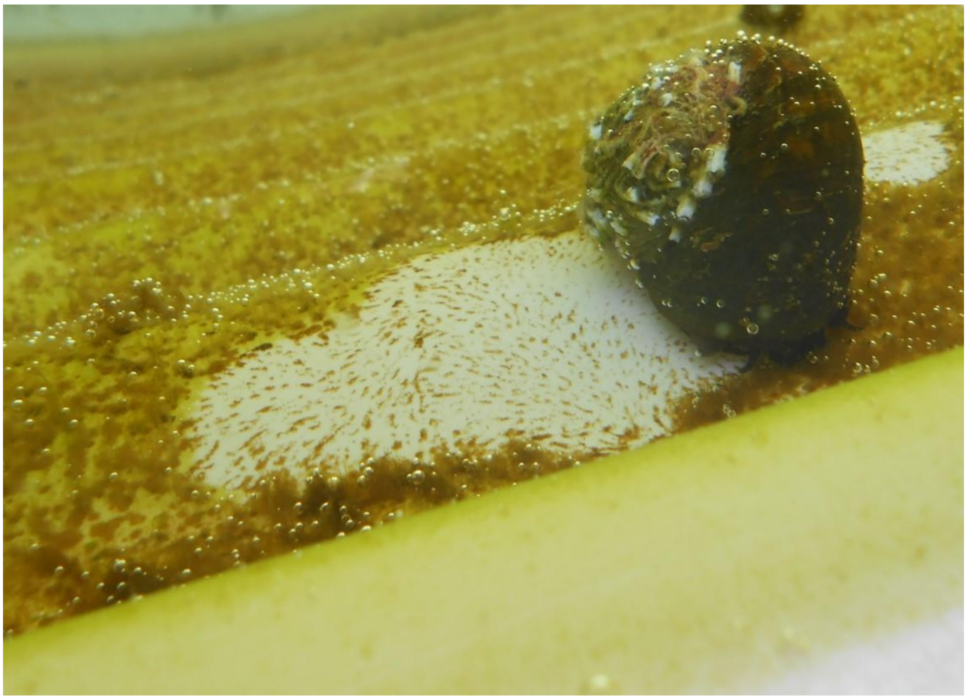
Changing Consumer Strength in a Changing Climate



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Cover image: *Turbo undulatus* (common warrener) grazing on turf algae. Photo credit: Nicole Mertens.

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Nicole Mertens

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ABSTRACT

The intensity at which organisms interact is affected by abiotic conditions. Ocean warming and acidification alter the metabolic demands of organisms and the strength at which they interact with each other. The metabolic costs of changing abiotic conditions vary between interacting pairs of species, and as such, their strength of influence on one another may change with changing climate.

Ocean warming and acidification are anticipated to alter competitive dominance among primary producers such as perennial kelp and ephemeral turf algae, increasing the potential for ecosystems to undergo phase shifts, e.g. from kelp-dominated to persistent turf-dominated states. However, in order to meet greater metabolic demands imposed by elevated temperature, herbivorous invertebrates need to increase feeding rates and may counter turf productivity as a result. Whilst strong top-down control of primary productivity is supported by metabolic theory of ecology (MTE), it assumes that consumption rates of herbivores keep pace with metabolism and mirror increased growth of producers.

At moderate warming, both metabolic rates and feeding of herbivorous gastropods were elevated, yet as temperature increased further consumption rates peaked earlier than turf growth rates. Imposed costs to resource allocation where consumption does not meet metabolic demands may result in reduced fitness and survivorship. These results suggest that future strength of top-down control is dependent on whether consumer-producer responses are synchronous, with mismatches between interacting pairs producing outcomes not predicted by metabolic theory. Further, moderate increases of temperature and CO_2 lead to reduced herbivore ingestion efficiency, ultimately resulting in reduced growth.

Elevated metabolism generally requires increased foraging to meet energetic demands; however, foraging may also need to be mediated by predator avoidance. This thesis identified that the need for greater foraging activity imposed by future warming and ocean acidification was opposed by elevated predation risk. Avoidance may be heightened in calcifying herbivores such as gastropods as a way to mitigate increased costs of inducible defences like shell building. Nevertheless, reduced foraging rates may compound energetic deficiencies and lead to reduced fitness.

Compensatory responses of gastropod and amphipod herbivores that buffered the accelerated effects of ocean warming and acidification on turf productivity may indicate the potential for this kelp-turf system to resist abiotic change. Moreover, this role was filled by more than one species, such that the one species could compensate for the effects of climate in the absence of the other, but not over compensate when together. Such functional redundancy of trophic compensation was underpinned by individual and population level responses to altered conditions, and offers an account for why some systems may be able to withstand both short- and long-term disturbances.

Species interactions are mediated by the abiotic environment, and the strength of interactions may be altered through the influence of abiotic change on physiological demands. This thesis contributes new knowledge to recognising idiosyncratic and predictable responses of interacting species to future conditions and their ensuing consequences for ecological communities. Finally, it expands on the theory of compensatory dynamics by exploring adjustability in strength of buffering responses of consumers to the effects of altered environments on productivity.

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Chapter 2

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CHAPTER 1

GENERAL INTRODUCTION

The world's marine ecosystems are set to be affected by climate change through change in species distribution and relative abundance (Harley *et al.* 2006; Cheung *et al.* 2009; Hoegh-Guldberg and Bruno 2010). Elevated temperature and carbon dioxide may directly impact upon the physiology of many marine species (Peck *et al.* 2004; Pörtner and Farrell 2008; Somero 2010), as well as *via* ecological processes such as competition; e.g. competitive subordinates turning into dominates (Kordas *et al.* 2011; Poore *et al.* 2013). Such changes can have cascading effects, altering the composition and function of entire ecological communities (Hawkins *et al.* 2008; Johnson *et al.* 2011; Harley *et al.* 2012; Vergés *et al.* 2014). However, systems that are exposed to considerable environmental stress do not necessarily shift to different states, as interactions between biotic components of the system may also serve to buffer some of the impacts of changing abiotic factors (Menge *et al.* 2011; Alsterberg *et al.* 2013). To better understand the potential for species loss and phase shifts in a given ecosystem there is a need to determine the main biotic and abiotic drivers that respond to elevated ocean warming and acidification.

In this introduction I discuss how a changing abiotic environment may affect individual species and their biotic interactions. I examine how interacting pairs of organisms in different functional groups (e.g. primary producers, grazers) respond to elevated temperature and $p\mathrm{CO}_2$, and whether these changes in physiological response result in a shift in the interaction strength of consumers. I investigate the mechanisms through which the broader effects of altered environmental conditions may be absorbed to varying extents *via* biotic interactions. I also consider the current predictions of how temperate marine systems will respond to global climate change, and discuss the merits of incorporating findings from studies across a broad range of scales in order to improve our understanding of how to mitigate the effects of changing environments.

1.1 PHYSICAL CHANGES TO THE WORLD'S OCEANS

Anthropogenic sources of carbon dioxide emission are contributing to atmospheric CO_2 concentrations 40% higher than pre-industrial levels, and well above those experienced by the planet in over 800,000 years (Lüthi *et al.* 2008; IPCC 2013). Warming in response to elevated CO_2 levels has seen global average surface temperature increase at a rate of approximately 0.2 °C per decade in the last three decades (Hansen *et al.* 2006). During this time, the world's surface waters have experienced an average decrease of 0.02 pH units per decade (Caldeira and Wickett 2005; Raven *et al.* 2005; Doney *et al.* 2009). Increased CO_2 dissolution into the oceans alters the carbonate chemistry of seawater, affecting the concentration of the three main forms of dissolved inorganic carbon (aqueous carbon dioxide, $CO_{2(aq)}$, bicarbonate, HCO_3^-, and carbonate, CO_3^{2-}) (Kleypas *et al.* 1999; Feely *et al.* 2004; Fabry *et al.* 2008). CO_2 dissolving into seawater forms carbonic acid, H_2CO_3, which readily dissociates into a proton (H^+) and HCO_3^- (Fabry *et al.* 2008). Through a series of chemical reactions, CO_2 dissolution results in an increase in carbonic acid and bicarbonate, a decrease in carbonate and carbonate saturation levels and lower pH (Kleypas *et al.* 1999; Fabry *et al.* 2008).

Predictions of future global temperature rise based on 'business as usual' scenarios of CO_2 emissions correspond to a global average warming of at least 2°C by the end of the century, with an average warming of 4°C more than likely (IPCC 2013). Concomitantly, the pH of the world's oceans will be reduced by 0.3-0.4 units on average (Feely *et al.* 2009). However, the pH of coastal habitats is influenced by many other factors, and likely to be subject to more daily and seasonal fluctuations in carbonate chemistry than the open ocean (Takahashi *et al.* 2002; Duarte *et al.* 2013). Metabolic processes in coastal ecosystems can cause daily pH fluctuations of over 0.3 units (Frieder *et al.* 2012; Duarte *et al.* 2013), and eutrophication from upwelling or nutrient run-off from terrestrial inputs can alter the carbonate chemistry of coastal waters more so than direct increases in $p\mathrm{CO}_2$ (Borges and Gyphens 2010; Duarte *et al.* 2013). This existing variability may mean some systems show greater tolerance of fluctuations in abiotic factors (Frieder *et al.* 2012), however, predicted increases in temperature variability may have negative outcomes for many ectothermic species (Vasseur *et al.* 2014). Daily fluctuations of temperature and carbonate chemistry are an important consideration when designing coastal climate change experiments (Melzner *et al.* 2013).

Whilst other factors associated with climate change such as increased UV radiation and altered coastal upwelling will also impact upon marine organisms and communities (Harley *et al.* 2006), this thesis focuses on the effects of rising CO_2 levels and concomitant increases in temperature.

1.2 PHYSIOLOGICAL RESPONSES TO A CHANGING CLIMATE

All organisms have a thermal window within which biological processes can occur, therefore factors that influence environmental temperature may also impact upon an organism's physical performance (Pörtner and Farrell 2008). If organisms are living below their thermal optima, warming may increase their performance (e.g. Huey *et al.* 2012). The metabolic theory of ecology predicts that metabolic rates will increase with increasing temperature (Brown *et al.* 2004). Higher energetic demands as a result of elevated metabolism will lead to increased feeding rates (O'Connor 2009; Carr and Bruno 2013). However, if environmental temperatures exceed physiological thresholds for extended periods, and the organism is unable to adapt, heat stress and eventual death ensue. Poikilothermic organisms (organisms for which internal temperature varies considerably) that live in thermally stressful environments, such as the intertidal zone, have developed mechanisms to survive periods of extreme warming which may allow them to persist under future conditions. Heat shock proteins, metabolic depression and behavioural responses are all examples of adaptation to unfavourable temperatures (Williams and Morritt 1995; Helmuth and Hofmann 2001; Angilletta Jr *et al.* 2006; Marshall *et al.* 2011). However, if an organism is pushed outside of its thermal limits for an extended or indefinite time, such as during rapid global warming, it faces limited options: move, acclimate or perish (Williams *et al.* 2008).

Carbon dioxide can have multiple and contrasting effects on organisms. For autotrophs, it may be a resource; although the extent to which CO_2 enrichment has a positive effect depends on the carbon limitation and tolerance of ocean acidification in the autotroph in question (Doney *et al.* 2009; Porzio *et al.* 2011; Harley *et al.* 2012; Connell *et al.* 2013). Importantly for marine biota, decreasing carbonate lowers the saturation state of carbonate and calcium carbonate ($CaCO_3$) (Gattuso and Buddemeier 2000). $CaCO_3$ is used by many marine organisms to build shells, and increasing dissolution of shells in environments undersaturated with respect to CO_3^{2-} can impose energetic costs (Feely *et al.* 2004; Orr *et al.* 2005; Fabry *et al.* 2008). For example, a calcifying organism may require greater energetic investments to maintain defensive structures or change their behaviour to avoid predators, with both outcomes potentially altering the time spent acquiring resources or resulting in energetic deficiencies and trade-offs (Bibby *et al.* 2007; Wood *et al.* 2008; Nienhuis *et al.* 2010; Melatunan *et al.* 2013; Kroeker *et al.* 2014). Physiological stress associated with ocean acidification including hypercapnia (elevated CO_2 in the internal fluid) tend to result in compromised metabolic rates (Michaelidis *et al.* 2007; Fabry *et al.* 2008; Melatunan *et al.* 2011), however increased feeding rates have been shown in several species as a mechanism to compensate for energetic costs (Gooding *et al.* 2009; Li and Gao 2012).

The effects of CO_2 on extant taxa are varied; however, most heavy calcifiers display overall negative responses in terms of growth, reproduction and survivorship under reduced pH regimes (Shirayama and Thornton 2005; Widdicombe and Spicer 2008; Ries *et al.* 2009; Gazeau *et al.* 2013). For organisms that display lower rates of calcification such as fleshy algae, crustaceans and fish, the results are less clear (Hendriks *et al.* 2010; Kroeker *et al.* 2010; Wittmann and Portner 2013). Recently, CO_2 has been shown to affect the ability of many species of fish, as well as several invertebrates, to detect chemical cues associated with habitat recognition and predator/prey detection (Briffa *et al.* 2012; Nilsson *et al.* 2012; Leduc *et al.* 2013). The variation in nature and severity of responses to increased CO_2 dissolution in marine organisms highlight the importance of context dependency when attempting to predict the outcomes of ocean acidification on a given ecosystem.

CO_2 and temperature will increase concomitantly; therefore it is important to investigate their combined effects as well. As previously discussed, both CO_2 and temperature can alter the metabolic demands and physiological performance of an organism (Portner *et al.* 2005). Synergies between related factors can have unexpected results, exacerbating or ameliorating the effects of these factors in isolation. Warming acts synergistically with OA to lower thermal bleaching thresholds in corals (Anthony *et al.*

2008), increase mortality of giant kelp spores (Gaitán-Espitia *et al.* 2014), and reduce calcification in crustose algae (Martin and Gattuso 2009). Increased temperatures and CO_2 dissolution had a synergistic increase on predation rate for reef fish, but an antagonistic effect on predator selectivity (Ferrari *et al.* 2015). The effects of temperature and CO_2 in combination can have synergistic, additive or antagonistic effects on biological responses (Crain *et al.* 2008; Byrne and Przeslawski 2013); as such, they should be studied in combination to address context-specific questions.

1.3 RECENT RESPONSES TO GLOBAL CHANGE AND CURRENT PREDICTIONS

Warming at regional scales is seasonally and spatially variable, yet over 70% of the world's coastlines have experienced significant warming at a mean rate of 0.25 ± 0.13 °C per decade during the last 30 years (Lima and Wethey 2012). Rosenzweig *et al.* (2008) demonstrated that between 1970 and 2004, 90% of changes in biological systems documented in peer reviewed literature are consistent with predictions of the impacts of warming. Whilst the oceans are warming at a slower rate to terrestrial environments, the response of marine systems in terms of velocity and seasonal timing of shifts of isotherms is higher (Burrows *et al.* 2011).

In general, range shifts are predicted to be a common response to ocean warming, with many instances of range contractions and expansions already documented (Southward *et al.* 1995; Sagarin *et al.* 1999; Wernberg *et al.* 2011). However, predicting range shifts and local extinctions of marine species based solely on changing environmental conditions and mismatches with physiological optima can be problematic. Including biotic interactions when investigating climate change scenarios can result in very different outcomes than those predicted using abiotic factors alone (Araújo and Luoto 2007; Van der Putten *et al.*

2010) highlighting the need to identify the strength of such interactions and whether they are likely to be altered with changing climate. Indeed, it is likely that accurate predictions of community responses to climate change will need to involve biotic responses to multiple stressors at multiple scales (Queirós *et al.* 2015).

1.4 THE INFLUENCE OF SPECIES INTERACTIONS IN ECOSYSTEMS UNDERGOING ENVIRONMENTAL CHANGE

1.4.1 BIOTIC INTERACTIONS MODIFY THE IMPACT OF ABIOTIC FACTORS

Biotic interactions have been shown to reverse the effects of climate change on grassland communities (Suttle *et al.* 2007), exacerbate the effects of climate change on aspen communities (Brodie *et al.* 2012) and invalidate the predictions of simple climate change models on species distribution by shifting the physiological optima of competing species (Davis *et al.* 1998). Other organisms can be individually affected by climate factors, but the net effect on their interaction may amount to zero (Landes and Zimmer 2012). Therefore, it is unrealistic to base predictions of how an individual or community will respond to change by looking at individual tolerances and responses alone. Recently, attention has been given to the role of herbivory in controlling primary production under warming and increased resources. Whilst these factors may increase the growth of certain producers (Connell and Russell 2010; Diaz-Pulido *et al.* 2011), heterotrophic metabolism is more temperature dependent than autotrophic respiration (Allen *et al.* 2005). Metabolic theory predicts stronger consumer control of primary productivity as a result of climate change (López-Urrutia *et al.* 2006; Yvon-Durocher *et al.* 2010; O’Connor *et al.* 2011). Indeed, consumers may be able to mediate or even counter the effects of climate in certain systems (O'Connor *et al.* 2009; Alsterberg *et al.* 2013).

1.4.2 COMPENSATORY FEEDING

The extent to which a system can absorb stress underpins its stability, and how likely it will switch between alternative states (Scheffer *et al.* 2001). For example, when changes to environmental conditions could facilitate a switch in the competitive dominance of primary producers through increased resource availability, the same conditions may favour an increase in herbivory. Increased *per capita* feeding rates act as a countervailing mechanism to increased productivity, and the stress of resource addition is absorbed. Herbivore ability to control primary productivity under resource enhancement occurs in many different systems (Burkepile and Hay 2006). The countervailing mechanism of increased consumption has been recently demonstrated in seagrass (McSkimming *et al.* 2015a) and kelp systems (Falkenberg *et al.* 2014; Ghedini *et al.* 2015; McSkimming *et al.* 2015b), and offers an explanation as to why systems under environmental stress do not always undergo a change of state.

The physiological reasons for compensatory feeding are inherently linked to an organism's threshold and their metabolic needs. In order for an organism to maintain crucial biological processes, consumption must meet energetic costs. Failure to do so will lead to sublethal trade-offs in resource allocation, reducing fitness, or eventual death (Angilletta Jr *et al.* 2003; Lemoine and Burkepile 2012). Whilst increases in consumption as a result of warming generally outpace increasing metabolism (Vasseur and McCann 2005), intraspecific responses to warming indicate that as temperatures approach an ectotherm's upper thermal limits, consumption declines (Lemoine and Burkepile 2012; Twomey et al. 2012). Such mismatches lead to increased risk of consumers becoming energetically deficient even when food is in abundance and consumption rates increase (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011).

Several factors influence an organism's ability to convert ingested food into energy for cellular metabolism. These include the edibility and quality of the food source (Calow 1975; Granado and Caballero 2001) as well as the digestive adaptations and abilities of the consumer (Steneck and Watling 1982; Cox and Murray 2006). Ingestion efficiency (I) is a unitless metric used to determine how much energy from consumed food is left after cellular maintenance costs for other biological functions. It is calculated by determining the amount of food actually absorbed in digestion (assimilation efficiency, w), the energetic content of the food source ingested over time (J), and the consumer's metabolic rate (R), such that $I = wJ/R$. If $I > 1$, there is sufficient energy left over after basic metabolic costs for functions such as growth; if $I < 1$, reductions in fitness can occur (Rall *et al.* 2010; Lemoine and Burkepile 2012).

