

Mass mortality events of echinoderms: Global patterns and local consequences

by

Jessica Anne Schultz

B.Sc., University of British Columbia, 2013

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

© Jessica Anne Schultz 2016
SIMON FRASER UNIVERSITY
Summer 2016

All rights reserved.

However, in accordance with the *Copyright Act of Canada*, this work may be reproduced, without authorization, under the conditions for Fair Dealing. Therefore, limited reproduction of this work for the purposes of private study, research, education, satire, parody, criticism, review and news reporting is likely to be in accordance with the law, particularly if cited appropriately.

Approval

Name: Jessica Anne Schultz
Degree: Master of Science
Title: *Mass mortality events of echinoderms: Global patterns and local consequences*
Examining Committee: Chair: Dr. Margo Moore
Professor

Dr. Isabelle Côté
Senior Supervisor
Professor

Dr. Michael Hart
Supervisor
Professor

Dr. Nicholas Dulvy
Internal Examiner
Professor
Department of Biology
Simon Fraser University

Date Defended/Approved: August 23, 2016

Abstract

Wildlife mass mortality events can have profound ecological consequences and may be becoming more frequent or severe due to climate change, anthropogenic factors or other stressors. Mortality events involving echinoderms are of particular concern because of the important role echinoderms play in structuring marine ecosystems. In this thesis I explore the local consequences of a widespread sea star mortality event, and investigate the global trends in echinoderm mass mortality events. I found that the mass mortality of the sunflower sea star *Pycnopodia helianthoides*, which began in the summer of 2013 as a result of a wasting syndrome, resulted in a trophic cascade involving urchins and kelp at the local scale (i.e., Howe Sound, BC). A global review of reports of echinoderm die-offs revealed that these events have not become more frequent or extensive since 1897. However, disease and climate change may be playing an increasing role. This study provides some of the first evidence of subtidal community shifts following sea star wasting syndrome, and highlights the need for consistent and comprehensive documentation of echinoderm population trends in the literature to increase our understanding of mass mortality events.

Keywords: biological disturbance; community shifts; sea star wasting syndrome; marine diseases; climate change, benthic invertebrate populations.

Dedication

“A hundred times every day I remind myself that my inner and outer life are based on the labors of other men, living and dead, and that I must exert myself in order to give in the same measure as I have received and am still receiving.”

- Albert Einstein, *The World As I See It*

I would like to dedicate this work to my family. Through ways you may not even realize, your labours have allowed me the privilege of following my curiosity and dreams to explore the natural world. Mom, Dad, Leslie, Jason, Oma, Gunter, Grandma, Grandpa, Blaine, and all of my extended family: thank you for your patience and support as I bumble through life's mysteries and choices. You've cultivated my love of nature, inspired me to dream, and challenged me to improve. Wherever I am in the world, your love and encouragement always make me feel at home. I am ever grateful for what I have learned from you. I hope that in some small way this work will allow me to get a little bit closer to giving in the same measure as I have received. Hopefully, in learning more about the natural world, we can become better stewards, citizens and decision makers. With all my heart, thank you.

Acknowledgements

I am truly grateful for all of the support I've received throughout my degree. Without the help of others, this thesis would not have been possible. I would firstly like to thank my Senior Supervisor, Dr. Isabelle Côté. Not only have you been a tremendous source of guidance and support, but for many years, I have also considered you both a role model and a friend. Thank you for being an excellent teacher and for leading by example in academia and beyond. I couldn't have asked for better. I would also like to thank my supervisory committee member, Dr. Michael Hart for your input and advice throughout. Funding for my work primarily came from the Vancouver Aquarium, and the project was also supported by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada.

I am also greatly indebted to Dr. Jeff Marliave, at the Vancouver Aquarium. I cannot thank you enough for giving me the opportunity to learn and grow while being a part of the Howe Sound Research team. Few graduate students are fortunate enough to learn from two exceptional mentors of differing perspectives, and I very much appreciate your knowledge, experience and guidance. Your passion for exploration and natural history is contagious, and I know it will continue be a guiding theme throughout my career.

In addition, I've had the fortune of working with exceptional team members at the Vancouver Aquarium. In particular, I would like to give special thanks to Donna Gibbs and Laura Borden for their support and friendship throughout my thesis. Thank you for your patience, hard work, and sense of humour, and for having my back on the many occasions when I had a few too many balls in the air. I would also like to thank the staff and volunteer divers who assisted me greatly with my fieldwork and other tasks: Boaz Hung, Charlie Gibbs, Roya Esragh, Marielle Gilmour, Brian Caron, Justin Lisaingo, Crystal Kulstar, and Alex Clegg, I couldn't have done it without you.

Similarly, the Côté Lab and Earth 2 Ocean research group were a valued source of encouragement and guidance throughout my degree. Although I didn't spend as much time at SFU as I would have liked, I always looked forward to the opportunity to be around such fun and likeminded people, and I appreciated your advice on everything

from statistical approaches and presentations, to life as a graduate student in general. I would also like to thank Ryan Cloutier for providing the invaluable baseline data for this study. Thanks to everyone who has supported me these past few years, I have grown professionally, intellectually and personally, and I've had a great deal of fun in the process. Thank you!

Table of Contents

Approval.....	ii
Abstract.....	iii
Dedication.....	iv
Acknowledgements.....	v
Table of Contents.....	vii
List of Tables.....	viii
List of Figures.....	viii
List of Acronyms.....	ix
Chapter 1. General introduction	1
Chapter 2. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia	5
2.1. Introduction.....	5
2.2. Materials and Methods	9
2.2.1. Subtidal surveys.....	9
2.2.2. Citizen-contributed (REEF) surveys.....	12
2.2.3. Data analyses.....	12
2.3. Results.....	14
2.3.1. Sea star mortality.....	14
2.3.2. Benthic Community Composition.....	16
2.4. Discussion.....	21
Chapter 3. Long-term patterns in echinoderm mass mortality events.....	25
3.1. Introduction.....	25
3.2. Materials and Methods	27
3.3. Results	29
3.4. Discussion.....	35
Chapter 4. General Discussion	39
References	46

List of Tables

Table 2.1.	Taxa recorded during subtidal surveys in Howe Sound, British Columbia.....	11
Table 2.2.	Differences in pre- and post-mortality benthic assemblages.....	18

List of Figures

Figure 2.1.	Progression of sea star wasting disease.	7
Figure 2.2.	Rocky reef survey sites in Howe Sound, British Columbia.....	10
Figure 2.3.	Mortality of sea stars, and subsequent change in sea urchin abundance and kelp cover after sea star mortality.	15
Figure 2.4.	Sunflower star and green sea urchin abundance trajectories.	16
Figure 2.5.	Rocky reef species assemblages before and after sea star mortality.	19
Figure 2.6.	Relative difference in abundance of sea stars, sea urchins and kelp by site.	20
Figure 3.1.	Temporal pattern of mass mortality events (MMEs) and of published research on echinoderms.....	31
Figure 3.2.	Number of echinoderm mass mortality events (MMEs) from 1897 to 2015.....	32
Figure 3.3.	The number of echinoderm mass mortality events (MMEs) attributed to either cold-related (blue) or heat-related (red) thermal stress from 1897 to 2015.....	33
Figure 3.4.	Relationship between median latitude of echinoderm mass mortality events and year of event (linear model: $F_{1,156} = 0.37$, $R^2 = 0.002$, $p = 0.54$, $n = 175$ events).....	34

List of Acronyms

ANOSIM	Analysis of Similarity
CR	Consistency Ratio
df	Degrees of Freedom
GPS	Global Positioning Satellite
LME	Linear Mixed Effects Model
m	Meter
MDS	Multi-Dimensional Scaling plot
MME	Mass Mortality Event
n	Sample size
p	Significance value
R	Correlation coefficient
REEF	Reef Environmental Education Foundation
SCUBA	Self-Contained Underwater Breathing Apparatus
SD	Standard Deviation
SIMPER	Analysis of Similarity Percentages
SSWS	Sea Star Wasting Syndrome
t	t-statistic for linear mixed effects models
ρ	Rho; Spearman's Rank correlation coefficient

Chapter 1.

General introduction

Mass mortality events are defined as a considerable reduction in the abundance or biomass of a population at all life stages in a relatively short period of time (Fey *et al.*, 2015; Lawrence, 1996). Sudden reductions in the abundance of one or more species can have far-reaching consequences for marine communities. At the population level, mortality can result in a loss of genetic diversity, potential Allee effects and increased extinction risk (Lande, 1993). At a wider scale, reductions in biomass can impact productivity (Tilman, Reich, & Isbell, 2012), ecosystem services (Worm *et al.*, 2006), or have consequences that span multiple trophic levels (Worm & Lenihan, 2013). As management practices struggle to keep pace with changing environmental conditions, there is need for an improved understanding and prediction of ecosystem responses to mass mortality events.

As human populations continue to expand, mounting anthropogenic stressors are likely to increase the prevalence of mass mortality events (De'ath *et al.*, 2012; Seidl *et al.*, 2014). In the marine realm, the greatest threats are posed by exploitation, habitat loss, invasive species, climate change, pollution and disease (Dulvy, Sadovy, & Reynolds, 2003; Halpern *et al.*, 2007; Worm & Lenihan, 2013). Multiple threats often act in concert (Lotze *et al.*, 2006), and can produce synergistic effects (Ramirez-Llodra *et al.*, 2011). For instance, while climate change can cause disturbance directly through increasing storm activity (e.g. Feehan, Scheibling, & Lauzon-Guay, 2012b; Scheibling, Feehan, & Lauzon-Guay, 2013) or thermal stress (e.g. Garrabou *et al.*, 2009; Perez *et al.*, 2000), it can also cause indirect mortality by increasing disease risk (Harvell *et al.*, 2002) or facilitating the spread of invasive species (Harley *et al.*, 2006; Rahel & Olden, 2008). Coastal ecosystems, where human activities frequently overlap with biodiverse habitats, face the greatest risk of biodiversity loss (Gray, 1997).

Mortality events that involve echinoderms are of particular interest because of the important ecological role that echinoderms play in many marine communities. Echinoderms are notorious for exhibiting dramatic population fluctuations, and can be important drivers of biodiversity, population dynamics and ecological shifts (Uthicke, Schaffelke, & Byrne, 2009). For example, outbreaks of the crown-of-thorns star (*Acanthaster planci*) in the tropical Pacific are responsible for widespread coral declines (De'ath *et al.*, 2012; Sano, Shimizu, & Nose, 1984), and a catastrophic mortality of the black sea urchin (*Diadema antillarum*) in the Caribbean in the 1980s caused a long-lasting shift to algae-dominated reefs (Carpenter, 1990). In addition, many sea stars species are important predators (Lambert, 2000), often exerting strong ecological influences in their environment (Duggins, 1981; 1983; Paine, 1966).

Echinoderms are often involved to top-down or bottom-up trophic cascades. In a classic example, historical exploitation of the sea otter (*Enhydra lutris*) caused prey release of herbivorous purple sea urchins (*Strongylocentrotus purpuratus*). Destructive grazing of canopy-forming kelps by the urchins created widespread barrens in many areas (Estes & Duggins, 1995; Estes & Palmisano, 1974). Similarly, disease outbreaks in the green sea urchin (*Strongylocentrotus droebachiensis*) in Nova Scotia drive cyclic transitions between kelp forests and urchin barren states (Feehan & Scheibling, 2014; Scheibling *et al.*, 2013). In cases where habitat-forming species like kelps are impacted, the effects can continue even farther through the trophic web. Sedimentation and increased turf grass growth in California facilitated the sudden dominance of rocky reefs by the sea cucumber *Pachythyone rubra*. Because *P. rubra* filters algal spores from the water column, the outbreak caused a persistent decline in macroalgae (Rassweiler, Schmitt, & Holbrook, 2010). As a result, species like amphipods that rely on kelp also declined, as did reef fish that consume the amphipods as an important food item (Okamoto *et al.*, 2012).

Starting in the spring of 2013, the west coast of North America underwent an unprecedented mass mortality of sea stars. Afflicted sea stars exhibited arm curling, a loss of turgor pressure, body wall lesions, tissue necrosis, and in later stages, arm automatization and death. The sea star wasting syndrome has so far impacted some 20 species of sea stars from Alaska to Mexico, causing rapid population declines at many

locations (Stokstad, 2014). Because of the important predatory role of many sea star species (Lambert, 2000), their rapid declines are likely to have cascading impacts at multiple trophic levels of the communities they inhabit. While there has been recent progress in understanding the 2013 wasting epidemic (Eisenlord *et al.*, 2016; Fuess *et al.*, 2015; Hewson *et al.*, 2014; Menge *et al.*, 2016a), the ecological consequences remain poorly understood.

Although there have been other recorded cases of sea star wasting diseases in the past, the 2013 event was unprecedented in terms of geographic scope and the number of individuals affected (Stokstad, 2014). The earliest report of sea star wasting was from 1972-1974 on the Atlantic coast of North America, where populations of the common sea star, *Asterias vulgaris*, were decimated (Menge, 1979). In recent years, there have also been anecdotal reports of chronic wasting in *Asterias forbesi*, and possibly other species, from Maine to New Jersey (DeSesto, 2015). On the west coast of North America, wasting was first observed in 1978 in *Heliaster kubiniji* in the Gulf of California (Dungan, Miller, & Thomson, 1982), and between 1978 and 1998, wasting has been repeatedly observed in the Channel Islands, CA, where multiple species of asteroids, and often other echinoderm species, were affected (Blanchette *et al.*, 2005; Eckert, Engle, & Kushner, 2000; Engle, Halvorson, & Maender, 1994). Sea star wasting syndrome has also been used to describe a gonad-infecting ciliate protozoan that causes castration and mortality in male sea stars (Bates, Hilton, & Harley, 2009; Leighton *et al.*, 1991; Stickle, Weidner, & Kozloff, 2001). In addition, disease-related sea star mortality has been reported in the south Pacific (Zann, Brodie, & Vuki, 1990) and the Mediterranean (Staehli *et al.*, 2009). Although previous disease outbreaks reached mortality rates exceeding 99% (e.g. Zann *et al.*, 1990), they were comparatively isolated and affected fewer populations than the 2013 outbreak, which has been observed along most of the west coast of North America with mortality rates reaching 100% in some areas (Stokstad, 2014).

Climate has played a key role in many echinoderm disease outbreaks. The 1978 *H. kubiniji* mortality occurred during unusual weather conditions, including warm sea surface temperature, strong winds and heavy rains (Dungan *et al.*, 1982), and the recurring wasting events in the Channel Islands appeared to follow warmer, El Niño

years (Blanchette *et al.*, 2005; Eckert *et al.*, 2000; Engle *et al.*, 1994). Wasting was especially prevalent following strong El Niño years, such as 1982-1983 and 1997-1998 (Blanchette *et al.*, 2005; Eckert, Engle, & Kushner, 2000; Engle, Halvorson, & Maender, 1994). Similarly, the prevalence of castrating parasites in *Pisaster ochraceus* is greater at higher temperatures (Bates, Hilton, & Harley, 2009). The relationship between climate and disease is also evident in echinoids. For instance, bald sea urchin disease is associated with warm sea surface temperature and low wave height in the Mediterranean (Girard *et al.*, 2011), and urchin disease outbreaks in Nova Scotia are associated with storm outbreaks (Feehan, Scheibling, & Lauzon-Guay, 2012b; Scheibling *et al.*, 2013). As the impacts of climate change intensify, there is a need to understand both how echinoderm mortality events impact marine communities, and how the prevalence of such events may be changing over time.

In this thesis, I explore the ecological consequences and global patterns of echinoderm mass mortality events. Chapter 2 evaluates local-scale community shifts following the rapid decline of sea stars in Howe Sound, British Columbia. Using a combination of subtidal transect surveys and citizen science data, I quantify the mortality of the sunflower star, *Pycnopodia helianthoides*. I also evaluate whether concomitant changes in the abundance of invertebrates and algae are consistent with the hypothesis of a trophic cascade. In Chapter 3, I use an extensive literature review to explore whether the frequency or severity of mass mortality events involving echinoderms has changed over time. I distinguish changes in the number of mortality events from changes in reporting effort by comparing the frequency of mortality events reported in the literature with the overall number of echinoderm-related ecology studies. I also examine reports for trends in the cause, affected taxa, and geographic location of die-off events. This thesis provides some of the first evidence of a trophic cascade following the unprecedented mortality of sea stars that began in 2013. In evaluating global trends in echinoderm mortality events, I place the 2013 wasting event in an historical context, and highlight the need for consistent, comprehensive monitoring of echinoderm population dynamics during this period of global change.

