Direct and Indirect Effects
of Marine Protection:
Rockfish Conservation Areas as a Case Study

by

Ryan Nelson Cloutier

B.Sc. (Biology), Simon Fraser University, 2007

THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the

Department of Biological Sciences

Faculty of Science

© Ryan Nelson Cloutier 2011

SIMON FRASER UNIVERSITY

Fall 2011

Approval

Name: **Ryan Nelson Cloutier**

Degree: **Master of Science**

Title of Thesis: ***Direct and Indirect Effects of Marine Protection: Rockfish Conservation Areas as a Case Study***

Examining Committee:

           Chair: Carl Lowenberger, Professor

Dr Isabelle Côté
Senior Supervisor
Professor

Dr Andrew Cooper
Supervisor
Associate Professor

Dr Wendy Palen
Supervisor
Assistant Professor

Dr Anne Salomon
External Examiner
Assistant Professor, Resource and Environmental
Sciences, Simon Fraser University

Date Defended/Approved: December 2, 2011

Declaration of
Partial Copyright Licence

STATEMENT OF ETHICS APPROVAL

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

(a) Human research ethics approval from the Simon Fraser University Office of Research Ethics,

or

(b) Advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University;

or has conducted the research

(c) as a co-investigator, collaborator or research assistant in a research project approved in advance,

or

(d) as a member of a course approved in advance for minimal risk human research, by the Office of Research Ethics.

A copy of the approval letter has been filed at the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Simon Fraser University
Burnaby, BC, Canada

Last update: Spring 2010

Abstract

Fishing is one of the most pervasive anthropogenic stressors to the world's oceans. As a result, reversing declining trends in fish populations and restoring the health of the world's oceans will largely depend on the efficacy of future fisheries management. In 2002, Canada's Department of Fisheries and Oceans (DFO) announced the creation of a series of Rockfish Conservation Areas (RCAs), a type of marine protected area, along the coast of British Columbia, Canada. In this thesis I explore the direct and indirect consequences of RCAs in the Strait of Georgia. I found that RCAs currently harbour higher densities of rockfish than do ecologically equivalent unprotected areas but these differences in meso-predator numbers have not induced detectable effects at lower trophic levels (i.e., trophic cascades). This study is the first to assess on a large scale the effectiveness of this federal marine management strategy, implemented for a group of threatened species.

Dedication

"Life is about balance; stay balanced or you will eventually fall."

   - Frank Cloutier

I'd like to dedicate this work to my family and friends who truly make this life worth living. I appreciate all the support, laughter, adventure, growth, and love that we've shared together. Without you, this journey would be meaningless. In the time that I've spent at SFU working on my master's degree I've learned much more than just how to write a thesis; I've learnt about life, about passion, about sharing and about myself. The experiences I will remember most are hardly captured in the pages of this thesis. Instead, they are embodied in all of the people that I shared time with at SFU. Thank you to all those people. In closing, I will hesitantly say that I've come a little closer to keeping my balance.

Acknowledgements

This work would not have been possible without the help of many people; I am indebted to you all. I'd like to thank my senior supervisor, Dr. Isabelle Côté, for supporting me and encouraging me to do the best job possible. Your knowledge, experience, and patience have truly been beneficial and are clearly visible in the high-calibre of this thesis. I'd like to thank my supervisory committee, Dr. Andrew Cooper and Dr. Wendy Palen, for ongoing advice and guidance regarding complex ecological and statistical dilemmas. Funding for this project came largely from a partnership involving Isabelle Côté, the Canadian Healthy Oceans Network (CHONe), and NSERC. In addition to these funds, the Garfield Weston and BC Packers Ltd fellowship in Marine Sciences provided me with support for one year.

A special thanks goes out to my primary research assistants, Erika Grebeldinger and Kevin Swoboda, with whom I shared many amazing and unforgettable experiences above and below the water's surface. During the summer of 2009, Erika G. and I called the aging 'Pelagic' our beloved research vessel. We faced mechanical, navigational, and challenging dive conditions on a daily basis that always kept us on our toes. Despite these difficulties we persevered and accomplished a truly amazing amount of work. Erika, you were (and are!) a great diver and I thank you for your expertise, patience and dedication to the project. In 2010, Kevin joined me for yet another epic four-month field season, but this time we used the research vessel the 'C.J. Walters'. We weathered unpredictable challenges in the Gulf Islands, enjoyed hectic logistics in Howe Sound and had some of the best times in Sechelt working with my Dad and brother off of the O'Sea II. Kevin, I was lucky to have you as a 'dive-tec' and appreciate the skills, motivation, and laughs you brought to the project. Also, I thank my Dad and brother for all of their help during both field seasons.

The Earth2Ocean Group and Côté lab provided invaluable insight and feedback throughout the duration of this project. This group of researchers were especially helpful with regard to giving modeling advice, suggestions on presentations, and for knowing how to throw wicked parties! As a result of being surrounded by all these people I've become a more proficient scientist by gaining experience in experimental design, statistical analyses, writing, and project management. Finally, I thank Parks Canada, the

Table of Contents

List of Tables

List of Figures

List of Acronyms

AICc	Akaike information criterion corrected for small sample size
BMTs	Behaviourally-mediated traits
°C	Degrees celsius
CI	Confidence interval
cm	Centimeter
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CR	Consistency ratio
DFO	Department of Fisheries and Oceans
DISTLM	Distance-based linear model analysis
ESA	Endangered Species Act
GLMMs	Generalised linear mixed-effects models
GPS	Global positioning system
GI	Gulf Islands
HS	Howe Sound
IUCN	International Union for the Conservation of Nature
k	Degrees of freedom
km	Kilometer
m	Meter
MANOVA	(parametric) Multivariate analysis of variance
min	Minute
MPA	Marine protected area
N	Sample size
nMDS	Non-metric multidimensional scaling (plot)
PERMANOVA	Permutational analysis of variance
PERMDISP	Permutational analysis of dispersion
r	Correlation coefficient
R^2	Coefficient of determination
RCA	Rockfish Conservation Area
ROV	Remotely operated vehicle
SC	Sechelt
SD	Standard deviation

SIMPER	Analysis of similarity percent
VIF	Variance inflation factors
wi	Model weight

Chapter 1.

General introduction

Humans have been influenced by the world's oceans for millennia. We have depended on the oceans for a wide variety of goods and services (Holmlund and Hammer 1999; Jackson 2001; Worm et al. 2006) which once seemed inexhaustible. However, scientists and society alike are now beginning to understand that the oceans' resources are finite (see Worm et al. 2006 and Adger et al. 2005 for examples). This realization is prompting increased efforts, at local and regional scales, to assess and curtail human influences on the marine environment (Jessen et al. 2011).