These calculations are an important aspect of Dynamic Energy Budget modelling, a theory that seeks to identify and quantify how all organisms uptake and utilise energy from their environment (Nisbet *et al.* 2000; Koiijman 2001). DEB models usually assume that all assimilated energy enters a single reserve, from which a fixed amount is allocated to cellular maintenance and growth (k) and the remainder towards reproduction (1-k) (Nisbet *et al.* 2000; Kooijman 2001; van der Meer 2006). Thus, any reduction in ingestion efficiency will likely first affect processes such as reproduction and development (Nisbet *et al.* 2000), and if an organism is still energetically compromised the organism will suffer reduced growth and finally, the ability to regulate homeostasis (van der Meer 2006).

Temperature has the potential to greatly influence feeding rates and metabolism (Vasseur and McCann 2005). Warming may influence consumption and feeding preferences by also altering the importance of nutrients required for cellular metabolism (Lemoine *et al.* 2013). Ingestion efficiency in ectotherms has been shown to decrease at increased temperatures, leading to reduced fitness through lower growth rates (Lemoine and Burkepile 2012) and weaker interaction strength of consumers on their food sources (Rall *et al.* 2010). As such, mismatches between consumer metabolism and ingestion may actually lead to reduced control of productivity under future warming. The ability of consumers to compensate for increases in productivity therefore depends on physiological thresholds of the consumers in question.

Some species perform similar roles in ecological communities based on the way that they utilise ecosystem resources (e.g. “guilds”, see Root 1967). Where multiple species exist in such a guild or functional group, loss of certain species may have little impact on ecosystem processes if the remaining species can maintain the function of the group (Lawton and Brown 1993). Such functional redundancy, often used interchangeably with the term functional compensation, has been used to describe how ecosystem properties remain stable despite disturbance resulting in species loss or change in relative abundance (Loreau and de Mazancourt 2013, for review). Recently the theory has been broadened to include processes that buffer disturbances before species loss or species change, such as compensatory feeding in response to environmental conditions that favour increased productivity (Connell and Ghedini 2015). If multiple taxa within a guild can respond in a compensatory way to future change, as well as adjust their compensation in response to loss of alternate species, such functional redundancy may stabilise communities in the face of environmental change. Thus, the ability of a system to resist environmental disturbance may depend on the diversity of species within and among functional groups and the individual responses of those species to changing abiotic conditions (Naeem 1998; Ruesink and Srivastava 2001).

It is important to also consider the ability of individuals to acclimate to environmental variability, and for that of populations to adapt to long term environmental change. Whether an animal is already close to its tolerance limits for a certain stressor will likely determine its potential to acclimate to climate change within its lifetime, and the ability to respond to altered abiotic conditions will affect the potential of populations to adapt over generations (Somero 2010). Some organisms may display plasticity in their behaviour or morphological characteristics as a response to shifts in environmental variables. For behavioural examples, intertidal animals such as mussels increase the time spent with shell valves closed when exposed to higher air temperatures (Anestis *et al.* 2007), whilst mobile gastropods may cease activity and move to cooler refuges such as tide pools and crevices to avoid thermal stress (Garrity 1984).

Phenotypic plasticity can manifest at the scale of molecules through to whole organisms (Kingsolver and Huey 1998; Hoffman and Todgham 2009). Common examples of plastic physiological responses to changes in environmental temperature are the induction of heat shock protein production in thermally stressed organisms (Horowitz 2001; Hamdoun *et al.* 2003) and seasonal differences in melanin concentration in butterfly wings regulating ideal body temperature for flight (Kingsolver and Huey 1998). Organisms that display plasticity in response to stress may increase their chances of surviving in increasingly harsh or variable environments; as such the presence of plasticity has been considered an adaptive response (Gotthard and Nylin 1995; Kingsolver and Huey 1998) and presence of plasticity of traits in a population may allow it to persist despite increasing abiotic stressors (Chevin and Lande 2009). However, rates of environmental change predicted under current scenarios may mean that an organism's response is uncoupled from important seasonal changes, and microevolution of plastic traits will be required for populations to successfully adapt to changing climate (Visser 2008).

1.4.3 IDIOSYNCRATIC RESPONSES OF INTERACTING PAIRS

If warming or associated factors such as increased OA occur within an organism's physiological optima, positive responses are predicted; but if future conditions fall outside of optima it is reasonable to predict a decline in performance. As such, some consumers may increase their utilisation of primary productivity and in doing so, increase the influence of top down control in a system (O'Connor 2009); whilst others may not (Lemoine and Burkepile 2012). The challenge then is identifying how different organisms will respond to altered abiotic environments, and how this will affect their interactions with other species. Indeed, even functionally similar organisms living in the same environments can have very different responses to warming, either at the individual or species level (Winder and Schindler 2004; Iles 2014; Lemoine *et al.* 2014). Variation in response is also apparent across trophic levels (Voigt *et al.* 2003; Twomey *et al.* 2012). Whilst metabolic theory can assist us in making broad predictions about how systems will respond to warming, it is important to investigate the context-specific nature of consumer responses based on underlying physiological thresholds if we are predicting how an individual system may change (Schulte 2015).

When herbivores and their food sources are exposed to climate change, warming is predicted to favour an increase in herbivory, and thus strengthen the top-down control of primary productivity in a given system (Yvon-Durocher *et al.* 2010; O'Connor *et al.* 2011). But if a concomitant increase in CO_2 adversely affects the herbivore, herbivory may not be able to control increases in primary productivity. Poore et al. (2013) demonstrated that decreased pH and elevated temperature negatively affected the growth and survival of an herbivorous amphipod. They also found that these factors in combination altered the palatability of its food source, reducing its feeding rates under future conditions. If the producer in a given pair is positively affected by CO_2 as a resource (Connell *et al.* 2013;

Falkenberg *et al.* 2013), primary production may instead outpace consumption through such a reduction in consumer fitness.

Idiosyncratic responses to environmental change between predators and prey have also been documented, and thus the outcome of these interactions may be altered. Whilst CO_2 alters the sensory abilities of fish prey and their predators alike, prey species were disproportionately negatively impacted compared to their predators (Cripps *et al.* 2011). Likewise, a carnivorous gastropod was capable of detecting prey under elevated CO_2, but showed reduced ability to detect predator cues (Manríquez *et al.* 2014). Again, predator feeding rates may also be altered through enhanced metabolism and changes to the energetic content of their prey, requiring greater time spent foraging to meet energetic demands (Kroeker *et al.* 2014). If both predators and prey spend more time foraging under future climate, increased frequency of encounters may impact negatively on prey numbers and have resounding effects throughout the system.

1.5 KELP FORESTS OF THE FUTURE: INVESTIGATING HOW CHANGING CONSUMER STRENGTH MAY INFLUENCE ECOSYSTEM STRUCTURE AND FUNCTION

Kelp forest communities are highly productive systems that provide a range of ecosystem services, such as supporting secondary productivity, creating three dimensional habitat and coastal defence through buffering of water movement and storm surges (Steneck *et al.* 2002; Smale *et al.* 2013). They also provide economic benefits by supporting commercially targeted benthic animals, functioning as nursery habitats for commercial fish species, use as feed for livestock, direct consumption by humans and their role in coastal tourism (Smale *et al.* 2013). However, these temperate communities are also at risk of degradation loss with changing climate. There are many ways that climate change may adversely affect kelp communities. Kelp are directly impacted by warming waters through mortality and reduced growth (Wernberg *et al.* 2010; Wernberg *et al.* 2011), whilst the calcifying coralline algae that serve as substrate for kelp are negatively affected by ocean warming and acidification (Kuffner *et al.* 2008; Russell *et al.* 2009). Additionally, fleshy turfing algae (Connell *et al.* 2014) perform better under elevated $p\mathrm{CO}_2$ and warming, increasing their competitive dominance of the substrate and further eroding the ability for kelp to recover after disturbance (Connell and Russell 2010; Connell *et al.* 2013; Kroeker *et al.* 2013b). Whilst turfs can serve as habitat and food to some benthic species, they typically only grow to < 5 mm in height and do not provide the structure to support the same biodiversity, nor ecosystem services, as kelp (Benedetti-Cecchi *et al.* 2001; Airoldi *et al.* 2008).

Kelp communities are also home to a diverse array of ectothermic consumers which form functional groups such as herbivores and predators. Many of these consumers are also calcifiers, and as such, the effects of both warming and ocean acidification may have profound impacts on their physiology and feeding responses (Kroeker *et al.* 2013a). For example, calcifying grazers such as gastropods readily consume turf algae associated with kelp systems (Steneck and Watling 1982; Worthington and Fairweather 1989). These herbivores are then preyed upon by other calcifiers such as carnivorous snails and crabs. Gastropods and crustaceans display a variety of responses to ocean warming and acidification, and not all of them are negative (Melatunan *et al.* 2013; Russell *et al.* 2013; Wittmann and Portner 2013). The effects of climate within and amongst functional groups will influence the outcome of interactions between trophic levels, and ultimately, whether kelp forests will be able to persist into the future.

1.6 THESIS SCOPE AND OUTLINE

How multiple climate change factors acting across trophic levels will shape the future of temperate reefs is unclear. In this thesis, I investigate how climate change (e.g. elevated temperature/pCO$_2$) may impact upon individual organisms and their interactions with species from different functional groups. I then expose key components of a typical kelp forest assemblage to warming and ocean acidification conditions and quantify the outcomes in terms of how species interactions have modified or mitigated the effects of climate change on composition and abundance.

Manipulative experiments were conducted to address the following specific aims:

1. To test whether the metabolic rates of grazers and primary producers increase under a gradient of future warming scenarios, and whether this corresponds to an increase in feeding/productivity. Further, to determine whether any increase in productivity is countered by a corresponding increase in grazer feeding rates, or if mismatches in physiological response to warming lead to a change in the interaction strength of grazers (Chapter 2)
2. To investigate the combined effects of warming and elevated pCO$_2$ on grazer ingestion efficiency and metabolism, and whether these grazers will be energetically compromised under future conditions (Chapter 3)
3. To test whether the ability of grazers to detect predation risk is impaired under climate change, and whether predation risk reduces grazer foraging activity despite increased energetic costs (Chapter 4)
4. To determine whether functional redundancy of consumers exists in the kelp-turf system, whereby the preservation of one or more of these consumers results in a

compensatory response to increased productivity under future conditions of temperature and $p\mathrm{CO}_2$ (Chapter 5).

1.6.1 THESIS INTENT

Chapter 2

According to the Metabolic Theory of Ecology (Brown *et al.* 2004), warming will lead to increased consumer control of primary productivity (López-Urrutia *et al.* 2006). This is because heterotrophic respiration is more temperature dependent than autotrophy (Allen *et al.* 2005). Warming has indeed been shown to enhance top-down controls (O'Connor *et al.* 2009; Carr and Bruno 2013). However, idiosyncratic responses to warming in interacting pairs may produce unexpected outcomes (Iles 2014; Lemoine *et al.* 2014). If a consumer is pushed outside its thermal optima, metabolic stress occurs and consumption can decline (Lemoine and Burkepile 2012). Here, I test whether the metabolism and consumption of herbivorous gastropods keep pace with primary production of turf algae under a range of elevated temperatures corresponding to warming scenarios, or if differences in thermal optima result in decreased consumer control of turf growth.

Chapter 3

Environmental change can increase the metabolic demands of an organism, and consequently their food consumption, in order to avoid energetic deficits (Kingsolver and Woods 1997). If energetic demands are not met, reduced growth and survivorship are likely (Angilletta Jr *et al.* 2003; Lemoine and Burkepile 2012). In Chapter 3 I investigate the effects of future environmental conditions of temperature and CO_2 on the metabolism, feeding and ingestion efficiency of grazers. I then test whether failure to meet metabolic demands through any changes in feeding efficiency will lead to reductions in physical fitness.

Chapter 4

Increased energetic costs as a result of warming and elevated CO_2 lead to an increased demand for resources, which must be met by increased consumption. Foraging activity may be mediated by predator avoidance, however, the ability to detect predators is predicted to be reduced by elevated CO_2 (Leduc *et al.* 2013; Lienart *et al.* 2014). In Chapter 4, I test the hypothesis that future climate conditions will lead to an increase in prey activity due to increases in energetic demands. I also investigate the impact of predators on foraging behaviour and whether elevated CO_2 alters prey ability to perceive predation risk.

Chapter 5

Compensatory dynamics provide explanation for how ecosystem properties may remain stable despite a disturbance causing species loss or change in relative abundance. Future conditions are known to facilitate the expansion and dominance of turfs (Connell and Russell 2010; Connell *et al.* 2013), but these same conditions may strengthen trophic compensation by coexisting herbivores (Ghedini *et al.* 2015; McSkimming *et al.* 2015b). In this chapter I expose herbivorous gastropods and amphipods to future conditions of ocean warming and acidification to test the extent to which these species adjust their compensatory responses to increased productivity. Further, I test whether loss of alternate species results in an increase in compensation by the remaining taxa, thereby demonstrating functional redundancy of herbivores in the kelp-turf system.

Chapter 6

In Chapter 6 I discuss the key findings of previous chapters and suggest areas where future research could build on such findings as well as investigate gaps in knowledge identified therein.

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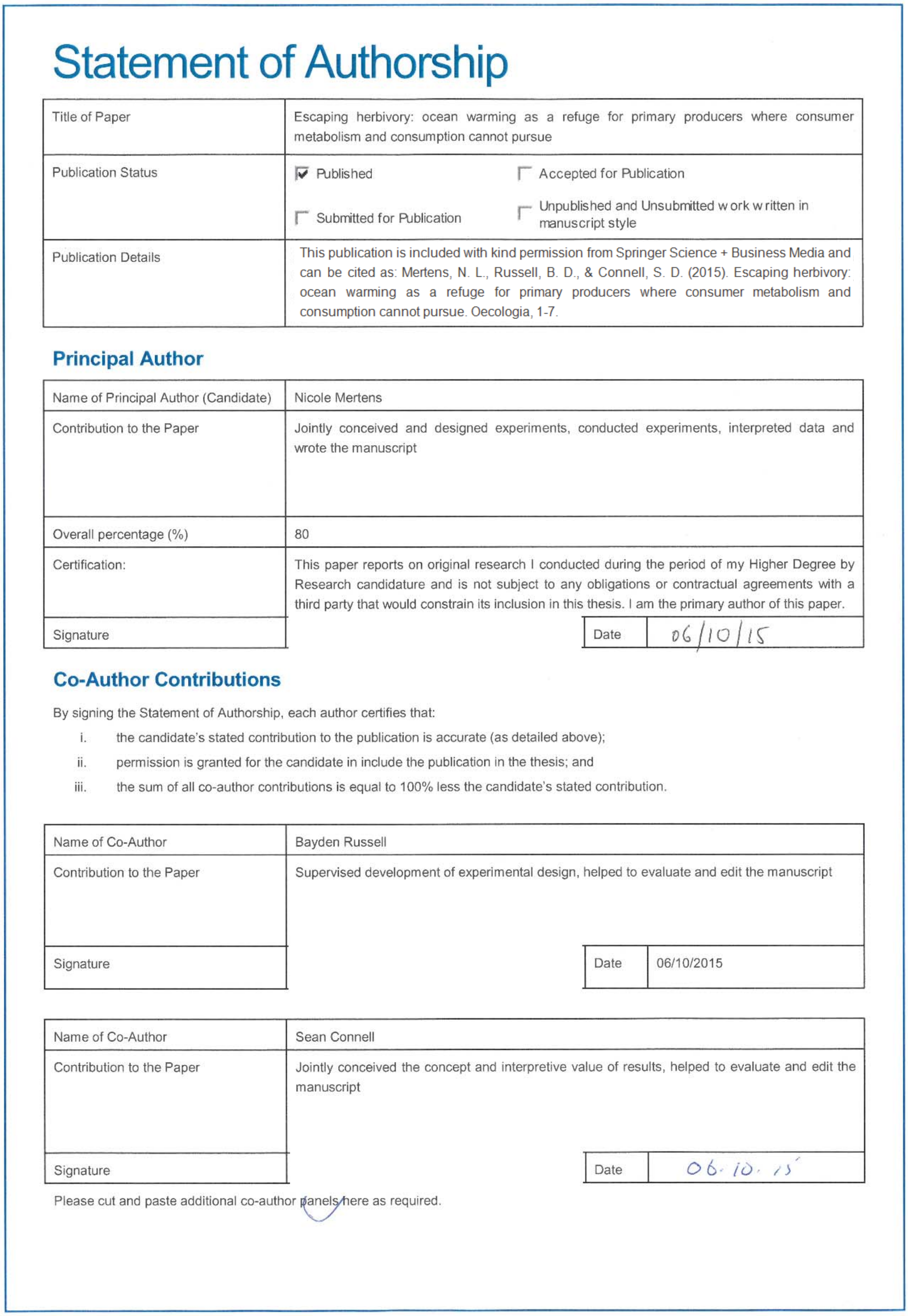
CHAPTER 2

ESCAPING HERBIVORY: OCEAN WARMING AS A REFUGE FOR PRIMARY PRODUCERS WHERE CONSUMER METABOLISM AND CONSUMPTION CANNOT PURSUE

