos* sp. will not be affected by exposure to UV-B levels up to 60 μW cm^{-2}. Further study, however, is needed to establish how much UV-B these sponges can withstand before negative effects on oxygen consumption rates are observed. It would be

valuable to conduct further work using oxygen consumption rates and some other internal measure, such as, stress protein expression, to give a clearer picture of UV-B radiation effects at a cellular level. In conclusion, rising ultraviolet radiation levels due to ozone depleting pollution and global climate change may not affect the physiological functioning of sponges. This outcome was surprising, though it is possible that exposing the sponges to longer periods of higher energy UV-B may have detrimental effects. The impact of UV-B radiation on sponges is a field worthy of more detailed research.

Chapter Four

The effect of sediment on the oxygen consumption of a model temperate sponge

High sediment loads are generally assumed to be detrimental to sponges, yet diverse and abundant sponge fauna often inhabit sites with such sediment loads. This study examined the effects of different levels of 'high' sediment (2.5, 8.5 and 16.5 g L^{-1}) compared to no sediment, on the oxygen consumption rates of a model temperate sponge, *Tethya bergquistae*. Oxygen consumption is required for all energetic processes in an organism, and a change in this uptake can indicate a response to stress. Here, it was expected that increased levels of sediment would cause a marked decrease in oxygen consumption, as pumping activity slowed or ceased in response to clogging of the filtration system. The results showed that oxygen consumption rates were similar for sponges exposed to 0 and 2.5 g L^{-1} of sediment, indicating that *T. bergquistae* may easily tolerate sedimentation between these levels. In contrast, oxygen consumption rates decreased by 70% for specimens under 8.5 and 16.5 g L^{-1}, which suggests that at these sedimentation levels long-term survival of *T. bergquistae* could be jeopardized. These results show the potential of *T. bergquistae* to tolerate moderately high levels of sedimentation, but its susceptibility to more excessive levels of sediment. The generality of this finding, in terms of both species-specific responses, and the duration and intensity of exposure to increased sedimentation are discussed.

4.1 **INTRODUCTION**

Sediment is known to influence the distribution of a variety of benthic marine species (Konnecker 1973; McClanahan & Obura 1997). Extreme sediment deposition can limit settlement success (Bakus 1968) and combined with hydrodynamic forces may have a deleterious and abrasive effect on living organisms (Carballo & Garcia-Gomez 1994). A long-held assumption in sponge research has therefore been that high sedimentation is generally detrimental to this phylum (Dayton & Oliver 1977; Hiscock 1983; Naranjo *et al.* 1996; Kowalke 2000; Carballo *et al.* 2008). Numerous authors attribute low sponge abundance to high sedimentation, but give little supporting evidence regarding sediment rates or the influence of other abiotic or biotic factors (Seddon *et al.* 1992; Naranjo *et al.* 1996; Kowalke 2000; de Voogd & Cleary 2007). It has been assumed, consequently, that these organisms will inhabit areas away from sediment pressure (Hiscock 1983; Bell & Barnes 2000d). Cliff overhangs, for example, are expected to have a high abundance of sponges as these areas are generally devoid of sediment (Hiscock 1983). Similarly, sponges in high sediment sites are thought to be avoiding silt settling on their surfaces by exploiting microhabitat on vertical cliffs (Bell & Barnes 2000d; Bell & Barnes 2000b; Bell & Barnes 2000a).

Ecological studies, however, support positive effects of sediment on sponge diversity and abundance (e.g. Barthel *et al.* 1991; Ilan & Abelson 1995; McClanahan & Obura 1997; Bell & Barnes 2000b; Bell & Smith 2004). Many sponge species are abundant in areas of increased sediment (Ilan & Abelson 1995; Carballo *et al.* 1996; Rutzler 1997; Kowalke 1998). Distribution studies frequently find high levels of diversity and abundance of sponges in sedimented environments (McClanahan & Obura 1997; Bell & Barnes 2000d, c; Bell & Smith 2004). Bell and Smith (2004), for example, found that species richness was almost as high in areas of low sediment as under increased sedimentation. McClanahan and Obura

(1997) argued that increased sedimentation could induce rapid growth of benthic invertebrates, such as sponges, in response to higher nutrient enrichment. Other papers report that sediment disturbance will increase diversity by preventing competitively dominant species from monopolizing space, and maintaining patchiness within the habitat (Foster 1975; Taylor & Littler 1982; Littler *et al.* 1983; McQuaid & Dower 1990). Bell and Barnes (2000b) also argued that high sediment reduced competition with algae for sponges at Lough Hyne, Ireland, and resulted in an increased abundance. Sedimentation can reach a critical level, however, where it causes a decrease in sponge abundance (Bell & Barnes 2000c), potentially because burial, or the smothering of sponges leads to the closure of their inhalant pores, and a shut-down of the normal pumping activity, affecting feeding and resulting in energetic stress (Gerrodette & Flechsig 1979; Cerrano *et al.* 1999; Tompkins-MacDonald & Leys 2008). It is highly likely, therefore, that the discrepancies identified above may be explained by different tolerance limits of sponges to sediment stress. Clearly there is a need to experimentally test the impact of sedimentation on sponges, especially in terms of metabolic costs and survival.

Aim and hypothesis

The aim of this study was to examine how different amounts of 'high' sediment exposure affected a model temperate sponge. This was accomplished by measuring sponge oxygen consumption in response to different levels of 'high' sediment stress over three days. Oxygen consumption is required for all energetic processes in an organism (Kleiber 1975) and can therefore be used as a proxy for 'health', where changes in consumption indicate a response to stress (e.g. Zocchi *et al.* 2003; Obermuller *et al.* 2007; Poirier *et al.* 2008). It was hypothesised that over time the oxygen consumption rates of the sponges would significantly decline for specimens exposed to higher levels of sediment due to a reduction in pumping activity (Gerrodette & Flechsig 1979; Yahel *et al.* 2007; Tompkins-MacDonald & Leys 2008).