Chapter 2.

Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia

2.1. Introduction

Echinoderms can be subject to dramatic population fluctuations (Uthicke *et al.*, 2009). Rapid declines are often driven by disease or extreme climatic events. For example, the spread of mass mortality of the black sea urchin, *Diadema antillarum*, in the 1980s suggests that it was most likely caused by a pathogen (Lessios *et al.*, 1984). The event impacted an estimated 3.5 million km² of the Caribbean region, causing up to 99% urchin mortality at some sites (Lessios, 1988). While the precipitous decline of *Diadema* was a unique occurrence, other echinoderm mass mortality events occur repeatedly. On the Atlantic coast of North America, an amoeboid parasite causes episodic mortality events in green sea urchins, *Strongylocentrotus droebachiensis* (Jones & Scheibling, 1985), which are linked to hurricanes and are predicted to increase in frequency with climate change (Scheibling & Lauzon-Guay, 2010). Similarly, recurring events of wasting disease involving asteroids (sea stars), echinoids (sea urchins) and holothurians (sea cucumbers) in the Channel Islands, California, are associated with climate regime shifts and extreme weather events (Engle, 1994; Eckert *et al.*, 2000).

Because sea stars and sea urchins play key ecological roles in many marine ecosystems, echinoderm population collapses can be important drivers of biodiversity, population dynamics and ecological shifts. In fact, the term 'keystone predator' was originally coined for the purple star, *Pisaster ochraceus*, after experiments showed that its absence led to significant decreases in intertidal biodiversity (Paine, 1966). Many other echinoderm species have since been shown to influence community composition through predation or herbivory. These effects are apparent on coral reefs following

echinoderm population booms (e.g., coral cover declines owing to eruptive crown-of-thorns star, *Acanthaster planci*; Sano *et al.*, 1984), or busts (e.g., the transition from coral- to algae-dominated reefs following the *D. antillarum* mortality event; Carpenter, 1990). On temperate rocky reefs, fluctuations in the abundance of herbivorous urchins can result in major community shifts, from kelp forests to urchin barrens and back again (Estes & Duggins, 1995; Steneck *et al.*, 2003).

The northeast Pacific region has recently experienced a protracted mass mortality of sea stars that might rival the magnitude of the *Diadema* die-off of the 1980s (Johnson, 2016). The event was first noticed on the Olympic coast of Washington in June 2013 (Hewson *et al.*, 2014). In affected sea stars, the signs progress from a loss of turgor pressure, to lesions and ruptures of the body wall and autotomization of arms, and ultimately, disintegration and death (Fig. 2.1). The wasting syndrome has continued through 2014 and 2015, and has so far affected some 20 species from Alaska to Southern California (Stockstad, 2014). A virus may be involved (Hewson *et al.*, 2014), but the precise causes and contributing factors remain poorly understood. Moreover, little is known so far of the extent and ecological consequences of this sea star mortality event at any location.

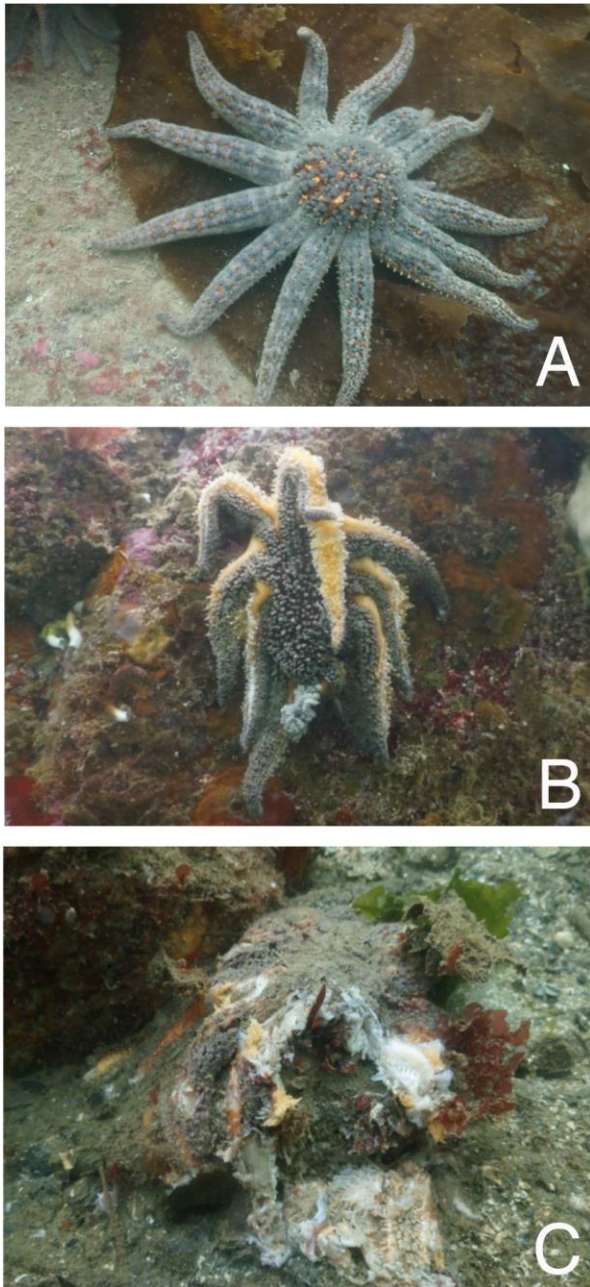


Figure 2.1. Progression of sea star wasting disease. (A) A healthy-looking specimen of *P. helianthoides* moves across the kelp, *Agarum fimbriatum*. (B) Afflicted sea stars exhibit a loss of turgor pressure and body wall ruptures, followed by (C) limb autotomization, disintegration and death. Photos by Donna Gibbs.

Many of the affected sea stars were predatory species, raising the possibility of top-down trophic cascades associated with their disappearance and marked community restructuring. In Howe Sound, southern Strait of Georgia, British Columbia, the sunflower star *Pycnopodia helianthoides* showed signs of advanced wasting in early September 2013. Dense aggregations disappeared from many sites in a matter of weeks (personal observations). This species is one of the world's largest predatory sea stars and it consumes a variety of prey, including echinoderms, gastropods and crustaceans (Herrlinger, 1983; Shivji *et al.*, 1983). In areas that lack other predators such as sea otters *Enhydra lutris*, such as in Howe Sound, sunflower stars can become the dominant predator of urchins (Duggins, 1983). By altering the abundance and/or distribution of sea urchins, which in turn can have a conspicuous impact on the abundance of kelp, sunflower stars can influence the formation and persistence of urchin barrens, i.e. areas devoid of kelp because of the grazing activity of urchins (Duggins, 1981). Indeed, most well-substantiated examples of tri-trophic cascades in rocky subtidal ecosystems involve urchins as prey and major herbivore (Pinnegar *et al.*, 2000). I therefore expected that *Pycnopodia* prey, in particular urchins, would increase in abundance following the disappearance of their major predator, leading to reductions in kelp cover.

Here, I evaluate the extent of mortality of *P. helianthoides* in Howe Sound and test whether changes in the benthic community following the rapid decline of this predatory sea star are consistent with the hypothesis of a top-down trophic cascade. I compare rocky reef community composition before and after the mass mortality using quantitative data derived from subtidal transects and qualitative information gathered by citizen scientists. In doing so, I provide empirical evidence that a trophic cascade quickly followed what might be one of the largest wildlife die-off events ever recorded (Johnson, 2016).

2.2. Materials and Methods

2.2.1. Subtidal surveys

I compared sunflower star abundance and benthic community composition before (2009/2010) and after (2014) the 2013 wasting event using scuba-based surveys of 20 sites in Howe Sound, British Columbia (BC), Canada (Fig. 2.2). Surveys before the wasting event were conducted as part of a study of rockfish (*Sebastes* spp.) habitat (Cloutier, 2011). I repeated these surveys after the wasting event using the same method, at the same GPS locations, depths (within 2 m) and time of year (within 14 days). Ten sites were surveyed in early summer (June – July) and 10 sites in late summer (August – October). In all surveys, I recorded the abundance of 18 taxa (species or species groups) of common benthic fishes and invertebrates (Table 2.1).

At each site I surveyed four transects (25 m long by 4 m wide) at depths between 8 and 15 m (chart datum). I quantified fish and invertebrate abundance by counting all individuals of the target taxa occurring fully or partly within 0.25 m² quadrats placed at 15 random positions along each transect. I also estimated visually the percent cover of kelp (mainly the genera *Agarum*, *Costaria*, *Laminaria* and *Saccharina*) within the same quadrats.

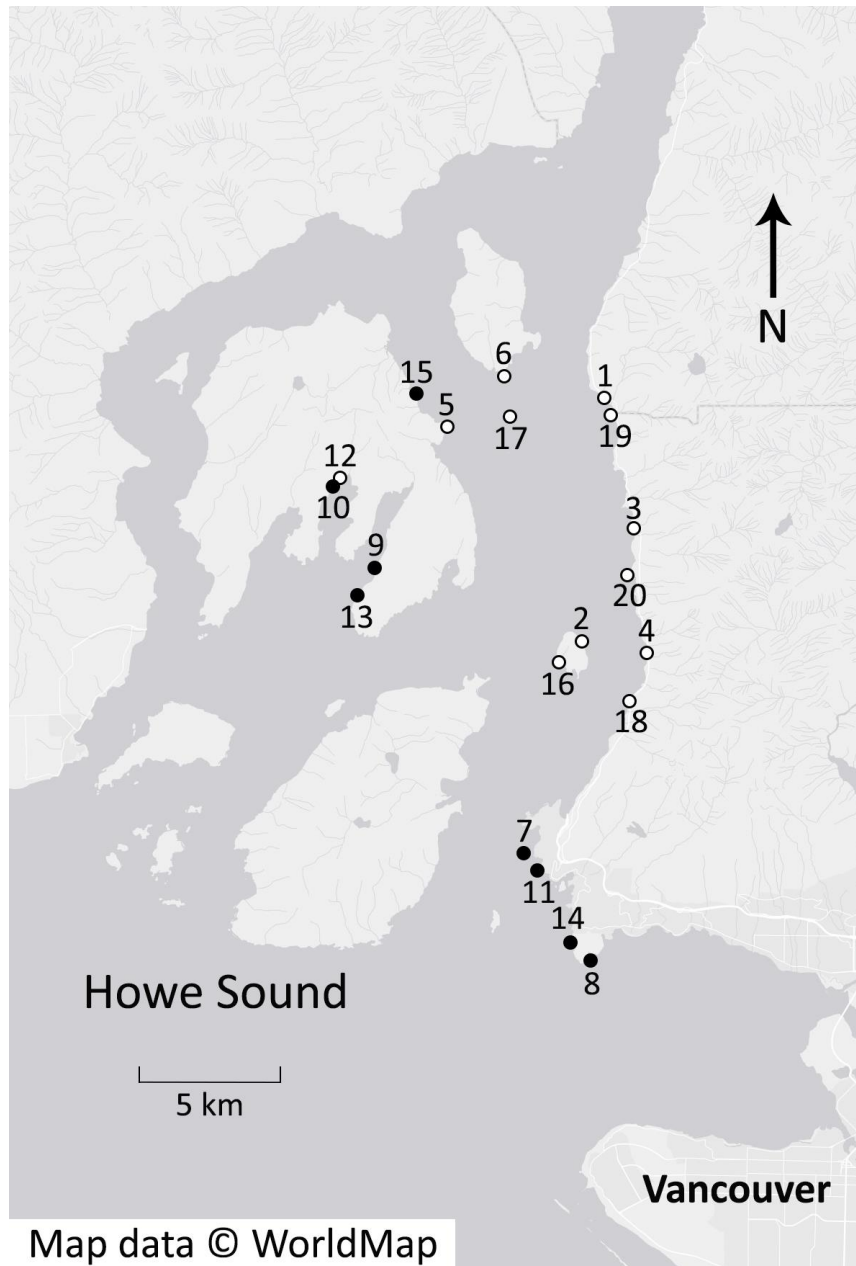


Figure 2.2. Rocky reef survey sites in Howe Sound, British Columbia. Benthic community composition was assessed at each of the 20 sites once in 2009 or 2010 and again in 2014. A mass mortality of sea stars occurred in the summer and fall of 2013 in this area. A site-level trophic cascade following the mortality was detectable at some sites (solid circles) but not others (open circles) (Map data © 2015 WorldMap).

Table 2.1. Taxa recorded during subtidal surveys in Howe Sound, British Columbia.

Mean density and standard deviation per 15 m² are given for each taxa as recorded before and after the sea star mortality event.

Taxon	Species or genera included in taxon	Mean density (SD)	
		Before	After
Invertebrates			
Sunflower star	<i>Pycnopodia helianthoides</i> (Brandt, 1835)	6.4 (11.4)	0.9 (3.3)
Green sea urchin	<i>Strongylocentrotus droebachiensis</i> (Müller, 1776)	18.3 (41.0)	77.2 (157.4)
Red sea urchin	<i>Mesocentrotus franciscanus</i> (Aggasiz, 1863)	0.4 (0.9)	0.3 (0.6)
White sea urchin	<i>Strongylocentrotus pallidus</i> (Sars, 1871)	1.1 (2.0)	0.3 (0.4)
California cucumber	<i>Apostichopus californicus</i> (Stimpson, 1857)	6.1 (9.0)	13.1 (8.9)
Dungeness crab	<i>Metacarcinus magister</i> (Dana, 1852)	0.1 (0.2)	0.0
Red rock crab	<i>Cancer productus</i> Randall, 1840	0.1 (0.3)	0.4 (0.7)
Spot prawn	<i>Pandalus platyceros</i> Brandt, 1851	22.1 (89.1)	0.3 (0.8)
Squat lobster	<i>Munida quadrispina</i> Benedict, 1902	4.0 (9.0)	0.3 (0.6)
Miscellaneous crabs	Primarily anomurans, including lithodid and hermit crabs; several brachyuran genera including <i>Cancer</i> , <i>Pugettia</i> , <i>Scyra</i> , and <i>Oregonia</i>	21.7 (35.0)	16.3 (23.5)
Miscellaneous shrimps	Primarily <i>Pandalus danae</i> Stimpson, 1857, but also other members of the genus <i>Pandalus</i> , as well as the genera <i>Lebbeus</i> , <i>Eualus</i> , <i>Heptocarpus</i> and possibly others	37.0 (38.6)	15.8 (11.2)
Giant Pacific octopus	<i>Enteroctopus dofleini</i> (Wülker, 1910)	0.1 (0.2)	0.0
Cup corals	<i>Balanophyllia elegans</i> Verrill, 1864, <i>Caryophyllia alaskensis</i> Vaughan, 1941	6.7 (15.8)	22.1 (19.0)
Benthic fishes			
Grunt sculpin	<i>Rhamphocottus richardsonii</i> Günther, 1974	0.1 (0.2)	0.1 (0.2)
Longfin sculpin	<i>Jordania zonope</i> Starks, 1895	0.2 (0.4)	2.7 (4.1)
Sailfin sculpin	<i>Nautichthys oculofasciatus</i> (Girard, 1858)	0.1 (0.2)	0.0
Scalyhead sculpin	<i>Artedius harringtoni</i> (Starks, 1896)	0.8 (1.6)	1.8 (2.3)
Miscellaneous sculpins	Cottid genera including <i>Artedius</i> , <i>Oligocottus</i> , <i>Radulinus</i> , <i>Chitonotus</i> and possibly others.	5.5 (4.6)	0.7 (1.2)

2.2.2. Citizen-contributed (REEF) surveys

To verify that the patterns of echinoderm abundance detected at the 20 study sites reflected local trends accurately, I compiled qualitative data on the abundance of sunflower star and green sea urchin in Washington and BC, from the Reef Environmental Education Foundation (REEF) citizen science database. Through REEF, scuba divers are trained in species identification and collect data on the abundance of species sighted during recreational dives. Divers assign an abundance score from 1 – 4 to each species they can positively identify: score 1 = a single individual, 2 = 2-10 individuals, 3 = 11-100 individuals and 4 = > 100 individuals. Species with no abundance score were assumed to be absent, which I deemed to be a fair assumption given that the target taxa were easy to identify.

I extracted the abundance scores of sunflower stars and green sea urchins for all REEF surveys submitted between January 1, 2010 and November 1, 2014 in Washington and BC. To depict trends in abundance over time, I plotted 60-day running averages of the abundance scores for both species. Missing values were filled in using linear interpolation.