STATEMENT OF AUTHORSHIP



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Principal Author

Name of Principal Author (Candidate)	Nicole Mertens		
Contribution to the Paper	Jointly conceived and designed experiments, conducted experiments, interpreted data and wrote the manuscript		
Overall percentage (%)	80		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Bayden Russell		
Contribution to the Paper	Supervised development of experimental design, helped to evaluate and edit the manuscript		
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Contribution to the Paper	Jointly conceived the concept and interpretive value of results, helped to evaluate and edit the manuscript		
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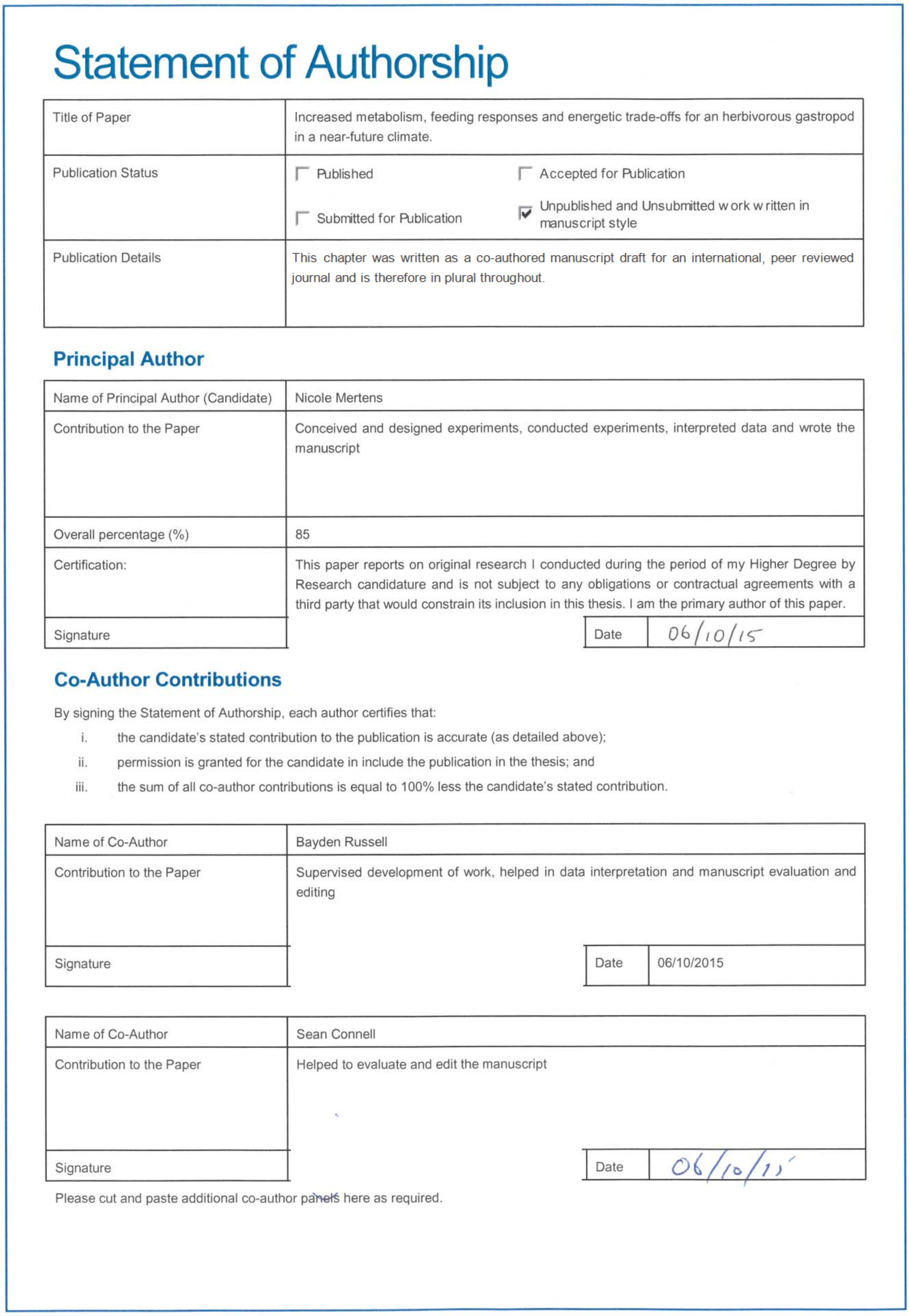
Mertens, N.L., Russell, B.D. & Connell, S.D. (2015). Escaping herbivory: ocean warming as a refuge for primary producers where consumer metabolism and consumption cannot pursue.
Oecologia, 179(4), 1223-1229.

CHAPTER 3

INCREASED METABOLISM, FEEDING RESPONSES AND ENERGETIC TRADE-OFFS FOR AN HERBIVOROUS GASTROPOD IN A NEAR-FUTURE CLIMATE

STATEMENT OF AUTHORSHIP



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Contribution to the Paper	Conceived and designed experiments, conducted experiments, interpreted data and wrote the manuscript		
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iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Bayden Russell		
Contribution to the Paper	Supervised development of work, helped in data interpretation and manuscript evaluation and editing		
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Contribution to the Paper	Helped to evaluate and edit the manuscript		
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CHAPTER 3

INCREASED METABOLISM, FEEDING RESPONSES AND ENERGETIC TRADE-OFFS FOR AN HERBIVOROUS GASTROPOD IN A NEAR-FUTURE CLIMATE

3.1 ABSTRACT

Environmental factors associated with climate change, such as elevated temperature, can increase the metabolic demands of an organism. Consequently, organisms must increase feeding or suffer energetic deficits that can lead to reduced growth and physical performance. We exposed a subtidal herbivorous gastropod, *Turbo undulatus*, to combinations of contemporary or predicted future temperature and carbon dioxide to test our hypotheses that a) gastropods will increase their feeding under climate change conditions to compensate for increasing metabolic demands and b) that failure to meet metabolic demands will lead to reduction in physical fitness. As predicted, both metabolic rate and consumption increased with elevated temperature, both alone and in combination with elevated pCO_2. Ingestion efficiency (the amount of ingested energy remaining after cellular maintenance costs) was negatively affected by future climate conditions, but efficiencies were still maintained at levels indicating that gastropods were able to meet their metabolic demands. However, weight loss was observed in elevated pCO_2 treatments despite having ingestion efficiencies above the minimum required for cellular maintenance. This weight loss was unlikely to be a result of shell dissolution, but may represent increased energetic costs of shell building. Trade-offs in body size and/or shell mass are likely to have consequences for gastropod survival as they are more susceptible to predation. Climate change will therefore pose a challenge to this species by altering energetic demands and allocation of resources.

3.2 INTRODUCTION

Metabolic responses to a changing climate have the potential to reshape ecological communities. Whilst climate change may increase primary productivity (Enquist *et al.* 2003; Allen *et al.* 2005), warming in particular may lead to increased consumer control of producers (López-Urrutia *et al.* 2006; O'Connor *et al.* 2009; Yvon-Durocher *et al.* 2010) as respiration is more temperature dependent than autotrophic processes (Allen *et al.* 2005). Indeed, increased consumption in response to increased energetic demands is well documented (Thompson 1978; Kingsolver and Woods 1997; Carr and Bruno 2013). Ectothermic consumers have physiological rates that are directly linked to the physical environment. The metabolic theory of ecology (MTE; Gillooly *et al.* 2001; Brown *et al.* 2004) predicts exponential increases in the metabolic rates of ectotherms with increasing temperature. However, organisms are constrained within thermal performance curves, and outside of thermal optima, reduced fitness and eventual death occurs (Angilletta Jr *et al.* 2002; Kingsolver 2009). Variation in individual responses to warming within and amongst coexisting taxa have been documented (Iles 2014; Lemoine *et al.* 2014). If we are to predict whether top-down control of a given system strengthens under future climate, we need to investigate the ability for individual species within that system to respond to environmental change (Lemoine and Burkepile 2012; Mertens *et al.* 2015).

Ocean acidification as a result of elevated atmospheric CO_2 dissolution may impose further metabolic costs and trade-offs to marine consumers, many of which are calcifiers that may be adversely affected by both lower pH and saturation states of calcium carbonate required for shell-building (Fabry *et al.* 2008; Nienhuis *et al.* 2010). The physiological effects of elevated pCO_2 have been shown to reduce growth, metabolism and survivorship of marine organisms (Pörtner *et al.* 2004; Shirayama and Thornton 2005; Michaelidis *et al.*

2007), however, several species have been shown to increase their feeding rates to compensate for increased physiological stress and metabolic costs (Gooding *et al.* 2009; Li and Gao 2012). In addition, the impacts of warming on an individual's metabolism can be exacerbated by elevated CO_2 levels (Pörtner 2008). However, effects of CO_2 on marine organisms vary considerably; as such, herbivore control of producers under elevated pCO_2 is likely to be dependent on individual adaptations and tolerances (Kroeker *et al.* 2010).

In order for an organism to maintain crucial biological processes, consumption must meet energetic costs, or energetic deficiencies must be compensated for by sublethal trade-offs in resource allocation (Angilletta Jr *et al.* 2003). Intraspecific responses to warming indicate that as temperatures approach an ectotherm's upper thermal limits, metabolism can outpace consumption (Lemoine and Burkepile 2012; Twomey *et al.* 2012). Such mismatches lead to lower energetic efficiencies, and increased risk of consumers becoming energetically deficient despite food abundance and elevated consumption rates (Vucic-Pestic *et al.* 2011). This not only impacts upon consumer fitness, but on their ability to control increases in primary productivity (Mertens *et al*. 2015).

In this study we assessed the effects of near-future levels of temperature and pCO_2 on the metabolic rate, total food consumption and ingestion efficiency of the herbivorous gastropod *Turbo undulatus*, and how this translated into loss or gain of biomass. We hypothesised a) gastropods will increase their feeding under climate change conditions to compensate for increasing metabolic demands and b) that failure to meet metabolic demands will lead to reductions in physical fitness.

3.3 METHODS

3.3.1 EXPERIMENTAL SET UP AND MAINTENANCE

The effects of temperature and CO_2 on grazer metabolism and growth were measured in a microcosm experiment. Five replicate microcosms were used *per* treatment, each containing one gastropod, *Turbo undulatus*, collected from subtidal rocky reefs (0.5-2 m depth) at O'Sullivan Beach, South Australia (35.1190°S, 138.4750°E) in June, 2013. Gastropods were chosen to be of similar initial size, with an average weight prior to experiments of 7.18 ± 0.25 g. The microcosms were kept in a glasshouse. Prior to commencement of experiments, gastropods were allowed to acclimate to ambient conditions of pCO_2 and temperature within the glasshouse for two weeks. Also within each microcosm were three 5 × 20 cm panels on which algal turfs were grown for grazing trials. Algal turfs comprise of densely packed filaments of algae less than 5 mm in height (Connell *et al.* 2014). Turfs were initially collected on rocks from the same field site as gastropods and allowed to establish on fibre-cement panels under ambient glasshouse conditions for 6 weeks prior to experiments in order to reach approximately 100 % cover on panels used in grazing trials. After this time, turfs were placed in microcosms and subject to treatment conditions for two weeks prior to introduction of grazers.

Microcosms were subjected to natural light cycles within the glasshouse (approximately 10:14 hours light:dark), and lighting was supplied *via* natural light shaded with shadecloth to approximately 21 μmol m^{-2} s^{-1} as measured with a quantum light meter (LI-COR, Lincoln, USA). Each microcosm had a volume of 5 L and to maintain water quality one third of the water volume in each tank was replaced with fresh seawater every four days.

Target temperature and partial pressure of CO_2 (pCO_2) were based on current field conditions and RCP 4.5 scenario for the year 2100 (Moss *et al.* 2010; IPCC 2013).

Temperatures were maintained at a daily average of 17°C (ambient) or 20°C (elevated) with thermostat controlled heater/chiller units (Teco, Smithfield, Australia). CO_2 levels were manipulated by constantly aerating the microcosms at either ambient atmospheric air (380 ppm, current) or air enriched with CO_2 *via* a gas mass flow mixer (650 ppm, future) (Columbus Instruments, Columbus Ohio, USA). Temperature and pH were monitored twice daily using a handheld pH/temperature meter (Hanna Instruments, Woonsocket, USA). Temperature and pCO_2 were allowed to fluctuate over a 24 hour period in response to biological processes and variation in non-climatic drivers (e.g. solar) in order to reflect the natural variability of coastal marine systems (Duarte *et al.* 2013). Recorded fluctuations in temperature over a 12 hour period in each treatment are presented in Table 1.

Salinity was monitored using a visual refractometer (Vertex Aquaristik, Köln, Germany) and maintained at 40 ppt. Total alkalinity (TA) was measured weekly using a potentiometric titrator (888 Titrando, Metrohm, USA). Concentrations of pCO_2, carbonate (CO_3^{2-}) and bicarbonate (HCO_3-), as well as the saturation state of calcite (Ω Ca) and aragonite (Ω Ar) were then calculated from measured TA, pH, salinity and temperature using the CO2SYS program for Excel (Pierrot *et al.* 2006) with constants from Mehrbach et al. (1973) as adjusted by Dickson & Millero (1987). Results of measured and calculated water parameters can be found in Table 2.

Table 1 Change in pH and temperature measured every 2 hours over a 12 hour daytime period (mean ± SE) per treatment

Treatment	Control	+T	+CO2	+T +CO_2
ph	0.058 ± 0.006	0.050 ± 0.007	0.098 ± 0.022	0.100 ± 0.007
Temperature (°C)	0.52 ± 0.06	0.84 ± 0.21	0.70 ± 0.08	0.82 ± 0.16

Control: ambient temperature and CO_2; +T: elevated temperature; +CO_2: elevated CO_2; +T +CO_2: elevated temperature and CO_2

Table 2 Water parameters during experimental run time (± SE) as determined by morning measurements of pH and temperature once daily for six weeks and results of titrations conducted every two weeks for six weeks.

Treatment	Control	+T	+CO_2	+T +CO_2
ph	8.11 ± 0.03	8.11 ± 0.03	7.95 ± 0.02	7.96 ± 0.02
Temperature (°C)	16.61 ± 0.11	19.97 ± 0.21	16.82 ± 0.14	19.56 ± 0.13
Salinity	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00
TA	2379.67 ± 114.46	2298.17 ± 144.38	2293.22 ± 92.84	2347.22 ± 136.66
pCO_2 (µatm)	328.51 ± 16.85	306.64 ± 8.44	486.29 ± 10.00	479.84 ± 17.27
CO_3^{2-} (µmol/kgSW)	216.68 ± 18.21	234.32 ± 27.21	157.42 ± 11.93	179.47 ± 15.91
HCO_3^- (µmol/kgSW)	1838.36 ± 80.28	1711.10 ± 85.34	1897.75 ± 66.64	1899.76 ± 104.23
Ω Ca	4.98 ± 0.42	5.39 ± 0.63	3.62 ± 0.27	4.12 ± 0.37
Ω Ar	3.22 ± 0.27	3.51 ± 0.41	2.34 ± 0.18	2.69 ± 0.24

Control: ambient temperature and CO_2; +T: elevated temperature; +CO_2: elevated CO_2; +T +CO_2: elevated temperature and CO_2

3.3.2 OXYGEN CONSUMPTION AND FEEDING

Metabolic rate was measured as oxygen consumption (mg O_2 min^{-1} g^{-1}) of resting gastropods in a closed respirometry chamber filled with filtered treatment seawater. Prior to measurements, gastropods had been exposed to treatment conditions for six weeks. Initially, gastropods were “chased” into their shells with a small brush to expel air from the mantle cavity. They were then removed from their microcosm, had their shells gently cleaned to remove microorganisms and placed inside the chamber. Once snails were acclimated to the chamber (time varied between individuals and was measured by emergence from shell), the chamber was sealed and oxygen levels were measured every 10 seconds for 10 minutes. Trials were stopped if air bubbles were detected, or if the snail was moving excessively or retreated back within the shell.

To control for metabolic activity of any microorganisms present in the seawater, trials of a chambers containing only experimental water (no gastropod) were run for each treatment and results of these were subtracted from gastropod-present trials. To standardise oxygen consumption *per* gram of gastropod, flesh weight was estimated by comparing whole fresh weight of live individuals to whole fresh weight versus tissue weight of destructively sampled individuals (n = 15, r^2 = 0.98).

Gastropod feeding activity was quantified as daily biomass of turf algae consumed standardised as percentage of gastropod flesh weight. Visual estimates of turf cover were recorded from grazing panels with initial 100 % turf cover (net consumption), as *per* Dethier *et al.* (1993). Turf cover was estimated on a daily basis so that it incorporated the growth of turf across a 24 hour period, and measured over a total of 2 weeks. To calculate gross consumption whilst taking into account differential growth rates of turf amongst treatments, turf growth on grazer-excluded panels also present within each microcosm was added to net consumption. Turf biomass removed from grazing panels was then estimated using scrapings taken from grazer-excluded panels at 100 % cover at the completion of the experiment.

3.3.3 INGESTION EFFICIENCY AND CHANGE IN WEIGHT

Ingestion efficiency is a unitless metric used to estimate the ingestion gains of a consumer relative to its energetic costs (Vasseur and McCann 2005). We estimated ingestion efficiency, I, as $I = wJ/R$, where w is the assimilation efficiency ((ingestion-faeces)/ingestion), J is the ingestion rate ($J\ s^{-1}$) of the consumer and R is consumer resting metabolic rate converted to $J\ s^{-1}\ g^{-1}$ (Rall *et al.* 2010; Lemoine and Burkepile 2012). Assimilation efficiency was estimated by quantifying food ingested and faecal mass for five individuals exposed to each treatment, and the average per treatment was used in further calculations. When measuring w, gastropods were fed *Ulva* sp. (sea lettuce) to obtain exact measurements of food consumed, and to ensure that all faecal matter was easily identified and separated from food remnants for calculations. J was calculated as total biomass of turfs consumed over a 24 hour period multiplied by the energetic content (J) turf tissues. Energetic content of turfs was determined by bomb calorimetry.

As ingestion efficiency is closely associated with biomass gains or losses, we also weighed gastropods throughout the duration of the experiment. Gastropod shells were blotted to remove excess water and the gastropods were then dried in air until shells were visibly dry prior to weighing. Whole fresh weights were converted to dry flesh weight as described above (see *Oxygen consumption and feeding*).

3.3.4 ANALYSES

For the relationship between oxygen consumption and algal biomass consumed, a linear regression was conducted, with assumptions tested and analyses performed in SPSS.

Calculation of the Durbin-Watson statistic (2.098) showed no serial correlation of residuals. Two-way analysis of variances (ANOVAs) were used to test assimilation efficiency, ingestion efficiency and change in weight of gastropods. These analyses were performed in PRIMER. The factors of temperature and $p\text{CO}_2$ were considered fixed and orthogonal with two levels in each factor (temperature: ambient vs. elevated; $p\text{CO}_2$: current vs. future). Individual microcosms were treated as replicates ($n = 5$). Post-hoc pairwise tests were used to determine which levels differed when a significant interaction was detected.

3.4 RESULTS

There was a positive relationship between oxygen consumption and algal biomass consumed (Fig. 1, $r^2 = 0.44$, $p = 0.001$). Elevated temperature treatments resulted in greater metabolic activity and consequently greater feeding rates.

There was an antagonistic effect of temperature and CO_2 on assimilation efficiencies (ANOVA $F_{1,16} = 9.64$, $p < 0.005$). Under elevated CO_2, ambient temperature resulted in greater w than elevated temperature (post hoc pair wise comparisons, $p < 0.05$; 0.98 ± 0.007 versus 0.95 ± 0.003 respectively). Control gastropods had assimilation efficiencies of 0.94 ± 0.013, and gastropods in elevated temperature only treatments had assimilation efficiencies of 0.96 ± 0.006.

Future temperature and CO_2 treatments resulted in lower ingestion efficiencies than the control, with an interactive effect of CO_2 and temperature on ingestion efficiency (Fig. 2a; ANOVA $F_{1,16} = 4.59$, $p < 0.05$). Under current CO_2, future temperature resulted in lower I than at current temperature (post hoc pairwise comparisons, $p < 0.01$). An $I > 1$ indicates that metabolic demands are being met by consumption. Whilst control I were all well above 1, climate change treatments were much closer to 1 (although still above the threshold required for cellular maintenance) (Fig. 2a). There was no significant effect of treatment on turf energetic content (ANOVA $F_{3,8} = 0.26$, $p = 0.87$) , resulting in an average energetic content of 10582.83 ± 322.33 J g^{-1}.

Gastropods exposed to future CO_2 had significantly lower weight gains than those in current conditions (Fig 2b; $F_{1,16} = 9.59$, $p = 0.01$), with the majority of gastropods exposed to future CO_2 exhibiting weight loss (change in flesh weight = -0.003 ± 0.027 g).