4.2 **METHODS**

Sponge species and collection sites

Tethya bergquistae was chosen as the study organism. This species is a good model for other demosponges as it is abundant and found in a range of habitats. Sponge specimens were collected from the Wellington South Coast of New Zealand at Breaker Bay and Barretts Reef (Figure 4.1) by SCUBA and snorkelling.
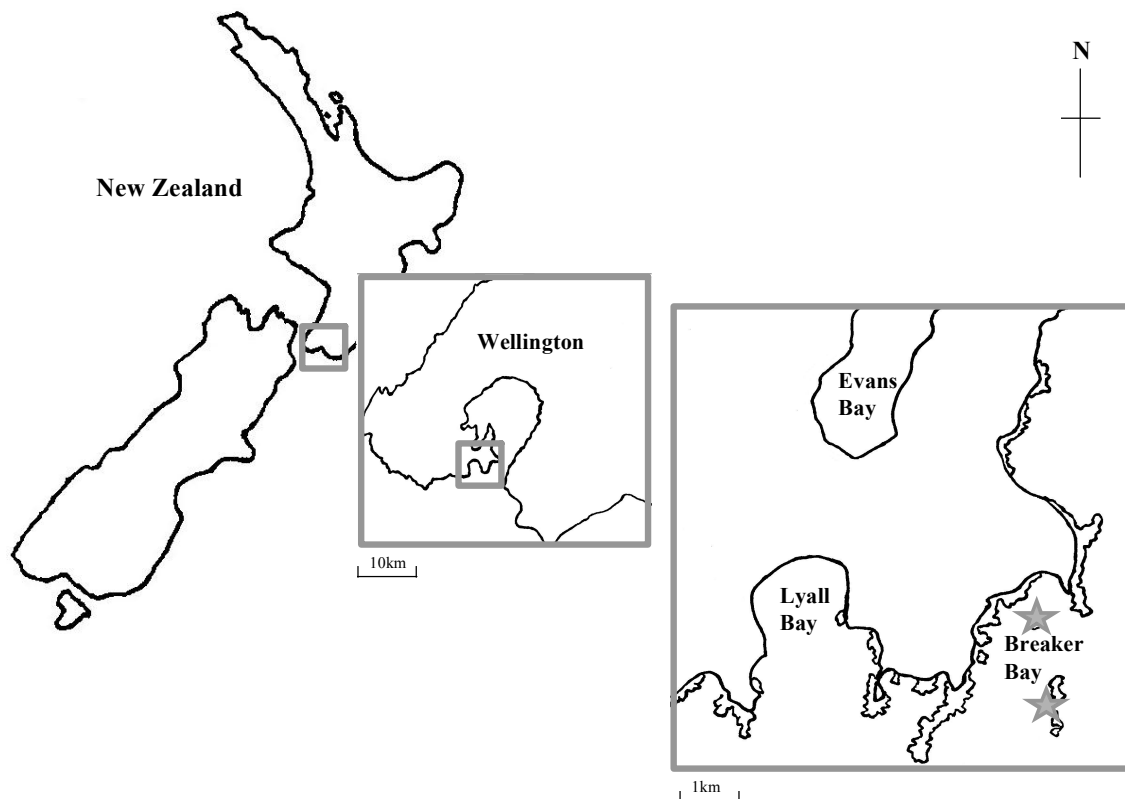
Figure 4.1 *Tethya bergquistae* collection sites at Breaker Bay and Barretts Reef (stars), Wellington South Coast, New Zealand.

Collection method and housing prior to the experiment

Collected specimens of *T. bergquistae* were transported in seawater to an aquarium and housed in glass tanks of approximately 100 L when not in experimental use. Fresh unfiltered seawater was constantly supplied to each tank at approximately 13.4 L min^{-1}, creating an open flow system, which is important for sponges (Vogel 1974, 1977, 1978). The sponges were

allowed to acclimate for 24 hours prior to experimentation, consistent with other sponge studies (Zocchi *et al.* 2003; Nickel 2004; Hadas *et al.* 2008).

Sediment preparation

The area used to gather sponges was inappropriate for collecting large amounts of fine sediment. Sediment for the experiment, therefore, was collected at low tide from a shallow estuary (Porirua Harbour) in the Wellington region (41°13'S 174°84'E). In the laboratory the sediment was rinsed with freshwater to prevent salt build up in the drying process (Airoldi & Cinelli 1997) and gradually sieved to remove particles larger than 250 μm. The sediment was transferred into a drying oven at 60°C for three days, and then incinerated in a muffle furnace at 500°C for five hours to remove organic matter.

Sampling design

Oxygen consumption rates were measured for five sponges per sediment treatment (Control 0 g L^{-1}, 2.5 g L^{-1}, 8.5 g L^{-1}, and 16.5 g L^{-1}) once a day, over three consecutive days. *Tethya bergquistae*, therefore, experienced a recovery period between sediment treatments (approximately 24 hours). This was important to help analyse whether sediment would cause irreversible damage, as some sponges have been found to recover normal activity after 3 - 25 hours following sediment exposure (Tompkins-MacDonald & Leys 2008). The treatments were chosen to test different levels of high sediment stress, based on reported 'high' sedimentation rates from coastal areas in the literature (1 - 15 g L^{-1} d^{-1} Naranjo *et al.* 1996; Crabbe & Smith 2002; Bell 2004). Unfortunately no information could be found for sedimentation rates around the Wellington South Coast, but the values chosen were useful to determine the crude effects of sediment. Oxygen consumption rates were also measured again after exposing sponges to the Control and 2.5 g L^{-1} treatments on day seven, as an extension to the main experiment (see results in Figure 6.3 Appendix).

Measuring net oxygen consumption rates

In an experimental tank, a closed-system cylinder (300 ml) was used to measure oxygen consumption (Figure 4.2), similar to that employed by Gatti *et al.* (2002). The clear plastic cylinder was placed over a sponge, and sediment was poured through a funnel in a hole at the top. Oxygen and temperature electrodes were fitted into a rubber bung, which sealed the hole at the top of the chamber. A magnetic spin bar rotating at 250 rpm kept water flow constant within the chamber and most of the sediment in suspension. The oxygen concentration in the chamber was then recorded every five seconds for 15 minutes in the light (20 μmol photons $m^{-2} s^{-1}$). At the completion of each oxygen measurement sediment was eliminated from the chamber to prevent build up in the experimental tank. Each sponge was transferred back into the holding tanks. The experimental procedure within each sediment treatment was repeated on the same five sponges over three consecutive days. Net oxygen consumption rates were calculated from the decrease in oxygen concentration (% saturation) over 15 minutes, taking into account temperature, salinity, and water volume (i.e. chamber volume minus sponge volume). These measurements were standardised for sponge dry weight and multiplied by four to represent the hourly net oxygen consumption rate (units mg O_2 g^{-1} DW h^{-1}). Sponge dry weight was obtained at the completion of the experiment by drying specimens in an oven at 60°C for three days (i.e. to a constant dry weight).
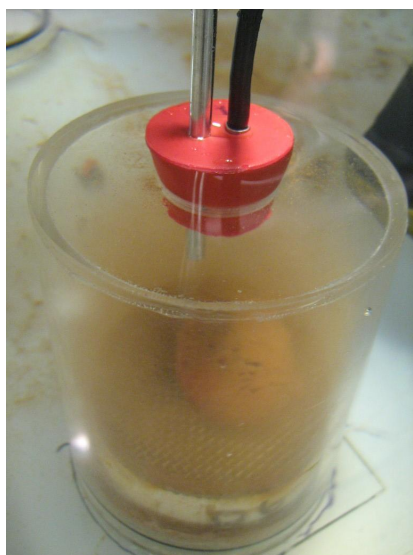
Figure 4.2 *Tethya bergquistae* inside the 300 ml closed-system cylinder exposed to the 16.5 g L^{-1} sediment treatment. The bung, and oxygen and temperature electrodes are shown in the top of the cylinder.