2.2.3. Data analyses

I used linear mixed-effects models in the R statistical platform (nlme package; Pinheiro *et al.*, 2015) to compare sunflower star abundance, green sea urchin abundance and kelp cover before and after the sea star mortality. I obtained sunflower and green sea urchin abundance for each transect by summing the number of sunflower stars and, separately, green sea urchins across all quadrats and log-transforming the values prior to analysis. Kelp cover was averaged across all quadrats within each transect. In all cases, I included 'site' as a random effect, and verified the assumptions of normally distributed residuals, homoscedasticity and the absence of leverage by visually examining quantile, residual vs. fitted and Cook's distance diagnostic plots, respectively.

To depict graphically site-level changes in the abundance of sunflower stars, green sea urchins and kelp, I plotted the relative difference in abundance for each group

at each site. Relative abundance was calculated as the abundance after the mortality event minus the abundance prior to it divided by the mean abundance for both time periods. Abundance was calculated as the total count of each species at each site for sunflower stars and green sea urchins, and as the average percent cover at each site for algae.

To compare overall benthic community composition before and after the sea star mortality, I ran a permutation-based, non-parametric analysis of similarity (ANOSIM; Clarke, 1993) using PRIMER (v. 6.1.9; Clarke & Gorley, 2006). Abundance matrices (species by site) were compiled for each period (i.e., pre- and post-mortality), in which abundance was estimated as the total count of each taxon across transects and/or quadrats at each site. The raw data were square-root-transformed to reduce the influence of very abundant or very rare species. Bray-Curtis similarity coefficients were computed between pairs of sites (Clarke & Warwick, 2001). The ANOSIM procedure was carried out on the similarity matrix. ANOSIM generates an R statistic, which varies between 0 (samples are as similar across groups as they are within group) and 1 (all samples within groups are more similar to each other than to any sample across groups) and is tested for difference from zero with a permutation test (in this study, N = 999 permutations). The differences in benthic assemblages were visualized in a non-metric, multidimensional scaling (MDS) plot in which samples that are more similar in community composition appear closer together than more dissimilar samples. Stress values of <0.1 suggest that distances among samples in an MDS plot accurately reflect the extent of community differences (Clarke & Warwick, 2001). Finally, I conducted an analysis of similarity percentages (SIMPER) to identify the main taxa responsible for any differences observed between pre- and post-mortality assemblages. I considered a taxon to be important to community differences if its individual contribution was 11% or more, which is twice the expected value if dissimilarity contributions were evenly distributed among all taxa in the analysis (i.e., 100 percent divided by 18 taxa, multiplied by 2). The SIMPER analysis also includes an indication of evenness, expressed as a consistency ratio (CR). CR is the average dissimilarity contribution of a taxon divided by the standard deviation in dissimilarity values of that taxon, for each time period. CR values greater than one suggest that the taxon contributed to dissimilarity between time periods equally across all sites (Terlizzi *et al.*, 2005).

2.3. Results

2.3.1. Sea star mortality

At the sites I monitored, the abundance of sunflower stars declined by $89\% \pm 29\%$ (mean \pm SD), from an average of $0.42 (\pm 0.76)$ sunflower stars per m^2 before the mortality event to $0.06 (\pm 0.22)$ individuals per m^2 after it (LME: $t = 4.62$, $df = 139$, $p < 0.0001$; Fig. 2.3). Three sites had no sunflower stars in 2009/2010, and were not included in the percent decline calculation. All 17 sites with sunflower stars in 2009/2010 had fewer sunflower stars in 2014.

The REEF data included 1568 surveys carried out at 28 sites broadly distributed across BC and Washington between 2010 and 2014. Although sunflower stars were sighted on 98% of surveys in the years before the mortality event and on 89% of surveys in the years afterward, a marked decline was evident in their abundance score trajectory (Fig. 2.4). At this larger geographic scale, sunflower stars started declining in approximately the third week of September, some 15 weeks after the first report of sea star wasting in the region.

I was unable to detect a geographic pattern in the spread of the sea stars mortality in the study area. Sea star wasting progressed so rapidly that by the time it was first observed in Howe Sound (at Whytecliff Park; $49^{\circ}22'18.4''N$, $123^{\circ}17'33.8''W$) on 2 September, 2013, it was soon present at all sites that were subsequently investigated.

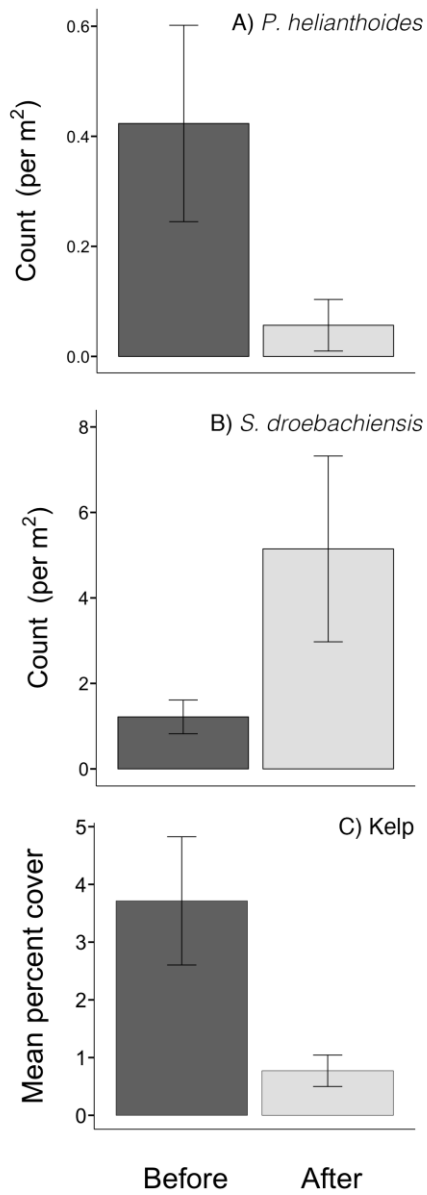


Figure 2.3. Mortality of sea stars, and subsequent change in sea urchin abundance and kelp cover after sea star mortality. Mean abundance (per m²) of (A) sunflower stars and (B) green sea urchins, and (C) percent cover of kelp on rocky reefs in Howe Sound, British Columbia, on 80 transects before and after the mass mortality of sea stars in 2013. Error bars represent standard error. The dominant kelp was the sea colander kelp, *Agarum fimbriatum*.

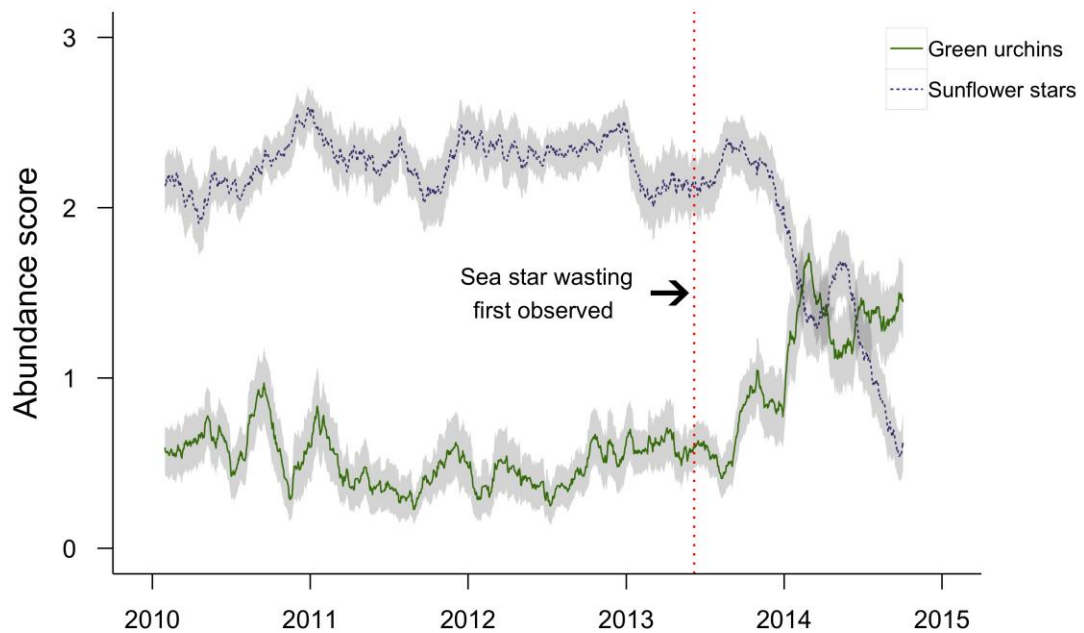


Figure 2.4. Sunflower star and green sea urchin abundance trajectories. Sixty-day running average abundance scores for green sea urchins (*Strongylocentrotus droebachiensis*; green solid line) and sunflower stars (*Pycnopodia helianthoides*; purple dashed line) recorded in REEF surveys from January 2010 to November 2014 in Washington and British Columbia (n = 1568 surveys). Grey bands indicate 95% confidence intervals of the running average. The vertical red dotted line indicates the date of the first recorded observation of sea star wasting syndrome (7 June 2013), which was on the Olympic coast of WA.

2.3.2. Benthic Community Composition

There was a significant shift in overall community composition following sea star mortality in Howe Sound (ANOSIM: $R = 0.326$, $p = 0.001$; Fig. 2.5), and many species changed in abundance from one period to the next (Table 1). The community shift was largely driven by an increase in abundance of green sea urchins (Table 2.2). Green sea urchin abundance quadrupled after the near-disappearance of sunflower stars (LME: $t = -3.10$, $df = 139$, $p = 0.0023$; Fig. 2.3). This trend is supported by the REEF surveys, although these qualitative data suggest that green sea urchin numbers began increasing in the first week of September, two to three weeks before the detectable onset of sea

star decline (Fig. 2.4). There was also an increase in the abundance of cup corals, while the numbers of small shrimps and crabs decreased (Table 2.2). Cumulatively, these four taxa accounted for nearly two-thirds (62%) of the dissimilarity in benthic community composition before and after the sea star mortality, and their contributions were consistent across sites (CRs > 1; Table 2.2). Despite their marked decline, sunflower stars did not contribute disproportionately to the dissimilarity between time periods (SIMPER; individual contribution to dissimilarity = 7.15%). Overall, within-year similarity was higher after than before sea stars died (SIMPER; average inter-site similarity before = 46.28%, after = 58.11%; Fig. 2.5), suggesting that communities became more homogeneous following the sea star mortality.

In addition to shifts in benthic animal community composition, there was also a change in the abundance of kelp. Kelp cover decreased from 4% (\pm 10%) in 2009/2010 to <1% (\pm 2%) in 2014 (LME: $t = 2.669$, $df = 139$, $p = 0.0085$; Fig. 2.3). In all years, the kelp species at the study sites was almost exclusively the sea colander kelp, *Agarum fimbriatum*, but also included *Saccharina latissima*.

At the regional scale, the changes in abundance of sunflower stars (decline), green sea urchins (increase) and kelp (decline) were consistent with a top-down trophic cascade (Fig. 2.3). At the site level, the patterns were more variable (Fig. 2.6). Eleven of the 17 sites that had some *P. helianthoides* before the sea star mortality showed increases in green sea urchin abundance concomitant with declines in sea star abundance (Fig. 2.6). Eight of these 17 sites showed declines in kelp cover concomitant with increases in green sea urchin abundance (Fig. 2.6). A clear alternation of population trajectories from predators to herbivores to kelp was clear at eight of the 17 sites (Fig 2.6).

Table 2.2. Differences in pre- and post-mortality benthic assemblages.

The four taxa that contributed disproportionately to dissimilarity in benthic community composition on rocky reefs before and after the 2013 sea star mass mortality. Mean densities (# per 30 m² ± 1 SD), consistency ratios, and individual and cumulative contributions (in %) to differences between years are shown. The consistency ratio is calculated as a species' average dissimilarity contribution divided by the standard deviation of dissimilarity values. A consistency ratio > 1 indicates an even contribution to community dissimilarity across sites. The analysis was conducted on square-root-transformed data (see Methods) but untransformed densities are presented here. Differences in pre- and post-mortality benthic assemblages. The four taxa that contributed disproportionately to dissimilarity in benthic community composition on rocky reefs before and after the 2013 sea star mass mortality. Mean densities (# per 30 m² ± 1 SD), consistency ratios, and individual and cumulative contributions (in %) to differences between years are shown. The consistency ratio is calculated as a species' average dissimilarity contribution divided by the standard deviation of dissimilarity values. A consistency ratio > 1 indicates an even contribution to community dissimilarity across sites. The analysis was conducted on square-root-transformed data (see Methods) but untransformed densities are presented here.

Taxon	Mean density (SD)		Consistency ratio	Individual contribution (%)	Cumulative contribution (%)
	Before	After			
<i>Strongylocentrotus droebachiensis</i>	18.3 (41.0)	77.2 (157.5)	1.09	18.91	18.91
Cup corals	6.7 (15.8)	22.2 (19.1)	1.41	13.04	31.95
Misc. shrimps	37.0 (38.7)	15.9 (11.2)	1.3	11.29	43.23
Misc. crabs	21.7 (35.0)	16.3 (23.5)	1.05	11.15	54.38
<i>Pycnopodia helianthoides</i>	6.4 (11.4)	0.9 (3.3)	1.18	7.15	69.05

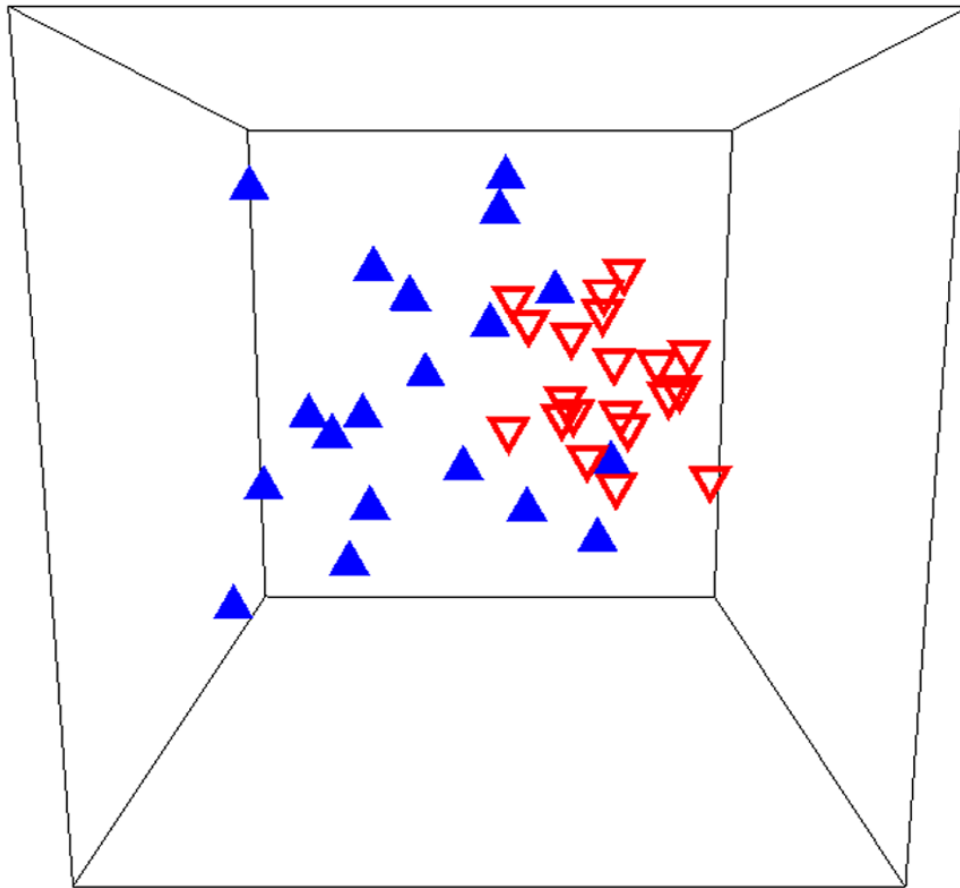


Figure 2.5. Rocky reef species assemblages before and after sea star mortality. Multidimensional scaling plot of benthic community composition on rocky reefs before (blue triangles) and after (inverted red triangles) the 2013 sea star mass mortality event in Howe Sound, British Columbia. The analysis included 18 fish and invertebrate taxa at 20 sites, surveyed both in 2009/2010 and 2014. The associated stress value (0.13) suggests some distortion in the multivariate representation of the data.