Among the many anthropogenic stressors that affect the oceans today (e.g., pollution, agricultural run-off, coastal development, invasive species, aquaculture, global climate change, an ocean acidification; Lelieveld et al. 2001; Anderson et al. 2002; Walther et al. 2002; Halpern et al. 2008; Danovaro et al. 2011), fishing is arguably the most pervasive and damaging (Jennings and Kaiser 1998; Jackson et al. 2001). While fishing has been practised for thousands of years with seemingly little effect, its impact is now evident in oceans across the globe (Halpern et al. 2008). Recent advances in fishing technology (e.g., the advent of GPS navigation equipment, fish finders, larger, more efficient and mechanized gear, and increases in vessel size, power and capacity) coupled with our general inability to limit effort are largely responsible for the collapse of fisheries around the world. For example, the biomass of large predators (e.g., bluefin tunas, marlins, sharks, and codfishes) has decreased by 90% between ~ 1950-1990, coinciding with the onset of commercial long-line fisheries (Myers and Worm 2003; Ward and Myers 2005). In addition, the analysis of global fisheries landings from the same period indicates an overall shift from large-bodied, high trophic level species to smaller invertebrates and planktivorous fish species (Pauly et al. 1998), further indicating that current exploitation rates are unsustainable. However, the extent to which the mean trophic level of fisheries catches represents ecosystem mean trophic level is uncertain

(Branch et al. 2010) since either the addition of 'new' lower trophic level fisheries or the decline of existing high trophic level species would have the same expected result (Essington et al. 2006; Branch et al, 2010). Nonetheless, these examples serve to highlight deep concern about the fate of marine fisheries in general, and of stocks of predatory species in particular.

The removal of top predators by fisheries may have consequences that reverberate through marine communities, affecting non-target species indirectly. Trophic cascades, in which changes in the abundance of one species affect other species at two or more lower trophic levels away (Paine et al. 1980; Carpenter 1985), have been demonstrated in many ecosystems (Pace et al. 1999; Pinnegar et al. 2000; Shurin et al. 2002). In the marine environment, coastal ecosystems and benthic habitats may be particularly sensitive (Shurin et al. 2002). For example, the extirpation of sea otters in Alaska led to sharp declines in kelp forests via the increase of grazing sea urchin populations, which were released from sea otter predation (Estes and Palmisano 1974, but see Pinnegar et al. 2000 and Shurin et al. 2002 for reviews). Likewise, declines in abundance of large benthic predators (e.g. Atlantic cod, pollock, and redfish) associated with overexploitation of their stocks may have triggered a four-level trophic cascade in waters off the coast of Nova Scotia (Frank et al. 2005, Frank et al. 2011). Declines in groundfish landings coincided with increases in small pelagic fish and invertebrates, which led to increased predation on large zooplankton, which subsequently declined, leading ultimately to increases in phytoplankton biomass (Frank et al. 2005). While alternate explanations for both examples of trophic cascades have been offered (Greene and Purshings 2007; Steneck et al. 2002), they seem unlikely given the predictable effects that sea otter reintroductions have had (Steneck et al. 2002) and the extent to which changes in the biomass of cascading trophic levels are congruent with now increasing cod stocks (Frank et al. 2011).

The implementation of marine protected areas (MPAs), "clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley 2008), may provide a way to mitigate or even reverse some of the effects of fishing, and restore ecosystem health. Indeed, there is mounting evidence showing increased species abundance, biomass, richness, size,

and reproductive output of fishes and invertebrates inside MPAs (Alcala and Russ 1990; Polunin and Roberts 1993; Russ and Alcala 1996; Bohnsack 1998; Mosqueira et al. 2000; Côté et al. 2001; Gell and Roberts 2003; Harmelin-Vivien et al. 2008; Lester et al. 2009; Molloy et al. 2009). Reserves may also generate subsidies (e.g., increased catches and revenue for commercial fisheries from larval or adult spillover) beyond their boundaries (Roberts et al. 2001; Murawski et al. 2005; Goñi et al. 2006, 2009; Tupper 2007). In addition to direct effects, MPAs may also induce changes in ecosystem structure that stem from restored predator abundances (Babcock et al. 1999; Pinnegar et al. 2000; Shears and Babcock 2002; Salomon et al. 2009). However, predicting such indirect effects remains difficult since many factors may prevent or promote trophic cascades from occurring in marine ecosystems (Salomon et al. 2008; Shears et al. 2008). For example, increasing food web complexity, dietary breadth, recruitment variability, and the existence of thresholds and time lags can make detecting cascades a complex task (Hunter and Price 1992; Pinnegar et al. 2000; Baum and Worm 2009; Salomon et al. 2009; Babcock et al. 2010). Despite these large knowledge gaps, marine managers are increasingly recognizing the utility of marine reserves, which are now being implemented around the world (Spalding et al. 2008).

In Canada, the implementation of marine protected areas, and of marine reserves from which all forms of extraction are forbidden, has been slow (Jessen et al. 2011). However, in 2002, the Department of Fisheries and Oceans (DFO) announced the creation of a network of Rockfish Conservation Areas (RCAs) along the coast of British Columbia, as part of its commitment to a rockfish conservation strategy. The creation of RCAs, along with reducing catch quotas, accounting for all harvest mortality (targeted and bycatch), and improving stock assessments for these bottom fishes are the guiding tenets that will be used to rebuild depleted nearshore rockfish populations (Yamanaka and Lacko 2001; DFO 2002). Furthermore, in 2006 DFO launched the integrated fisheries management plan (IFMP) as a pilot program that reorganised how the groundfish fishing fleet is managed. Most notably, the introduction of transferable quota between all groundfish fishing vessels and 100% at-sea and dockside catch monitoring minimizes bycatch and promotes more sustainable fishing practices (Fraser 2008). The addition of the integrated fisheries management plan should effectively complement the rockfish conservation strategy.

In the Pacific northeast, nearshore rockfish (*Sebastes* spp.) have been harvested at modest levels as bycatch from the directed lingcod fishery that commenced in the 1860s (King 2001). However, recent advancements in fishing technology and an expanding market for rockfish, particularly the live rockfish fishery in Vancouver, created a higher demand during the ladder half of the 20th century (Love et al. 2002; Yamanaka and Logan 2010). This led to steep increases in the total landings of rockfish in BC, which peeked in 1990 at ~ 1800 metric tonnes (Yamanaka and Logan). As a result of growing concerns of overexploitation of rockfish stocks (DFO 2000; Parker et al. 2000; Yamanaka and Lacko 2001; Haggarty and King 2004; Yamanaka et al. 2004; COSEWIC 2009; Yamanaka and Logan 2010), DFO implemented a series of management actions that were intended to decrease rockfish fishing mortality, beginning in 1986 (e.g., vessel licensing, catch quotas, at-sea observer coverage, recreational bag limits etc., were introduced).

Nearshore rockfish share a number of traits that make them both susceptible to over-fishing and amenable for marine protection. They are slow growing, have a late age at maturity (e.g., ~ 6 – 20 years old when 50% of the population reaches sexual maturity), long lifespan (e.g., yelloweye can reach 120 years old) and attain large sizes (e.g., ~ 90 cm) (Love et al. 2002; Parker et al. 2000; Yamanaka et al. 2006), which increase their susceptibility to human exploitation (i.e., they have a low intrinsic rate of population growth; Jennings et al. 1998; Dulvy et al. 2003; Reynolds et al. 2005). However, nearshore rockfish are also highly sedentary and have relatively small home ranges (i.e., ~ 10 – 4000 m^2; Mathews 1990a, b; Tolimieri et al. 2009), which may make them amenable to protection by provision of spatial refuges such as MPAs, since they are less likely to across MPA boundaries. While RCAs are primarily being implemented to protect rockfish, they may also benefit lingcod, which are also large benthic predators (up to 150 cm) and occupy similar habitats (King 2001). Moreover, they reach sexual maturity at a young age (age 2 – 5; King and Withler 2005) and thus might respond rapidly to RCA protection, which could have negative effects on rockfish recovery. The commercial fishery for lingcod in BC began in ~ 1860 (King 2001) and was later closed in the Strait of Georgia in 1990 due to growing concerns of overexploitation, with some studies suggesting that lingcod biomass had declined by 95% compared to 1950-levels (Wallace et al. 2000). The loss of lingcod as a dominant predator and the associated ecological consequences may have been buffered by the presence of rockfish in the

system, which could have acted as functional equivalents. Rockfish may now be the major predators structuring rocky reef ecosystems in the absence of lingcod. However, this may not always be the case; when present, lingcod are important predators in rocky reef ecosystems (Frid and Marliave 2010). Nonetheless, the repercussions of declining rockfish stocks could be magnified and may carry substantial ecosystem consequences.