Analysis of data

A two-way mixed model ANOVA was used to analyse whether net oxygen consumption rates of *T. bergquistae* differed over the three-day period, and between sediment levels. To satisfy the assumption of equal variance, + 1 was added to all the values and this new data set was log transformed to correct for negative data points (Winer 1971). A significant interaction between sediment and time made it difficult to distinguish discrete patterns in the results. To further examine patterns in the data therefore, several one-way ANOVAs were used to investigate the effect of sediment treatment on sponge net oxygen consumption rates for each day. The analysis for Day One was carried out on x + 1 log transformed data due to violations in equal variances (Winer 1971), while untransformed data were used for Day Two and Three. Effect sizes (*r*) were calculated to indicate the strength of the relationship between sediment treatments on each day (large effect size $\geq$ 0.50, medium $\geq$ 0.30, and small $\leq$ 0.10, which account for over 25%, 9%, or 1% of the total variance, respectively) (see Field 2005). Net oxygen consumption rates from the two lowest (Control and 2.5 g L^{-1}), and highest (8.5 and 16.5 g L^{-1}) treatments were combined to clearly identify trends over time and analysed using two one-way repeated measure ANOVAs, as similar patterns were found between these treatments.

4.3 RESULTS

The effect of sediment on net oxygen consumption in *Tethya bergquistae*

The net oxygen consumption rate of *Tethya bergquistae* in both the Control and 2.5 g L^{-1} sediment treatments (0 and 2.5 g L^{-1}) followed the same pattern, increasing over the three-day period (Figure 4.3). Net oxygen consumption rates of the sponges in the 8.5 and 16.5 g L^{-1} sediment treatments, however, were similar to the Control on the first day but dropped considerably by the third day (Figure 4.3). Statistical analysis revealed an effect of both time

and sediment treatment on the net oxygen consumption rates of *T. bergquistae* (Table 4.1). The *post-hoc* test for the effect of sediment (irrespective of time) revealed that the net oxygen consumption rates of *T. bergquistae* were significantly higher in the Control and 2.5 g L^{-1} treatments compared to the 8.5 and 16.5 g L^{-1} treatments ($p < 0.05$). The interaction term was also significant (Table 4.1), indicating that the effect of sediment treatment on net oxygen consumption rates varied with time.

Analysis of sediment treatment effects on each day

Net oxygen consumption rates of *T. bergquistae* were significantly different between sediment treatments on each day (Table 4.2). For Day One the *post-hoc* analysis showed that net oxygen consumption rates were higher in the 16.5 g L^{-1}, 8.5 g L^{-1} and Control treatments than in the 2.5 g L^{-1} sediment treatment ($p < 0.05$). On Day Two, however, net oxygen consumption rates were higher in the 2.5 g L^{-1} sediment treatment than in the 8.5 g L^{-1} sediment treatment ($p < 0.05$), but not for any other comparisons ($p > 0.05$). On Day Three net oxygen consumption rates were higher in the 2.5 g L^{-1} and Control sediment treatments than in the 8.5 and 16.5 g L^{-1} sediment treatments ($p < 0.05$).

Analysis of sediment treatment effects between days

Net oxygen consumption rates from the two lowest (Control and 2.5 g L^{-1}) and highest (8.5 and 16.5 g L^{-1}) sediment treatments were combined to clearly identify patterns in the data. There was an effect of time on net oxygen consumption rates within the Control and 2.5 g L^{-1} treatments ($F_{2,18} = 36.577$, $p < 0.001$). The *post-hoc* analysis showed that net oxygen consumption rates within the Control and 2.5 g L^{-1} sediment treatments were higher on Day Three compared to Day Two and Day One ($p < 0.05$). Net oxygen consumption rates in these treatments on Day Two were also higher than on Day One ($p < 0.05$). There was an effect of time on net oxygen consumption rate within the 8.5 and 16.5 g L^{-1} sediment treatments ($F_{2,18}$

= 24.749, *p* < 0.001). The *post-hoc* analysis showed that net oxygen consumption rates on

Day One and Day Two were 70% higher than on Day Three (*p* < 0.05).

Table 4.1 Results of the two-way mixed model ANOVA for the effects of sediment treatment over time on the net oxygen consumption rates of *Tethya bergquistae* (*** *p* < 0.001).

Variable	df	F	P
Time	2, 32	30.441	***
Sediment	3, 16	20.678	***
Time x Sediment	6, 32	23.467	***

Table 4.2 Results of the one-way ANOVAs for the effects of sediment treatment on the net oxygen consumption rates of *Tethya bergquistae* for each day (* *p* < 0.05).

Variable	df	F	Effect size (*r*)	P
Day One	3, 16	7.943	0.722	*
Day Two	3, 16	4.077	0.659	*
Day Three	3, 16	74.771	0.966	*