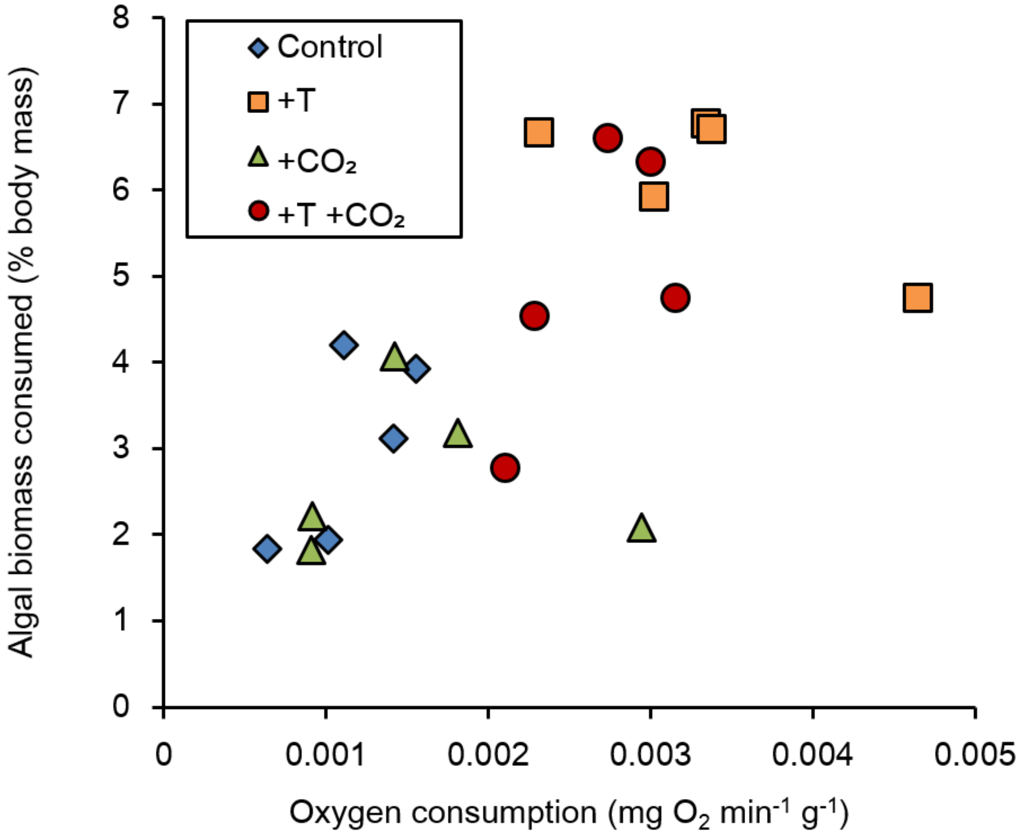

Figure 1 Oxygen consumption (mg O_2 min^{-1} g^{-1}) versus the percentage body weight of biomass consumed daily by gastropod grazers. Control: ambient temperature and CO_2 (blue diamonds); +T: elevated temperature (orange squares); +CO_2: elevated CO_2 (green triangles); +T +CO_2: elevated temperature and CO_2 (red circles)

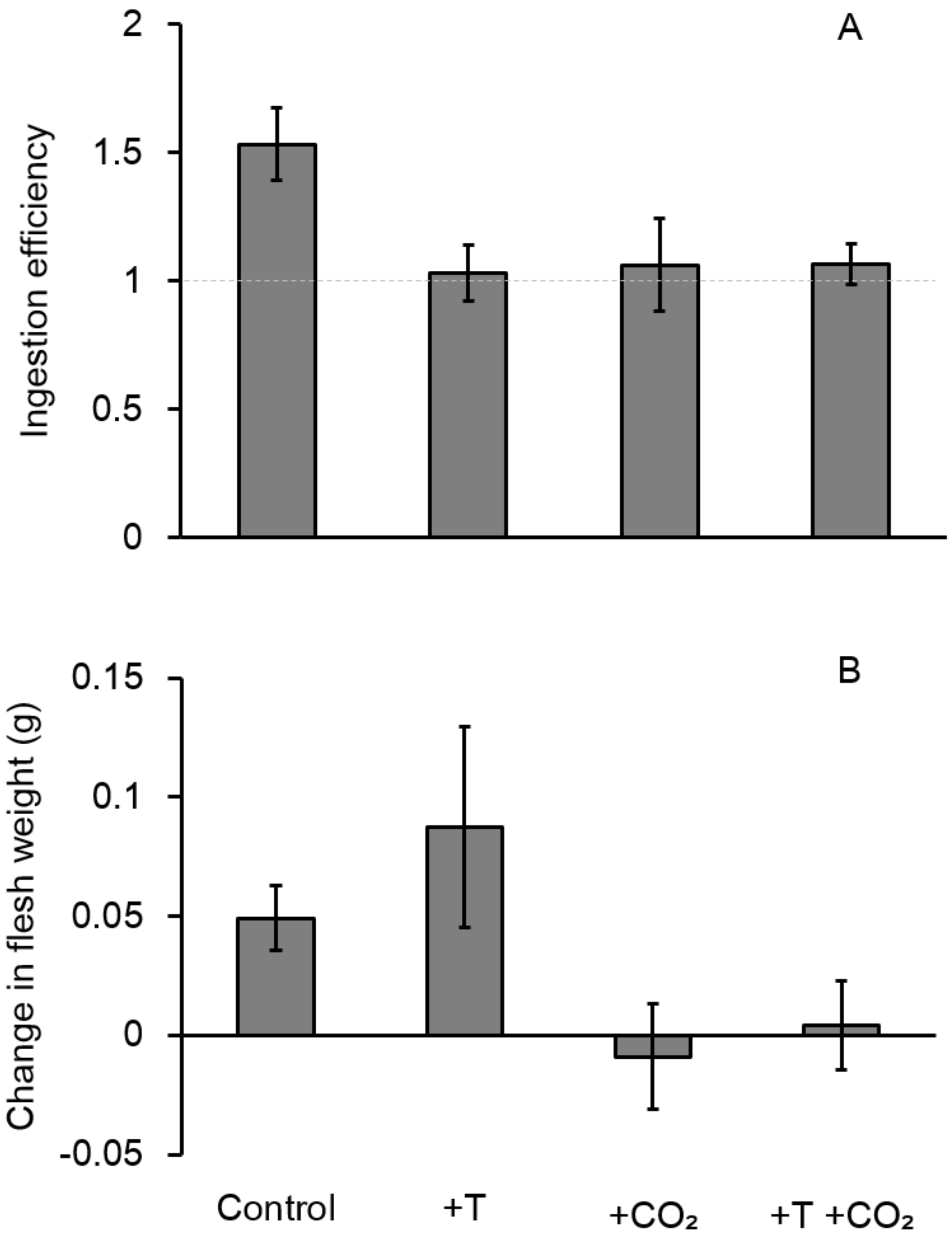

Figure 2: (A) Ingestion efficiency and (B) change in flesh weight (g) in grazers over one month (mean ± SE). Control: ambient temperature and CO_2; +T: elevated temperature; +CO_2: elevated CO_2, +T +CO_2: elevated temperature and CO_2. Dashed line indicates minimum ingestion efficiency required for cellular maintenance.

3.5 DISCUSSION

Elevated temperature resulted in increased metabolic rates and a concomitant increase in feeding. Increased top-down control of algal turfs by gastropod grazers under these conditions would serve to regulate turf expansion on rocky reefs, as predicted by metabolic theory (O'Connor 2009; Carr and Bruno 2013). However, reductions in ingestion efficiency and lower weight gain under a combination of elevated pCO_2 and temperature indicate that these grazers may be reaching a physiological threshold under these physical conditions, after which metabolism outpaces consumption and results in reduced fitness (Rall *et al.* 2010; Lemoine and Burkepile 2012). Such a threshold has been reported in this species, where consumption peaks at approximately 20 °C despite increased metabolic activity at higher temperatures (Mertens *et al.* 2015).

Assimilation efficiency was above 90 % for all treatments, which is considerably higher than estimates based on previous empirical studies ($w = 0.45$ for herbivorous consumers, see Yodzis and Innes (1992)). These values were determined by comparing the w of a broad range of carnivores and herbivores comprising of endothermic and exothermic examples as well as terrestrial and marine animals. These w are suggested to be linked to differences in digestibility of plant and animal tissues, such that more energy is lost in the process of digesting plant material, leading to lower assimilation efficiencies for herbivores in general (Calow 1977; Yodzis and Innes 1992). However, assimilation efficiencies much greater than 0.45 have been documented in marine herbivorous invertebrates (Grahame 1973; Cox and Murray 2006; Lemoine and Burkepile 2012). Both filamentous turfs and *Ulva* sp. lack hard structures and are considered palatable and easily digested by herbivorous marine snails (Lubchenco 1978; Steneck and Watling 1982). As such, these herbivores appear to be able to utilise most of the algal tissues they consume, which should correspond to higher assimilation efficiencies.

Ingestion efficiency was lower in the future CO_2 and temperature treatments. Consumption generally kept pace with increases in metabolic rate, meaning that grazers are at least partially compensating for these increased metabolic demands through consumption under future conditions (Lemoine and Burkepile 2012). However, change in weight varied between treatments. Gastropods exposed to elevated temperature alone had the highest consumption rates and greatest weight gain. Thus, we could consider that the energetic demands of these grazers are indeed being met by feeding rates, with ingestion rates and efficiencies providing enough energy for growth.

Under elevated $p\mathrm{CO}_2$ conditions snails experienced either low weight gain compared to controls, or weight loss, despite having ingestion efficiencies greater than 1. Net calcification rates can be maintained under ocean acidification scenarios, however, this may come at an energetic cost to other vital processes such as inducible defences and growth (Kroeker *et al.* 2014). Results of seawater analysis in our study revealed that saturation states of calcite and aragonite were greater than 1 in all treatments, regardless of reductions in saturation levels in elevated $p\mathrm{CO}_2$ treatments. Thus, shell dissolution was unlikely to be contributing to reduced weight gain. However, a reduction in calcification rate can occur as a result of any reduction in saturation level, even if levels remain above saturation (Feely *et al.* 2004). Coleman *et al.* (2014) found that *Turbo undulatus* were able to repair damaged shells as efficiently under low pH conditions as at ambient conditions, and shell strength and thickness did not differ amongst treatments. Wood et al. (2008) demonstrated that brittlestars can increase their calcification rates in low pH environments, but the cost of upregulating their metabolism to compensate lead to muscle wastage. Increased $p\mathrm{CO}_2$ alone did not affect gastropod metabolism but still resulted in weight loss. Hence, these gastropods do not appear to be upregulating their metabolic rates to compensate for increasing cost of shell building or growth.

Flesh weight or shell weight loss both adversely affect survival by increasing risk of predation. Many predators select for smaller body size and thinner shells as these factors reduce handling time, an important trade-off for predator survival (Menge 1974; Bertness and Cunningham 1981; Boulding 1984; Moran 1985; Juanes 1992). As gastropods responded to increased metabolic demands through increasing their feeding rates we may predict that they will persist under future conditions of $p\text{CO}_2$ and temperature. However, slower growth and smaller body size may lead to increased mortality through predation. Common gastropod predators include other ectothermic calcifiers such as crabs. These predators will also likely increase their feeding rates in response to elevated warming (Thompson 1978; Kingsolver and Woods 1997; Rall *et al.* 2010). Ocean acidification has the potential to adversely affect crab physiology, especially in the presence of warming (Pörtner 2008; Harvey *et al.* 2013). The effects of ocean acidification on animal fitness are, however, highly variable and crustaceans and fish (another type of common gastropod predator) may display less negative responses to elevated CO_2 than their gastropod prey (Kroeker *et al.* 2010; Kroeker *et al.* 2013; Wittmann and Portner 2013).

3.6 CONCLUSIONS

Warming resulted in increased metabolic and feeding rates, suggesting that these grazers have the potential to increase regulation of algal turfs as predicted by MTE. However, ingestion efficiencies of gastropods exposed to future conditions were just above the minimum required to meet energetic needs. Therefore, end-of-century $p\text{CO}_2$ and temperature, which are predicted to be higher than used here, are likely to worsen physiological performance and fitness. Notably, grazers suffered reduced weight gain under the combination of elevated temperature and $p\text{CO}_2$ (conditions which will occur in the future), which may negatively impact their survival. Any reduction of grazer abundance will likely have consequences for the broader system as grazer food sources such as turf algae will experience less consumer-mediated control.

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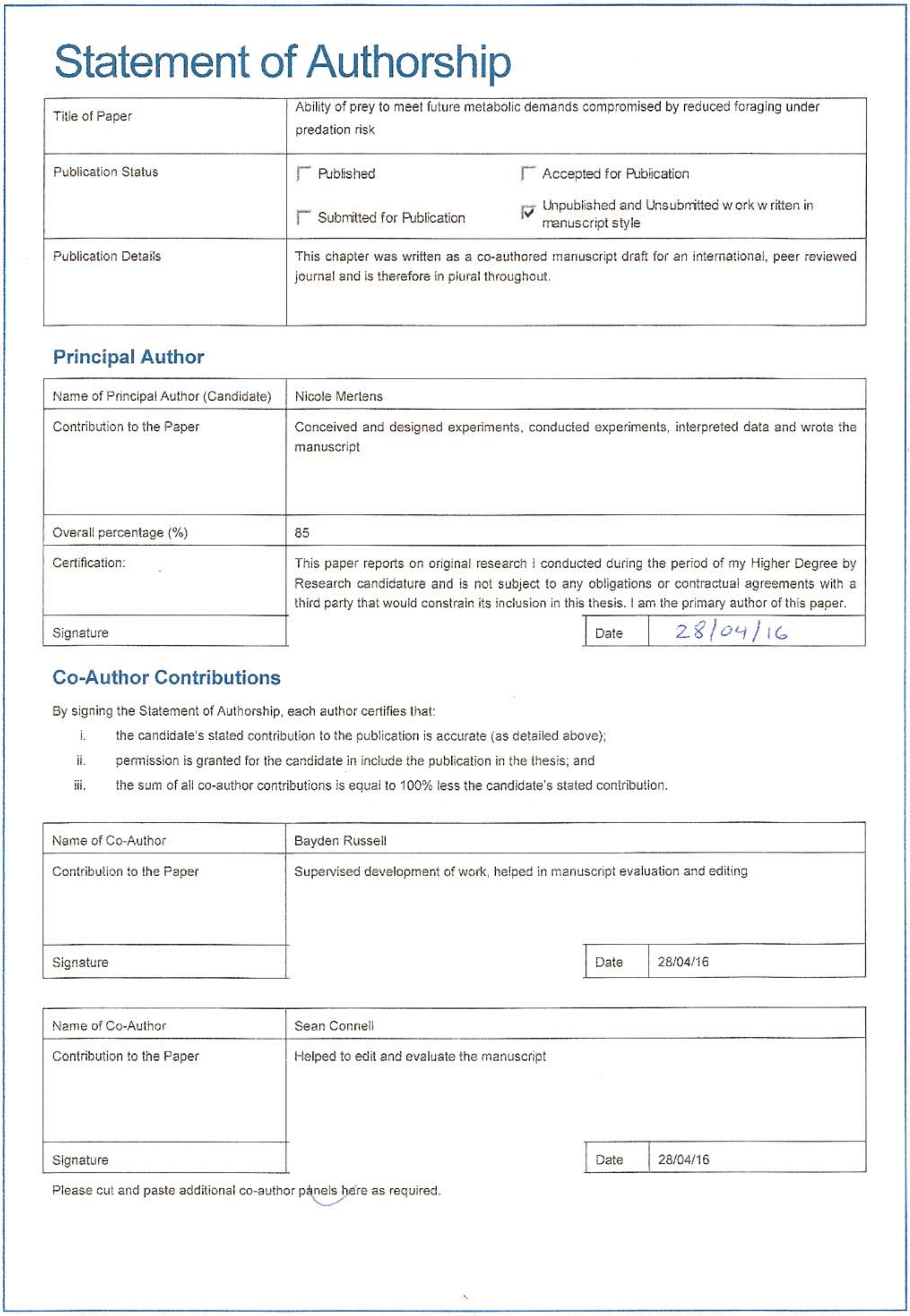
CHAPTER 4

ABILITY OF PREY TO MEET FUTURE METABOLIC DEMANDS COMPROMISED BY REDUCED FORAGING UNDER PREDATION RISK

STATEMENT OF AUTHORSHIP



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By signing the Statement of Authorship, each author certifies that:

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iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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CHAPTER 4

ABILITY OF PREY TO MEET FUTURE METABOLIC DEMANDS COMPROMISED BY REDUCED FORAGING UNDER PREDATION RISK

4.1 ABSTRACT

Elevated temperature and CO_2 generally increases metabolic rate and energetic costs in ectotherms, leading to an increased demand for resources. Yet, increases in foraging needed to meet these energetic demands may be mediated by predator avoidance. The ability to respond to predation risk is, however, predicted to be reduced by elevated CO_2. Therefore, climate change poses a complex challenge to prey species by simultaneously affecting multiple aspects of physiology and behaviour. We exposed a subtidal gastropod, *Turbo undulatus*, to combinations of elevated CO_2 and temperature to test the hypothesis that future climate conditions will lead to an increase in activity due to increases in energetic demands. As anticipated, foraging activity increased with increasing metabolic rate caused by future climate in the absence of predators. Elevated predation risk, however, opposed this increase in foraging rate because prey spent less time foraging, potentially limiting their ability to service increased energetic costs under future climate.

4.2 INTRODUCTION

Ocean warming increases the energetic demands of marine organisms, resulting in a greater need to forage for food (López-Urrutia *et al.* 2006). Concurrently, ocean acidification can affect calcification rates, development, extracellular acid-base regulation and survival (Orr et al. 2005, Hendriks et al. 2010). Changes to these vital processes will come with energetic costs. Of its nature, increased foraging time to meet energetic needs will also increase prey exposure to predation (Lienart *et al.* 2014). Understanding the outcomes of such interactions between predators and their prey assists models of how species and systems respond to global change.

The outcome of a predator-prey interaction is mediated by the ability of individuals to detect, identify and respond to certain cues (Brown 2003). These cues may be visual, but often more important in the marine environment are chemical cues released from predators and the tissues of damaged individuals as the result of predation events (Wisenden 2000, Jacobsen and Stabell 2004). For the prey species, the ability to identify risk associated with proximity to predators is crucial when determining how long to spend foraging to meet energetic requirements (Houston et al. 1993, Lima 1998, Brown 2003). Prey may reduce risk to predation by reducing foraging activity and hence food intake (Connell 2002) such that growth rates are reduced (Connell 1998). Calcifying prey such as gastropods may also show phenotypic plasticity in their protective structures, growing thicker shells when predators are present (Trussell 1996). However, this response may be disrupted by low seawater pH (Bibby *et al.* 2007).