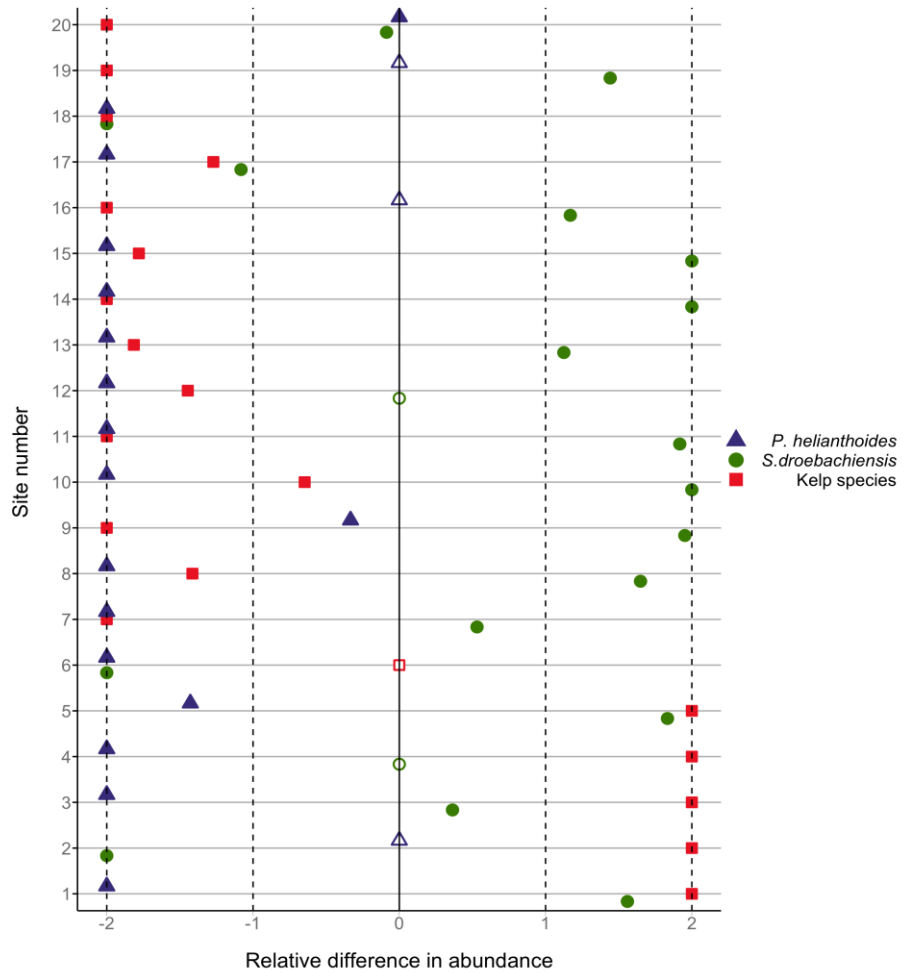


Figure 2.6. Relative difference in abundance of sea stars, sea urchins and kelp by site. The relative difference in total count of sunflower stars (blue triangles) and green sea urchins (red circles), and the relative difference in the mean percent cover of algae (green squares) before and after the sea star mass mortality. Open symbols show sites where density of a taxon was zero before and after the mass mortality. Relative difference was calculated as the change in abundance divided by the mean abundance of both time periods. Sites are numbered chronologically according to the order in which they were surveyed, from June to August, 2014.

2.4. Discussion

The wasting disease that affected echinoderms in the northeast Pacific in 2013/2014 heavily impacted populations of sunflower stars, the sea stars that formerly dominated subtidal communities. I found a noticeable shift in benthic community structure following the sea star decline. Community changes were largely driven by changes in the abundance of green sea urchins, cup corals, shrimps and crabs. The temporal coincidence of the alternating trajectories of abundance of sea stars, sea urchins and kelp, as well as the overlapping distributions and documented trophic linkages among these three taxa, meet the diagnostic criteria of a tri-trophic cascade (Grubbs *et al.* 2016), triggered by the mass mortality of predatory sunflower stars.

Sunflower star densities declined by almost 90%, on average, at the sites I surveyed in Howe Sound, BC. Such a decline in sea stars rivals the largest magnitudes reported for disease-induced echinoderm mass mortalities (e.g., 70% of *Strongylocentrotus droebachiensis* in Nova Scotia, Scheibling & Stephenson, 1984; 95% of *Mesocentrotus franciscanus* in California, Pearse *et al.*, 1977; 97% of *Diadema antillarum* across the Caribbean, Lessios, 1988). The percent change in biomass of *P. helianthoides* must be even greater than the change in relative abundance because the sea stars we observed following the mortality event were almost exclusively juveniles (< 6 cm diameter). The very large individuals (>50 cm diameter) present before the mortality event likely played a larger role in structuring benthic communities than the juveniles present after the event. The steep decline in sunflower star numbers, occurring some 15 weeks after the first official sighting of sea star wasting, was clearly evident in the qualitative density scores generated by citizen science (REEF) surveys, which covered a broader geographic area. The time-series of REEF data suggests that sunflower star population levels were somewhat variable, perhaps reflecting variation in the sites surveyed by divers, but largely stable between the first snapshot in 2009/2010 and the onset of the wasting event in 2013. More generally, the benthic species composition of the Strait of Georgia region has remained remarkably stable in recent decades, even in the face of climate regime shifts (Marliave *et al.* 2011). It therefore seems unlikely that the sea star population declines, and concomitant changes in

benthic community composition, could be ascribed to a different, unreported disturbance occurring prior to 2013.

The most striking change I observed in community composition was a marked increase in the abundance of green sea urchins. Overall, green sea urchins were nearly four times more numerous following the sea star mortality event than before. However, the mechanism of this population increase remains unclear. One possibility is that a recruitment pulse of green sea urchins coincided with sea star wasting disease, which would have generated a large sea urchin cohort even in the presence of sunflower stars. Another possibility is that sea urchin recruits – whether part of a normal or a large cohort – were able to survive better in the absence of abundant sea star predators (Duggins, 1981). However, the majority of sea urchins present a year following the sea star mortality were approximately 3 - 5 cm in diameter. Green sea urchins of this size on the east coast of North America are at least three years of age, and possibly more than a decade old (Russel, Ebert & Petraitis, 1998; Vadas *et al.*, 2000). If these growth rates are similar on the Pacific coast, then most of the sea urchins we saw could have settled several years before the sea star mortality event. However, sea urchin growth rates can be highly variable (Vadas *et al.*, 2000), depending on food supply and temperature (Thompson, 1983; Meidel & Scheibling, 1999; Pearce *et al.*, 2005), and sea urchin growth rates have not yet been estimated in BC. A third possible explanation is that the observed increase in sea urchin abundance resulted from a shift in sea urchin behaviour following the sea star mortality event. The impact of ‘intimidation’ on predator–prey interactions can be as important as direct consumption (Lima & Dill, 1990; Preisser, Bolnick & Benard, 2005). Under risk of predation, prey individuals alter a suite of behaviours, including habitat choice, foraging range, and time under cover. (Werner *et al.*, 1983; Peacor & Werner, 2001; Trussell, Ewanchuk & Bertness, 2003; Schmitz, Krivan & Ovadia, 2004). The effect of sunflower star on sea urchin behaviour is well documented. In field experiments in Alaska, both green and purple (*S. purpuratus*) sea urchins moved away after *P. helianthoides* arms were placed in the centre of urchin aggregations (Duggins, 1981), and sea urchin distribution shifted rapidly when sea star abundance was experimentally increased (Duggins, 1983). Fear-released sea urchins could therefore respond by moving from refuges, perhaps in very shallow or deep

habitats or in sheltered crevices inaccessible to sea stars (and divers), to more open substrates, making them easier to see and count.

The data from REEF surveys support a behavioural rather than a consumptive mechanism for the increase in sea urchin numbers. Whereas one would expect a delayed increase in sea urchin numbers following a release from predation (Wangersky & Cunningham, 1957), green sea urchin numbers began to increase at approximately the same time as the decline in sunflower stars was evident (Fig. 2.4). The observed change in green sea urchin abundance may therefore be due, at least in part, to green sea urchins modifying their distribution in response to the decline of sunflower stars.

Another conspicuous change I observed was a ~80% reduction in kelp cover (Fig. 2.3), pointing to a potential trophic cascade triggered by the sea star mortality event. There are many documented examples of sea urchin abundance directly influencing the abundance of algae (e.g., Fletcher 1987; Carpenter, 1990; Estes & Duggins, 1995; McClanahan *et al.* 1996; Scheibling, Hennigar & Balch, 1999; Villouta *et al.* 2001). As sea urchin numbers rise, either due to a large recruitment event (Hart & Scheibling, 1988) or the absence of a predator (Watson & Estes, 2011), kelp is rapidly depleted. The alternating directions of population trends of sea stars, sea urchins and kelp observed here are consistent with the hypothesis of a top-down trophic cascade triggered by the sea star disease. The tri-trophic cascade was clearly evident at the larger scale of Howe Sound (Fig. 2.3), but detectable at only half of the sites, with a few additional sites showing only part of the cascade (Fig. 2.6). It is notable that the sites surveyed earliest (i.e., sites 1-5 on Figs 2.2 and 2.6) showed an increase in kelp cover, perhaps because not enough time had passed for changes to take place. At other sites where the trophic cascade was not detectable, it is possible that sea urchins moved elsewhere in search of better food sources (e.g., at sites 17 and 18 on Fig. 2.6), or that the presence of juvenile sea stars (i.e., site 20 on Fig. 2.6) resulted in different trophic interactions.

In contrast to green sea urchins, the abundance of many prey species did not increase in the near-absence of sunflower star predators. For example, there was no change in abundance of red sea urchins (*M. franciscanus*) and white sea urchins (*S.*

pallidus). Neither species is common in Howe Sound, and little is known about the ecology of *S. pallidus*. However, *M. franciscanus* may generally be less susceptible to sea star predation than other sea urchin species because they grow too large to be consumed (Duggins, 1981). Moreover, although crustaceans constitute a significant portion of the diet of sunflower stars (Shivji *et al.*, 1983; Estes & Duggins, 1995; Lambert, 2000), shrimps and crabs declined following the sea star mortality. Several of the crustaceans I monitored use kelp for both food and habitat. The spot prawn, *Pandalus platyceros*, for instance, specifically uses the sea colander kelp as nursery habitat (Marliave & Roth, 1995). The decline of some crustacean taxa could result from the reduced kelp cover and therefore be a fourth step in the cascade documented here.

Another fourth link in the ecological cascade triggered by sea star mortality might involve cup corals. Their increase in abundance was surprising as cnidarians are not normally consumed by *P. helianthoides* (Shivji *et al.*, 1983; Herrlinger, 1983). However, cup corals are known to fare poorly in areas dominated by macroalgae (Fadlallah, 1983). Contact with algae causes coral polyp retraction, which in turn allows overgrowth by filamentous and coralline algae (Coyer *et al.*, 1993). Increases in density of cup corals can be swift (< 1 year), and of the magnitude observed here (3-4 times), after algae disappear (Coyer *et al.*, 1993). Of course, the reduced abundance of kelp and of sea stars may also have allowed for less obstructed view of the substrate by the observers. As a number of taxa were not monitored in this study, there were likely other changes following the sea star mortality event that we did not detect.

In conclusion, this study contributes to understanding the ecological consequences of the northeast Pacific sea star mass mortality. The most notable change was a marked increase in the number of green sea urchins, which might have already had trickle-down effects on other levels of the ecosystem by the time I detected it. It is unclear whether the changes observed will persist as long-term consequences of the near-disappearance of sea stars. Nonetheless, further monitoring will help elucidate the resilience of this ecosystem in the face of acute biological disturbances. Although such a sudden and drastic decline in sea star populations is alarming, it provides a large-scale natural experiment that may advance our understanding of subtidal trophic cascades and invertebrate population dynamics.

Chapter 3.

Long-term patterns in echinoderm mass mortality events

3.1. Introduction

Large-scale mortality events can have significant consequences on marine ecosystems. Depressed populations can be slow to recover and are subject to a loss of genetic diversity, potential Allee effects and increased extinction risk (Lande, 1993). Where affected species are of commercial interest, there can also be important economic costs. Mortality events involving harvested species such as lobster (Pearce & Balcom, 2005) or abalone (Raimondi *et al.*, 2002) have direct economic implications, while widespread coral or seagrass die-offs can have indirect consequences through their effects on fisheries, tourism and ecosystem services (Grandcourt & Cesar, 2003; McArthur & Boland, 2006).

Marine ecosystems are facing growing strain from climate change and other anthropogenic factors (Harley *et al.*, 2006). As a result, the prevalence of mass mortality events, especially those caused by diseases, is increasing for many taxa (Ward & Lafferty, 2004; Harvell *et al.*, 2004; Fey *et al.*, 2015). Climate change increases the risk of disease by compromising host immunity and by shifting pathogen or host home ranges (Harvell *et al.*, 1999; Mydlarz, Jones & Harvell, 2006). Such an increase in risk is visible, for example, in Nova Scotia, Canada, where the probability of disease in sea urchins increases with storm activity (Feehan, Scheibling & Lauzon-Guay, 2012b; Scheibling, Feehan & Lauzon-Guay, 2013). Warming can also lead to mortality more directly. For example, record heat waves in both 1999 and 2003 caused large scale die-offs in the Mediterranean in corals, sponges and other invertebrates (Perez *et al.*, 2000). In 2003, mortality rates reached up to 80% and affected thousands of kilometers of

coastline (Garrabou *et al.*, 2009). The impacts of climate on marine mortality are exacerbated by human activities such as habitat fragmentation, aquaculture, the transport of invasive species or parasites, overfishing and pollution (Altizer, Harvell & Friedle, 2003; Lafferty, Porter & Ford, 2004; Feehan & Scheibling, 2014a). As climate change intensifies and the human population expands, there is the potential for widespread die-offs to become more frequent and severe.

Mass mortality events involving echinoderms are of particular concern because of the large impacts that echinoderms can have on marine communities. Sea urchins are notorious for driving phase shifts between urchin barrens and kelp communities in the northeast Pacific (Dayton *et al.*, 1992; Steneck *et al.*, 2013) and on both sides of the Atlantic (Norway: Hagen, 1983; 1997; Nova Scotia: Scheibling, Feehan & Lauzon-Guay, 2013). Sea urchins are also important herbivores in tropical regions. For example, following the catastrophic mortality of *Diadema antillarum* in 1983, many coral reefs became overgrown with algae (Hughes, 1994; Lessios, 2004). In addition, sea stars function as keystone predators in many marine communities and mass mortalities involving sea stars are likely to have large-scale ecological consequences. For instance, an unprecedented sea star wasting event recently occurred on the west coast of North America (Hewson, Button & Gudenkauf, 2014; Stokstad, 2014), and marked benthic community shifts were observed in some areas following the sea star decline (Schultz, Cloutier & Côté, 2016). Not all of the factors contributing to this sea star wasting event are fully understood; the disease appeared to become more severe with warming water in some areas (Eisenlord *et al.*, 2016), but not others (Menge *et al.*, 2016). However, most previous cases of sea star wasting have been associated with climate regime shifts and weather events (Dungan, Miller & Thomson, 1982; Bates, Hilton & Harley, 2009; Eckert, Engle & Kushner, 2000; Blanchette *et al.*, 2005).

Given increasing pressures from climate change and other stressors associated with human populations, I predicted that the frequency and severity of mass mortality events involving echinoderms have increased over time. To test this hypothesis, I collated reports of mass mortality events involving echinoderms to construct a temporal trend. To try to distinguish between true patterns of mass mortality events and simple changes in reporting frequency, I established a null expectation in the form of a temporal

trend in annual number of publications on echinoderm ecology. I assumed a priori that if the two trends mirror one another, changes in frequency of echinoderm mortality events over time might be in part due to better reporting (e.g., Ward and Lafferty, 2004; Hassall *et al.*, 2007; Jones *et al.*, 2008; Oliver *et al.*, 2008; Feehan and Scheibling, 2014). Because the impacts of climate change may be greatest at higher latitudes (Solomon, 2007), I also evaluated whether there was a change in the median latitude of echinoderm mass mortality events over time.