In this thesis I explore the direct and indirect effects of marine protection using Rockfish Conservation Areas as a case study. Chapter 2 consists of an assessment of the effectiveness of RCAs at rebuilding rockfish populations (i.e., direct effects). Specifically, I evaluate the effect of protection on rockfish abundance using underwater visual survey methods carried out in RCAs in three regions of the Strait of Georgia. Chapter 3 is devoted to characterizing the community composition of rocky reefs at protected and unprotected sites. I was specifically interested in determining if any changes in rockfish abundance detected in Chapter 2 were associated with altered community structure in ways that are consistent with trophic cascades (i.e., indirect effects). This study is one of the first to empirically document the progress of RCAs since their establishment in 2002, and hence provides the first estimates of whether or not RCAs are contributing to their stated goals of preventing further declines and rebuilding existing rockfish populations (DFO 2002; DFO 2007). Thus, the findings in this thesis have direct implications for management, and add to the growing body of knowledge surrounding the effects of marine protection, both direct and indirect, in temperate marine ecosystems.

Chapter 2.

Do Rockfish Conservation Areas Work?

Introduction

Fishing is one of the most pervasive and damaging anthropogenic stressors to the world's oceans (Jennings and Kaiser 1998; Jackson et al. 2001; Halpern et al. 2008). Its consequences range from reductions in species abundance, diversity and size to large-scale habitat loss and ecosystem phase shifts (Pauly et al. 1998; Jackson et al. 2001; Myers and Worm 2003; Dulvy et al. 2004; Worm et al. 2006; Frank et al. 2009; Salomon et al. 2009). As a result, reversing declining trends and restoring the health of the world's oceans will largely depend on the efficacy of future fisheries management.

While traditional fisheries management has largely focused on single species trajectories, more recent interventions have taken an ecosystem approach. This philosophy recognizes the importance of incorporating species interactions and the preservation of critical habitat into management objectives (Browman and Stergiou 2004; Pickitch et al. 2004; Levin et al. 2009). For example, no-take marine protected areas (MPAs) or marine reserves, where extraction is prohibited, provide refugia for depleted stocks to rebuild (Alcala and Russ 1990; Bohnsack 1998; Mosqueira et al. 2000; Côté et al. 2001; Gell and Roberts 2003; Lester et al. 2009; Molloy et al. 2009) while preserving sensitive habitat and ecosystem function. This form of management is fundamentally different from the single-species focus as it is premised on the notion that intact, whole ecosystems function better and are worth more than the sum of their parts (Browman and Stergiou 2004).

Rockfishes (*Sebastes* spp) are iconic species of the Pacific coast of North America. Species in this highly diverse genus vary widely in morphology, coloration, maximum age and size as well as the depth ranges and habitats they occupy. However, many species share life-history characteristics such as slow growth, late age at maturity, long lifespan and attain large sizes (Love et al. 2002) that make them vulnerable to human-exploitation (Jennings et al. 1998; Parker et al. 2000; Dulvy et al 2003; Reynolds et al. 2005; Yamanaka and Logan 2010). Indeed, numerous rockfish species are listed as imperilled by the International Union for Conservation of Nature (IUCN), the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and by the Endangered Species Act (ESA) in the United States (Table S2.1).

In an effort to curb the decline of inshore rockfishes (DFO 2000; Parker et al. 2000; Yamanaka and Lacko 2001; Haggarty and King 2004; Yamanaka et al. 2004; COSEWIC 2009; Yamanaka and Logan 2010) and to guard against scientific uncertainty in stock assessments, the Canadian government committed to a federal rockfish recovery plan in 2002 (DFO 2002). This strategy included reducing catch quotas, accounting for all harvest mortality (targeted and bycatch) and improving stock assessments for these bottom fishes (Yamanaka and Lacko 2001; DFO 2002). It also included the establishment of Rockfish Conservation Areas (RCAs) along the coast of British Columbia (DFO 2007). Rockfish Conservation Areas are a type of marine protected area designed to protect inshore rockfishes (i.e., Quillback *S. maliger*, Copper *S. caurinus*, Tiger *S. nigrocincus*, China *S. nebulosus* and Yelloweye *S. rubberimus* rockfish) and their habitat. Both commercial and recreational activities that target inshore rockfish are prohibited inside RCAs. This includes all bottom trawling gear (except scallop trawls, which reportedly do not fish in RCAs) and numerous types of directed hook and line fisheries, which effectively results in the protection of benthic habitats in RCAs (DFO 2007). However, nearly a decade after establishment there is still no systematic monitoring program in place to evaluate the effects of the 164 RCAs currently in place.

The aim of this study was therefore to examine the effectiveness of RCAs (relative to unprotected sites) at rebuilding shallow-water rockfish populations in the Strait of Georgia, British Columbia, Canada. I quantified effectiveness by comparing the presence/absence, as well as the density when present, of rockfish species in and out of

RCAs. I accounted for the contributions of other important biotic and abiotic environmental variables as well as their interactions in both analyses so as to disentangle, as best as possible, the effect of protection from other variables such as rugosity, kelp and boulder cover, depth, and geographical location.

Materials and Methods

Study regions and sites

I conducted scuba-based assessments of the abundance of rockfish within RCAs and at adjacent, ecologically equivalent unprotected sites in the Strait of Georgia. All sites were surveyed over a two-year period, between June and October in 2009 and 2010. The sites were located in three different regions in the Strait of Georgia: The Gulf Islands, Howe Sound and Sechelt (Figure 2.1). These regions have different oceanographic regimes characterized by varying currents and levels of primary productivity. High freshwater influx and little tidal mixing combine to boost annual primary productivity in both the northern and central Strait of Georgia (i.e., in Sechelt and Howe Sound, respectively), while waters around the Gulf Islands are less productive (Yin et al. 1997; Masson and Peña 2009). Moreover, fishing pressure or disturbance levels may also differ among the regions. The inclusion of these three areas allowed me to quantify potential regional effects on density and on the strength of rockfish recovery (i.e., through the inclusion of interactions terms in the modeling process).