Excessive amounts of photosynthetic particles caught in the chamber near the oxygen electrode is the only reasonable explanation for the negative oxygen consumption rates found on the first day under the 2.5 g L^{-1} sediment treatment (Figure 4.3). The significant increase in oxygen consumption rates over time for both the Control and 2.5 g L^{-1} treatments (Figure 4.3) was potentially due to natural variation induced by nutrient availability, as rates recorded after seven days in these treatments had declined to a similar level as those for Day Two (see Figure 6.3 Appendix).
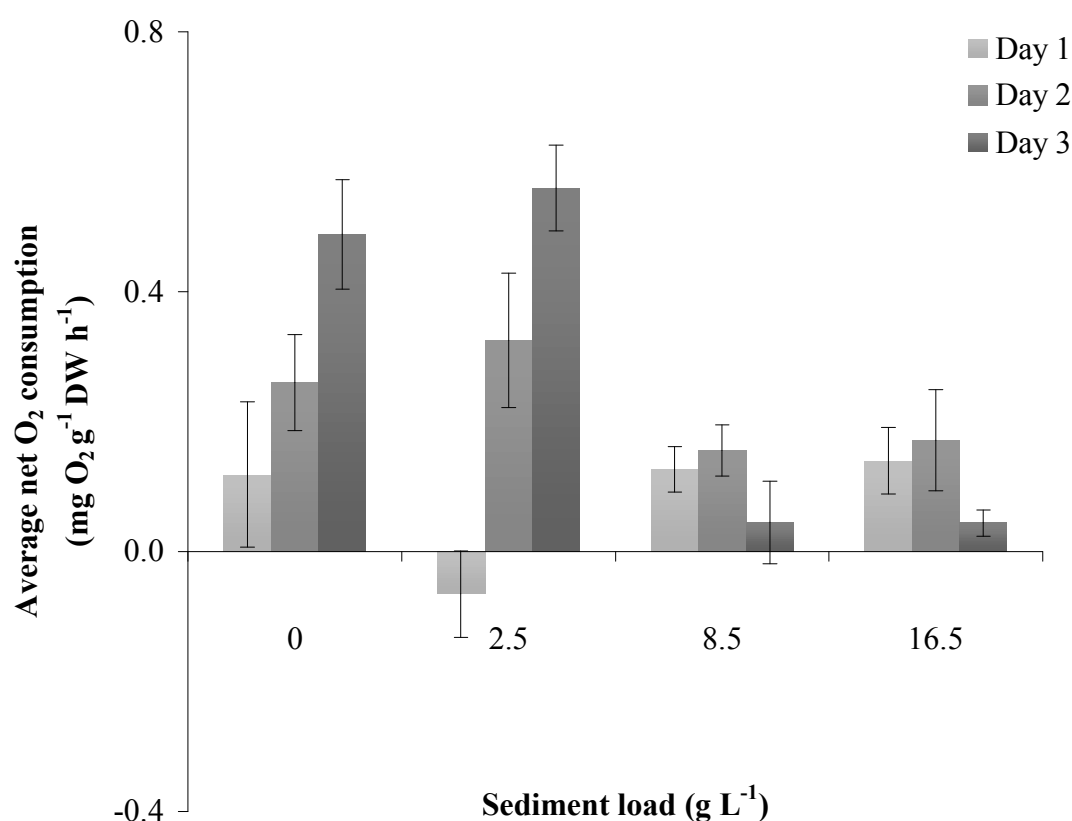
Figure 4.3 Average net oxygen consumption rates (mg O_2 g^{-1} DW h^{-1}), ± 95% confidence intervals, of *Tethya bergquistae* exposed to repetitive sediment stress over three days (Control 0 g L^{-1}, 2.5 g L^{-1}, 8.5 g L^{-1}, and 16.5 g L^{-1}) ($N = 5$ for each treatment). Negative values indicate oxygen production.

4.4 DISCUSSION

Many studies report physiological damage or disruption to sponges from sediment (Gerrodette & Flechsig 1979; Cerrano *et al.* 1999; Tompkins-MacDonald & Leys 2008), yet ecological research finds great diversity and abundance of these organisms in silt-laden sites (Carballo *et al.* 1996; McClanahan & Obura 1997; Bell & Barnes 2000d; Bell & Barnes 2000b). This study investigated the influence of different levels of 'high' sediment on the oxygen consumption rates of a model temperate sponge, *Tethya bergquistae*. Oxygen

consumption rates were expected to significantly decline under increasing concentrations of sediment, due to reductions in the water pumping activity of the sponges (Gerrodette & Flechsig 1979; Jorgensen *et al.* 1986; Yahel *et al.* 2007; Tompkins-MacDonald & Leys 2008). The results showed that oxygen consumption rates were similar for sponges exposed to 0 and 2.5 g L^{-1} of sediment, but decreased by 70% on the third day for specimens under 8.5 and 16.5 g L^{-1} of sediment.

The effects of sediment on oxygen consumption in *Tethya bergquistae*

Oxygen consumption rates of *T. bergquistae* were similar between the Control treatment and sediment treatment of 2.5 g L^{-1}, indicating that this sponge may tolerate sedimentation rates between these levels. This result was surprising, as sediment exposure of 2.5 g L^{-1} is within the range of high loadings reported in the literature (1 - 15 g L^{-1} d^{-1} Naranjo *et al.* 1996; Crabbe & Smith 2002; Bell 2004), and significant reductions in pumping activity have been found for sponges exposed to considerably lower levels (0.01 - 0.04 g L^{-1}) (Gerrodette & Flechsig 1979; Tompkins-MacDonald & Leys 2008). The tolerance of *T. bergquistae* to sediment above 2.5 g L^{-1}, however, appears to be much lower, as oxygen consumption rates were reduced by 70% under treatments of 8.5 and 16.5 g L^{-1}. It seems likely that a threshold occurs between the sediment levels of 2.5 and 8.5 g L^{-1}. Bell and Barnes (2000c) suggested that when sedimentation reaches a critical level it causes a decrease in sponge abundance potentially due to the blocking of inhalant ostia (Reiswig 1971a; Gerrodette & Flechsig 1979). More research is necessary to determine if a critical level exists between the sediment treatment of 2.5 and 8.5 g L^{-1} or whether the response to sediment is more gradual.

The results from the two highest sediment treatments, 8.5 and 16.5 g L^{-1}, indicate that *T. bergquistae* suffered reduced metabolic activity (and presumably pumping activity) after the second day of exposure. It is likely that the sediment exposure on Day One and Day Two

had a cumulative effect on the sponge, gradually clogging the filtration system (Hiscock 1983; Barthel & Gutt 1992; Tompkins-MacDonald & Leys 2008). Reductions in oxygen consumption rates may have occurred more quickly if the sponges had been exposed to longer periods of sediment stress within the same day. Significantly low oxygen consumption under sedimentation rates of 8.5 and 16.5 g L^{-1} may therefore limit the energy available for reproduction, growth, and long-term survival, which would impact on the distributional ecology for *T. bergquistae*. It has been suggested, however, that lower oxygen consumption rates may enable a species to survive longer under periods of environmental stress (Paffenhofer 1993; Castellani *et al.* 2005). In this case *T. bergquistae* may 'hibernate' until sediment stress is alleviated. Further experiments over a longer period of time would help establish whether *T. bergquistae* can sustain long-term sediment pressure in a 'hibernation' state or if mortality occurs at rates of more than 8.5 g L^{-1}.

Ecological implications of sediment tolerance

In the literature high sedimentation has been considered detrimental to sponges (Gerrodette & Flechsig 1979; de Voogd & Cleary 2007; Wulff 2008), yet various ecological studies have found diversity and abundance of these organisms at silt-laden sites (McClanahan & Obura 1997; Bell & Barnes 2000d; Bell & Smith 2004). The results from this study suggest that *T. bergquistae*, and perhaps other sponges, can withstand some levels of sediment that are considered 'high', as demonstrated in the 2.5 g L^{-1} treatment. The effects of sediment in this experiment, however, were significantly influenced by both the duration and intensity of treatments. This is important, as sedimentation pressure in the marine environment is also likely to vary in time and intensity due to local hydrography, which makes it difficult to predict what impact this will have on a sponge. Sponges may persist in areas with 'high sediment', for example, by reducing pumping and oxygen consumption activities until local conditions change in favour of growth and reproductive activity. The large range of values

presented in the literature representing 'high' sedimentation makes interpretation difficult. This was demonstrated well by the results from the 2.5 g L^{-1} sediment treatment, which was clearly within the range of 'high' sedimentation reported in the literature, yet no effects of stress were observed. It is important that sponge research investigating the effects of sediment should provide quantitative values for sedimentation, which is more meaningful than a description of 'high' or 'low'.