Research into the potential for elevated levels of CO_2 to disrupt the sensory ability of prey and reduce anti-predator behaviour is growing rapidly, especially for both freshwater and marine fishes (see Leduc *et al.* 2013). Fish exposed to near-future ocean acidification predictions (year 2100) have shown reduced or even reversed responses to predator olfactory cues (Dixson *et al.* 2010; Munday *et al.* 2010). Altered anti-predator and resource choice behaviour under elevated CO_2 regimes in some marine invertebrates have also been observed (de la Haye *et al.* 2011; Watson *et al.* 2013). Failure to respond to cues may expose prey to increased predation risk (Munday *et al.* 2010). If the ability of calcifying prey to detect predators under ocean acidification is reduced, and their defensive structures are weaker as a result of dissolution of carbonate or increased cost of shell building, mortality through predation events may be even greater.

Few studies to date combine the effects of co-dependent environmental factors such as temperature and CO_2 on foraging activity and response to predation risk. The potential for opposing effects on physiology and behaviour in these co-dependent environmental factors complicate our ability to predict responses to climate change. If the response to predation risk is compromised but energetic demands are increased by future climate, prey species will spend more time exposed to danger. If sensory ability is not impaired, prey species will either be forced to expose themselves for longer times or become energetically compromised.

Here we test whether the need to forage under future climate conditions outweighs the risk of predation. We exposed a subtidal gastropod prey to elevated temperature and CO_2 levels under increasing levels of cues associated with predation. We hypothesised that future climate conditions would lead to an increase in activity due to increases in energetic demands. Further, if the response of gastropods to predation cues were unaffected by climate change we predicted that the presence of cues would result in reduced foraging times compared to risk-free conditions, with consequences for their energetic requirements.

4.3 METHODS

4.3.1 STUDY ANIMALS AND TREATMENTS

Herbivorous marine gastropods, *Turbo undulatus*, and predatory rock crabs, *Ozius truncatus*, were collected by hand from the shallow subtidal waters (0.5-2 m depth) adjacent to Adelaide, South Australia in May, 2013. *T. undulatus* of similar size were chosen with an average weight of 7.58 ± 0.23 g. *O. truncatus* with carapace lengths between 5–7 cm only were used in trials. During acclimation, predators and prey were kept separate to ensure prey were naïve when exposed to predator cues during trials. Throughout the acclimation period gastropods and crabs were fed *ad libitum* on macroalgae and shellfish, respectively. New gastropods and crabs were collected and handled identically for each trial.

Animals were introduced to experimental water conditions of temperature and pH and acclimated for 6 weeks in outdoor mesocosms (1,800 L) before being housed in indoor aquaria (25 L) for the duration of trials. Prior to commencement of trials, animals were allowed to acclimate to laboratory conditions for 24 hours. Light:dark cycles in the laboratory were set to mimic natural light cycles for the season (10:14 hours).

Throughout acclimation and trials gastropods were exposed to one of four crossed combinations of temperature (ambient vs. elevated) and CO_2 conditions (current vs. future). Temperature and CO_2 conditions chosen to encompass likely outcomes for the year 2100 under RCP 4.5 and 6.0 scenarios (Moss *et al.* 2010; IPCC 2013), with ambient or elevated (+3°C) for temperature treatments and current or future CO_2 scenarios corresponding to pH values of 8.10 and 7.95, respectively. Temperature was maintained in the larger mesocosms using individual heater/chiller units (TC-60 Aquarium Chillers, TECO Refrigeration Technologies, Ravenna, Italy), whilst elevated temperatures in the laboratory were achieved using bar heaters (150W Glass Heaters, Aqua Pacific UK Ltd, Southampton, UK). Manipulation of seawater pH was achieved *via* bubbling water with elevated-CO_2 air from a gas mixer (Pegas 4000 MF, Columbus Instruments, Columbus Ohio USA). Temperature and pCO_2 were allowed to fluctuate slightly over a 24 hour period in response to biological processes in order to reflect the natural variability of coastal marine systems (Duarte *et al.* 2013). Measurements of pH and temperature were measured three times throughout the day using a handheld pH meter (Hanna Instruments, Woonsocket, USA). Salinity was measured daily using a visual refractometer (Vertex Aquaristik, Cologne, Germany). Total alkalinity (TA) measured weekly using a potentiometric titrator (888 Titrando, Metrohm, USA). Concentrations of pCO_2, carbonate (CO_3^{2-}) and bicarbonate (HCO_{3-}), as well as the saturation state of calcite (Ω Ca) and aragonite (Ω Ar) were then calculated from measured TA, pH, salinity and temperature using the CO2SYS program for Excel (Pierrot et al. 2006) with constants from Mehrbach et al. (1973) as adjusted by Dickson and Millero (1987). The results analysis of seawater chemistry can be found in Table 1.

After acclimation to experimental conditions, gastropod behaviour in response to predation risk was tested in two separate trials with either (1) implied risk (predator cue only) or (2) predator and conspecific cues (“predation” trial) presented to gastropod prey.

Table 1 Water parameters for predation cue trials as determined by titration and daily measurements of pH, salinity and temperature for a) predator cue only trials and b) predation trials. pH and temperature were recorded in each tank three times a day over three days and results are therefore daily averages. One titration per trial was conducted at the completion of trials, with 3 replicates per treatment.

Treatment	Control	+T	+CO$_2$	+T +CO$_2$
a) Predator cue				
ph	8.07 ± 0.00	8.07 ± 0.00	7.95 ± 0.00	7.95 ± 0.00
Temperature (°C)	16.69 ± 0.03	20.04 ± 0.04	16.84 ± 0.03	20.04 ± 0.05
Salinity	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00
TA	2574.94 ± 43.15	2587.78 ± 48.90	2567.67 ± 40.06	2533.17 ± 28.96
pCO$_2$ (µatm)	424.57 ± 36.75	413.81 ± 34.94	519.64 ± 39.94	526.79 ± 48.52
CO$_3^{2-}$ (µmol/kgSW)	215.83 ± 10.418	233.46 ± 10.65	184.96 ± 8.27	197.58 ± 10.26
HCO$_3^-$ (µmol/kgSW)	2043.27 ± 46.75	2014.27 ± 47.83	2111.46 ± 49.82	2045.84 ± 44.01
Ω Ca	4.96 ± 0.24	5.36 ± 0.25	4.25 ± 0.19	4.54 ± 0.19
Ω Ar	3.21 ± 0.16	3.49 ± 0.16	2.75 ± 0.12	2.95 ± 0.15
b) Predation				
ph	8.09 ± 0.01	8.10 ± 0.01	7.96 ± 0.01	7.97 ± 0.01
Temperature (°C)	18.34 ± 0.12	21.53 ± 0.08	18.74 ± 0.08	21.59 ± 0.06
Salinity	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00	40.00 ± 0.00
TA	2429.33 ± 8.31	2435.89 ± 5.60	2426.56 ± 5.66	2432.67 ± 4.14
pCO$_2$ (µatm)	317.93± 11.63	342.51± 14.64	548.14 ± 36.15	521.40 ± 30.06
CO$_3^{2-}$ (µmol/kgSW)	244.79 ± 9.27	244.84 ± 6.08	174.58 ± 12.95	189.16 ± 7.88
HCO$_3^-$ (µmol/kgSW)	1820.72 ± 21.66	1828.35 ± 12.73	1993.20 ± 29.03	1963.95 ± 19.42
Ω Ca	5.63 ± 0.21	5.63 ± 0.14	4.01 ± 0.30	4.35 ± 0.18
Ω Ar	3.67 ± 0.15	3.68 ± 0.09	2.62 ± 0.20	2.85 ± 0.12

C: current CO$_2$ conditions, ambient temperature; +T: elevated temperature; + CO$_2$: future CO$_2$ conditions.

4.3.2 PREDATOR CUE ONLY TRIALS

Following acclimation, gastropods were reassigned to aquaria exposed to orthogonal combinations of temperature (ambient vs. +3°C), CO_2 (current vs future) and predation cue (absent vs. predator cue). Temperature and CO_2 levels corresponded to individual gastropod acclimation conditions. Fifteen individuals were randomly and evenly split into three replicate aquaria per treatment combination (120 gastropods total). Predator cues were maintained throughout the duration of the experiment by the inclusion of a caged crab in the cue-present treatment. An empty cage was included in the aquaria for the control (predator cue absent) treatments.

Present in each tank was a 15 × 15 cm square panel covered with algae to provide an adequate food source for the gastropods. A PVC cylinder (15 cm in length, 5 cm diameter), devoid of algae, was provided as a potential refuge from predation risk.

Once predator cues were introduced to the tanks *via* the inclusion of caged crabs, gastropods were kept in these conditions for three days and their behaviour quantified over five minute periods, three times per day. Behaviour was recorded as the percentage of time spent undertaking different activities; active (consuming food or actively foraging with antennae protruding from shell) or avoiding predation (moving above water line, withdrawn into shell or hiding in refuge). As *T. undulatus* are subtidal and do not need to move above the water line to forage, we consider movement above the waterline as an escape mechanism. During trials water parameters were also measured three times per day, with measurements taken after the completion of behavioural observations.

4.3.3 PREDATION TRIALS

The methods for the predation trials (no predation vs predation) were the same as above except that the predator cue was replaced with actual predation risk using an uncaged crab. Crabs were able to freely capture and consume gastropods throughout the duration of the trial. Whilst mortality was recorded during behavioural observations, shells and remnant tissues of consumed gastropods were left in tanks to elicit conspecific predation cues, another important chemical cue in predation risk detection (Appleton and Palmer 1988; Wisenden 2000). Gastropod behavioural response was quantified as per the predation cue trials.

4.3.4 METABOLIC RATE

To assess the effects of temperature and CO_2 on the metabolic rates of *T. undulatus*, resting metabolic rate was measured as oxygen consumption by gastropods exposed to orthogonal combinations of temperature (ambient vs +3°C) and CO_2 (current vs future). Five additional individuals per treatment (n= 20 gastropods total) were allowed to acclimate to experimental conditions over 6 weeks. Oxygen consumption of individual gastropods was then measured using an optical oxygen sensor system (Ocean Optics, Dunedin, USA) in a closed respirometry chamber filled with filtered experimental seawater (68 mL total volume), kept at experimental temperature *via* a temperature controlled water bath. Gastropods were first gently “chased” into their shells underwater using a fine paintbrush to expel any air from the mantle cavity. They were then removed from seawater, their shells lightly scrubbed with ethanol to remove external organisms, rinsed again in seawater and then placed in the unsealed chamber. Once they emerged from their shells the chamber was sealed and measurements commenced. Measurements were stopped and repeated at a later time if the gastropod was moving excessively or if air bubbles were detected. For detailed methods regarding oxygen measurements in marine gastropods, see Brown et al. (1978) and Sokolova and Pörtner (2001). Oxygen levels were measured every 10 seconds for 10 minutes. To account for any microorganisms still present in the seawater, trials of chambers containing only experimental water (no gastropod) were run for each treatment and the results of these were subtracted from trials where gastropods were present.

4.3.5 ANALYSES

Three-factor ANOVAs (analyses of variance) were used to test time spent active and above the water line for gastropods exposed to CO_2 (current vs future), temperature (ambient vs +3 °C) and cue (control vs predator cue vs predation). A two-factor ANOVA was used to test gastropod oxygen consumption and predation rate in response to CO_2 (current vs future) and temperature (ambient vs +3 °C). All factors were considered fixed and orthogonal. Post-hoc pairwise tests were used to determine which levels differed when a significant interaction was detected. All analyses were performed in PRIMER.

4.4 RESULTS

Elevated temperature and CO_2 influenced the activity levels of prey in opposing ways. Elevated temperature had an overall positive effect on activity, whilst future CO_2 levels had an overall negative effect (Fig. 1, Table 2). Movement above water line (avoidance response) accounted for the majority of time not spent actively foraging in all treatments. The presence of predation risk cues caused a reduction in foraging, and therefore an increase in avoidance, in *T. undulatus* across all levels of temperature and CO_2 (Fig. 1). When exposed to predator cues only, activity decreased by between 18-40 %. The presence of active predators and conspecific cues resulted in the greatest reduction in activity (Fig.

1, Table 2). Crushed conspecifics and presence of mobile predator cues intensified anti-predator responses, with at least a 44 % reduction in activity compared to cue-free trials.

Along with increasing foraging activity, elevated temperature also had a positive effect on metabolic rate, with oxygen consumption approximately three times greater in gastropods at +3 °C above ambient (Fig. 2, Table 3). There was no effect of elevated CO_2 on gastropod oxygen consumption (Fig. 2, Table 3).

There was no significant difference in predation rate within or between treatments ($F_{1,8} = 0.08$, $p = 0.73$), with crabs taking gastropods in all treatments.

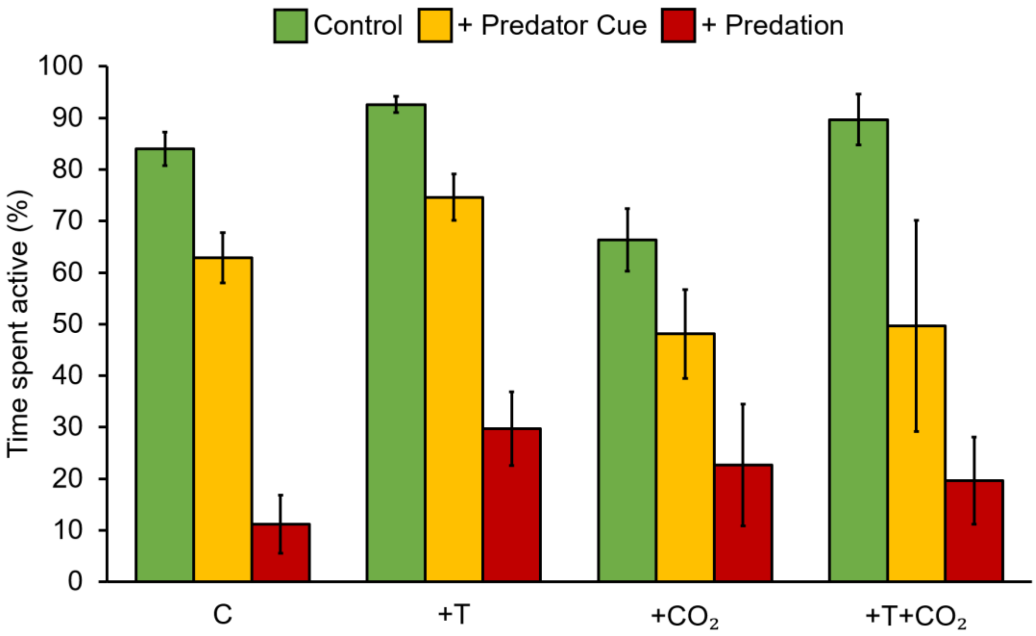

Figure 1 Percentage of time spent active by *T. undulatus* (mean ± S.E) exposed to differing levels of temperature, CO_2 and predation risk. C: ambient temperature and current CO_2. +T: +3 °C. +CO_2: future CO_2. Control (green bars): no predation cue present. +Predator Cue (yellow bars): caged crab present. +Predation (red bars): uncaged crab + damaged snail tissue present.

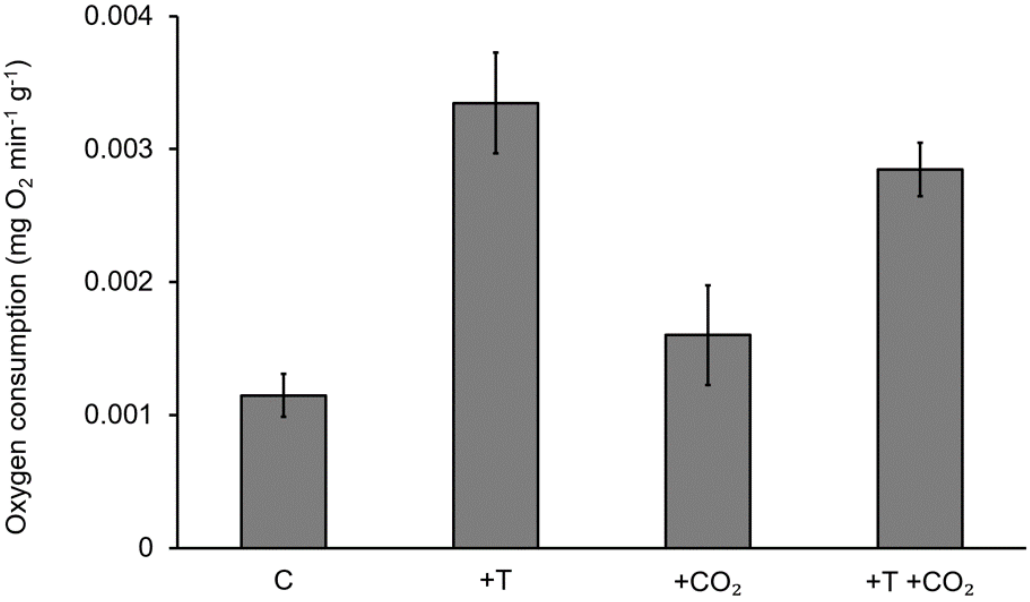

Figure 2 Oxygen consumption (mg O_2 min^{-1} g^{-1}) by *T. undulatus* (mean ± S.E) exposed to differing levels of temperature and CO_2. C: ambient temperature and current CO_2. +T: +3 °C. +CO_2: future CO_2.

Table 2 The combined effects of temperature (Ambient vs. +3 °C), CO_2 (current vs. future) and predation risk cue (control, predator cue or predation) on the time *T. undulatus* spent active, as determined by a three-factor ANOVA.

Source	**df**	**MS**	***F***	***P***
CO_2	1	866.19	4.70	0.0425
Temperature	1	921.78	5.00	0.0381
Cue	2	11860.00	64.29	0.0001
CO_2 × Temperature	1	71.58	0.39	0.5344
CO_2 × Cue	2	318.36	1.73	0.1956
Temperature × Cue	2	78.20	0.42	0.6552
CO_2 × Temperature × Cue	2	257.91	1.40	0.2601
Residual	24	184.48		

Pairwise comparisons for significant terms in Table 1: for CO_2, current > future; for Temperature, ambient < +3 °C; for Cue, control > predator cue > predation.

Table 3: The combined effects of temperature (Ambient vs. +3 °C) and CO_2 (current vs. future) on oxygen consumption by *T. undulatus*, as determined by a two-factor ANOVA.

Source	**df**	**MS**	***F***	***P***
Temperature	1	1.48×10^{-5}	33.82	0.0010
CO_2	1	2.45×10^{-9}	5.57×10^{-3}	0.9430
Temperature × CO_2	1	1.13×10^{-6}	2.58	0.1180
Residual	16	4.39×10^{-7}		

Pairwise comparison for significant term in Table 2: Temperature, +3 °C > Ambient.