A total of 15 different RCAs and associated control (i.e., unprotected) sites were selected (five per region), primarily to maximize the range of duration of protection (Table 2.1). Within each site, two locations were chosen, which were in predicted 'good' rockfish habitat according to the rockfish habitat model of Parks Canada - the federal agency responsible for national parks. This model attempts to identify and map suitable rockfish habitat by combining select seafloor features (e.g. slopes, depressions and ridges) with areas of high rugosity (defined as the fourth quartile of log-transformed values) using bathymetric data generated on a 25 m grid and the Benthic Terrain Modeller tool in ArcGIS (see Lundblad et al. 2006). Note that the Department of Fisheries and Oceans Canada (DFO), the agency responsible for RCAs, used a similar model to identify potential locations during the RCA establishment period. The maps

produced by the two models are generally similar; however, because the Parks Canada model used higher resolution bathymetric data (e.g., multibeam bathymetry data when available) and did not use CPUE data as a surrogate for rockfish habitat (Yamanaka and Logan 2010), it was more suitable for selecting study locations. Hence, I produced a haphazardly generated list of potential survey locations in predicted 'good rockfish habitat' for each site, and surveyed the first two that met or exceeded the minimum habitat requirement of having continuous cobble with sparse boulders or continuous bedrock upon initial inspection of the site (i.e., I searched a circular area with diameter ~ 10 m^2 to determine if it was suitable for inclusion in this study). Restricting site selection to those sites of adequate habitat suitability was an attempt to minimize the influence of habitat quality on rockfish density, however since rugosity, percent cover of boulders and kelp, region, and depth are accounted for in the models, variation in these metrics should not have biased the estimates of the effect of protection.
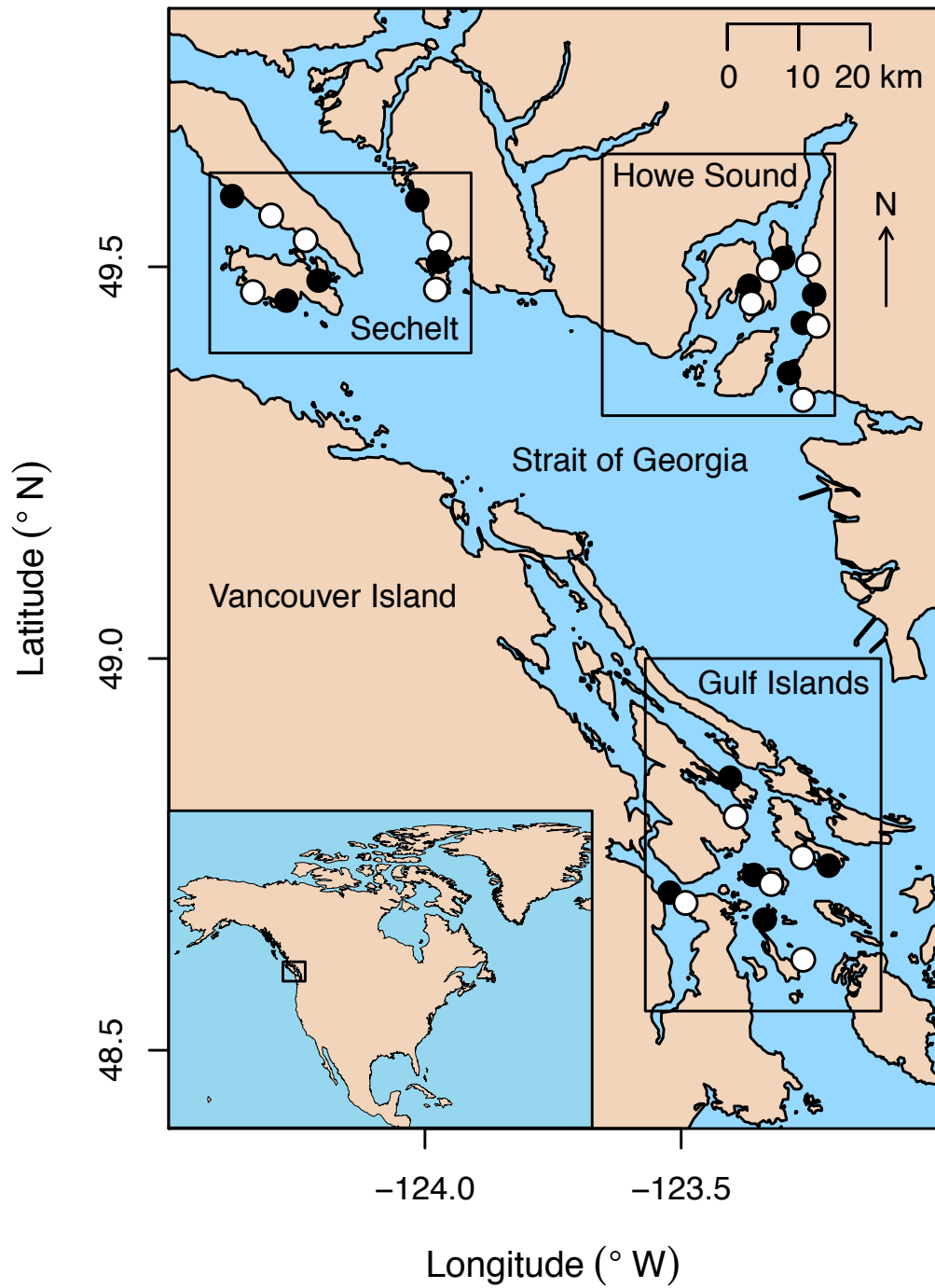
Figure 2.1. The Strait of Georgia, British Columbia, Canada, with the three focal geographic regions examined in this study. The locations of Rockfish Conservation Areas (black dots) and unprotected sites (white dots) are shown.

Table 2.1.   Summary information for the 15 RCAs surveyed in this study.

Geographic region	Rockfish Conservation Area	Area km²	Year of protection	Year of survey	Duration of protection	Protection duration category
Gulf Islands	Bedwell Harbour	2.5	2002	2009	7	Old
	Portland Island	3.0	2002	2009	7	Old
	Brethour Islands*	18.8	2004	2010	6	Old
	Patey Rock	0.9	2007	2010	3	Young
	Prevost Island	9.1	2007	2010	3	Young
Howe Sound	Bowyer Island	3.2	2004	2009	5	Old
	Lions Bay	4.8	2007	2009	2	Young
	Pam Rock	5.7	2004	2009	5	Old
	West Vancouver	2.8	2007	2010	3	Young
	Upper Centre Bay	1.1	2007	2010	3	Young
Sechelt	Lasqueti Island South	18.5	2004	2009	5	Old
	Thormanby Island	3.3	2004	2009	5	Old
	McNaughton Point	2.2	2004	2009	5	Old
	Davie Bay	10.2	2007	2010	3	Young
	Sabine Channel Islands	22.4	2007	2010	3	Young

* The portion of the Brethour Islands RCA that was surveyed has been protected since 2004; at that time the RCA was 7.79 km².

Fish and benthic surveys

At each site I performed a total of eight belt transects (25 m long x 4 m wide) (four transects in each of two locations per site) to survey fish at depths from 8 to 15 m (chart datum). Search effort was standardized by controlling swimming speed (3 – 4 m•min^{-1}). I recorded the species and length (visual assessment, to nearest cm) of each rockfish encountered. To minimize the potentially confounding effect of varying fish detectability throughout the survey period (due to changes in fish behaviour and activity levels, and water visibility), half of the surveys at each site were carried out in early summer (June – early August) and the remaining during early fall (late August – October). Water temperature ranged from 8 to 14 °C and visibility from 4 m to 25 m. Visibility was recorded as the maximum distance at which two divers could see each other's hand signals while wearing white gloves.