The results found here for *T. bergquistae* compared to other sponges in the literature demonstrate that sediment tolerance appears to be species specific. Lohrer *et al.* (2006) found no differences in the oxygen consumption rates of *Aaptos* spp. exposed to three weeks of sediment deposits of 0 mm, 10 mm, and 20 mm thickness. Yet sediment has been found to cause significant reductions in growth, reproductive status, and chlorophyll *a* presence from symbiotic phototrophs in the sponge *Cymbastela concentrica* (Roberts *et al.* 2006b) and sediment burial has been found to cause 15 - 50% 'tissue' death in several sponge species after four weeks (Wulff 1997). Carballo *et al.* (1996) concluded that there is a clear distinction in sponge species that are sensitive to sediment and those that favoured sedimented sites. Areas of 'high' sediment, therefore, will not necessarily be detrimental to all sponges, and large reductions in abundance may only occur in more sensitive species.

Sensitivity of a species may be determined by whether the sponges have mechanisms to prevent the detrimental effects of sediment. Many suspension-feeding organisms, for example, temporarily reduce or cease filtration to avoid being clogged by sediment (e.g. Mackie *et al.* 1974; Bock & Miller 1996; Ellis *et al.* 2002), but over a long period reduced pumping activity may result in considerable losses to the sponge volume (Hadas *et al.* 2008). Some sponges have been found to remove sediment from their surface by actively producing and then shedding a layer of mucous (Turon *et al.* 1999; Kowalke 2000), and other species

can reverse their water flow direction to force sediment from blocked canals (Simpson 1984). Sponge morphology is also considered important for species experiencing high sediment loads. Branching morphology is considered adaptive with respect to sedimentation for sponges and other organisms like corals, by preventing large amounts of sediment from settling on their surface layers (Chappell 1980; Bell & Barnes 2000c). This body form, however, is often restricted to lower flow environments due to the delicate nature of their basal attachment and branches (Bell *et al.* 2002a). Morphological features, such as the positioning of ostia, protruding spicules, and hairy or bristly surfaces have also been suggested to prevent sediment from clogging the inhalant systems of sponges (Bidder 1923; Barthel & Tendal 1993; de Voogd & Cleary 2007). Sponges may also combat abrasion from larger sediment particles by increasing spicule densities to enhance colony stiffness and strength and preventing significant losses of biomass (Vicente 1978; Palumbi 1984, 1986; Meroz & Ilan 1995; Bell *et al.* 2002b). The mechanisms mentioned above will help some sponge species to be more tolerant of high sedimentation rates of both fine and large sediment particles. Future research should investigate whether ecological surveys in areas of high sediment are more likely to find species with these characteristics.

Conclusions

This study confirms that 'high' sediment levels do not always cause negative effects on sponges, as found under the 2.5 g L^{-1} treatment for *Tethya bergquistae*. Sedimentation of 8.5 g L^{-1}, however, is at or above the critical level for *T. bergquistae*, as this amount of sediment potentially reduces the energy available for reproduction, growth, and survival, though long-term studies are necessary to support this. It was concluded from the results in this study, and those in the literature, that the long-term effects of sediment on sponges seem to depend on the particular species concerned and the local hydrography, which changes the duration and intensity of this environmental stress.

General Discussion

5.1 OVERVIEW

Marine environments are changing globally: coastal waters are warming (Southward *et al.* 1995; Levitus *et al.* 2000; Southward *et al.* 2005; Vargas-Yanez *et al.* 2008), ultraviolet-B radiation is increasing in the water-column (Crutzen 1992; Harris *et al.* 1995; Schindler *et al.* 1996; Madronich *et al.* 1998), sediment discharge into the ocean is expected to grow (Dunne 1979; Takeuchi 2004), pH is decreasing (Solomon *et al.* 2007), and rises in sea level and storm events are predicted - the latter also enhancing run-off, flooding and turbidity (Solomon *et al.* 2007). The rate and frequency of these changes is concerning as little information is available on the effects of these factors on important benthic species, such as sponges.

Over the last century reports of mortality and the prevalence of disease in sponges and other organisms have increased (Gaino *et al.* 1992; Vacelet 1994; Cerrano *et al.* 2000; Perez 2000; Wulff 2006b; Webster 2007; Garrabou *et al.* 2009). In some areas long-term declines have caused a more than 50% loss of sponge species and cover (Wulff 2006b). Sponge disease, meanwhile, has significantly affected commercially-grown species, with some almost becoming extinct (Gaino *et al.* 1992). Warming temperatures are thought to be the main reason for increasing disease and mass mortality events, though, salinity, sedimentation, pollution, nutrient enrichment, and a host of anthropogenic disturbances have also been implicated (Harvell *et al.* 1999; Cerrano *et al.* 2000; Perez 2000; Wulff 2006b; Lesser *et al.* 2007; Webster 2007). It has been acknowledged that any environmental stress reducing the

fitness of sponges is likely to increase susceptibility to disease or cause higher levels of mortality (Webster 2007). The predicted changes for global marine environments may therefore have significant adverse effects on sponge assemblages, but there is still a relatively poor understanding of their natural variation, due to limited monitoring and lack of physiological and ecological information (Wulff 2006b; Becerro 2008). The overall aim of this thesis was to better understand sponge physiology and the effects of environmental stressors on these organisms. Oxygen consumption was chosen as an indicator of physical condition and stress because this process determines the energy available for all physiological activities. The environmental factors, ultraviolet-B radiation and sediment, were selected because their input into the marine environment has been predicted to increase, yet little is known about their effects on individual sponges and sponge assemblages.

5.2 FINDINGS & APPLICATIONS

The following discussion addresses the main findings of the preceding chapters and, in a broader context, identifies how these results may relate to the survival of sponge assemblages within marine benthic systems. Long-term subsistence of sponges will depend on their rates of reproduction, recruitment, growth and mortality (Hall & Hughes 1996), but factors that negatively influence the energy available for these processes will change their survival rates.

Oxygen consumption rates

The study on oxygen consumption rates found significant variability within and between some species, and an interesting relationship was discovered between oxygen consumption rates and the proportion of inorganic material (spicule load) for temperate sponges. Variability in oxygen consumption rates may reflect better efficiency in energy use by some species over others, which could have consequences for their survival. Lower oxygen

consumption rates, for example, have been suggested to enable a copepod species to survive for longer when food sources are scarce, explaining their abundance and ubiquity (Paffenhofer 1993; Castellani *et al.* 2005). This could hold true for some of the sponges investigated, such as *Tethya bergquistae* and *Aaptos* sp., but not *Mycale* sp. which is found abundantly and in a number of different habitats (H.J.R. Murray, personal observation) and had one of the highest oxygen consumption rates of the temperate sponges. Further research into other physiological parameters is needed to determine those species that are more efficient at utilising energy in periods of food scarcity.