4.5 DISCUSSION

Predators are primarily thought to affect prey populations through death, but prey are also strongly affected by the presence of their predators with broader consequences for the demography of prey populations (Connell 1998, 2002). Whilst increased temperature had an overall positive effect on gastropod activity, and CO_2 had an overall antagonistic effect, there were significant reductions in foraging activity between no predation cue and increasing predation cue scenarios. Our findings demonstrate that CO_2 concentrations at near future levels are unlikely to adversely affect the ability of *T. undulatus* to respond to predation cues. Importantly, warming had a positive effect on metabolic activity and corresponding foraging rates of gastropods. Assuming that the levels of activity observed in risk-free trials indicates optimal foraging times under future climate scenarios, we suggest that predation risk would either lead to greater rates of direct predation or energetic deficiencies *via* predator avoidance behaviours.

Altered abiotic conditions can influence the palatability and nutritional content of algal tissues, and therefore herbivore preference and feeding rates (Zou 2005; Duarte *et al.* 2016). Responses are variable, however, and while previous work has shown reduced C:N ratios in turf algae exposed to elevated CO_2 (Falkenberg *et al.* 2012), ocean warming and acidification does not increase the energetic content of turf tissues (N.L. Mertens, unpublished data). Therefore, the reduced time spent foraging in gastropods exposed to predation cues is likely to impose energetic trade-offs under future conditions.

Gastropods exposed to predation cues demonstrated an ability to respond to predation risk at all levels of treatment. That these subtidal animals moved above the waterline when exposed to predation risk indicates that their primary method of avoiding predation lies in escape, rather than withdrawing into their shell. The low proportion of time spent withdrawn in response to predation cues is likely due to the ineffective nature of this behaviour- temperate turbinid snails have relatively thin operculums (Vermeij and Williams 2006) and once captured by *O. truncatus*, their shells are easily broken (personal observation). Morphological responses to predation risk such as thicker shells come at a greater energetic cost (DeWitt 1998), which would be less desirable to maintain as changing environmental conditions increase metabolic demands. Movement as an avoidance behaviour has been previously documented in other species (Trussell *et al.* 2004; Dalesman *et al.* 2006; Bibby *et al.* 2007). Indeed, mobility and the ability to accurately sense predation risk with enough time to escape may be key to the survival of these gastropods in future.

Acidification has negatively affected the response to predation cues in most aquatic species studied to date (Leduc *et al.* 2013). However, the vast majority of studies focus on fishes (> 90%), with very few studies considering the effects of acidification on the anti-predator behaviour of gastropods (see Bibby et al. 2007, Watson et al. 2014). Our results suggest that the mechanisms proposed to explain anti-predator behaviour documented in fishes (Leduc et al. 2013) may not apply to other marine organisms, or may be dependent on other environmental or biological variables. Differences in sensitivity to CO_2 amongst taxa may explain disparities in responses seen amongst gastropods. For example, anti-predatory behaviour was reversed in a marine conch shell at near future levels (Watson et al. 2013). In contrast, we found no response in a turbinid gastropod at similar CO_2 levels, and continued avoidance behaviour has been documented in littorinid snails at CO_2 concentrations far exceeding those predicted for the year 2100 (Bibby et al. 2007). The same variability may apply to ability of *T. undulatus*' predators to detect prey under ocean acidification, although research has shown lower sensitivities to increased pCO_2 in fish and crabs (Wittman and Pörtner 2013), and a reduced effect on locating prey (Cripps *et al.* 2011; Manríquez et al. 2014). Context is therefore crucial when predicting the response of prey to future conditions as elevated CO_2 may not have consistent effects on their ability to detect or react to predation cues.

In conclusion, our results concur that warming will lead to increased activity and foraging demands of these gastropods in line with metabolic theory (López-Urrutia et al. 2006, Russell et al. 2013). Consequently, gastropods not exposed to predation cues displayed greater time spent foraging than those subject to predation cues. Animals under long-term risk of predation must, however, make decisions to expose themselves to potential mortality or to suffer energetic deficiencies known to hamper growth, reproduction and ultimately survival (Houston et al. 1993, Lima 1998). Due to greater metabolic demands as a result of ocean warming, animals may find themselves under greater stress to allocate sufficient time to feed whilst avoiding predation.

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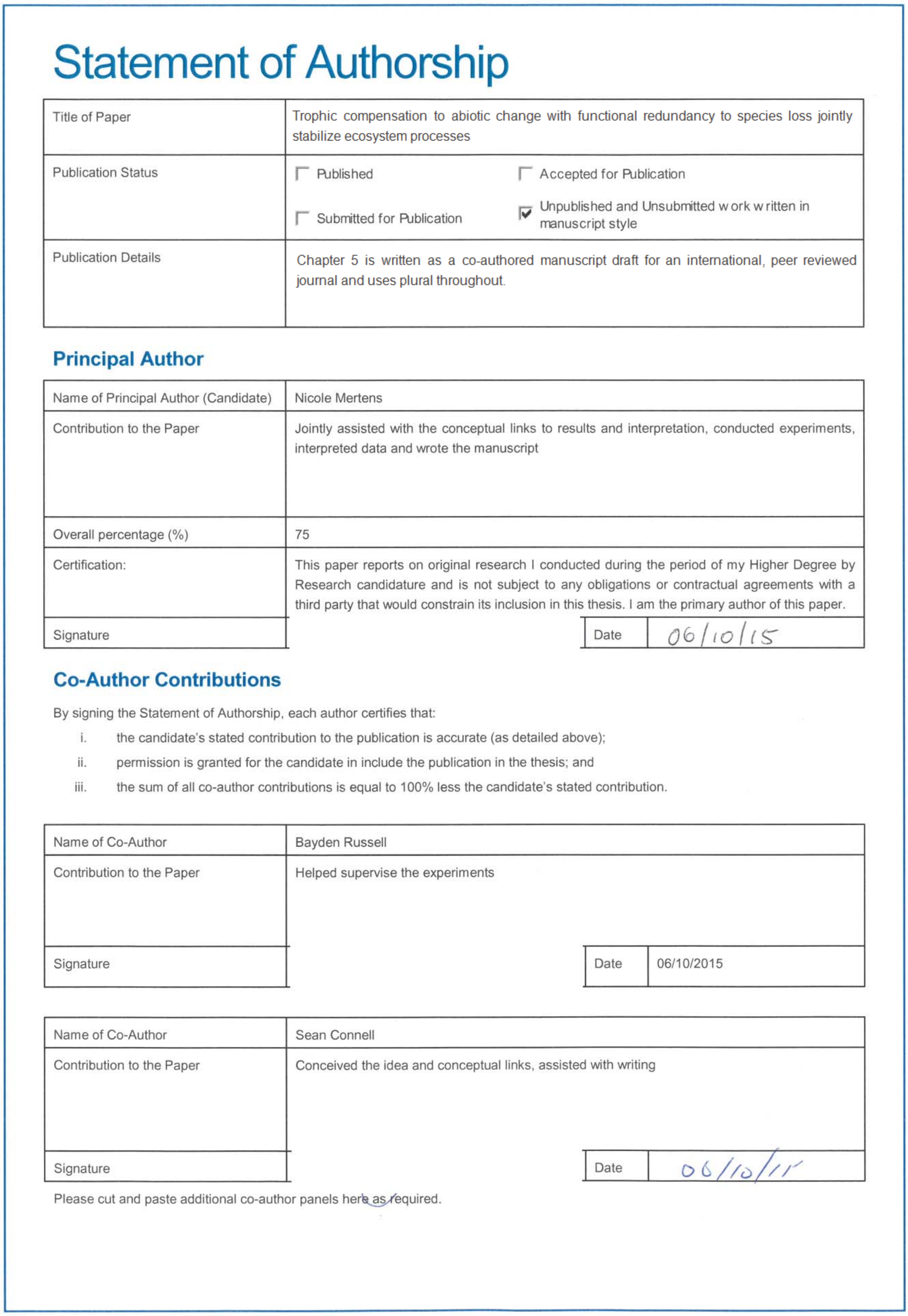
CHAPTER 5

TROPHIC COMPENSATION TO ABIOTIC CHANGE WITH FUNCTIONAL REDUNDANCY TO SPECIES LOSS JOINTLY STABILIZE ECOSYSTEM PROCESSES

STATEMENT OF AUTHORSHIP



Statement of Authorship

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Name of Principal Author (Candidate)	Nicole Mertens		
Contribution to the Paper	Jointly assisted with the conceptual links to results and interpretation, conducted experiments, interpreted data and wrote the manuscript		
Overall percentage (%)	75		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	06/10/15

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

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CHAPTER 5

TROPHIC COMPENSATION TO ABIOTIC CHANGE WITH FUNCTIONAL REDUNDANCY TO SPECIES LOSS JOINTLY STABILIZE ECOSYSTEM PROCESSES

5.1 ABSTRACT

If ecosystems are to remain stable, they require an internal dynamic that adjusts to variation in identity and strength of abiotic and biotic disturbance. Compensatory dynamics provide an account of how ecosystem properties remain stable despite a disturbance causing species loss or change in relative abundance. Nevertheless, ecosystems also appear to have compensatory processes that act well in advance of species loss or decline, involving early responses that adjust in proportional strength to the initial biological imprint of the disturbance. We used mesocosm experiments to test the extent of adjustability in compensatory responses of two herbivore species to disturbances under no species loss (i.e. herbivores compensate for enhanced productivity under future climate) and species loss of alternate species able to fulfill the former function (i.e. functional redundancy). These responses were tested under both current and predicted future conditions of temperature and $p\mathrm{CO}_2$. Overall, net production remained stable under abiotic change without species loss and despite change to species abundance and composition. This result highlights the remarkable adjustability of compensatory processes and suggests that such adjustability of response to be a hallmark of research into compensatory processes.

5.2 INTRODUCTION

If ecosystems are to remain stable, they require an internal dynamic that adjusts to variation in strength of abiotic and biotic disturbance. Compensatory dynamics stabilize communities against change by buffering the effects of disturbance in its various forms, combinations and intensities (Ghedini *et al.* 2015). Hence, in the face of change to whole ecosystem attributes (e.g. net production and biomass), there is adjustability in processes that resist change (e.g. rates of consumption or population growth), generating compensatory dynamics that reinforce stability (Gonzalez and Loreau 2009; Ghedini *et al.* 2015). Such adjustability in response to disturbance appears to be a hallmark of compensation.

Historically, the terms functional compensation and functional redundancy have been used interchangeably to describe how ecosystem properties remain stable despite a disturbance causing species loss or change in relative abundance (Loreau and de Mazancourt 2013, for review). Functional redundancy in particular is based on the well-understood idea that some species perform similar roles in communities and ecosystems, and may therefore be substitutable with little impact on ecosystem processes (Lawton and Brown 1993). Where an ecosystem function is underpinned by the activity of a single species, loss of this species would reduce the stability of the system (i.e. functional redundancy is low). Hence, functional redundancy is higher where alternate species are able to fulfill the function of another, should that species be unable to fill that role (e.g. by loss).

Recently, the theory of compensatory dynamics was broadened to include processes that buffer disturbances that drive direct change to ecosystem properties before species loss or species change (Connell and Ghedini 2015). Ecosystems appear to have processes that act well in advance of species loss or decline, involving early responses that adjust in proportional strength to the initial biological imprint of the disturbance. For example, herbivory adjusts in proportion to the expansion of opportunistic species favoured by human-driven increases in resource availability (Ghedini *et al.* 2015). Here, trophic compensation acts as an adjustable function to negate the effects of alternate types and combinations of pollution on primary production without change to species diversity.

Here, we explore the extent of adjustability in compensatory responses where no species loss occurs (i.e. trophic compensation) and where this function is shared by alternate species so that their responses are sufficiently adjustable that they stabilize productivity whether together (i.e. no over compensation) or apart (i.e. no under compensation). We explore the capacity for trophic compensation to stabilize otherwise accelerated productivity caused by elevated ocean temperature and CO_2 concentrations, and maintain stability during change to species abundance and composition (Fig. 1). Such evidence would suggest that the overall stability of a system might be underpinned by multiple species which not only support processes that adjust in strength to counter disturbances, but also adjust to compensate for species loss.

Our experimental assessment focuses on a model kelp system that has an intensive history of research, including the processes that drive shifts from one ecosystem state (i.e. kelp-dominated) to another (i.e. turf-dominated). Resource enhancement increases the probability of normally subordinate, turf-forming algae displacing the naturally dominant kelp forests (i.e. nutrient pollution; Gorman and Connell 2009) and turf expansion is exacerbated by elevated temperature and carbon dioxide (Connell and Russell 2010). Processes that oppose turf expansion, such as herbivory, enable kelp replenishment and persistence. For herbivory to compensate for resource-disturbance, rate of consumption by grazers must proportionally increase to match the rate of expansion of turfs (i.e. the rate at which canopies are lost). Whilst urchin herbivores are important in structuring algal habitats in many regions (Connell and Irving 2008), the consumers of turfs that are known to counter increase in turf productivity under resource enrichment in this study system are gastropods (Ghedini *et al.* 2015; McSkimming *et al.* 2015) and amphipods (Munguia and Connell unpubl. data).

We hypothesized that grazers would increase intensity of feeding in proportion to the effects of climate on productivity (i.e. elevated temperature and CO_2) and this effect would be maintained by both taxa in combination and continue to be maintained by each taxa in isolation. Hence, the stability of productivity would not only be a function of the ability of herbivores to compensate for environmental change, but also for this role to be performed by multiple taxa so that loss of species has little impact on the ecosystem.

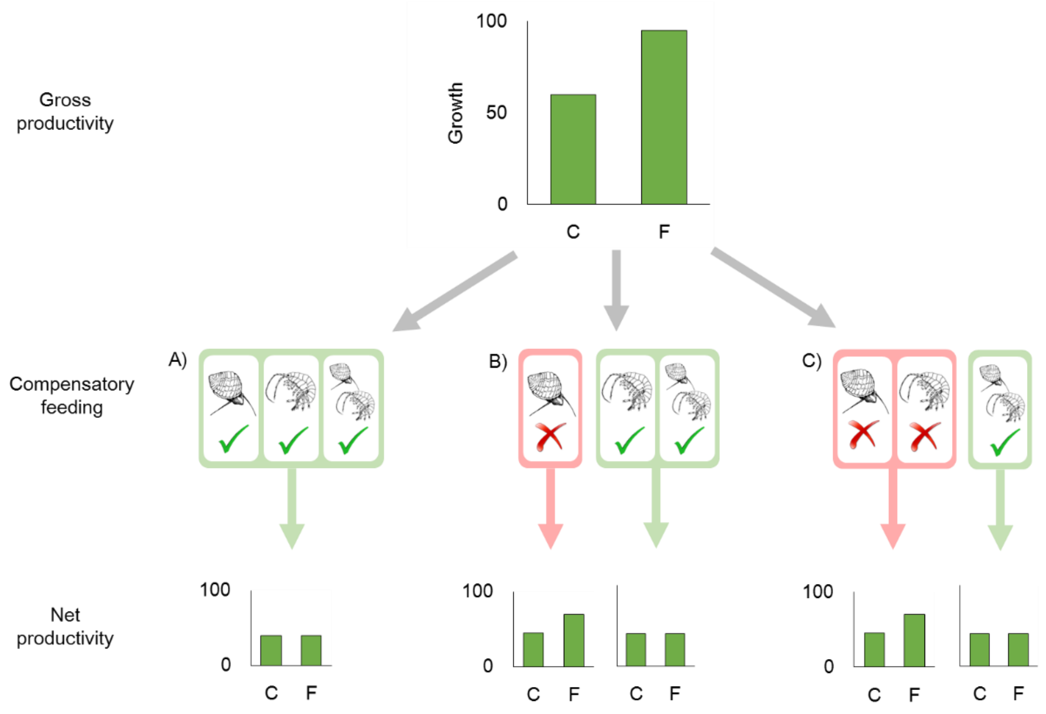

Figure 1 A conceptual diagram showing the net productivity of primary producers as a result of differential responses of herbivores to current (C) and future (F) conditions. In the absence of herbivores (gross productivity), future conditions result in greater growth of primary producers. A) When two individual herbivore species demonstrate trophic compensation through increased feeding (*per capita* response) or increased numbers (population response) under future conditions both alone and in combination, the outcome for primary producers is a net neutral change in growth. Loss of one or the other herbivores will still result in trophic compensation. B) When only one species compensates alone and in combination, loss of that species will result in loss of trophic compensation, and increased net growth of primary producers under future conditions. C) When both species compensate only in combination, loss of either species will result in loss of trophic compensation.

5.3 METHODS

5.3.1 EXPERIMENTAL SET UP AND MAINTENANCE

Experimental mesocosms (polyethylene, TeamPoly, Australia) were located at SARDI (South Australian Research and Development Institute) Aquatic Sciences, West Beach, South Australia (34.9453 °S, 138.5038 °E). Each mesocosm was covered with high density polyethylene with woven scrim (SolarPro, PolyFab, Australia) to prevent intrusion of rainwater into the system. Mesocosms were filled to 2000 L total volume with natural filtered seawater; therefore, seawater chemistry prior to experimental manipulation was characteristic of these waters (see Table 1, Current for details). A flow-through system with a flow rate of 4 L min^{-1} was used to maintain water quality.

Two scenarios of temperature and $p\text{CO}_2$ were chosen to represent current and future conditions for these factors in combination, as they will increase concomitantly, with future water temperature and pH levels based off IS92a model prediction for 2050 (Meehl *et al.* 2007). Temperature was maintained at either current (seasonal ambient) or future (+3 °C) using individual heater/chiller units (TC-60 Aquarium Chillers, TECO Refrigeration Technologies, Ravenna, Italy). CO_2 was maintained at either current ambient concentration (corresponding to a pH of approximately 8.10) or future concentration (corresponding to a target pH of approximately 7.95) by aerating the tanks at a rate of 15 L min^{-1} with either ambient atmospheric air, or air enriched with CO_2 *via* a gas mixer (Pegas 4000 MF, Columbus Instruments, Columbus Ohio, USA). Temperature and pH were measured daily using a handheld pH meter (Hanna Instruments, Woonsocket, USA). Temperature and $p\text{CO}_2$ were allowed to fluctuate over a 24 hour period in response to biological processes and variation in non-climatic drivers (e.g. solar) in order to reflect the natural variability of coastal marine systems (Duarte *et al.* 2013). Total alkalinity (TA) was measured weekly using a potentiometric titrator (888 Titrando, Metrohm, USA).

Concentrations of pCO_2, carbonate (CO_3^{2-}) and bicarbonate (HCO_3-), as well as the saturation state of calcite (Ω Ca) and aragonite (Ω Ar) were then calculated from measured TA, pH, salinity and temperature using the CO2SYS program for Excel (Pierrot *et al.* 2006) with constants from Mehrbach et al. (1973) as adjusted by Dickson & Millero (1987). For measured and calculated water parameters throughout experimental run time, see Table 1.

Table 1: Water parameters during experimental run time (± SE) as determined by daily measurements of pH and temperature and weekly titrations. Mean pH and temperature reported below were taken from morning measurements over total experimental run time (147 days). Titrations were taken throughout trials, data presented here are the means of twelve titrations ($n = 3$ per titration). Current: ambient temperature and CO_2, Future: elevated temperature and CO_2.