I assessed three habitat variables (rugosity, kelp and boulder cover) along each transect since they have been shown to be important determinants of rockfish density (Table 2.2). Substratum rugosity was measured three times at random locations along each transect using a 5 m-long beaded stainless steel chain. The chain was draped

over the substratum so as to conform to surface irregularities, and the linear distance between the ends of the chain was recorded. Rugosity was calculated as the ratio of the chain's total length to the linear distance measured; a ratio of 1 indicates a flat surface, while ratios > 1 indicate more complex substrata. Kelp cover and boulder cover were determined using 1 m^2 quadrats placed at 15 random positions along each transect. Kelp cover (mainly the genera *Laminaria*, *Nereocystis*, *Macrocystis* and *Pterygophora*) was estimated visually and recorded as a percentage for each quadrat and used as a proxy for biotic structure. In contrast, the percent cover of boulders was estimated for each transect as the proportion of quadrats with boulders as the dominant substratum type. Boulders were defined as rocks of > ~ 30 cm diameter and the dominant substratum type was identified as that occupying the largest area of any given quadrat. The mean transect-level rugosity, kelp cover, and boulder cover was calculated and used in the analyses.

Data analysis

I evaluated the effectiveness of RCAs using two different response variables: rockfish presence and rockfish density. I examined rockfish presence by converting the count data into a binary response variable (presence or absence) (N = 192 transects). In contrast, the analysis of rockfish density considered non-zero counts as the response variable (N = 157 transects). Transects with no rockfish present were removed from the density analysis to avoid problems of zero-inflation and thus parameter estimates are contingent on rockfish being present at a site (Zuur et al. 2009). I conducted an exploratory analysis to remove outliers, detect multicollinearity and identify the variables that best explained rockfish density across sites. Prior to modelling, some variables were standardized to facilitate the comparison of all parameters and to aid in the interpretability of main effects in the presence of interaction terms (Gelman 2008; Shielzeth 2010; see below). I then evaluated the relative importance of protection, region, and the variables identified in the exploratory step in explaining the presence or density of rockfish by comparing multiple generalised linear mixed-effects models (GLMMs) using the Akaike Information Criterion (corrected for small sample size, AICc). Table 2.2 lists all the fixed effects that were estimated using identical random structures (i.e., transects (8) nested within sites (30)). Results for both analyses are presented as model-averaged parameter estimates with the 95% unconditional standard errors as

calculated from standardized data (Burnham and Anderson 2002; Anderson 2008; Gelman 2008). This approach allowed me to examine which variables are useful predictors of rockfish presence and density at average conditions.

An initial exploration of the data allowed me to reduce the number of potential explanatory variables. I omitted some variables (e.g. month, visibility, search time and tidal height) because dotcharts and boxplots showed no trend with rockfish counts, which suggests that they will have little explanatory power and can be dropped from the analysis (Zuur et al. 2009). The boxplots also revealed three data points as outliers. These points were removed prior to further analyses because they were clearly unrepresentative of the rest of the data (i.e., they were up to ~ 9 times larger than the average count) and could have exerted undue leverage on the results (Zuur et al. 2009). I checked for multicollinearity using variance inflation factors (VIF) and pairwise correlation plots. All VIF scores had values below two, indicating that the assumption of non-collinearity was met (Zuur et al. 2009). Pairwise correlation coefficients (r) of all continuous variables were below the recommended threshold (r = 0.6) and thus no further variables were excluded from the analyses (Zuur et al. 2009). A final list of the seven predictors used in my analyses is shown in Table 2.2, along with *a priori* predictions of the direction of correlations with rockfish presence and density. Note, that my goal was not to model all the factors that may influence the distribution of rockfish; instead, it was to assess the effect of protection (2 metrics: RCA protection and protection duration; see Table 2.2) while still accounting for the contribution of other variables (e.g., rugosity, kelp and boulder cover, depth and geographic region). Thus, the Results and Discussion focus mainly on protection metrics and, to a lesser extent, on another few biologically relevant variables (i.e., rugosity and geographic region).

Table 2.2.   A priori predictions of the influence of seven variables on rockfish presence or density.

Variable	Metric	Variable type	Justification for inclusion	Expected correlation	References
Region	mean annual chlorophyll (mg/m^3)*	categorical: HS, SC, GI	Primary productivity differs by region and may influence fish biomass and recovery rate	HS = SC > GI **	Ware and Thomson 2005; Masson and Peña 2009
Rugosity	ratio of chain length to linear distance measured	continuous: 1.0 - 1.6	Complex habitats provide more shelters and food and can foster higher fish densities	positive	Love et al. 2002; Alvarez-Filip et al. 2009
Boulder cover	percentage of benthic cover	continuous: 0 - 100	Inshore rockfish have a known affinity for habitats with large boulders	positive	Richards 1987; Johnson et al. 2003; Love et al. 2002; Murie et al. 1994; Marliave and Challenger 2009
Kelp cover	percentage of benthic cover	continuous: 0 - 98	Several *Sebastes* spp associate with kelp	positive	Love et al. 1991; Love et al. 2002
Depth	datum depth of transect	continuous, range: 8 - 15 m	Fish abundance can vary with depth depending on fish demographics	positive or negative	Love et al. 2002
Protection status	unprotected or protected	categorical: 0 and 1	Reduced fishing pressure on target species can lead to increased fish density	positive	Mosqueira et al. 2000; Côté et al. 2001; Gell and Roberts 2003; Lester et al. 2009
Protection duration	control, young and old RCAs	categorical: 0 years, 2-3 years, 5-7 years	Relative improvements in fish density have been shown to increase with longer protection intervals	positive	Claudet et al. 2008; Molloy et al. 2009

*Note that mean chlorophyll density wasn't analysed per se, but was used to generate predictions about expected differences in rockfish abundance among regions
**GI = Gulf Islands, HS = Howe Sound, SC = Sechelt

Several variables (i.e., rugosity, percent boulder, percent kelp, and depth) were standardized (i.e., centered and scaled) prior to analysis, following the recommendations of Gelman (2008). First I centred the data, by subtracting the global mean from each value, and then scaled it, by dividing by two times the standard deviation (SD). This procedure has two main benefits. First, centering the data causes each parameter to be estimated while all others are at their mean values (which adds biological context when variables can never have a value of zero i.e., depth and rugosity). The centered estimate can be interpreted independently from any interactions it may be involved in. This is because centering has decoupled the correlation between the intercept and slope (see Shielzeth 2010), hence main effects have direct meaning regardless of presence of

interaction terms. The second benefit is derived from the scaling procedure. Traditionally, the parameter estimates represent the expected change in the response given a one unit change in the covariate. Because covariates are often on different scales and can have very different ranges, a direct interpretation of the parameter estimates is not possible. Scaling by two standard deviations puts all variables on a common scale so that each can be directly compared to each other (Gelman 2008). Thus, overall, the parameter estimate for protection status can be interpreted as the effect of RCA protection on rockfish density when rugosity, percent kelp, percent boulder, and depth are at their average values (global means).

I initially combined six variables (only one protection metric was allowed per model) in all possible ways (additive combinations plus all two-way interactions). However, because this resulted in a very large number of models, many of which would have likely generated spurious results, I reduced the candidate model set based on the ratio of data points to the number of parameters estimated in each model. As a basic rule of thumb, it is acceptable to estimate one parameter for every 10 data points (Anderson 2008; Grueber et al. 2011). I therefore eliminated models for which this ratio was less than 10 (i.e. $N/k \geq 10$, where N is the sample size and k is the degrees of freedom) to remove models that over-fit the data. I also considered biologically plausible second-order interactions (see Table S2.2 for complete list), but did not include higher-order interactions because these are often difficult to interpret (Zuur et al. 2009) and because I had no *a priori* predictions about these interactions. The candidate model set including protection status was identical to that including duration of protection (i.e., each protection metric was present in the same number and combinations of models). The two candidate model sets were then combined into a single set for AICc analyses.