The relationship between increasing oxygen consumption rates and higher inorganic content in the temperate sponges demonstrated that specific habitat features, namely wave energy and nutrient concentrations in the water column, could have a significant influence on physiology. Increased production of spicules in sites with high water flow, however, may limit the energy available for reproduction, as oocyte size has been found to be smaller in wave-exposed areas compared to sheltered environments (Meroz-Fine *et al.* 2005). Meroz-Fine *et al.* (2005) suggested that a trade-off might exist between spicule abundance and reproduction. If a trade-off in reproductive activity is occurring for the sponges on the Wellington South Coast, then other forms of environmental stress could be quite damaging to their long-term survival.

Ultraviolet-B radiation

It was expected that damage by ultraviolet-B (UV-B) radiation to the surface layers of the sponges would impair important functions, such as, the inter-cellular transfer of electrical pulses (Yahel *et al.* 2007), waste excretion (Bergquist 1978), or the production of buds in reproduction (Brusca & Brusca 2003), which would increase oxygen consumption for the costs of repair. Experimentation, however, revealed surprising results. Two sponges, *Tethya bergquistae* and *Aaptos* sp., which live in vastly different habitats, showed no response to

damaging UV-B wavelengths, as the accumulated exposure to this radiation had no effect on their oxygen uptake. This indicated that increased levels of UV-B radiation penetrating into the water column may not be a concern for the long-term survival and distribution patterns in *T. bergquistae* and *Aaptos* sp., and perhaps other sponge species too. Despite this conclusion, increases in UV-B radiation may still have the potential to influence sponge survival in other ways. Ultraviolet-B radiation may negatively impact sponges directly through the greater sensitivity of gametes or juveniles (Damkaer *et al.* 1980; Pennington & Emlet 1986; Biermann *et al.* 1992; Adams & Shick 1996), or UV-B radiation may act synergistically with warming temperatures (Vincent & Roy 1993; Roos & Vincent 1998).

Gametes or juvenile sponges may be more susceptible to damage from UV-B wavelengths than are adult sponges. Several studies have found that invertebrate embryos and larvae are particularly sensitive to ultraviolet radiation (Damkaer *et al.* 1980; Pennington & Emlet 1986; Biermann *et al.* 1992; Adams & Shick 1996). Larvae may combat UV-B radiation, however, by containing high levels of protective compounds, or by alternating their brooding and spawning times so that larval production does not coincide with peak UV-levels, as found for some ascidian species (Bingham & Reyns 1999; Bates 2005).

The predicted increase in global sea surface temperatures of marine systems may reduce the ability of sponges to withstand damage from UV-B radiation. Physiological stress can lower the ability of cells to prevent damage from ultraviolet radiation (Vincent & Roy 1993; Roos & Vincent 1998), and increased temperature can therefore exacerbate the negative effects of ultraviolet radiation in aquatic organisms (MacFadyen *et al.* 2004; Harley *et al.* 2006). Little is known about sponge thermal tolerance (Bell & Smith 2004), but responses to temperature appear to be species specific (Blidberg *et al.* 2000; Przeslawski *et al.* 2008). Some sponges have been reported to tolerate extremes in temperature (Gaino *et al.* 1996), while others

experience symbiont bleaching or mortality in response to thermal extremes (Roberts *et al.* 2006b; Lopez-Legentil *et al.* 2008). The interaction between UV-B radiation and temperature on sponges may also be species specific, but it seems likely that the combined stress of these factors will be detrimental. The compounding effects of multiple stressors may be of highest concern on coral reefs where sponges already live close to their thermal tolerance limits and where UV-B penetration is significant due to high irradiances and the clarity of water.

Sedimentation

It was shown here that *Tethya bergquistae* can continue to function under relatively large sediment pulses, although at extreme levels a negative impact on the uptake of oxygen was found. It was concluded that predicted increases of sediment deposition into the marine environment may not have a negative influence on survival rates of this species, which is important given than *T. bergquistae* is abundant in shallow coastal waters where sediment is expected to increase (Syvitski *et al.* 2005).

From the literature it was clear that responses to sediment are species specific, and that, while the survival of *Tethya bergquistae* may not be affected by increased sedimentation, the distribution and abundance of a number of other sponges may change. Carballo *et al.* (1996) observed a clear distinction between sponge species that were very sensitive to environmental change and those that favoured extreme conditions. These authors found that several species of sponge were absent in areas where sedimentation was high, yet a number of other species preferentially settled in these sites (Carballo *et al.* 1996). Global increases in sedimentation, therefore, may simply change the species composition of sponge assemblages rather than cause large-scale mortalities.

One aspect not considered thus far is the effect of burial, as opposed to increased suspended sediment. The deposition of sediment into the water column from coastal landslips can result in a silt layer of up to 100 mm thick (Shaffer & Parks 1994; Konar & Roberts 1996; Wheatcroft *et al.* 1997; Thrush *et al.* 2004). This type of deposition may give rise to substantial tissue necrosis or rapid mortality of sponges (Wilkinson & Vacelet 1979; Wulff 1997, 2008). It appears that the tolerance of sponges to increased sediment depends on how much tissue is buried. Wulff (2008), for example, found that sponges experiencing shallow burials had full recovery, while mortality and significant 'tissue' disintegration occurred for those under deep layers. The impact of burial on sponge assemblages may depend, therefore, on local water flow and wave activity, as stormy or high wave-energy conditions could flush sediments from these organisms, facilitating their survival (Maldonado *et al.* 2008).

The effect of suspended sediment, in contrast, may present a significant problem for areas dominated by phototrophic sponges. Large increases in suspended sediment over long periods will reduce light levels reaching benthic habitats, and limits photosynthetic production in symbiotic sponges (Cheshire *et al.* 1997; Roberts *et al.* 2006b). This is not likely to cause drastic mortality, but may slow growth rates of affected sponges, as has been seen in phototrophic giant clams (Elfwing *et al.* 2003).

Grain sizes of sediment entering the marine environment may also have different impacts on sponges. Large-grained sand is more likely to cause abrasion to sponge assemblages (Carballo & Garcia-Gomez 1994) while small particles have the potential to clog the filtration systems of these organisms (Maldonado *et al.* 2008). Storms can re-suspend sediment sizes of 2.5 - 6 mm to a depth of 50 - 80 m (Logan *et al.* 1969); predicted increases in the frequency and severity of these events may reduce the biomass of sponges but total mortality may be avoided by species that increase their spicule density enhancing colony stiffness and strength

(Vicente 1978; Palumbi 1984; Meroz & Ilan 1995; Bell *et al.* 2002b). Small grain sizes (less than 30 μm), however, may present a bigger risk by enhancing the chances of clogging and subsequent mortality (Maldonado *et al.* 2008).