3.2. Materials and Methods

To compile a list of unique mass mortality events (MMEs) involving echinoderms, I conducted an extensive search of literature published up to the end of 2015 using three scientific abstract indexing services: Web of Knowledge, Aquatic Science and Fisheries Abstracts (ASFA), and Google Scholar. I used a Boolean keyword search string that included terms related to echinoderms (echinoderm* OR seastar* OR "sea star*" OR starfish* OR asteroid* OR urchin* OR "sand dollar*" OR echinoid* OR "brittle star*" OR ophiuroid* OR "sea cucumber*" OR holothuroid* OR "feather star" OR crinoid*) and terms related to MMEs ("mass mortalit*" OR "die-off*" OR "mass death*" OR "mass kill*" OR "unusual mortality event"). I read the title and abstract of each paper returned to assess its relevance, and recorded all spatially and temporally distinct events described in each, since some papers contained descriptions of more than one MME. Accounts of MMEs were rejected if (1) the year of the event was not documented, (2) the account was from the fossil record, (3) the die-off occurred as a result of harvest or experimentation, or (4) the event occurred in a laboratory, aquarium or aquaculture setting. I considered a mortality event a MME if it was identified as such by authors or review papers. Generally, MMEs were defined by reductions in biomass affecting a considerable portion of a population at all life stages in a relatively short period of time (Lawrence, 1996; Fey *et al.*, 2015).

To broaden the search further, I also examined the bibliography of each relevant study to identify additional references describing mass mortality events. News articles and other non-peer reviewed accounts were included when they were mentioned in the scientific literature. In addition, I contacted experts in the field, posted on scientific

forums and social media (Twitter), and made appeals at scientific meetings for knowledge of echinoderm mortality events.

From each qualifying description (i.e., published paper, news item, personal account), I recorded the year of the event, the proposed primary cause, the duration, the echinoderms and other taxa involved, the location and continent, and the median latitude of the die-off. I classified the primary proposed cause into one of six categories: disease, physical stress (e.g., thermal stress, hypoxia, volcanic activity), weather (e.g., storms, wave action, extreme rainfall), human perturbation (e.g., oils spills, pollutants), biotoxicity or unknown. I also scored the taxonomic extent (species = 1, class = 2, phylum = 3, invertebrates = 4, kingdom = 5, or kingdom+ = 6), defined as the lowest-level taxonomic grouping encompassing all organisms affected by the mass die-off. The 'invertebrates' category included cases involving multiple invertebrate phyla but no fish or other vertebrates. 'Kingdom+' indicated events involving one or more animal taxa and algae.

To construct a temporal trend in MMEs, I counted the number of events documented each year from 1897 (the first MME record found) to 2015. For events lasting longer than one year, I included one data point for each year of the event; including only one data point for multi-year events produced a similar pattern. In cases where more than one study reported the same event occurring in the same year, I included only one account of this event for that year. I examined graphically how the frequency of reported MMEs varied over time in relation to primary cause, taxon affected, geographic distribution, duration of event and taxonomic extent. I examined selected patterns in more detail: changes over time in the proportion of events caused by disease, weather or physical stress, the proportion of events involving echinoids, the duration of MMEs and the taxonomic extent of MMEs were analyzed using Spearman's rank correlations. To tease apart potential relationships with climate change, I also looked specifically at events caused by physical stress, and categorized events attributed to thermal stress as either 'cold' stress or 'heat' stress events. I then used Spearman's Rank correlations to determine whether the proportion of thermal stress-related mortality events caused by heat vs. cold stress changed over time. For all correlations, MMEs were grouped into five-year intervals, and proportions were

calculated for each interval. Because a large proportion (49 %) of records were obtained from a previous review (Lawrence 1996), I also considered the temporal distribution of reports added to this seminal paper. To determine whether there was a change in median latitude or median absolute latitude of MMEs over time, I used Spearman's rank correlations.

Finally, I sought to identify any effect of better reporting by providing a general background of publication activity on echinoderm ecology against which the pattern of echinoderm MMEs could be compared. To do so, I performed an additional search on ASFA. I used the same keyword search for echinoderm terms as described above, with the addition of the word ecology (AND ecolog*), and noted the total number of publications for each year from 1897 to 2015.

3.3. Results

I found accounts of 175 echinoderm MMEs occurring between 1897 and 2015, which were described in 193 publications (Fig. 3.1). Nearly half (49%, $n = 77$; Fig. 3.2A) of these events were reported in Lawrence (1996). My searches added many new records of MMEs occurring during the period covered by the previous review (Fig. 2A). Over the 119-year span of the study, 4212 papers were published on echinoderm ecology. The annual number of echinoderm ecology publications increased nearly exponentially between 1897 and 2014; however, there was a marked drop in publications in 2015 (Fig. 3.1), which probably reflects a delay in indexing of published works.

The highest number of mortality events occurred between 1980 and 1989 ($n = 45$; Figs 3.1 & 3.2). The three most commonly proposed causes of mortality were disease ($n = 65$), physical stress ($n = 43$), and weather ($n = 38$; Fig. 3.2B). Human perturbation and biotoxicity were the suggested cause in 12 and 7 cases, respectively, with the remainder ($n = 10$ cases) having unknown causes (Fig. 2B). Of MMEs with known causes ($n = 165$), the proportion attributed to disease increased over time (Spearman's rank correlation, $\rho = 0.64$, $n = 25$, $p < 0.001$; Fig. 3.2B), while the proportion attributed to physical stress or to weather did not vary significantly (physical

stress: Spearman's rank correlation, $\rho = -0.35$, $n = 25$, $p = 0.13$; weather: Spearman's rank correlation, $\rho = -0.18$, $n = 25$, $p = 0.44$; Fig. 3.2B). The majority of MMEs caused by physical stress were attributed to thermal stress (79%), and within the thermal stress subcategory, the proportion of events associated with heat stress rather than cold stress increased over time (Spearman's rank correlation, $\rho = 0.84$, $n = 12$, $p < 0.001$; Fig. 3.3).

Echinoids were involved in more mortality events than all other echinoderm classes combined ($n = 99$; Fig. 3.2C). The proportion of echinoid-specific mass mortality events did not change over time (Spearman's rank correlation, $\rho = 0.15$, $n = 25$, $p = 0.53$; Fig. 3.2C). More events were reported from North America than from all other regions combined ($n = 109$; Fig. 3.2D). There was a non-significant tendency for die-off events reported more recently to be shorter than earlier MMEs (Spearman's rank correlation, $\rho = -0.14$, $n = 175$, $p = 0.07$; Fig. 3.2E). Taxonomic extent also declined over time (Spearman's rank correlation, $\rho = -0.46$, $n = 175$, $p < 0.0001$; Fig. 3.2F). There was no change in either median latitude (Spearman's rank correlation, $\rho = -0.002$, $n = 175$, $p = 0.97$; Fig. 3.4) or median absolute latitude (Spearman's rank correlation, $\rho = -0.004$, $n = 175$, $p = 0.95$) over time.

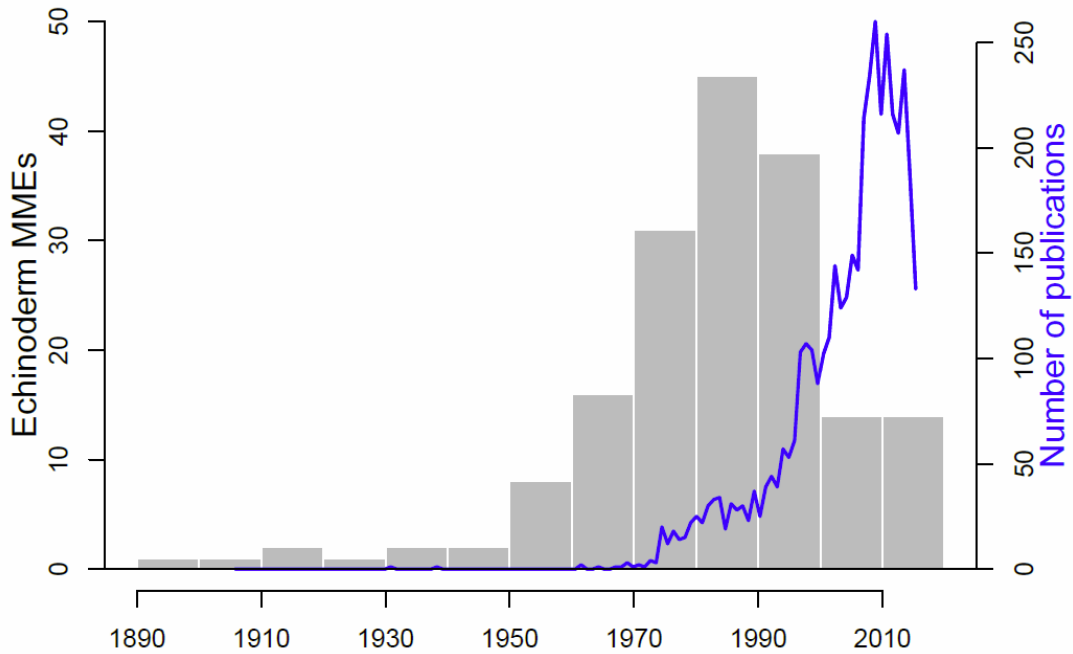


Figure 3.1. Temporal pattern of mass mortality events (MMEs) and of published research on echinoderms.
 The number of echinoderm mass mortality events ($n = 175$; grey bars) is shown by decade. The decadal intervals are left-closed such that the year labels indicate the start of an interval. The number of publications on echinoderm ecology ($n = 4212$; blue solid line) are shown for each year between 1897 and 2015.

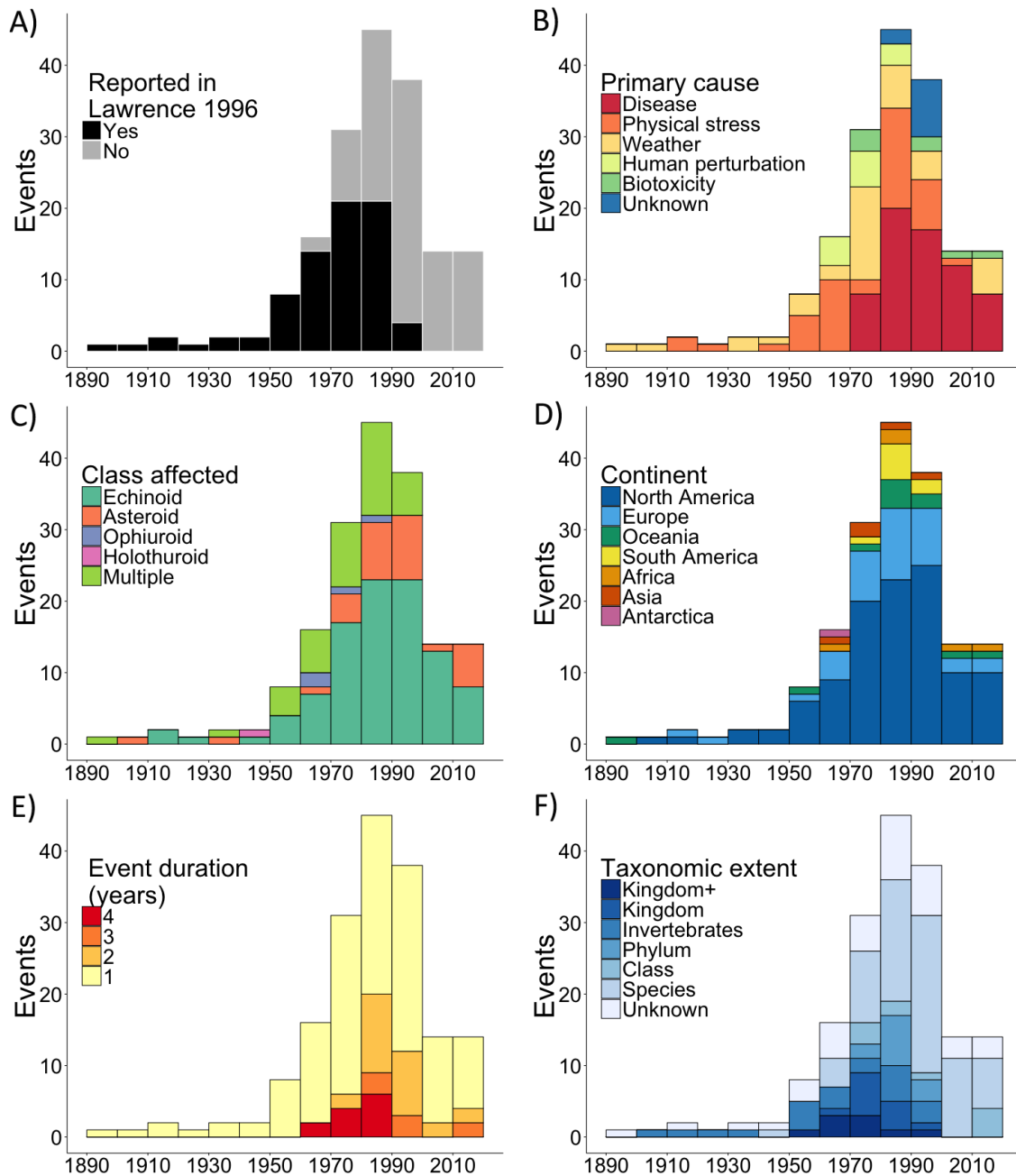


Figure 3.2. Number of echinoderm mass mortality events (MMEs) from 1897 to 2015. Bars are coloured according to (A) whether the event was reported in Lawrence (1996), (B) proposed primary cause, (C) echinoderm class affected, (D) continent, (E) event duration, and (F) taxonomic extent. MMEs are shown by decade. The decadal intervals are left-closed such that the year labels indicate the start of an interval.

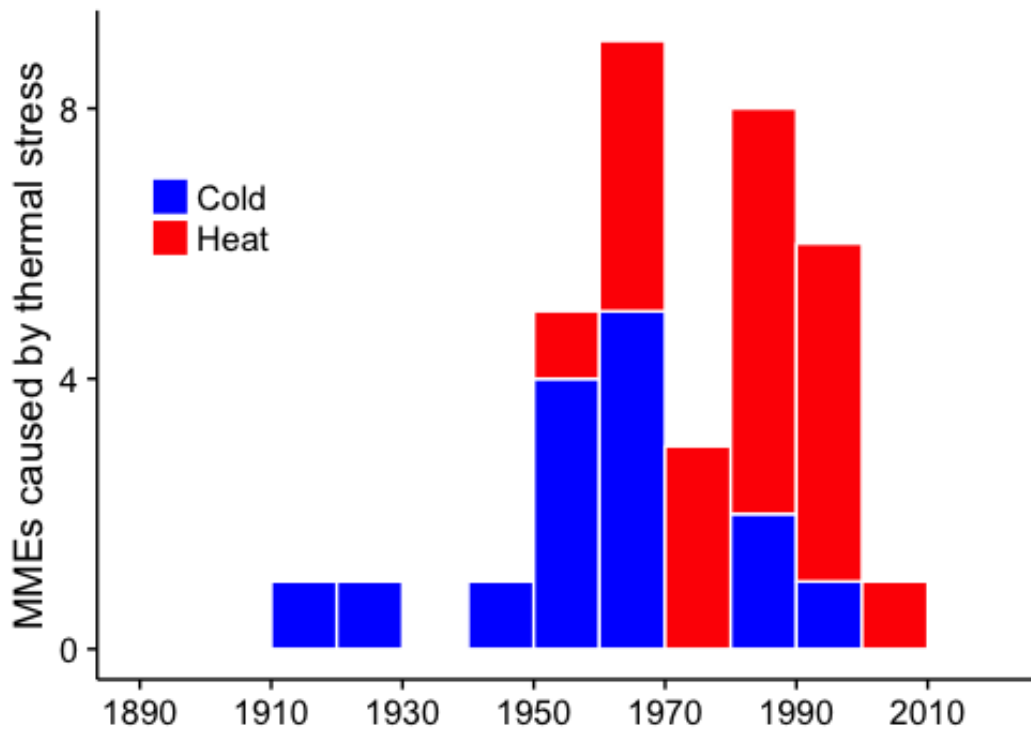


Figure 3.3. The number of echinoderm mass mortality events (MMEs) attributed to either cold-related (blue) or heat-related (red) thermal stress from 1897 to 2015. MMEs are shown by decade. The decadal intervals are left-closed such that the year labels indicate the start of an interval.