I opted for a generalised linear mixed-effect model (GLMMs) framework. This modeling technique was well suited to the hierarchical structure of my data (i.e., transects are nested within site) and permitted the specification of a non-normal error distribution when appropriate. The inclusion of random effects (i.e., site) allowed me to account for spatial autocorrelation, minimize the loss of degrees of freedom and most importantly, expand the conclusions from the models to other RCAs in these regions (Lai and Hessler 2004; Bolker et al. 2009; Zuur et al. 2009; O'Hara and Kotze 2010). All GLMMs were then compared using Akaike Information Criterion (corrected for small

sample size, AICc; Bolker et al. 2009; Grueber et al. 2011). With AICc, the best-supported model has the lowest score (Burnham and Anderson 2002; Anderson 2008). I accounted for model selection uncertainty, i.e. when no single model has overwhelming support (wi >0.90; see Results), by calculating the averaged parameter estimates and the unconditional standard errors. This was achieved by selecting the models in which the variable of interest appeared, renormalizing the model weights, and then summing the product of the model weight and the parameter estimate (Burnham and Anderson 2002; Anderson 2008; Grueber et al. 2011). Finally, I plotted the averaged parameter estimates and the 95% unconditional confidence intervals for all variables, in separate plots for each of my two rockfish response variables. Individual parameter weights were not calculated because parameters were not present in an equal number of models, and thus prohibited a fair comparison of the resulting parameter weights.

For the density analysis, I present some estimates as back-transformed (i.e., using the inverse natural logarithm) values in the text to facilitate their interpretation (e.g., to allow me to state 'there were x more rockfish in protected areas given average environmental conditions). In addition, I provide the pseudo-R^2 values, which were derived from the regressions of the observed data (i.e., rockfish counts, on the y-axis) versus the predicted values (derived from each model, on the x-axis) and provide a measure of how much of the variation in the count data is explained by the models (see Piñeiro et al. 2008 for details). For the presence/absence analysis, parameters of logistic regressions cannot easily be handled in the same way. They were therefore not back-transformed nor were the pseudo-R^2 values examined (Mittlbock and Schemper 1996; Menard 2000).

Results

The complete set of averaged parameter estimates for the models of rockfish presence/absence and of rockfish density are shown in Table S2.2 and Figure S2.3. However, for the purpose of this chapter I will focus on a smaller subset of these parameters. Details of the top models are presented in Tables S2.6 and S2.7 and show that no model obtained overwhelming support in either analysis, reemphasizing the need for a parameter averaging approach.

Rockfish presence or absence

Rockfish Conservation Areas were not more likely to harbour rockfish than unprotected sites, when all other variables are held at average conditions (Figure 2.2). The same held for young and old RCAs, when compared to unprotected areas. However, in all three cases, the central tendency of the effect of protection is positive (Figure 2.2; Table S2.2). Rugosity was the only predictor that was strongly correlated with rockfish presence/absence, indicating that rockfish are more likely to be present at sites with high rugosity (Figure 2.2). Finally, rockfish were equally likely to be present in all three geographical regions studied (Figure 2.2; Table S2.2). The negative interaction between RCA protection and rugosity (RCA protection*Rugosity) suggests that the effect of RCA protection on occurrence is less pronounced in high rugosity sites; however, the interaction is associated with much uncertainty.
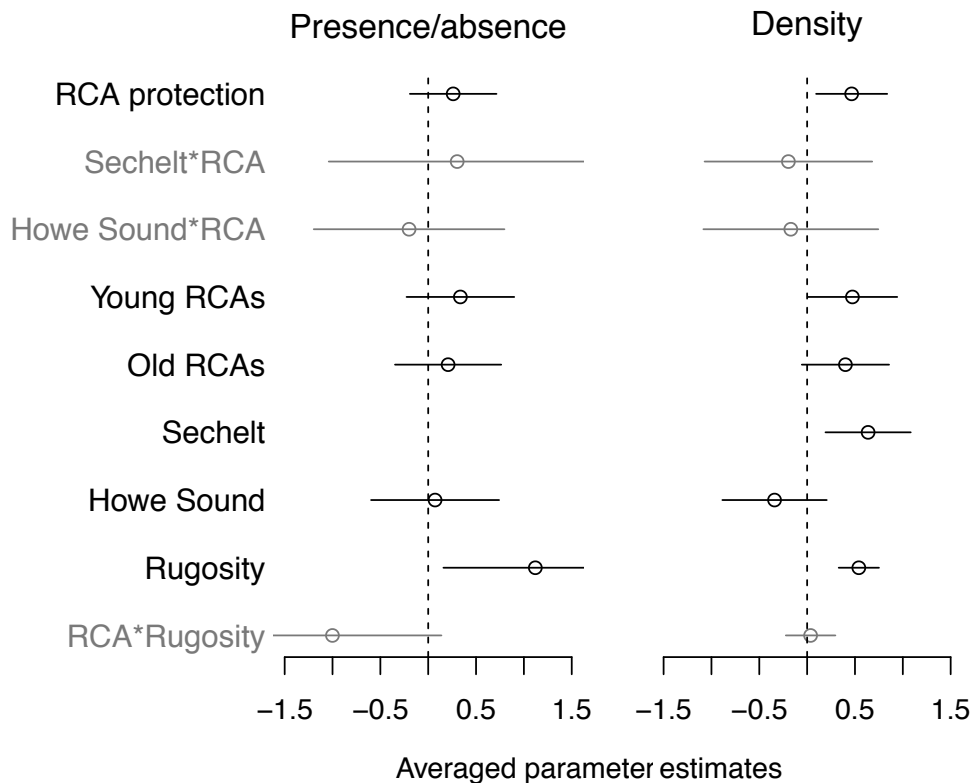
Figure 2.2. *Standardized model-averaged parameter estimates and unconditional 95% confidence intervals for models of rockfish presence/absence (left) and density (right). Black type indicates main effects; grey type indicates interactions. Parameter estimates represent the effect of each variable on the response going from -2SD to +2SD from the mean while all other variables are at their mean or baseline values (see Methods). Table S2.2 and Figure S2.3 show all effects. The parameter estimate for Sechelt lies outside the scale shown.*

Rockfish density

There was a positive effect of RCAs on the density of rockfish: RCAs had on average 1.6 times (95% CI = 1.1x – 2.3x) more rockfish within their boundaries than unprotected areas when all other variables were at average conditions (Figure 2.2; Table S2.2). There was no obvious effect of duration of protection as 'young' and 'old' RCAs had rockfish densities that were 1.5 times (1.0 – 2.6) and 1.6 times (0.94 – 2.4) higher, respectively, than unprotected areas, although the prediction associated with 'old' RCAs is slightly less certain (Figure 2.2; Table S2.2). There were regional differences in

rockfish density. Sechelt had 1.9 times (1.2 – 3.0) more rockfish than the Gulf Islands (the baseline region) while the central tendency for Howe Sound suggests lower densities (0.71 time fewer rockfish; 0.41 – 1.2). There was strong evidence for a positive correlation between rugosity and rockfish density. Rockfish density increased by a factor of 1.7 (1.4 – 2.1) from transects with the lowest to highest recorded substratum rugosity in this study. Finally, the effect of protection on rockfish density was similar across regions, as evidenced by the parameter estimates for the protection by region (RCA*Region) interactions (i.e., the error associated with each estimate is large), and it did not interact with rugosity (Figure 2.2; Table S2.2).

