Changing Consumer Strength in a Changing Climate

Nicole Lee Mertens

Presented for the degree of Doctor of Philosophy

School of Biological Sciences

The University of Adelaide

October 2015
Cover image: *Turbo undulatus* (common warrener) grazing on turf algae. Photo credit: Nicole Mertens.
THESIS DECLARATION

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

The author acknowledges that copyright of published works contained within this thesis resides with the copyright holder(s) of those works.

I also give permission for the digital version of my thesis to be made available on the web, via the University’s digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Nicole Mertens

October 2015
# TABLE OF CONTENTS

**Thesis declaration** ................................................................. i

**Table of Contents** ........................................................................................ ii

**Abstract** ........................................................................................................ vi

**Acknowledgements** .................................................................................. viii

**Chapter 1** ........................................................................................................... 1

1.1 Physical changes to the world’s oceans ...................................................... 2

1.2 Physiological responses to a changing climate ........................................ 3

1.3 Recent responses to global change and current predictions ................. 6

1.4 The influence of species interactions in ecosystems undergoing environmental change ........................................................................................................ 7

1.4.1 Biotic interactions modify the impact of abiotic factors .................... 7

1.4.2 Compensatory feeding ......................................................................... 8

1.4.3 Idiosyncratic responses of interacting pairs ....................................... 12

1.5 Kelp forests of the future: investigating how changing consumer strength may influence ecosystem structure and function .................................................. 13

1.6 Thesis scope and outline ...................................................................... 15

1.6.1 Thesis intent ......................................................................................... 16

1.7 References ............................................................................................. 19

**Chapter 2** ........................................................................................................... 37

**Statement of Authorship** ........................................................................... 38
Escaping herbivory: ocean warming as a refuge for primary producers where consumer metabolism and consumption cannot pursue........................................................................39

Chapter 3.........................................................................................................................46

Statement of Authorship.................................................................................................47

Increased metabolism, feeding responses and energetic trade-offs for an herbivorous gastropod in a near-future climate........................................................................48

3.1 Abstract ....................................................................................................................48
3.2 Introduction ..............................................................................................................49
3.3 Methods....................................................................................................................51
  3.3.1 Experimental set up and maintenance .................................................................51
  3.3.2 Oxygen consumption and feeding ........................................................................54
  3.3.3 Ingestion efficiency and change in weight............................................................55
  3.3.4 Analyses...............................................................................................................55
3.4 Results.....................................................................................................................56
3.5 Discussion ...............................................................................................................59
3.6 Conclusions ............................................................................................................61
3.7 References .............................................................................................................63

Chapter 4.........................................................................................................................69

Ability of prey to meet future metabolic demands compromised by reduced foraging under predation risk ........................................................................................................69

Statement of Authorship.................................................................................................70
Ability of prey to meet future metabolic demands compromised by reduced foraging under predation risk .................................................. 71

4.1 Abstract ........................................................................... 71

4.2 Introduction ...................................................................... 72

4.3 Methods ........................................................................... 74

4.3.1 Study animals and treatments ........................................ 74

4.3.2 Predator cue only trials ................................................ 77

4.3.3 Predation trials ............................................................. 78

4.3.4 Metabolic rate .............................................................. 78

4.3.5 Analyses ........................................................................ 79

4.4 Results ............................................................................. 79

4.5 Discussion ....................................................................... 84

4.6 References ....................................................................... 87

Chapter 5 ............................................................................. 92

Statement of Authorship .......................................................... 93

Trophic compensation to abiotic change with functional redundancy to species loss jointly stabilize ecosystem processes ........................................... 94

5.1 Abstract ........................................................................... 94

5.2 Introduction ...................................................................... 95

5.3 Methods .......................................................................... 99

5.3.1 Experimental set up and maintenance .......................... 99

5.3.2 Producers and grazers .................................................. 101
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.
ACKNOWLEDGEMENTS

Firstly I want to express my sincere thanks to my supervisors, Sean Connell and Bayden Russell, for their guidance and support throughout this PhD. Sean, I thank you for your enthusiasm, insight and critical opinion; and for first introducing me to temperate marine science. Bayden, I thank you for your advice, encouragement and eye for detail; and for always being approachable (even when we were in different time zones). Both of you have helped shape my early career choices in a positive and pragmatic way.

Thanks to members past and present of the Southern Seas Ecology laboratories for their assistance and camaraderie in the field, lab and office. To everyone involved in the MESO experience, I thank you all for making long days and never ending nights much more bearable and ultimately rewarding. In particular thanks to Kat Anderson, Giulia Ghedini, Jennie Pistevos, Katherine Heldt and Tullio Rossi, who were always creating a cheerful and uplifting work environment. Also to Roger, the lab’s trusty old twin cab ute, without whom numerous, memorable field trips and adventures with the water trailer would not have been had.

A special mention to Chloe McSkimming for being there to lend a hand every step of the way, and providing a refuge when this particular organism found herself under considerable environmental stress. Also to Laura Falkenberg for her sage advice and expertise, and for her understanding. Chloe and Laura, your friendship helped me overcome many frustrations and failures, and for that I give my earnest thanks.

I thank my family for their multifaceted support. To all my friends, thankyou for keeping me in good humour, and for giving me perspective. To Alex and Max, thankyou for housing (and quite often feeding) me. And to Jono, thankyou for everything.
CHAPTER ACKNOWLEDGEMENTS

Chapter 2
We thank Laura Falkenberg for her valuable assistance. We thank Deron Burkepile for sharing his deep insights on this topic and the anonymous reviewers for their valuable comments. This research was partly funded by the Dr Paris Goodsell Marine Ecology Research Grant and an Australian Research Council (ARC) Project to Bayden Russell and Sean Connell and an ARC Future Fellowship to Sean Connell.

Chapter 3
We thank volunteers from the Southern Seas Ecology laboratories, in particular Giulia Ghedini and Chloe McSkimming, for their assistance in collection of organisms from the field and with maintenance of the experimental mesocosms. We thank Sophie Hambour for her assistance in gathering data. This research was partly funded by the Dr Paris Goodsell Marine Ecology Research Grant and an Australian Research Council (ARC) Project to Bayden Russell and Sean Connell and an ARC Future Fellowship to Sean Connell.

Chapter 4
We thank Alyssa Lumsden for her valuable assistance collecting data and maintaining experiments. This research was funded by an Australian Research Council grant to BDR and SDC and a Future Fellowship to SDC.

Chapter 5
We thank the members of Southern Seas Ecology laboratories who assisted in the field and in maintenance of experimental conditions. Katherine Heldt and Kathryn Anderson
assisted in data collection and analysis. Laura Falkenberg assisted with the technical design and maintenance of the mesocosms. Giulia Ghedini provided input into the theoretical development of compensatory dynamics. These experiments were funded by an ARC Future Fellowship to Sean Connell (FT0991953).