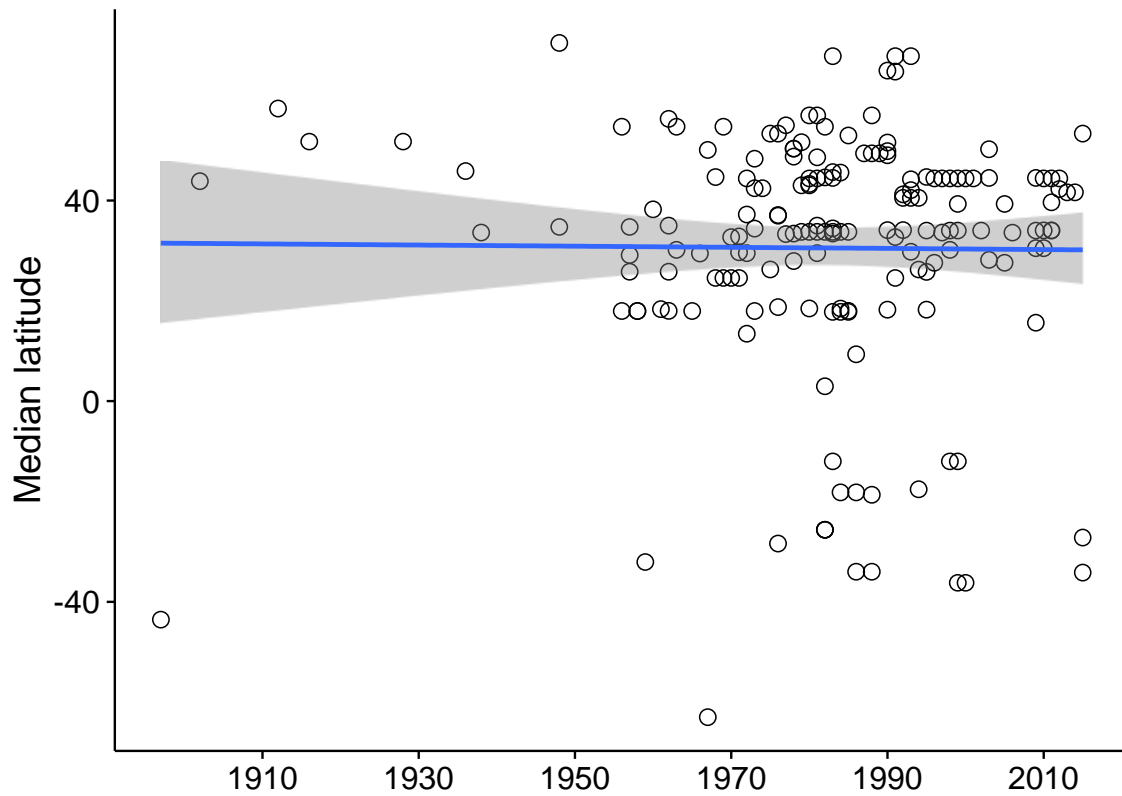


Figure 3.4. Relationship between median latitude of echinoderm mass mortality events and year of event (linear model: $F_{1,156} = 0.37$, $R^2 = 0.002$, $p = 0.54$, $n = 175$ events). Grey bands indicate the 95% confidence interval around the line of best fit (solid line).

3.4. Discussion

Overall, I found no evidence of an increase in the frequency or intensity of reported echinoderm mass mortality events over time. Instead, the annual number of echinoderm MMEs peaked in the 1980s, and has declined since then. The majority of reports have involved echinoids and have stemmed from North America. Echinoderm MMEs have become somewhat shorter over time, and recent events are more limited in taxonomic extent than earlier events. There has been no change in average latitude of mortality events but I still detected a potential signature of climate change. The proportion of MMEs caused by disease has increased over time, and although the proportion of MMEs caused by physical stress has not changed, events caused by heat stress have become relatively more frequent than those caused by cold conditions.

A challenge in reconstructing historical trends of ecological events is accounting for changes in reporting effort. Temporal variation in reporting effort is common and has been noted in records of climate-induced range and phenology shifts in animals (e.g., Hassall *et al.*, 2007; Hassall & Thompson, 2010), emergence of infectious diseases (Jones *et al.*, 2008) and coral bleaching (Oliver, Berkelmans & Eakin, 2009). To control for potential temporal variation in recorder effort, I compared trends in numbers of echinoderm MME reports and of ecological publications on echinoderms (see also Ward and Lafferty 2004, Jones *et al.* 2008, Feehan and Scheibling 2014 for use of a similar method). The rise in numbers of echinoderm MMEs up to the late 1980s mirrors a rise in scientific interest in echinoderm ecology, and an increasing proportion of publications has been interpreted as an indication of a real increase in event frequency (Ward & Lafferty, 2004). However, the peak in MMEs evident in my data from 1980-1989 may be the result of several keen echinoderm observers during that time period. For example, Lawrence (1996) described many small-scale, localized mortality events that may not have otherwise been reported in the peer-reviewed literature. In addition, events tend to be reported from geographic regions where the majority of ecologists live and conduct fieldwork (i.e., North America and Europe; Fig. 3.2D; see also Fey *et al.*, 2015), and other regions are likely underrepresented. However, the drop in reported MMEs despite the continued rise in echinoderm ecology publications and the increasingly frequent use of technologies such as SCUBA and remote observation equipment in subtidal habitats

suggests that the frequency of MMEs observed post-1980s might be a real pattern in nature.

Disease was the most common cause of echinoderm mass mortality. Moreover, the proportion of echinoderm MMEs attributed to disease increased over time. This pattern is consistent with previous studies reporting an increase in the prevalence of disease for other marine taxa (Harvell *et al.*, 1999; Ward & Lafferty, 2004; Harvell *et al.*, 2004) and is a predicted response to climate change (Harvell *et al.* 2002 Science). On the other hand, Feehan and Scheibling (2014b) found no evidence of an increase in reports of sea urchin disease. Escalating disease prevalence in some areas, such as Nova Scotia, Canada, was offset by a decline in other areas, such as the Caribbean, where populations of *Diadema antillarum* had not recovered following the widespread mortality in 1983 (Lessios, 2004; Kissling *et al.*, 2014). As a result, sea urchin mortality events in that region remained short-lived and highly localized (Feehan & Scheibling, 2014a). Despite the increase in proportion of disease-related die-offs, the decline in the absolute number of events caused by disease since the 1980s could reflect an absolute decline in emerging diseases in general (Jones *et al.*, 2008).

Another cause of echinoderm mortality that might be linked to climate change is physical stress. Although the proportion of MMEs caused by physical stress did not increase over time, nearly 80% of physical stress mortality events were attributed to thermal stress. In a global review with a small sample of marine invertebrate die-offs, Fey *et al.* (2015) found that the number of events related to cold stress declined over time, while those related to heat stress did not occur until after 1980. I observed similar, complementary trends across my longer time-series focused on echinoderms in that heat-related thermal stress events did not appear until the 1950s and increased thereafter as a proportion of all MMEs caused by heat stress. Both patterns can be attributed to the milder winters and more extreme summers associated with climate change (Donat *et al.*, 2013; Pairaud *et al.*, 2014).

Although informative, the patterns I observed regarding the causal factors of echinoderm mass mortality likely do not reveal the full complexity of mechanisms underpinning these events. A number of authors acknowledged a lack of certainty about

the ultimate factors leading to large-scale die-offs, even where a proximate cause was suggested (e.g., Skadsheim, Christie & Leinaas, 1995; Eckert, Engle & Kushner, 2000; Hewson, Button & Gudenkauf, 2014). In addition, there are likely multiple contributing factors involved in many mortality events (Fey *et al.*, 2015). Disease risk in particular can be compounded by environmental or human-caused factors that are not always readily apparent (Harvell *et al.*, 1999; Ward & Lafferty, 2004; Harvell *et al.*, 2004). Despite the importance of disease in regulating echinoderm populations (Uthicke, Schaffelke & Byrne, 2009; Feehan, Scheibling & Lauzon-Guay, 2012a), there is relatively limited knowledge of echinoderm pathogens compared to other taxa. For instance, although a virus may play a key role in the ongoing sea star wasting epidemic in the Northeast Pacific (Hewson *et al.*, 2014), the first known echinoderm-associated virus was only described in 2014 (Gudenkauf *et al.*, 2014). Furthermore, the pathogen responsible for the near-demise of *Diadema antillarum* in the Caribbean remains unidentified (Lessios, 2016).

The severity of echinoderm mass mortality events was difficult to evaluate. Although the duration of die-off events might have become shorter and the taxonomic extent appeared to decline over time, there was a paucity of consistent information on mortality levels or geographic extent. Often population-level impacts were unknown or expressed only in qualitative terms (e.g., “large numbers” of invertebrates killed by a toxic algal bloom; Olive & Cadman, 2002). Where mortality levels were mentioned, reports often used different metrics such as biomass (e.g., Miller & Colodey, 1983), density (e.g., Dungan, Miller & Thomson, 1982), approximate number of individuals (e.g., Rosenberg, Loo & Moller, 2002), or percent mortality (e.g., Lessios, 1988; Carpenter, 1990; Eckert, Engle & Kushner, 2000), which were not comparable among reports. While duration and taxonomic extent may provide a rough indication of severity, these metrics do not reflect the relative impacts on populations, loss of biomass, potential for recovery or ecological impacts. To understand long-term ecological trends, there is a need for consistent, comprehensive monitoring and reporting of population-level impacts and geographic extent (Feehan & Scheibling, 2014a).

In conclusion, contrary to expectation, the frequency of mass mortality events affecting echinoderm populations has not increased demonstrably over time. In fact,

they appear to have become less frequent over the past three decades, despite an increase in publication output. A lack of baseline data, inconsistent reporting and limited knowledge of the factors driving echinoderm population dynamics make it difficult to assess with certainty how echinoderm mass mortality events have been changing in frequency and intensity through time. However, patterns in my data suggest disease and warming conditions may play an increasing role in echinoderm die-offs. Given the importance of echinoderms in structuring marine communities (Dayton *et al.*, 1992; Scheibling, Feehan & Lauzon-Guay, 2013; Steneck *et al.*, 2013), the need for consistent, long-term population monitoring and improved understanding of population drivers cannot be overstated (Feehan & Scheibling, 2014b; Fey *et al.*, 2015).

Chapter 4.

General Discussion

In this thesis I investigated the global trends and local patterns surrounding echinoderm mass mortality events. In Chapter 2, I looked at the local-scale ecological consequences of a widespread sea star wasting event in British Columbia. The changes in community composition I observed following the sea star mortality were consistent with a trophic cascade. In particular, I found that the abundance of green sea urchins, an important sea star prey item, increased drastically, while the percent cover of kelp declined. Data from citizen science surveys in British Columbia and Washington suggest that the trophic cascade likely also occurred at a larger spatial scale. In Chapter 3, I conducted an extensive literature review to determine whether the frequency or severity of echinoderm-related mass mortality events changed over time on a global scale. Contrary to my initial expectation, the number of reports, duration and taxonomic extent of echinoderm mass mortality events did not increase through time. However, trends in the causes of mortality events suggest that disease and climate change are playing an increasing role in echinoderm die-offs.

Chapter 2 provides some of the first evidence of community shifts following the 2013 sea star die-off, which might be one of the largest wildlife mortality events known. While most recent research regarding the aftermath of sea star wasting syndrome has focused on intertidal habitats (e.g., Eisenlord *et al.*, 2016; Menge *et al.*, 2016), Chapter 2 is unique in its focus on the subtidal, where trophic interactions are not as well documented. As such, Chapter 2 expands our understanding of marine systems beyond the foreshore, and suggests that *Pycnopodia helianthoides* may play an important role in structuring communities in the subtidal, analogous to that of *Pisaster ochraceus* in the intertidal (Duggins, 1983; Paine, 1966).

Scientists have been cautioned recently about the pitfalls of identifying true trophic cascades (Grubbs *et al.*, 2016). However, it is highly unlikely that my conclusion that *Pycnopodia* mortality induced an ecological cascade is erroneous. The trophic link between sunflower stars and green sea urchins is well established (Duggins, 1983), and there are no other major predators of green sea urchins at the local scale of Howe Sound. Sea urchins are notoriously destructive grazers (Feehan, Scheibling, & Lauzon-Guay, 2012a), and respond rapidly to changes in predation pressure (Duggins, 1981). Although sea urchin settlement and growth rates can be highly variable (Vadas, Smith, & Beal, 2002), the tight temporal correlation between the increase in sea urchins and the sea star die-off (Figs. 2.3 and 2.6), and the lack of any comparable outbreak in sea urchin numbers in historical records (Fig. 2.4), lend confidence to the purported cascade at a time when other documented marine trophic cascades have been called into question (Grubbs *et al.*, 2016).

Chapter 3 highlighted the potentially increasing role of climate in disease outbreaks and mortality events. Climate was related to many of the mortality events I identified (e.g., Blanchette *et al.*, 2005; Dungan *et al.*, 1982; Feehan, Scheibling, & Lauzon-Guay, 2012b), and warm temperatures played an increasing role in mortality events compared to cold temperatures (Fig. 3.3). However, the overall relationship between climate and disease in echinoderms remains unpredictable (Lessios, 2013). For instance, the onset of the *Diadema antillarum* mortality throughout the Caribbean preceded the temperature increases associated with the 1982-1983 El Niño event (Lessios, 2013). Similarly, the 2013 sea star wasting event began before the very large El Niño of 2014-2015, and while disease risk increased with temperature in some areas (Eisenlord *et al.*, 2016), other areas witnessed higher disease prevalence during the cooler winter months (Menge *et al.*, 2016). In the tropics, herbivorous sea urchins survive well on reefs where coral has bleached and died (Lessios, 2005) and they may even indirectly benefit from the increase in available space for algal growth (Lessios, 2013). As climate change continues to shift benthic assemblages, the impact on echinoderms is likely to be highly variable, and some species may become more prevalent (Lessios, 2013).

Chapter 3 also places the 2013 sea star wasting event in an historical context. With the exception of the widespread *D. antillarum* mortality in the 1980s (Carpenter, 1990), no mortality events rivalled the 2013 wasting event in terms of geographic scope or total number of individuals affected. The *D. antillarum* mortality resulted in 87-100% declines in population sizes (Lessios, 1988), and spread from Panama to the rest of the Caribbean, Florida and Bermuda within one year (Lessios, Robertson, & Cubit, 1984). Furthermore, it is possible that the die-off spread to other areas of Central and South America but was not recorded due to the scarcity of observers in the area at that time. However, the 2013 wasting event was at least comparable as high mortality was observed from Alaska to Baja California (Stokstad, 2014), and possibly farther north or south where fewer observers are present. It also affected at least 20 different species (Stokstad, 2014), making it unique among previous sea star wasting events (e.g. Bates *et al.*, 2009; Blanchette *et al.*, 2005; Dungan *et al.*, 1982; Eckert *et al.*, 2000).

Despite the severity of the 2013 sea star die-off, there is potential for sea star populations to recover. Echinoderms are notorious for extreme population fluctuations (Uthicke *et al.*, 2009), and their life history characteristics may make them better equipped to rebound quickly. Plankotrophic larvae, which are common among echinoderms (Uthicke *et al.*, 2009), allow for substantial larval dispersal, and may allow populations to break cycles of parasitism or disease (Strathmann *et al.*, 2002). Long-distance dispersal may allow remote, healthy populations of sea stars to re-colonize areas that were heavily impacted by sea star wasting disease. However, recovery will depend on the existence of healthy, founder populations, and the complexity of larval dispersal and uncertainty regarding marine invertebrate population connectivity (Cowen & Sponaugle, 2009; Strathmann *et al.*, 2002) make it difficult to predict when and how sea star recovery may take place. In addition, recovering populations may be subject to Allee effects and genetic bottlenecks.

There may also be challenges to recovery from the community shifts associated with sea star wasting in Howe Sound and elsewhere. Ecological perturbations can shift communities to alternative stable states that may persist even after the drivers of change return to their previous levels (i.e., hysteresis; see Beisner, Haydon, & Cuddington, 2003). In some cases, complex trophic interactions can cause negative feedbacks that

slow or prevent recovery. For example, when Atlantic cod (*Gadus morhua*) stocks collapsed following intense fishing pressure, many of their prey species, including herring and other pelagic fish, increased in number (Frank, Petrie, & Shackell, 2007). In an example of predator-prey reversal, herring and other pelagic fish fed on Atlantic cod eggs, and inhibited the recovery of cod (Minto & Worm, 2012; Worm & Lenihan, 2013). A similar interaction is possible on temperate rocky reefs, for instance, if green sea urchins consume sea star larvae while grazing, and thereby impede sea star recovery following mortality.