Discussion

This study is the first study to empirically document the effectiveness of Rockfish Conservation Areas at rebuilding nearshore rockfish populations in British Columbia. My data show that after 2 – 7 years of protection, rockfish densities are 1.1 – 2.3 times higher in BC's RCAs. Marliave and Challenger (2009) had previously reported no effect of protection on rockfish density using a comparison of sites from one RCA (~ 2 years old) to several unprotected sites that were chosen because they were not in predicted 'good' rockfish habitat. However, my conclusions differ substantially. Using an expanded dataset of 15 RCAs and 15 control areas (eight transects per site), all in confirmed rockfish habitat, in three different geographical regions in the Strait of Georgia, I found that rockfish density is on average 1.6 times higher in RCAs than in unprotected areas while still accounting for habitat variables such as boulder and kelp cover, geographical region, depth, and rugosity (and many other associated interactions; see Table S2.2). My results also suggest geographical differences in rockfish density and a strong effect of substratum rugosity on both rockfish presence/absence and on density. The presence or absence of rockfish in an area was not associated with either protection metric or any other factor examined.

More rockfish in protected areas

There are four direct mechanisms by which rockfish densities could be higher in protected than unprotected areas: (1) through relatively higher recruitment or

immigration of rockfish in protected boundaries, (2) through relatively higher mortality of rockfish in unprotected areas, (3) through an initial bias in RCA site selection (i.e., there were already more rockfish at sites that became RCAs), (4) or through a combination of all processes. The possibility of higher recruitment is unlikely for two reasons. First, the observed effect of protection occurred after only two to seven years of implementation. Rockfish have slow life histories, with characteristics such as slow growth and late maturity (Love et al. 2002; Yamanaka et al. 2006), which are not congruent with rapid population increases (Mosqueira et al. 2000; Molloy et al. 2009). For instance, many of the copper and quillback rockfish observed in RCAs were sub-adults or adults (e.g. 15 – 25 cm total length), which would have likely been already present at the time of RCA implementation. Second, larval rockfish released in an area do not necessarily recruit locally. For example, the analysis of elemental otolith signatures revealed that juvenile rockfish (kelp *S. atrovirens* and black *S. melanops*) off the coast of California and Washington were recruited 10s – 100s km away from where parturition occurred (Miller and Shanks 2004; Standish et al. 2011). This is largely attributed to the extended larval pelagic phase common to all rockfish, which lasts between 2 – 6 months depending on species (Moser and Boehlert 1991; Ralston and Howard 1995; Love et al. 2002). However, oceanographic conditions, water temperature, and larval behaviour may also enhance or restrict dispersal distances (Miller and Shanks 2004). At present, without genetic information, it is not clear to what extent RCAs in the Strait of Georgia might be self-seeding. Finally, population densities could also be higher if adult rockfish immigrate into protected areas, although this is unlikely since rockfish are known to have small home ranges (i.e., 10 – 4000 m^2; Mathews 1990a, b) and can be very sedentary and site-attached as adults (Hixon et al. 1991; Tolimieri et al. 2009). However, in poorer habitat (e.g., low relief areas) rockfish have been observed to have larger home ranges (Mathews 1990a, b; Love et al. 2002), and thus may be more likely to displace from these areas. Depending on the relative difference in habitat quality between RCA and unprotected sites, rockfish movement in to RCAs may contribute to the positive effect of RCA protection. A more thorough investigation of rockfish movement patterns is needed in order to quantitatively assess the importance of post-settlement immigration/emigration of adult rockfish in and out of RCAs.

Alternatively, rockfish densities may appear to be higher inside of RCAs not because fish have accumulated within these protected areas but because populations in

unprotected areas have been depleted. It is clear that fishing pressure on rockfish was historically high in BC. For example, an estimated ~ 1800 metric tonnes of quillback and yelloweye rockfish were landed in the commercial fisheries and ~ 155 thousand individual rockfish were caught by recreational fishers in BC in 1990 (Collicutt and Shardlow 1992; Yamanaka and Logan 2010). While landings have been substantially reduced (by ~ 80% and 97% respectively; data taken from Yamanaka and Logan 2010; Zetterberg and Carter 2010) in the last ~ 20 years, fishing effort is likely to still be high in relation to rockfish life histories and their current stock status.

If the effect of protection is occurring without any contribution of enhanced recruitment or immigration but solely because unprotected rockfish populations are increasingly depleted, it would mean that RCAs may be effective at stopping the decline of rockfish within their boundaries, but that they may be failing, at least so far, to achieve their goal of rebuilding inshore rockfish populations within RCAs. Differences in size frequency distributions of rockfish between protected and unprotected areas would help to distinguish between these alternative scenarios. More specifically, a contribution of enhanced recruitment is expected to be manifested as a relatively higher frequency of small size classes of rockfishes in protected areas. However, visual inspection of size class distributions revealed no such pattern (Figure S2.4). In fact, there appears to be more small rockfish (0-5 cm) in unprotected areas. This may be a result of 'better' juvenile rockfish habitat occurring outside of RCAs or from increased predation on the smallest size class rockfish in RCAs (from either lingcod or rockfish or a combination of both). While it is clear that rockfish densities are higher inside RCAs, further research is required to determine if rockfish are indeed cannibalizing their young more often in protected sites. In contrast, a preliminary assessment of lingcod densities revealed that they are not more abundant in RCAs (R.Cloutier, unpublished data), which suggests that they are not responsible for generating the observed differences in juvenile rockfish. Perhaps lingcod have not benefitted from RCAs because their home ranges are larger than those of rockfish and as a result, lingcod spend less time within the protected boundaries (see Tolimieri et al. 2009 for a discussion of rockfish and lingcod home range sizes). An analysis of lingcod density that included 'RCA size' as a covariate might reveal whether or not this hypothesis has merit. Finally, it remains possible (though unlikely given my sample size and method for site selection) that groundfish fishing

21

pressure was particularly elevated in the sites selected as controls. If this is the case, then the partial success of RCAs documented here is an artefact of a control area bias.

The best way to show a definite effect of marine protection is by means of comparisons between pre- and post-reserve establishment. Before-After-Control-Impact (BACI) designs can effectively control for spatial and temporal variation in the abundance of the taxa of interest. However, most studies of marine protected areas, including the present one, do not use this design (see Osenberg et al. 2006; Lison De Loma et al. 2008), largely because of the lack of pre-establishment data. In the present study, differences owing to spatial habitat variation were minimized by using rigorous criteria for site selection and by modeling *a priori* rockfish covariates. However, it is still possible that pre-existing differences influenced the results of this study. For example, RCA site selection was non-random and may have consisted of areas that already had higher rockfish densities, thereby promoting the detection of an RCA effect. In addition, temporal variation, such as changes in the strength of predation, competition, and reproductive success (acting both on rockfish and other predator/prey species of rockfish), could have also influenced the results. For these reasons BACI designs are desirable and are one of the best ways to assess the effects of marine protection in light of potential confounding factors.