Sediment may also prevent sponge recruitment by reducing bud formation or decreasing available rocky substrate for attachment, and burying or scouring settlers (Gaino *et al.* 2006; Maldonado *et al.* 2008). Gaino *et al.* (2006) found that *Tethya aurantium* covered by a heavy sediment layer was unable to produce buds. Sponges that had only a small amount of sediment discontinuously affecting the surface, however, continued to produce buds (Gaino *et al.* 2006). Maldonado *et al.* (2008), meanwhile, found that early sponge settlers exposed to silt experienced significant morality. In this case, increased levels of settling sediment will be detrimental to sponge recruitment, although juveniles and early settlers may be able to prevent mortality by crawling away from areas of high sediment, as observed by Maldonado and Uriz (1999).

Interactions between sediment and UV-B

If UV-B radiation does have a negative impact on sponges this may be ameliorated by increases in suspended sediment and sedimentation. Coastal areas experiencing silt deposition from run-off often have lower penetration of ultraviolet radiation (Hader *et al.* 2007). Thin layers of sediment on the surface of sponges have also been assumed to protect these animals from ultraviolet damage (Mercurio *et al.* 2006). Sponges that prefer sedimented environments may therefore be at an advantage over those that cannot tolerate silt-laden sites at least in terms of UV-B protection.

5.4 **FUTURE RESEARCH**

Further research is needed, not only on sponge physiology but also ecology. The paucity of literature on sponges made it difficult to find explanations for many of the trends in this study. From this study various areas were recognised for future research and these are highlighted below.

Oxygen consumption rates and spicules

- Future research needs to address the major gaps in oxygen consumption information for calcareous and hexactinellid sponges, and for species from temperate and polar ecosystems.

- Future research into sponge oxygen consumption rates should include measurements of other physiological processes, such as, pumping activity, filtration of nutrients, symbiont abundance, and reproductive activity to enable a better description of specific oxygen consumption levels.

- More information is needed on spicule content and type, and their relation to oxygen consumption rates, specifically:

  1. Whether sponges maintaining or producing greater amounts of spicules require higher oxygen consumption rates. This would help to support conclusions about the identified link between inorganic content and oxygen consumption in the Wellington South Coast sponges.

  2. Whether calcareous sponges always have greater inorganic contents to combat the fragility of their spicules compared to those in demosponges.

Ultraviolet radiation and sponges

- Future work with UV-B radiation and sponges should use a combination of response variables to identify changes at molecular, cellular and organismal levels, such as oxygen

consumption rates, pumping activity, symbiont density, stress gene production (e.g. *hsp* genes), or chemical defence compounds.

- Laboratory experiments with UV-B radiation should be carried out over periods greater than 7 hours, to assess the long-term viability of sponges under this environmental stress.

- Identifying mycosporine-like amino acids and whether changes occur in these protective compounds when sponges are exposed to ultraviolet radiation would also benefit investigations.

- Future research should also look at the impacts of UV-B radiation on more sensitive parts of the sponge life cycle e.g. juveniles or gametes, as this would allow better predictions of the survival of these organisms in the long-term.

Sediment and sponges

- Future work with sedimentation and sponges should use a combination of different response variables, including oxygen consumption rates and pumping activity, filtration rates, symbiont density and sponge growth.

- Long-term sedimentation studies are needed. Experimental work with increased sedimentation levels should be carried out for longer than 7 - 30 days, as starved sponges have been found to survive this period with only minimal water pumping activity (Hadas *et al.* 2008).

- Separate studies should be conducted on the effects of burial versus suspended sediment, and the impact of different grain sizes and wave energies.

- To improve predictions of survival for sponge assemblages, the effect of sedimentation on oxygen consumption rates in species with different morphologies should be performed. Arborescent or tubular sponges, for example, have been predicted to reduce the amount of sediment settling on their surfaces, avoiding negative impacts caused by increased levels of silt (Chappell 1980; Maldonado & Young 1998; Bell & Barnes 2000b; Bell 2004).

5.5 **CONCLUSIONS**

Identifying and understanding the environmental pressures that affect any organism is fundamental for ecology and effective conservation (Williams *et al.* 2002; Tuomisto *et al.* 2003). The results from this thesis show that some sponge species may have the ability to withstand the challenges of global climate change and anthropogenic impacts. A lot more research is necessary, however, as the species-specific nature of sponge physiology, and in particular the responses of these organisms to environmental factors, often means that generalisations are unhelpful. Investigations into the effects of globally increasing environmental pressures may be better focused on particular sponge species that contribute significantly to coral and rocky reef systems. That is, for example, sponge species that make up a major part of the biomass, contribute large amounts to primary production, or have significant impacts on bentho-pelagic coupling.