Several suggestions for promoting ecosystem recovery following the 2013 sea star wasting event target management of specific species. One suggestion is formal protection for the species most heavily impacted by sea star wasting disease (Harvell, 2016). In particular, listing *P. helianthoides* as endangered could raise awareness about existing threats to the species. However, given that sea stars are not harvested, formal protection may not have a large impact on population recovery. Another proximate solution to reverting the community shifts resulting from sea star wasting might be to artificially restore kelp beds in areas where they have been depleted by overabundant grazers. Restoration efforts for giant kelp (*Macrocystis* spp.) and bull kelp (*Nereocystis luetkeana*) have been successful (Carney *et al.*, 2005; Wilson & North, 1983), and similar techniques could be applied to *Agarum* spp. Restored kelp beds may mitigate trickle-down effects on other levels of the food web (Wilson & North, 1983). However, because it may be difficult to protect cultivated kelp from overabundant grazers or competitors, kelp restoration may not be a viable long-term solution. A third suggestion is to promote commercial or recreational sea urchin harvest in areas where sea urchins are overabundant. A fishery already exists for *S. droebachiensis* on both the east (Chen & Hunter, 2003) and west (Perry, Zhang, & Harbo, 2002) coasts of North America. In British Columbia, green sea urchin harvest peaked in 1992 and 1993 and has declined steadily since then, largely due to poor market conditions (DFO, 2013). An assessment of the economic sustainability of sea urchin harvest and a revised active management plan (Perry *et al.*, 2002) are needed to determine the feasibility of sea urchin harvest as a solution to mitigate the impacts of sea star wasting syndrome on kelp.

An alternative approach is to incorporate conservation measures that promote ecosystem health and integrity as a whole. Changes in biomass can make ecosystems less stable and more prone to environmental fluctuations (Elmqvist *et al.*, 2003) because diversity within and among species provides a larger suite of traits to draw on in response to change (Hsieh *et al.*, 2006; Schindler *et al.*, 2010). Therefore, practices that reduce biomass or diversity can compromise ecosystem resilience (Hsieh *et al.*, 2006). Protecting diversity and reducing exploitation through establishing marine protected areas or other management strategies could be an important way to mitigate echinoderm mass mortality events when they occur.

However, there are also examples of ecosystems demonstrating recovery following mass mortality without intervention. Coral and fish assemblages on the Great Barrier Reef have been shown to recover following mortality from storms (Halford, Cheal, Ryan, & Williams, 2004), and benthic fauna recolonized when conditions improved after a mass mortality resulting from low oxygen conditions in a Swedish fjord (Rosenberg *et al.*, 2002). Physical processes can also facilitate ecosystem resilience. Overfishing of predatory fish and crabs in a salt marsh in New England led to an increase in the herbivorous crab, *Sesarma reticulatum*, causing 40-90% declines in smooth cordgrass (*Spartina alterniflora*; (Coverdale *et al.*, 2013). The resulting desertification was not reversed until bank erosion allowed the cordgrass to recolonize the area (Altieri *et al.*, 2013). Such examples of ecosystem resilience lend promise to the notion that communities will recover following sea star wasting or other echinoderm mass mortality events.

In addition, echinoderm overabundance may be a main contributing factor in disease outbreaks. The two largest echinoderm mass mortality events (the 1980s *D. antillarum* die-off and the 2013 Pacific sea star wasting mortality) were both preceded by high echinoderm population densities (Hay, 1984; Mah, 2010; Lessios, 2013). In Howe Sound in particular, *P. helianthoides* was exceptionally abundant in the years leading up to the sea star die-off (Mah, 2010). In some systems, disease has replaced predation as a population control mechanism for echinoderms (e.g., *S. droebachiensis* in Nova Scotia; Feehan and Scheibling 2014a). Therefore, it is possible that the 2013 die-off of sunflower stars in Howe Sound reset the community structure to a more typical state.

Despite the ecological importance of echinoderms, our current knowledge of some of the basic life history characteristics of echinoderms remains rudimentary. Approximations of age based on size are difficult for species such as *P. helianthoides* or *S. droebachiensis*. There is debate on how best to determine age (Russell, Ebert, & Petraitis, 1998). Estimates of growth rate vary from 1-2 mm per year (Himmelman, 1986) to > 1 cm per year (Munk, 1992) for *S. droebachiensis*, and depend on environmental conditions and food supply (Perry *et al.*, 2002; Vadas *et al.*, 2002). In addition, there are many unanswered questions regarding recruitment patterns and population connectivity (Perry *et al.*, 2002). A better understanding of echinoderm demography would paint a clearer picture of trophic linkages and ecosystem processes.

There are also many unknowns regarding 2013 sea star mass mortality in particular. Although a potential causative agent was identified (Hewson *et al.*, 2014), the factors contributing to the outbreak are not fully understood. There are likely multiple drivers involved. Hewson *et al.* (2014) identified a densovirus associated with symptomatic sea stars. However, the virus was also present in apparently healthy sea stars, other echinoderm taxa, plankton, sediments, and museum specimens, suggesting the virus has been in the environment for at least several decades and that its effects are not consistent (Hewson *et al.*, 2014). Asymptomatic sea stars or other taxa may serve as vectors for the disease (Hewson *et al.*, 2014), but the pathology, geographic spread and drivers of resistance of invertebrate diseases are poorly understood (Stokstad, 2014). In addition, the ecological consequences of the disease remain unknown for most regions of the west coast. While the present work provides some insight into subtidal community shifts, there is a need for a deeper understanding of trophic interactions and the impacts of the mortality across a wider geographic range. The event highlights the need to understand echinoderm diseases in greater detail, and to establish cause-and-effect linkages in echinoderm population dynamics.

Because of the ecological importance of echinoderms, widespread and continued monitoring of echinoderm population dynamics is important for understanding the drivers of ecosystem trends. One way to increase the geographic reach of monitoring is to incorporate citizen science (Dickinson *et al.*, 2012). The 2013 sea star die-off was an example of the utility of citizen science. Hundreds of observations by citizen scientists

and partner organizations allowed researchers to track the progression of the disease in a way that otherwise would not have been possible (see www.seastarwasting.org). Citizen science surveys submitted through the Reef Environmental Education Foundation (Fig. 2.4) provided evidence for a trophic cascade at the regional scale. Although there are limitations with data acquired in this way, public involvement increases the geographic and temporal scope of data collection (Dickinson *et al.*, 2012) as well as popular awareness of changes occurring in the ocean. In this era of global communication, the importance of collaboration and coordination in ecological monitoring remains critical to understanding the causes and consequences of echinoderm mass mortality events (Fey *et al.*, 2015).

References

- Altieri, A. H., Bertness, M. D., Coverdale, T. C., Axelman, E. E., Herrmann, N. C., & Szathmary, P. L. (2013). Feedbacks underlie the resilience of salt marshes and rapid reversal of consumer-driven die-off. *Ecology*, 94(7):1647–1657.
- Altizer S., Harvell D., Friedle E. (2003) Rapid evolutionary dynamics and disease threats to biodiversity. *Trends in Ecology and Evolution*, 18(11):589-596.
- Bates, A. E., Hilton, B. J., & Harley, C. D. G. (2009). Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. *Diseases of Aquatic Organisms*, 86:245–251.
- Beisner, B. E., Haydon, D. T., & K, C. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1(7):376–382.
- Blanchette, C. A., Richards, D. V., Engle, J. M., Broitman, B. R., & Gaines, S. D. (2005). Regime shifts, community change and population booms of keystone predators at the Channel Islands. *Proceedings of the California Islands Symposium*, 6:435-441.
- Carney, L. T., Waaland, J. R., Klinger, T., & Ewing, K. (2005). Restoration of the bull kelp *Nereocystis luetkeana* in nearshore rocky habitats. *Marine Ecology Progress Series*, 302: 49–61.
- Carpenter, R. C. (1990). Mass mortality of *Diadema antillarum*. *Marine Biology*, 104:67–77.
- Chen, Y., & Hunter, M. (2003). Assessing the green sea urchin (*Strongylocentrotus drobachiensis*) stock in Maine, USA. *Fisheries Research*, 60:527–537.
- Cloutier, R. N. (2011). Direct and indirect effects of marine protection: rockfish conservation areas as a case study. MSc Thesis, Simon Fraser University.
- Coverdale, T. C., Herrmann, N. C., Altieri, A. H., & Bertness, M. D. (2013). Latent impacts: The role of historical human activity in coastal habitat loss. *Frontiers in Ecology and the Environment*, 11(2):69–74.
- Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1:443–466.

- Coyer, J. A., Ambrose, R. F., Engle, J. M., & Carroll, J. C. (1993). Interactions between corals and algae on a temperate zone rocky reef: mediation by sea urchins. *Journal of Experimental Marine Biology and Ecology*, 167(1): 21-37.
- Dayton, P. K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs*, 45:137–159.
- Dayton, P. K., Tegner, M. J., Parnell, P. E., & Edwards, P. B. (1992). Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs*, 62:421–445.
- De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences*, 109(44):17995–17999.
- Del Sesto, C. J. (2015). Assessing the pathogenic cause of sea star wasting disease in *Asterias Forbesi* along the east coast of the United States. MSc Thesis, University of Rhode Island.
- DFO. (2013). Green sea urchin - Pacific region 2013-2016. Department of Fisheries and Oceans, Integrated Fisheries Management Plan Summary.
- Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Phillips, T., & Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10(6), 291–297.
- Donat, M. G., Alexander, L. V., Yang, H., Durre, I., Vose, R., Dunn, R. J. H., Willett, K. M., Aguilar, E., Brunet, M., Caesar, J., Hewitson, B., Jack, C., Klein Tank, A. M. G., Kruger, A. C., Marengo, J., Peterson, T. C., Renom, M., Oria Rojas, C., Rusticucci, M., Salinger, J., Elayah, A. S., Sekele, S. S., Srivastava, A. K., Trewin, B., Villarreal, C., Vincent, L. A., Zhai, P., Zhang, X., & Kitching, S. (2013). Updated analyses of temperature and precipitation extreme indices since the beginning of the twentieth century: The HadEX2 dataset. *Journal of Geophysical Research: Atmosphere*, 118(5):2098–2118.
- Duggins, D. O. (1981). Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia*, 48(2):157–163.
- Duggins, D. O. (1983). Starfish predation and the creation of mosaic patterns in a kelp-dominated community. *Ecology*, 64(6):1610-1619.
- Dulvy, N. K., Sadovy, Y., & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries*, 4(1):25–64.

- Dungan, M. L., Miller, T. E., & Thomson, D. A. (1982). Catastrophic decline of a top carnivore in the gulf of california rocky intertidal zone. *Science*, 216(4549):989–991.
- Eckert, G. L., Engle, J. M., & Kushner, D. J. (2000). Sea star disease and population declines at the Channel Islands. *Proceedings of the Fifth California Islands Symposium*, 5:390–393.
- Eisenlord, M. E., Groner, M. L., Yoshioka, R. M., Elliott, J., Maynard, J., Fradkin, S., Turner, M., Pyne, K., Rivlin, N., van Hooidek, R., & Harvell, C. D. (2016). Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371:20150212.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9):488–494.
- Engle, J. M., Halvorson, W. L., & Maender, G. L. (1994). Perspectives on the structure and dynamics of nearshore marine assemblages of the California Channel Islands. In: Halvorson, W. L. & Maender, G. J. (Eds.). *The Fourth California Channel Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, California.
- Estes, J. A., & Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs*, 65(1):75–100.
- Estes, J. A., & Palmisano, J. F. (1974). Sea otters: Their role in structuring nearshore communities. *Science*, 185(4156):1058–1060.
- Fadlallah, Y. H. (1983). Population dynamics and life history of a solitary coral, *Balanophyllia elegans*, from central California. *Oecologia*, 58(2): 200-207.
- Feehan, C. J., & Scheibling, R. E. (2014a). Disease as a control of sea urchin populations in Nova Scotian kelp beds. *Marine Ecology Progress Series*, 500:149–158.
- Feehan, C. J., & Scheibling, R. E. (2014b). Effects of sea urchin disease on coastal marine ecosystems. *Marine Biology*, 161:1467–1485.
- Feehan, C., Scheibling, R. E., & Lauzon-Guay, J. S. (2012a). Aggregative feeding behavior in sea urchins leads to destructive grazing in a Nova Scotian kelp bed. *Marine Ecology Progress Series*, 444:69–83.

- Feehan, C., Scheibling, R. E., & Lauzon-Guay, J. S. (2012b). An outbreak of sea urchin disease associated with a recent hurricane: support for the “killer storm hypothesis” on a local scale. *Journal of Experimental Marine Biology and Ecology*, 413:159–168.
- Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A., & Carlson, S. M. (2015). Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences*, 112(4), 1083–1088.
- Fletcher, W. J. (1987). Interactions among subtidal Australian sea urchins, gastropods and algae: Effects of experimental removals. *Ecological Monographs*, 57(1): 89-109.
- Frank, K. T., Petrie, B., & Shackell, N. L. (2007). The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution*, 22(5):236–242.
- Fuess, L. E., Eisenlord, M. E., Closek, C. J., Tracy, A. M., Mauntz, R., Gignoux-Wolfsohn, S., Moritsch, M., Yoshioka, R., Burge, C. A., Harvell, C. D., Friedman, C. S., Hewson, I., Hershberger, K., & Roberts, S. B. (2015). Up in arms: Immune and nervous system response to sea star wasting disease. *PLoS ONE*, 10(7):e0133053–17.
- Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Cheveltonné, P., Cigliano, M., Diaz, D., Harmelin, J. G., Gambi, M. C., Kersting, D. K., LeDoux, J. B., LeJeune, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J. C., Serrano, E., Teixido, N., Torrents, O., Zabala, M., Zuberer, F., & Cerrano, C. (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Global Change Biology*, 15(5):1090–1103.
- Girard, D., Clemente, S., Toledo-Guedes, K., Brito, A., & Hernández, J. C. (2011). A mass mortality of subtropical intertidal populations of the sea urchin *Paracentrotus lividus*: Analysis of potential links with environmental conditions. *Marine Ecology*, 33(3), 377–385.
- Grandcourt E.M., & Cesar H. (2003). The bio-economic impact of mass coral mortality on the coastal reef fisheries of the Seychelles. *Fisheries Research*, 60:539–550.
- Gray, J. S. (1997). Marine biodiversity: Patterns, threats and conservation needs. *Biodiversity & Conservation*, 6:153–175.
- Grubbs, R. D., Carlson, J. K., Romine, J. G., Curtis, T. H., McElroy, W. D., McCandless, C. T., Cotton, C. F & Musick, J. A. (2016). Critical assessment and ramifications of a purported marine trophic cascade. *Scientific Reports*, 6:20970.

- Gudenkauf, B. M., Eaglesham, J. B., Aragundi, W. M., & Hewson, I. (2014). Discovery of urchin-associated densoviruses (family Parvoviridae) in coastal waters of the Big Island, Hawaii. *Journal of General Virology*, 95:652–658.
- Hagen, N. T. (1983). Destructive grazing of kelp beds by sea urchins in Vestfjorden, northern Norway. *Sarsia*, 68:177–190.
- Hagen, N. T. (1997). Sea urchin outbreaks and epizootic disease as regulating mechanisms in coastal ecosystems. *Deep Sea Research, Part B*, 2(44):131.
- Halford, A., Cheal, A. J., Ryan, D., & Williams, D. M. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, 85(7):1892–1905.
- Halpern, B. S., Selkoe, K. A., Micheli, F., & Kappel, C. V. (2007). Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology*, 21(5):1301–1315.
- Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L., & Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, 9(2), 228–241.
- Hart, M. W., & Scheibling, R. E. (1988). Heat waves, baby booms, and the destruction of kelp beds by sea urchins. *Marine Biology*, 99:167–176.
- Harvell, C.D. (2016). Sea star wasting summit. Seattle, WA, 15 January, 2016.
- Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., Lipp, E. K., Osterhaus, A. D. M. E., Overstreet, R. M., Porter, J. W., Smith, G. W., & Vasta, G. R. (1999). Emerging marine diseases: Climate links and anthropogenic factors. *Science*, 285(5433):1505–1510.
- Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., & Samuel, M. D. (2002). Climate warming and disease risks for terrestrial and marine biota. *Science*, 296(5576):2158–2162.
- Harvell C. D., Aronson, R., Baron, N., Connell, J., Dobson, A., Ellner, S., Gerber, L., Kim, K., Kuris, A., McCallum, H., & Lafferty, K. (2004). The rising tide of ocean diseases: Unsolved problems and research priorities. *Frontiers in Ecology and the Environment*, 2(7):375–82.
- Hassall, C., & Thompson, D.J. (2010). Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution*, 1:343–350.
- Hassall, C., Thompson, D.J., French, G.C., & Harvey, I.F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, 13:933–941.