Parameter	Current	Future
pH	8.09 ± 0.01	7.92 ± 0.01
Temperature (°C)	16.32 ± 0.13	18.65 ±0.10
Salinity	40.00 ± 0.00	40.00 ± 0.00
TA (µmol/kgSW)	2457.08 ± 2.54	2452 ± 3.52
***p*CO2 (µatm)**	410.33 ± 15.63	520.96 ± 19.32
CO_3^{2-} (µmol/kgSW)	219.01 ± 6.61	189.31 ± 4.81
HCO_3^- (µmol/kgSW)	1914.24 ± 16.89	1983.42 ± 12.88
ΩCa	5.04 ± 0.15	4.35 ± 0.11
ΩAr	3.28 ± 0.11	2.84 ± 0.07

5.3.2 PRODUCERS AND GRAZERS

Each mesocosm contained an assemblage of turf or mat-forming algae (*sensu* Connell *et al.* 2014), five kelp (*Ecklonia radiata*) of similar size (average individual weight 284.37 ± 13.96 g) and two consumers of turfs; the subtidal gastropod *Turbo undulatus* (*n* = 10 per tank or 4 per m^2, average individual weight 7.78 ± 0.27 g) and the amphipod *Cymadusa pemptos* whose abundance was allowed to vary among treatments as a function of their rapid generation time. These consumers are ubiquitous to kelp forests of Australia's south coast and chosen for their impact on algal turfs. These taxa were collected by hand from the shallow subtidal waters (0.5-1 m depth) adjacent to Adelaide, South Australia, including turfs that were allowed to naturally develop on 10 x 15 cm fibre-cement settlement panels.

5.3.3 PRODUCTIVITY AND CONSUMPTION

This experiment was based on experimental observations of the joint effects of consumption of gastropods and amphipods on rates of turf productivity (i.e. grams per day) and three trails that estimated rates of consumption of gastropods and amphipods separately and together. The trials proceeded by estimating consumption rates of gastropods and amphipods alone and their joint rates by combining them. The trials were of different length so as to achieve a representative estimate of consumption by two quite different types of grazer; i.e. slower moving and sparser abundances of gastropods that cannot forage over the tank surface within a few days, versus the faster moving and densely populated abundances of amphipods that can consume from most surfaces immediately. Growth rates among trials were standardised to daily growth (grams per day).

Productivity of turfs in the presence and absence of both types of consumer was estimated for both current and future climate. For each mesocosm, this test involved estimating biomass on five panels (10 x 15 cm) open to both types of consumer and five panels in which cages prevented their access (0.5 mm mesh) over 45 days. Prior to commencement of this experiment, turfs and gastropods were exposed to treatments for 30 days for the purpose of acclimation.

The rate of gastropod consumption alone was estimated before amphipods were introduced to the tanks. Here, biomass of turf was estimated by visually quantifying turf cover on five panels (10 x 15 cm) open to gastropods and five panels in which cages prevented their access (1.5 mm mesh) over 47 days, and then converting cover to biomass using conversions derived from turf scrapings from panels grown under the same experimental conditions. Consumption was quantified as the difference between gross growth (absence of grazers) and net growth (presence of grazers) across 47 days.

On the completion of the first trial with gastropods, amphipods were introduced and the rate of amphipod consumption alone was estimated two months after they were introduced to the tanks. At this time their densities were estimated by first rinsing individual kelps in sea water then again in fresh water to remove amphipods and then passing the water containing amphipods through a 0.5 mm mesh filter (Heldt *et al.* in review). Amphipods were stored in 100% ethanol and those individuals that were visible under a 40x power dissecting microscope were counted. To assess the effects of amphipods consumption in isolation from gastropods, three feeding trials were conducted over three days with each trial separated by 2 days. Amphipods were placed inside plastic containers (250 mL) where the average number of amphipods per treatment of current climate (2.78 ± 1.07) was less than that of treatments future conditions (13.50 ± 0.95); reflecting the magnitude of differences in population size observed between these treatments. Turf of known weight was collected from the same tank and placed in these containers which were fitted with permeable mesh (0.5 mm) to allow water movement whilst retaining the set densities of amphipods (three containers per mesocosm).

The joint rates of consumption of gastropods and amphipods were also estimated two months after amphipods were introduced to the tanks. These estimates were derived from the 24 hour loss of biomass of turfs on five panels (10 x 15 cm) that were exposed to a single gastropod restrained by a fence, but exposed to amphipods. By constraining the gastropod in this trial of joint consumption of both consumers, we were able to achieve a time frame that enabled the surface to be fully accessed by both consumers. The suitability of this latter timeframe was identified by several pilot trials. To avoid grazing response being saturated (maximum grazing rate achieved or 100 % of turfs removed), all trials (gastropods only, amphipods only and gastropods and amphipods combined) were concluded at a time when all treatments maintained some turf cover.

5.3.4 ANALYSES

A two-way analysis of variance (ANOVA) was used to test effects of herbivory and treatment on turf growth. The factors of herbivores and treatment were considered fixed and orthogonal with two levels in each factor (herbivores: absent vs present; treatment: current vs. future). Individual turf-covered panels within mesocosms were treated as replicates (*n* = 15). Post-hoc pairwise tests were used to determine which levels differed when a significant interaction was detected. One-way analysis of variances (ANOVAs) were used to test daily consumption rates of herbivores and growth of turfs. Individual panels or containers within mesocosms were treated as replicates (*n* = 15 or *n* = 9 respectively).

5.4 RESULTS

Turf growth was regulated by an interaction between treatment and herbivores ($F_{1,8}$ = 26.49, $p < 0.001$). Herbivores had an effect on turf growth regardless of treatment (post-hoc pairwise comparisons; for current, absent > present, $p < 0.002$; for future, absent > present, $p < 0.003$). In the absence of grazers, there was a significant increase in turf growth under future conditions, approximately three times that of turf growing under current conditions (post-hoc pairwise comparisons, $p = 0.007$). However, the presence of grazing countered this effect so that turf growth was similar under current and future conditions (post-hoc pairwise comparisons, $p = 0.919$).

Rates of joint consumption by gastropods and amphipods were greater under future climate (Fig. 3a; $F_{1,4} = 11.52$, $p = 0.027$) such that net productivity between these treatments did not differ (Fig. 3a; $F_{1,4} = 0.01$, $p = 0.92$). This pattern of consumption balancing net productivity was also observed for each taxa in isolation. Rates of consumption by gastropods alone were greater under future climate (Fig. 3b; $F_{1,4} = 20.49$, p =0.01) such that net productivity between these treatments also did not differ (Fig. 3b; $F_{1,4} = 0.001$, $p = 0.98$). Similarly, rates of consumption by amphipods alone were greater under future climate (Fig. 3c; $F_{1,48} = 7.02$, $p = 0.01$) such that net productivity between these treatments did not differ (Fig. 3c; $F_{1,49} = 1.17$, $p = 0.28$).

Turf productivity in the gastropod only and gastropod and amphipod trials were similar; however, daily growth of turfs in the amphipod only trial was considerably greater (Fig. 3). This is likely to reflect differences in methodology which lead to greater exposure of turfs to light in amphipod only trials. Containers of amphipods and turf were submerged in experimental mesocosms at all times, but were suspended in the water column approximately 30 cm from the surface whilst tiles used in other trials were distributed on the floor of mesocosms. Whilst filamentous turfs are associated with subtidal benthos and can grow under low light regimes (e.g. shading, sedimentation) they respond positively to increases in light (Connell 2005).

Whilst the density of gastropods among treatments was maintained to be similar among treatments through replacement with acclimated individuals in the event of mortality (n = 10 per mesocosm), the density of amphipods was allowed to vary among treatments as a function of their rapid generation time. Whilst we assumed starting populations of amphipods would be similar due to randomly distributing kelp of equal size throughout treatments, after two months, treatments of future climate were estimated to support greater population sizes (mean = 9.41 ± 3.83 per kelp) than treatments of current climate (mean = 260.92 ± 111.64 per kelp) (Wilcoxans rank test: X^2 (1, N = 12) = 3.86, $P <$ 0.05).

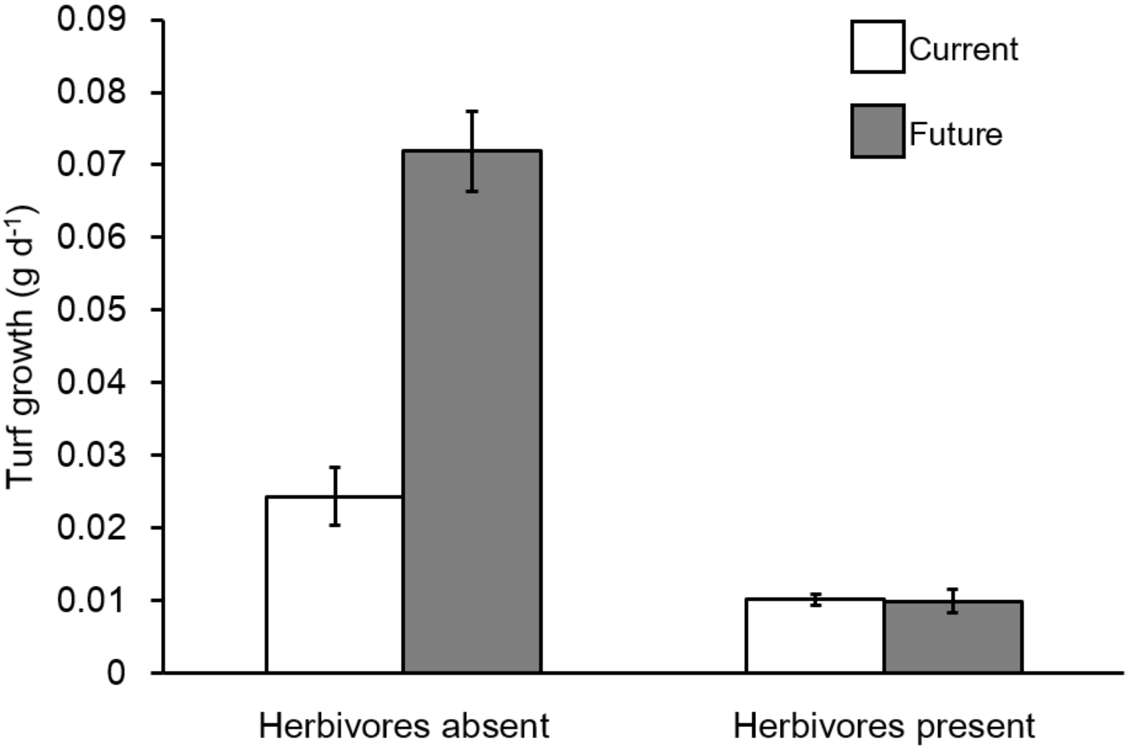

Figure 2 The growth of turfs (g d^{-1}; mean ± SE) exposed to current and future conditions of temperature and $p\mathrm{CO}_2$ for 47 days in the absence and presence of gastropod and amphipod herbivores.

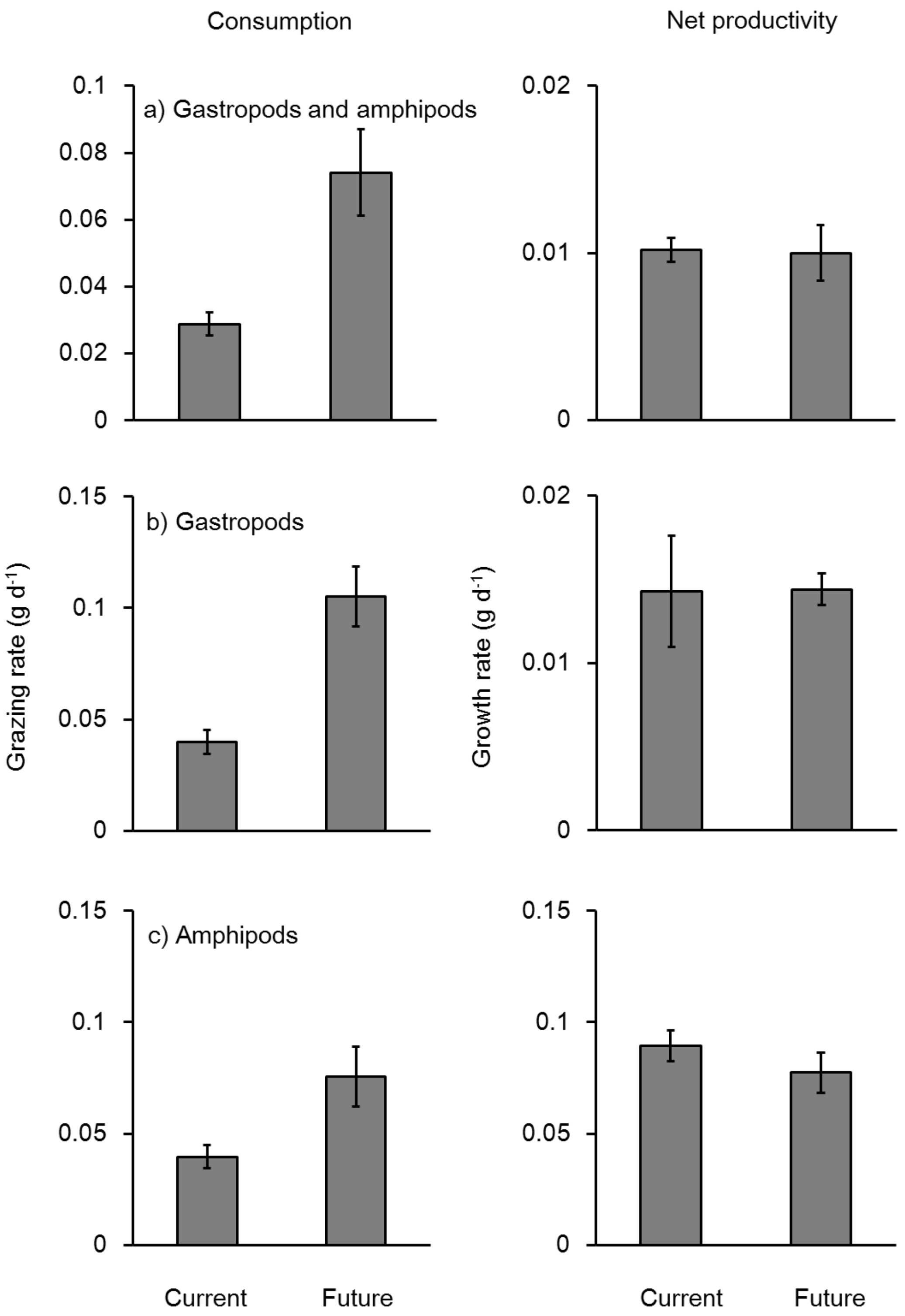

Figure 3 The effect of current and future climate on consumption of turfs (left hand graphs) and resulting net production of turfs (right hand graphs) in the presence of a) both gastropods and amphipods b) gastropods only and c) amphipods only (mean ± SE). Note the differences in scale on the y-axes.

5.5 DISCUSSION

In the face of abiotic change, enhanced productivity was not only compensated by herbivory (i.e. trophic compensation), but this function was also maintained when one taxa was lost such that the compensatory role of a taxa was compensated for by the other. This adjustability of response relates to well-studied property of functional redundancy where ecosystem function is maintained constant despite the loss a species. Here, however, we demonstrate that where ecosystem function is directly altered by environmental change (i.e. accelerated productivity), rather than species loss, compensation can occur across trophic levels to counter change.

This experiment demonstrated that compensation can act in advance of species loss or change, involving early responses (i.e. consumption) that adjust in proportional strength to the initial biological imprint of the disturbance (i.e. production). This stabilizing function is reinforced by the capacity for alternate species to fulfill this function, such that species loss causes the remaining species to increase the strength at which they counter change. Hence, the remaining species must increase consumption to compensate for the loss of additional consumption provided by the lost species. In this experiment, net production remained stable under abiotic change and subsequent species loss, such that there was no change in productivity when abiotic conditions improved productivity potential and then one taxa was deleted: herbivory adjusted so over-compensation was prevented when both taxa were together or under-compensation when they were apart.

The compensation we observed involved adjustments in both individual and population level responses. Adjustments in individual responses were demonstrated by gastropods (i.e. increases in *per capita* rates of consumption), whilst adjustments in population level responses were demonstrated by amphipods (i.e. increase in population size). Separate tests to understand the cause of increases in amphipod herbivory identified that *per capita* feeding rates actually declined (K.A. Anderson, P. Munguia and S.D. Connell unpublished data), hence population level change accounts for elevated rates of consumption. Together, these adjustments buffered increased production of turfs so that net productivity remained relatively fixed under a combination of ocean warming and elevated CO_2 concentrations. When environmental change (e.g. warming) stimulates increases in metabolism, population growth as a result of increased reproductive output is possible where resources are adequate (Savage *et al.* 2004). In this experiment, there was sufficient time for amphipod populations to cycle through multiple generations, allowing for population level change that was not possible for the longer generation times of gastropods.

Similar individual and population level responses have been observed to maintain ecosystem function in a community of stream insects in experiments simulating species loss (Ruesink and Srivastava 2001), suggesting when *per capita* or population size compensation can co-occur, stability of function should be increase with different types of disturbances. Pending the intensity and duration of disturbance, functional compensation may take both forms of individual and population level responses. Where disturbances are immediate and discrete (e.g. pulse disturbance), *per capita* change has the adjustability to respond instantly. Where disturbances are longer-term, population level increases may counter the effects through population growth. Both types of responses may be involved where disturbance is persistent; it may initially stimulate greater *per capita* rates of consumption that provides greater energy intake and ensuing fecundity at the individual level and growth at the population level.

How does compensation adjust so that grazing does not under or over compensate in a fluctuating environments? Ghedini and Connell (in preparation) suggest that the effect of additional energy in the system has similarities to naturally highly productive systems sustaining more intense herbivory than unproductive systems (McNaughton *et al.* 1989). That is, consumption continually adjusts to variation in production as function of energy use for basic organismal processes in fluctuating environments. It has been considered that such changes in metabolism represent a link between the individual organisms and their influence on community dynamics, because metabolism regulates the demand that organisms place on their environment and their collective metabolic processes largely determine ecosystem processes (Brown *et al.* 2004).

These results suggest substantial flexibility in compensatory processes that goes well beyond the often-documented stabilization of variation in species densities to maintain relatively stable ecosystem properties (Loreau and de Mazancourt 2013). Indeed, there appears to be considerable depth to the idea that compensation can also occur where abiotic change directly alters an ecosystem attribute; such as where trophic compensation counters the effects of resource-disturbance on productivity. Trophic compensation not only involves adjustments in proportional strength to the effect of disturbance (Ghedini *et al.* 2015), but also may itself be compensated *via* functional redundancy when species composition varies. To date, studies of compensation have focused on how species diversity maintains ecosystem stability through processes of density compensation (e.g., adjustments in species densities maintain overall community biomass; which may also provide functional compensation where the functional role of a species is taken up by another (MacArthur *et al.* 1972; Ernest and Brown 2001). However, the role of functional redundancy may be more adjustable than current thinking allows as it may also be involved in mechanisms that buffer the direct effects of abiotic change on ecosystem function.