Appendix

Experimental tank design

The experimental tank was specially designed to provide a constant flow of fresh seawater and a controlled irradiance (Figure 6.1, 6.2). This set up was used for all the experiments within in this study. The ultraviolet-B (UV-B) fluorescent bulb was only used in the UV-B experiment.
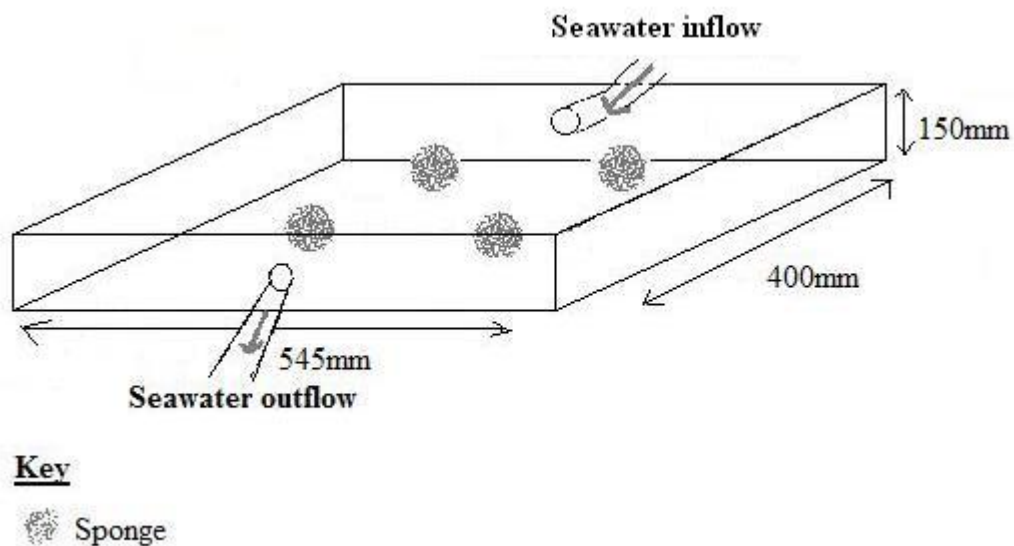
Figure 6.1 The experimental tank (150 mm deep, 545 mm wide and 400 mm long). An inflow tube supplied the tank with fresh unfiltered seawater. The outflow tube maintained the depth of water at 100 mm.
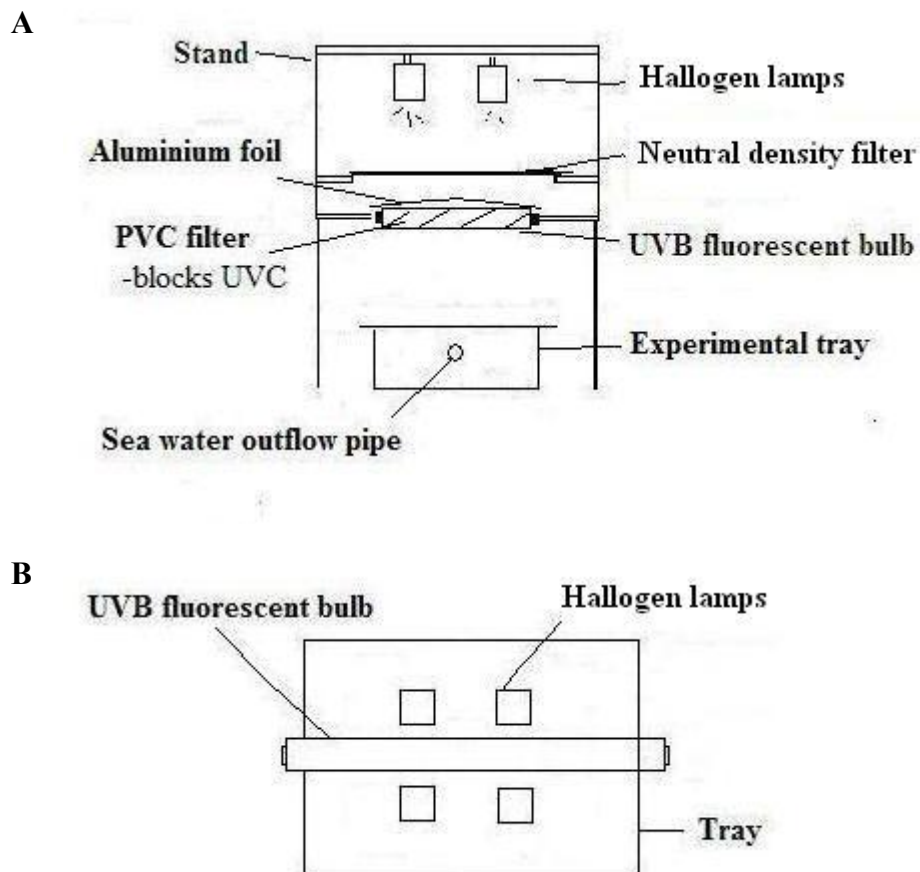
Figure 6.2   A front and birds-eye view of the experimental tank, stand, and lighting set up. **A.** The UV-B fluorescent bulb was anchored to a stand 350 mm directly above the experimental tank. Neutral density filter paper was fitted to alter the irradiance from halogen lights. **B.** The ultraviolet bulb was set up across the middle of the experimental tank, parallel to the in and outflow end.   Two halogen lamps were positioned each side of the UV-B fluorescent bulb. Sponges were placed under each light.

Sediment experiment extension

In the sediment experiment oxygen consumption rates were measured for five sponges per sediment treatment (Control 0 g L^{-1}, 2.5 g L^{-1}, 8.5 g L^{-1}, and 16.5 g L^{-1}) once a day, over three consecutive days. As an extension to the main experiment oxygen consumption rates were measured again after exposing sponges to the Control and 2.5 g L^{-1} treatments on day seven (Figure 6.3). The significant increase in oxygen consumption rates over time for both the Control and the 2.5 g L^{-1} sediment treatments was potentially due to natural variation induced by nutrient availability, as rates recorded after seven days in these treatments had declined to a similar level as those for Day Two (Figure 6.3).
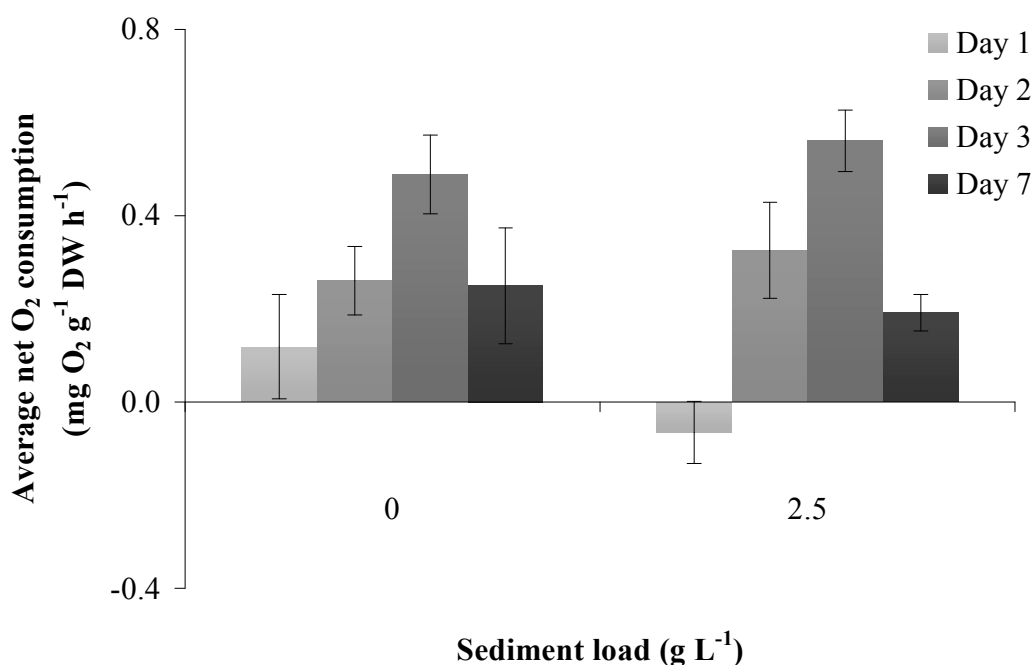
Figure 6.3 Average net oxygen consumption rates (mg O$_2$ g^{-1} DW h^{-1}), ± 95% confidence intervals, of *Tethya bergquistae* exposed to repetitive sediment stress over four days (Control 0 g L^{-1}, 2.5 g L^{-1}) ($N = 5$ for each treatment). Negative values indicate oxygen production.

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