- Hay, M. E. (1984). Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? *Ecology*, 65(2):446–454.
- Herrlinger, T.J. (1983). The diet and predator-prey relationships of the sea star *Pycnopodia helianthoides* (Brandt) from a central California kelp forest. MA Thesis, San Jose State University.
- Hewson, I., Button, J. B., Gudenkauf, B. M., Miner, B. G., Newton, A. L., Gaydos, J. K., Wynne, J., Groves, C. L., Hendler, G., Murray, M., Fradkin, S., Breitbart, M., Fahsbender, E., Lafferty, K. D., Kilpatrick, A. M., Miner, C. M., Raimondi, P., Lahner, L., Friedman, C. S., Daniels, S., Haulena, M., Marliave, J., Burge, C. A., Eisenlord, M.E., & Harvell, C. D. (2014). Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences, USA*, 111:17278–17283.
- Himmelman, J. H. (1986). Population biology of green sea urchins on rocky barrens. *Marine Ecology Progress Series*, 33:295-306.
- Hsieh, C. H., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., & Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature*, 443(7113), 859–862.
- Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265:1547–1551.
- Johnson, L. (2016). Sea star wasting disease among worst wildlife die-offs say scientists. CBC News. Retrieved from <http://www.cbc.ca/news/canada/british-columbia/sea-star-wasting-die-off-1.3414607>. 21 January, 2016.
- Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. *Nature*, 451(7181):990-993.
- Kissling, D.L., Precht, W.F., Miller, S.L., & Chiappone, M. (2014). Historical reconstruction of population density of the echinoid *Diadema antillarum* on Florida Keys shallow bank-barrier reefs. *Bulletin of Marine Science*, 90:665–679.
- Lafferty, K.D., Porter, J.W., & Ford, S.E. (2004). Are diseases increasing in the ocean? *Annual Review of Ecology, Evolution and Systematics*, 14:1566–1573.
- Lambert, P. (2000). Sea stars of British Columbia, southeast Alaska, and Puget Sound. Royal British Columbia Museum, UBC Press, Vancouver.
- Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, 142(6), 911–927.

- Lawrence, J. M. (1996). Mass mortalities of echinoderms from abiotic factors. In M. Jangoux & J. M. Lawrence (Eds.), *Echinoderm Studies* (Vol. 5, pp. 103–137). Rotterdam, The Netherlands: Balkema.
- Leighton, B. J., Boom, J. D. G., Bouland, C., Hartwick, B., & Smith, M. J. (1991). Castration and mortality in *Pisaster ochraceus* parasitized by *Orchitophrya stellarum* (Ciliophora). *Diseases of Aquatic Organisms*, 10:71–73.
- Lessios, H. A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics*, 19:371–393.
- Lessios, H. A. (2004). *Diadema antillarum* populations in Panama twenty years following mass mortality. *Coral Reefs*, 24:125–127.
- Lessios, H. A. (2005). Echinoids of the Pacific waters of Panama: Status of knowledge and new records. *Revista De Biología Tropical*, 53(3):147–170.
- Lessios, H. A. (2013). “Natural” population density fluctuations of echinoids. Do they help predict the future? In: J. M. Fernandez-Palacios, L. de Nascimento, J. C. Hernández, S. Clemente, A. Gonzalez, & J. P. Diaz-Gonzalez (Eds.), *Climate change perspectives from the Atlantic: Past, present and future*, (pp. 341–359). Servicio de Publicaciones, Universidad de La Laguna.
- Lessios, H. A. (2016). The great *Diadema antillarum* die-off: 30 years later. *Annual Review of Marine Science*, 8:267–283.
- Lessios, H. A., Robertson, D. R., & Cubit, J. D. (1984). Spread of *Diadema* mass mortality through the Caribbean. *Science*, 226(4672):335–337.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68:619–640.
- Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., & Jackson, J. B. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, 312(5781):1806-1809.
- Mah, C. M. (2010). Huge swarms of *Pycnopodia helianthoides* (sunflower stars) in British Columbia: Starfish swarms - has the invasion finally come? *The Echinoblog*, 16 November, 2010. <http://echinoblog.blogspot.ca/2010/11/huge-swarms-of-pycnopodia-helianthoides.html>.
- Marliave, J. B., Gibbs, C. J., Gibbs, D. M., Lamb, A. O., & Young, S. J. F. (2011). Biodiversity stability of shallow marine benthos in Strait of Georgia, British Columbia, Canada through climate regimes, overfishing and ocean acidification. In Grillo, O. and Verona, G. (Eds.), *Biodiversity loss in a changing planet*, (pp. 49-74). Rijeka, Croatia: InTech Publications.

- Marliave, J. B., & Roth, M. (1995). *Agarum* kelp beds as nursery habitat of spot prawns, *Pandalus platyceros* Brandt, 1851 (Decapoda, Caridea). *Crustaceana*, 68:27–37.
- McArthur, L. C., & Boland, J. W. (2006). The economic contribution of seagrass to secondary production in South Australia. *Ecological Modelling*, 196:163–172.
- McClanahan, T. R., Kamukuru, A. T., Muthiga, N. A., Gilagabher Yebio, M., & Obura, D. (1996). Effect of sea urchin reductions on algae, coral and fish populations. *Conservation Biology*, 10(1):136-154.
- Meidel, S. K., & Scheibling, R. E. (1999). Effects of food type and ration on reproductive maturation and growth of the sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*, 134:155–166.
- Menge, B. A. (1979). Coexistence between the seastars *Asterias vulgaris* and *A. forbesi* in a heterogeneous environment: A non-equilibrium explanation. *Oecologia*, 41(3):245–272.
- Menge, B. A., Cerny-Chipman, E. B., Johnson, A., Sullivan, J., Gravem, S., & Chan, F.. (2016). Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: Insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. *PLoS ONE*, 11(5):e0153994–28.
- Miller, R. J., & Colodey, A. G. (1983). Widespread mass mortalities of the green sea urchin in Nova Scotia, Canada. *Marine Biology*, 73:263–267.
- Minto, C., & Worm, B. (2012). Interactions between small pelagic fish and young cod across the North Atlantic. *Ecology*, 93(10):2139–2154.
- Munk, J. E. (1992). Reproduction and growth of green urchins *Strongylocentrotus droebachiensis* (Müller) near Kodiak, Alaska. *Journal of Shellfish Research*, 11:245–245.
- Mydlarz, L. D., Jones, L. E., & Harvell, C. D. (2006). Innate immunity, environmental drivers, and disease ecology of marine and freshwater invertebrates. *Annual Review of Ecology, Evolution and Systematics*, 37:251–288.
- Okamoto, D. K., Schmitt, R. J., Holbrook, S. J., & Reed, D. C. (2012). Fluctuations in food supply drive recruitment variation in a marine fish. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1747):rsbp20121862–4550.
- Olive, P. J. W., & Cadman, P. S. (2002). Mass mortalities of the lugworm on the South Wales coast: A consequence of algal bloom? *Marine Pollution Bulletin*, 21:542–545.

- Oliver, J. K., Berkelmans, R. & Eakin, C. M. (2009). Coral bleaching in space and time. In: van Oppen, M. J. H., Lough, J. M. (Eds). Coral bleaching. Springer, Berlin, Heidelberg, p 21–39.
- Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100(910):65-75.
- Pairaud, I. L., Bensoussan, N., Garreau, P., Faure, V. & Garrabou, J. (2014). Impacts of climate change on coastal benthic ecosystems: Assessing the current risk of mortality outbreaks associated with thermal stress in NW Mediterranean coastal areas. *Ocean Dynamics*, 64:103–115.
- Palacin, C., Giribet, G., Carner, S., Dantart, L. & Turon, X. (1998). Low densities of sea urchins influence the structure of algal assemblages in the western Mediterranean. *Journal of Sea Research* 39:281-290.
- Peacor, S. D. & Werner, E. E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy Science, USA*, 98:3904–3908.
- Pearce, C. M., Williams, S. W., Yuan, F., Castell, J. D. & Robinson, S. M. C. (2005). Effect of temperature on somatic growth and survivorship of early post-settled green sea urchins, *Strongylocentrotus droebachiensis* (Müller). *Aquaculture Research*, 36:600–609.
- Pearce, J., & Balcom, N. (2005). The 1999 Long Island Sound lobster mortality event: Findings of the comprehensive research initiative. *Journal of Shellfish Research*, 24:691-697.
- Pearse, J. S., Costa, D. P., Yellin, M. B., & Agegian, C. R. (1977). Localized mass mortality of red sea urchin, *Strongylocentrotus franciscanus* near Santa Cruz, California. *Fishery Bulletin*, 75(3):647-648.
- Pérez, T., Garrabou, J., Sartoretto, S., Harmelin, J.-G., Francour, P., & Vacelet, J. (2000). Mortalité massive d'invertébrés marins: Un événement sans précédent en Méditerranée nord-occidentale. *Academie Science Paris, Sciences De La Vie*, 323:853–866.
- Perry, R. I., Zhang, Z., & Harbo, R. (2002). Development of the green sea urchin (*Strongylocentrotus droebachiensis*) fishery in British Columbia, Canada: Back from the brink using a precautionary framework. *Fisheries Research*, 55:253–266.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2015) R Core Development Team. nlme: Linear and Nonlinear Mixed Effects Models. R-project. org/package= nlme. R package version.

- Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M. L., Hereu, B., Milazzo, M., Zabala, M., d'Anna, G., & Pipitone, C. (2000). Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. *Environmental Conservation* 27(2), 179-200.
- Preisser, E., Bolnick, D. & Benard, M. (2005). The high cost of fear: Behavioral effects dominate predator-prey interactions. *Ecology*, 86:501–509.
- Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, 22(3):521–533.
- Raimondi, P. T., Wilson, M. C., Ambrose, R. F., Engle, J. M., & Minchinton, T. E. (2002). Continued declines of black abalone along the coast of California: Are mass mortalities related to El Niño events? *Marine Ecology Progress Series*, 242:143–152.
- Ramirez-Llodra, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R., Escobar, E., Levin, L. A., Menot, L., Rowden, A. A., Smith, C. R., & Van Dover, C. L. (2011). Man and the last great wilderness: Human impact on the deep sea. *PLoS ONE*, 6(8):e22588.
- Rassweiler, A., Schmitt, R. J., & Holbrook, S. J. (2010). Triggers and maintenance of multiple shifts in the state of a natural community. *Oecologia*, 164(2):489–498.
- REEF. (2014). Reef Environmental Education Foundation. World Wide Web electronic publication. www.reef.org, downloaded 19 November 2014.
- Rosenberg, R., Agrenius, S., Hellman, B., Nilsson, H. C., & Norling, K. (2002). Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. *Marine Ecology Progress Series*, 234:43–53.
- Rosenberg, R., Loo, L-O, & Moller, P. (2002). Hypoxia, salinity and temperature as structuring factors for marine benthic communities in a eutrophic area. *Netherlands Journal of Sea Research*, 30:121–129.
- Russell, M. P., Ebert, T. A., & Petraitis, P. S. (1998). Field estimates of growth and mortality of the green sea urchin, *Strongylocentrotus droebachiensis*. *Ophelia*, 48(2):137–153.
- Sano, M., Shimizu, M., & Nose, Y. (1984). Changes in structure of coral reef fish communities by destruction of hermatypic corals: Observational and experimental views. *Pacific Science*, 38(1):1–29.

- Scheibling, R. E., Feehan, C. J., & Lauzon-Guay, J. S. (2013). Climate change, disease and the dynamics of a kelp-bed ecosystem in Nova Scotia. In J. M. Fernandez-Palacios, L. de Nascimento, J. C. Hernández, S. Clemente, A. Gonzalez, & J. P. Diaz-Gonzalez (Eds.), *Climate change perspectives from the Atlantic: Past, present and future* (pp. 361–387). Servicio de Publicaciones, Universidad de La Laguna.
- Scheibling, R. E. & Stephenson, R. L. (1984). Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Marine Biology*, 78:153–164.
- Scheibling, R. E., Hennigar, A. W., & Balch, T. (1999). Destructive grazing, epiphytism, and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, 56:2300–2314.
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298):609–612.
- Schmitz, O. J., Krivan, V. & Ovadia O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, 7:153–163.
- Schultz, J. A., Cloutier, R. N., & Côté, I. M. (2016). Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ*, 4:e1980.
- Seidl, R., Schelhaas, M.-J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 4(9):806–810.
- Shivji, M., Parker, D., Hartwick, B., Smith, M. J., & Sloan, N.A. (1983). Feeding and distribution study of the sunflower sea star *Pycnopodia helianthoides* (Brandt, 1835). *Pacific Science*, 37:133–140.
- Skadsheim, A., Christie, H. & Leinaas, H. P. (1995) Population reductions of *Strongylocentrotus droebachiensis* (Echinodermata) in Norway and the distribution of its endoparasite *Echinomermella matsi* (Nematoda). *Marine Ecology Progress Series*, 119:199–209.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (Eds.). (2007) IPCC, 2007: Summary for policymakers. *Climate change: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, United Kingdom and New York, USA.
- Staehli, A., Schaerer, R., Hoelzle, K., & Ribi, G. (2009). Temperature induced disease in the starfish *Astropecten jonstoni*. *Marine Biodiversity Records*, 2(e78):1–5.

- Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2003). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, 29(4):436-459.
- Steneck, R. S., Leland, A., McNaught, D. C., & Vavrinec, J. (2013). Ecosystem flips, locks, and feedbacks: The lasting effects of fisheries on Maine's kelp forest ecosystem. *Bulletin of Marine Science*, 89:31–55.
- Stickle, W. B., Weidner, E. H., & Kozloff, E. N. (2001). Parasitism of *Leptasterias* spp. (Echinodermata: Asteroidea) by the ciliated protozoan *Orchitophrya stellarum* (Scuticociliata). *Invertebrate Biology*, 120(1):88–95.
- Stokstad, E. (2014). Death of the stars. *Science*, 344:464–467.
- Strathmann, R. R., Hughes, T. P., Kuris, A. M., Lindeman, K. C., Morgan, S. G., Pandolfi, J. M., & Warner, R. R. (2002). Evolution of local recruitment and its consequences for marine populations. *Bulletin of Marine Science*, 20(1):377–396.
- Thompson, R. J. (1983). The relationship between food ration and reproductive effort in the green sea urchin, *Strongylocentrotus droebachiensis*. *Oecologia*, 56:50–57.
- Tilman, D., Reich, P. B., & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences, USA*, 109(26):10394–10397.
- Trussell, G. C., Ewanchuk, P. J. & Bertness, M. D. (2003). Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology*, 96:2049–2055.
- Uthicke, S., Schaffelke, B., & Byrne, M. (2009). A boom-bust phylum? Ecological and evolutionary consequences of density variations in Echinoderms. *Ecological Monographs*, 79(1):3–24.
- Vadas, R. L., Smith, B. D., & Beal, B. (2002). Sympatric growth morphs and size bimodality in the green sea urchin (*Strongylocentrotus droebachiensis*). *Ecological Monographs*, 72(1):113-132.
- Vadas, R. L., Beal, B., Dowling, T. & Fegley, J. C. (2000). Experimental field tests of natural algal diets on gonad index and quality in the green sea urchin, *Strongylocentrotus droebachiensis*: A case for rapid summer production in post-spawned animals. *Aquaculture*, 182:115–135.
- Villouta, E., Chadderton, W. L., Pugsley, C. W. & Hay, C. H. (2001). Effects of sea urchin (*Evechinus chloroticus*) grazing in Dusky Sound, Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 35(5):1007-1024.

- Wangersky, P. J., & Cunningham, W. J. (1957). Time lag in prey-predator population models. *Ecology*, 38:136-139.
- Ward, J. R., & Lafferty, K. D. (2004). The elusive baseline of marine disease: Are diseases in ocean ecosystems increasing? *PLoS Biol*, 2:0542–0547.
- Watson, J. & Estes, J. A. (2011). Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs*, 81:215–239.
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64:1540-1548.
- Wilson, K. C., & North, W. J. (1983). A review of kelp bed management in southern California. *Journal of the World Mariculture Society*, 14(1-4):345–359.
- Worm, B., & Lenihan, H. S. (2013). Threats to marine ecosystems: Overfishing and habitat degradation. In M. D. Bertness, J. F. Bruno, B. R. Sillman, & J. J. Stachowicz (Eds.), *Marine community ecology and conservation* (pp. 449–476).
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B., Lotze, H. K., Micheli, F., Palumbi, S. R., & Sala, E. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800):787–790.
- Zann, L., Brodie, J., & Vuki, V. (1990). History and dynamics of the crown-of-thorns starfish *Acanthaster planci* (L.) in the Suva area, Fiji. *Coral Reefs*, 9:135–144.