One renowned example that fits this model of functional redundancy, but is not often considered as such is the sequential loss of herbivores and sudden loss of coral reefs in Jamaica (Hughes 1994; Hughes *et al.* 2003). Here, fishing first reduced abundances of herbivorous fishes but corals remained. This loss was followed by mass mortality of an herbivorous sea urchin, which then enabled algal production to escape herbivory and replace corals as dominants (Hughes 1994). This sequence of near-elimination of distinct types of taxa performing similar functions (i.e. consumption of algal productivity) is almost always considered as an example of reduced resilience to additional disturbances. However, we suggest it may be better considered as an example of progressive loss of compensatory capability of the system (i.e. resistance). This example centers on the prevention of coral recovery after hurricane disturbance due to the expansion and space pre-emption by algae (Hughes 1994). From the perspective of compensatory dynamics, stability was maintained by herbivores whose functional redundancy was lost when urchins were eliminated following substantial loss of herbivorous fishes (Micheli and Halpern 2005).

The ability of a community to recover from disturbance by reorganizing while undergoing change, so as to retain essentially the same structure and function, has been the hallmark of resilience research (Scheffer *et al.* 2001; Folke *et al.* 2004). Yet, despite continuous disturbance, most communities are stable in that they dynamically persist in a certain state without switching to a contrasting state. This stability requires an internal dynamic that adjusts to variation in identity and strength of abiotic and biotic disturbance (Connell and Ghedini 2015). Hence, understanding how disturbance can be absorbed through compensation is necessary if resistance is to be better incorporated along with resilience into the conceptual framework of community ecology. We highlight the remarkable adjustability of compensatory processes, not only as a stabilizer after species loss, but also well before species loss, and suggest that this adjustability of response may well be the hallmark of research into compensatory processes.

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CHAPTER 6

GENERAL DISCUSSION

Ocean warming and acidification can lead to increased metabolic demands and consequently increased feeding. As such, consumers may mitigate and even counter the positive effects of warming and acidification on producer growth. The focus of my thesis has been to investigate the effects of altered abiotic conditions on consumer metabolism and feeding, and to identify in particular the capacity of herbivores to counter predicted expansion of opportunistic primary producers. How abiotic and biotic interactions influence consumer strength has been central to all chapters. Chapters 2, 3 and 4 sought to identify the underlying metabolic changes responsible for altered consumer responses. Chapter 5 then scaled up from more simplistic, mechanistic studies in order to compare these results with those obtained when more consumer species were present in combination. In a model kelp system, consumers were able to provide a countervailing mechanism to keep turf algae at ambient levels under moderate warming and CO_2 addition through adjustable compensatory responses, both alone and in combination. However, climate change poses direct and indirect challenges to consumer resource allocation, fitness and ultimately survival (Chapter 3). Warming of 3 °C resulted in reduced ingestion efficiency in gastropod consumers despite increased metabolism and consumption, and represented a peak in thermal performance (Chapter 2, 3). Further warming resulted in reduced consumption, despite continued productivity of turfs (Chapter 2). Additional trade-offs in foraging activity when consumers are exposed to predation risk are likely to increase energetic deficiencies and result in loss of fitness, or increase mortality through increased exposure (Chapter 4). Climate change fundamentally alters the metabolic balance of consumers, and requires compensatory responses and energetic trade-offs for consumers to meet increased demands. Whilst my results indicate that increased consumer control of primary productivity in kelp forests is possible under moderate levels of ocean warming and acidification, unmitigated warming will likely lead to weakened consumer strength, lowered ecosystem resilience, and phase shifts to turf-dominated states. This chapter summarises the key findings and significance of my research, as well as identifying areas where further research is required. I also outline the implications of my work for broad predictions of enhanced consumer strength under future climate, and argue how general theory must combine with knowledge of individual responses if we are to better predict how systems like kelp forests will be altered by a changing environment.

6.1 SUMMARY OF FINDINGS

The metabolic theory of ecology (MTE) predicts that ectothermic grazers will be more metabolically sensitive to changes in temperature than their food sources (López-Urrutia *et al.* 2006; Yvon-Durocher *et al.* 2010), and has been used to predict increases in top-down control of algal assemblages (O'Connor *et al.* 2009; Carr and Bruno 2013). Herbivores can absorb the effects of changing abiotic conditions through compensatory feeding (Connell and Ghedini 2015), and with an increase in temperature of up to 3 °C, grazers were able to counter increased primary productivity. However, at higher temperatures this trophic compensation failed (Chapter 2). These findings are important as they show that under likely warming scenarios predicted for 2100, consumer interaction strength begins to weaken and turfs have a greater capacity to persist than the capacity for their herbivores to compensate for their growth. These responses were underpinned by differing physiological responses to warming, such that grazers were unable to meet metabolic demands through feeding. Such mismatches between consumer feeding rates and metabolism have been documented in other ectothermic species (Lemoine and Burkepile 2012; Twomey *et al.* 2012). However, by also quantifying the responses of the food source (primary producers), I demonstrated the potential ecological consequences where consumers are unable to counter increased primary productivity as a result of asynchronous responses to warming between interacting consumers and producers. Therefore, tolerances and responses to warming within and amongst interacting taxa must be taken into account if we are to predict how warming will influence the strength and direction of interactions, and the outcomes for the broader system in question.

The addition of moderate future predictions of $p\mathrm{CO}_2$ to the grazer-turf dynamic studied in Chapter 2 yielded similar results in terms of consumption, where elevated temperature (+ 3°C) treatments alone resulted in increased metabolism and feeding rates (Chapter 3). However, reductions in ingestion efficiency and lower weight gain under a combination of elevated $p\mathrm{CO}_2$ and temperature indicated again that these grazers approach a thermal threshold at +3 °C, which appears to be exacerbated under ocean acidification scenarios. After this threshold is passed, metabolism is likely to outpace consumption and result in reduced fitness (Rall *et al.* 2010; Lemoine and Burkepile 2012). Indeed, even conservative loss of shell or body weight is likely to have detrimental effects on gastropod grazer ability to escape predation (Bertness and Cunningham 1981; Menge 1974; Juanes 1992). Energetic trade-offs to maintain shell thickness under predation risk would result in lower resource allocation to other biological processes such as reproduction and growth (Kroeker *et al.* 2014), also reducing overall fitness.

Warming up to 3 °C results in increased metabolism and feeding rates for these grazers with and without CO_2 addition, suggesting that they have the potential to counter the enhanced growth of algal turfs under future conditions as predicted by MTE (Chapter 2, 5). However, ingestion efficiencies of gastropods exposed to these conditions were just above the minimum required to meet energetic needs, therefore, further increases of pCO$_2$ and temperature are likely to have a more negative impact upon their ability to meet energetic demands through ingestion (Chapter 3). This is consistent with the results of metabolic rate versus consumption documented at higher temperatures (Chapter 2).

Higher trophic levels also influence herbivory under future climate, as grazers must balance the increased need to forage with the need to avoid predation (Lienart *et al.* 2014). Whilst predators are primarily thought to regulate prey populations through mortality, prey are also strongly affected by the presence of predation risk cues (Brown 2003). The implications of altered behaviour in response to risk have broader consequences for the demography of prey populations (Connell 1998; 2002). Future abiotic conditions had a positive effect on both gastropod metabolism and foraging activity in the absence of predators (Chapter 4). Contrary to results seen in fishes and some invertebrates (Leduc *et al.* 2013; Manríquez *et al.* 2013; Watson *et al.* 2014), the ability for these gastropod grazers to detect predation cues was not adversely affected by increased CO$_2$ concentrations. As such, there were significant reductions in foraging activity between risk-free and high predation risk scenarios (Chapter 4). Differences in sensitivity to climate variables (Kroeker *et al.* 2013; Wittmann and Portner 2013) may account for variability in response detected amongst taxonomic groups (e.g. Bibby *et al.* 2007; Watson *et al.* 2014). These findings demonstrate that context is again crucial when making predictions about how consumer strength will be altered by predation risk in future climates.

Predators are also likely to increase their feeding rates under future conditions due to increased metabolic demands. However, they often rely less on chemical cues alone to detect prey, and as such the effects of ocean acidification on predator behaviour may be smaller than those of their prey (Cripps *et al.* 2011). Assuming that the levels of activity observed in risk-free trials indicates optimal foraging times for grazers under future climate scenarios, predation risk may lead to either greater rates of direct predation or energetic deficiencies *via* predator avoidance behaviours. The outcome of either result would be less grazer control of primary productivity, with consequences for the broader community.

Scaling up prior work to include the effects of climate change on multiple consumer species yielded results in line with current predictions from smaller scale and field based studies (Connell *et al.* 2013). Turf algae showed increased productivity, demonstrating that climate change has the potential to result in greater coverage and persistence of these primary producers to the detriment of their kelp competitors (Chapter 5, Kennelly 1987; Gorman *et al.* 2009). However, conditions that facilitate expansion and dominance of turf can also strengthen trophic compensation and keep primary productivity in check (Connell and Ghedini 2015). These effects are known for both herbivorous gastropods and amphipods (Ghedini *et al.* 2015; McSkimming *et al.* 2015) through increases in *per capita* feeding. Whilst *per capita* rates of turf consumption did increase under future climate for the gastropod grazers in this system, amphipods did not show *per capita* increases, and instead the observed increase of turf consumption was a result of greater population size (Chapter 5).

Despite mechanistic differences in grazer response, trophic compensation occurred independently of the identity of taxa and whether they were together or apart. Hence, gastropods and amphipods are functional equivalents for maintaining resilience in kelp systems, and for which redundancy is possible. Differential mechanistic responses may increase the ability of a functional group to compensate, by allowing immediate response to pulse disturbances through individual, *per capita* change as well as response to longer-term change through population level increases in abundance. These findings suggest that whilst some taxa may experience severe and negative responses to ocean warming and acidification, preservation of functional groups may be possible, and systems may show unexpected resilience to change. Importantly, adjustability of compensatory processes by coexisting taxa acts not only as a stabilizer after species loss, but also well before species loss occurs (Connell and Ghedini 2015). In this system, experimental temperatures were at the peak of consumption for the gastropod grazer (Chapter 2), and further increases in temperature may lead to reduced compensatory response; however, amphipod grazers also demonstrated an ability to compensate for increased turf growth even in the absence of gastropods. Ideally, performance optima and temperature thresholds for the amphipod grazer in this system should be investigated to increase our understanding of the extent to which trophic compensation and functional redundancy may buffer against future change.

6.2 GAPS IN KNOWLEDGE AND FUTURE DIRECTIONS

The pace of climate change is generally slow, but exposure of animals to experimental treatments can be rapid. Such is also the case for measuring responses to such treatments. A search through the literature of manipulative climate change studies over the last 15 years reveals a wide array of acclimation times, experimental durations and justifications. Even when the search is narrowed to only those which manipulate carbon dioxide/temperature, disparities between studies involving very similar organisms are striking. Sea urchins have been exposed for 4 days through to 16 months to investigate basic physiological responses (Shirayama and Thornton 2005; Miles *et al.* 2007; Carr and Bruno 2013; Dupont *et al.* 2013). Gastropods of the genus *Littorina* have been exposed to treatments for 30 days to measure metabolic activity in one study (Melatunan *et al.* 2011) and 6-8 weeks in another (Sokolova and Pörtner 2001). Similar disparities can be seen measuring interspecific interactions, with response to predation risk in two separate studies being measured at 83 days and 5-7 days respectively (Manríquez *et al.* 2013; Watson *et al.* 2014). Whilst some studies argue that “long”-term acclimation is necessary to remove the effects of field acclimation prior to measuring treatment responses (e.g. Sokolova and Pörtner 2001; Yamane and Gilman 2009), very few give reasons for chosen experimental durations and due to the nature of sampling in some trials (e.g. destructive sampling, see Melatunan *et al.* 2011), there is no comparison of responses over time.

It then appears that acclimation times stated in many manipulation experiments are arbitrary, and as such, there exists a risk of measuring acute responses such as shock and interpreting these as valid results. Conversely, animals may perform at suboptimal temperatures for a length of time before mortality sets in. If experiments are ended before lethal limits are reached and appropriate measures of health such as growth, oxygen consumption or feeding behaviour have not been measured, the negative effects of climate could be underestimated. Care should be taken to allow appropriate time for acclimation to treatments, and where possible, to measure responses of organisms through time to reduce the risk of over- or underestimating the effects of climate. For our part, measures of oxygen consumption reported in various chapters of this thesis were taken at 6 weeks exposure to experimental conditions, however, measurements had been made every two weeks for the duration of the experiments in order to track any significant changes in magnitude or direction of response. Longer run times for these experiments were not logistically possible, but more long term studies would help us understand if we are at risk of over- or underestimating physiological responses.

Another way climate change studies may be overestimating long term effects is that most are restricted to a single generation. Where intergenerational manipulation experiments have been undertaken, they are usually on rapid developers that can cycle through multiple generations quickly, such as copepods, and often use the results of one or two generations to model outcomes over many more (e.g. Fitzer *et al.* 2012). However, recent work has investigated whether there is the potential for transgenerational acclimation to the effects of climate. Welch *et al.* (2014) found that response to chemical cues in damselfish remained dampened by elevated $p\mathrm{CO_2}$ over two generations, regardless of the level of $p\mathrm{CO_2}$ exposure of parent fish. Adaptations to current environmental conditions may reduce an organism's potential to acclimate to future warming, and inhibit their ability to adapt over generations (Somero 2005; Somero 2010). Once again, individual multigenerational studies may not give us great insight into broad patterns of adaptation to change, as physiological responses within and amongst taxa are so variable. More studies incorporating a wider range of taxonomic groups would be immensely beneficial to our understanding of the potential for adaptation at the rate of environmental change that we are witnessing. Modelling should not be discounted altogether, though, and when given appropriate parameters and robust data as determined by large ecological experiments may be able to address the logistical shortcomings of traditional studies (Queirós *et al.* 2015).

One important area of study that was not covered by this thesis was the effect of climate on early life stages and development of marine consumers. Environmental stressors can have a detrimental impact on hatching time, development and survival of embryos (Przeslawski *et al.* 2005; Deschaseaux *et al.* 2010; Davis *et al.* 2013). Effects of ocean warming and acidification vary throughout life stages, however, if embryos can survive until hatching early larval life stages may be at greatest risk of mortality (Byrne 2011; Ross *et al.* 2011; Pedersen *et al.* 2014). This not only has implications for a species' adaptive abilities, but may also mean that a population's risk of extinction could be underestimated if the effects of climate are only tested on late juvenile and adult life stages. More long term climate studies evaluating the response and survivorship of all life stages, especially in calcifiers, would improve our understanding of a particular consumer's ability to persist under future conditions.

Microcosm studies, whilst allowing tight control over variables and greater ability to identify mechanisms (Drake and Kramer 2012), are often criticised for over simplifying complex systems and lacking realism (Carpenter 1996). Field studies give us “realistic” results, however, the complexity of the natural system can leave limited ability to tease apart mechanisms responsible for observations (Stewart *et al.* 2013). Control of variables in the field can also be difficult through to impossible (Cadotte *et al.* 2005), especially in marine environments. Large manipulative mesocosm studies are not without their faults, but they do offer a way to incorporate more complexity whilst still exerting tight control over conditions (Stewart *et al.* 2013). Benton *et al.* (2007) argue that micro- and mesocosm studies are an integral part of understanding the mechanisms behind ecological processes, yet they should be combined with larger scale studies and ecological theory in order to address what they call the “credibility gap”. In this thesis, responses of producers and consumers observed in small scale laboratory experiments (Chapters 2, 3, 4) were also observed in much larger mesocosms incorporating multiple species and trophic levels (Chapter 5). Previous work on the turf-kelp system testing climate factors on one or two focal species was also reflected in the larger scale experiment undertaken in Chapter 5 (Connell and Russell 2010; Ghedini *et al.* 2015). The compensatory responses investigated in Chapter 5 do however suggest that we may over-estimate ecological change where pairs of species across trophic levels are not combined. Overall these results support the usefulness of smaller scale studies in predicting how broader communities may change over time, and show that continued work on small scale studies help to identify physical drivers of observed change. However, inclusion of multiple species and trophic levels in manipulation experiments where possible will increase our ability to predict the direction and magnitude of future change.

In marine climate change research, volcanic CO_2 vents provide a novel in-field "laboratory" to test a wide array of ecological interactions on acclimatised communities, although they are not without their limitations (Connell *et al.* 2013). They may give us insight into which species and taxonomic groups are at greatest risk of extinction under changing climate, and whether functional groups can be preserved into the future. Relevant to the work in this thesis, calciferous herbivores have still been found at natural CO_2 seeps where the pH reflects predicted end-of-century conditions (Kroeker *et al.* 2011), suggesting that these consumers may indeed be able to acclimate and potentially adapt to ocean acidification conditions. Yet, the mechanisms explaining these acclimations will likely be determined through further laboratory work. Ideally, when making predictions about how organisms and their broader ecosystems will respond to future conditions we should draw on findings collected over a range of scales in order to overcome the limitations of both laboratory and field studies.

6.3 CONCLUSIONS

Grazers are well known for their influence on the competitive abilities or relative dominance of primary producers, with implications for the stability and persistence of the system as a whole (Hughes *et al.* 2007; Ghedini *et al.* 2015). However, ectotherms can be pushed outside thermal optima with moderate environmental warming, causing energetic imbalances and leading to reductions in fitness. Sublethal effects of warming on metabolic processes may be compounded by ocean acidification, leading to reduced growth and shell size (Kroeker *et al.* 2014). This in turn may lead to increased risk of mortality through successful predation events (Menge 1974; Juanes 1992), and consequently, altered foraging behavior to compensate.

At warming above 3 °C from current ambient levels, gastropod herbivory was unable to keep pace with the increasing primary production of turfs. This has implications for management of anthropogenic activity and emissions targets; whilst warming of at least 2 °C is highly likely per current emissions scenarios, increases of 4 °C and above are also probable (IPCC 2013). My findings indicate that the ability for these grazers to regulate future primary productivity may hinge on global policy decisions made over the coming decade.

Imbalances between primary producers caused by an altered abiotic environment may have cascading effects throughout the broader ecosystem, leading to lower resilience and eventual phase shifts in kelp-dominated systems (Connell *et al.* 2013). However, under current business-as-usual scenarios of ocean warming and acidification, trophic compensation may provide a countervailing mechanism to increased turf dominance and expansion on temperate rocky reefs into the near-future (2050 and beyond). Functional redundancy of grazers from different taxonomic groups may mean that the eventual loss of one species (e.g. gastropods) would not alter the magnitude of grazer effects, and the net result would still be stronger consumer control of primary productivity. Thus, resistance of kelp forest systems under future climate may yet be maintained through top-down regulation of kelp competitors.

Throughout this thesis I have demonstrated that variability in physiological response to changing climate between coexisting species may yield unpredicted results in terms of changing interaction strength. Trophic compensation through increased and adjustable consumer control may counteract the positive effects of climate change on primary production, providing increased resistance of communities to environmental disturbance. However, compensatory responses are regulated by underlying consumer physiological demands and thresholds. As such, understanding individual optima and limits is therefore crucial when predicting how broader ecosystems may be affected by altered abiotic environments.

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