A final caveat in the interpretation of these results is that this study was conducted in relatively shallow depths. The rockfishes considered in this study occupy depths that range from barely subtidal to more than 500 m, in the case of Yelloweye rockfish (Love et al. 2002). Thus the depths I surveyed represent, in some cases, a small fraction of the total habitat potentially used. The effectiveness of RCAs at deeper depths remains unknown. It is possible, for example, that a depth refuge may exist in unprotected areas whereby rockfish can escape some recreational fishing pressure. If this is the case, then the inclusion of deeper sites would be expected to reduce the relative difference in rockfish density between protected and unprotected areas. Alternatively, if protection allows the persistence of older rockfish, which generally move deeper with age (Love et al. 1991), including deeper depths would enhance the RCA effect. Knowledge of fisher behaviour, detailed catch records (indicating fished depths), and the use of a Remotely Operated Vehicle to carry out deeper fish surveys may provide further insights regarding these hypotheses.

The importance of suitable habitat

At a large scale, differences in rockfish density emerged between geographic regions. I had predicted that these differences would mirror regional differences in primary productivity (Ward and Thomson 2005; Masson and Peña 2009), but this was not the case. Rockfish density in the Gulf Islands – the region with the lowest primary productivity estimate – was expected to be lowest, yet it was intermediate between that of Sechelt and Howe Sound, two regions with higher productivity. Other factors that vary regionally must have a larger impact on rockfish density. Possible candidates include historic and present-day fishing levels (commercial, recreational, First Nations, and illegal), the prevalence of predators (e.g., killer whales, seals, seabirds), and disease.

At a smaller scale, substratum rugosity, a proxy for habitat complexity, correlated strongly with both rockfish presence and density. Several other studies have reported this association (Richards 1987; Love et al. 2002; Johnson et al. 2003; Murie et al. 1994; Marliave and Challenger 2009). Rugosity could be important for rockfish because more complex sites may offer more or better shelter from predators and/or also provide more resources such as higher prey availability (Alvarez-Filip et al. 2009). Interestingly, neither rockfish presence nor density was strongly associated with the extent of boulders, which is a habitat association that has also been widely documented (Love et al. 2002; Marliave and Challenger 2009). It is possible that the method used to derive the percent cover of boulders had low resolution and did not capture the true importance of boulders for rockfish. In contrast, kelp cover was measured using a standard technique, which would have had better resolution for detecting differences in percent cover between transects and thus detecting an effect of kelp. A negative association of kelp cover and rockfish density emerged, which is surprising given that other studies have documented the opposite (Love et al. 1991; Love et al. 2002). I can think of no biologically reasonable explanation for this effect and suspect that some other 'hidden' covariate may have also been captured causing a spurious result. Finally, it is worth mentioning that the majority of transects had low kelp and boulder cover; thus, the paucity of transects with high kelp and boulder cover may be restricting the evaluation of these variables (i.e. there was not sufficient contrast in these predictor variables to detect their true effects).

The role of habitat complexity for predicting both rockfish presence and density highlights the critical importance of appropriate siting for the long-term success of RCAs. However, the extent to which the best rockfish habitat is represented in RCAs remains unclear. The process of site selection during this study allowed a preliminary evaluation of the accuracy of a rockfish habitat model, similar to that used during RCA establishment, at predicting good rockfish habitat. My tentative conclusions are that, at least in some RCAs, much of the habitat is sub-optimal and the rockfish habitat models have much room for improvement. However, it is clear that the locations of RCAs represent a trade-off between biological requirements and socio-economic impacts, and that compromises were necessary given DFO's tripartite mandate to support First Nations treaty rights, economic development, and marine conservation (Yamanaka and Logan 2010; http://www.dfo-mpo.gc.ca/us-nous/vision-eng.htm).

In conclusion, RCAs currently harbour higher densities of rockfishes (nine species evaluated; see Table S2.5) than unprotected areas, but the reasons for this pattern are unclear. They could stem from enhanced rockfish densities within RCAs or lower densities outside of protected boundaries. My results also suggest that habitat complexity (i.e. substratum rugosity) is important for predicting rockfish presence and density in the Strait of Georgia. I recommend that future work to evaluate the effectiveness of RCAs include mandatory baseline (pre-establishment) monitoring of all future RCAs and a thorough assessment of rockfish habitat models. Measuring the recovery (or lack thereof) of inshore rockfishes in RCAs is an essential part of assessing a federal marine management strategy which was implemented for these threatened species.

Chapter 3.

Community Impacts of
Rockfish Conservation Areas

Introduction

Marine protected areas (MPAs) have been implemented around the world to help rebuild
exploited stocks and to protect sensitive habitats (Côté et al. 2001; Spalding et al. 2008).
Although evidence of their effectiveness at enhancing fish populations continues to
accumulate (Alcala and Russ 1990; Bohnsack 1998; Mosqueira et al. 2000; Côté et al.
2001; Gell and Roberts 2003; Russ and Alcala 2003; Lester et al. 2009; Molloy et al.
2009), it is becoming clear that not all fish species respond to protection in the same way
or at the same rate (Mosqueira et al. 2000). For example, fish species targeted by
fishing generally respond more strongly to protection than do non-target species
(Polunin and Roberts 1993; Chapman and Kramer 1999; Tretreault and Ambrose 2007).
These species tend to be large-bodied and occupy high trophic levels (Pauly et al. 1998;
Mosqueira et al. 2000). Thus the target of marine protection is often focused on
predator populations, which can alter food web structure and interactions within MPA
boundaries (Pinnegar et al. 2000; Watson et al. 2007; Salomon et al. 2009).

Any protection-induced increases in the abundance of species occupying high
trophic levels could have effects that reverberate throughout the community. Trophic
cascades, in which changes in the abundance of one high-level species affect species at
two or more lower trophic levels (Paine 1980; Carpenter et al. 1985), have been
demonstrated in many ecosystems (Pace et al. 1999; Pinnegar et al. 2000; Shurin et al.
2002). Perhaps the most famous example of a marine trophic cascade is that arising
from sea otter extirpation in Alaska, which led to sharp declines in kelp forests via the
increase of grazing sea urchin populations, which were released from sea otter
predation (Estes and Palmisano 1974). However, cascades are not always triggered by

changes in predator abundance, and predicting the circumstances, interaction pathways and final community composition after direct effects (with imperfect ecological knowledge) remains a challenge (Sala 1997; Pinnegar et al. 2000; Shurin et al a. 2002; McCann 2007**;** Salomon et al. 2009). Several factors may prevent trophic cascades from occurring in marine ecosystems. For example, increasing food web complexity, dietary breadth, recruitment variability, and the existence of thresholds and time lags are factors that may supress predator-induced cascades (Pinnegar et al. 2000; Baum and Worm 2009; Salomon et al. 2009; Babcock et al. 2010).

Studying how rocky reef communities change in response to fishing prohibitions may help identify strongly interacting species and key food web pathways as well as provide information regarding the circumstances that trigger trophic cascades. This information could help managers better-predict the impacts of conservation interventions on rocky reef ecosystems. In this chapter I evaluate whether community composition in Rockfish Conservation Areas (i.e. protected sites) differs from that in ecologically equivalent but unprotected sites. I hypothesize that higher rockfish density within RCAs (Chapter 2) could have community-altering effects since rockfish are opportunistic meso-predators and thus have the potential to interact with many benthic and pelagic fish and invertebrates (Murie 1995), especially since the biomass of lingcod, a formerly dominant rocky reef predator, is estimated to have been reduced by 95% in recent decades (Martell et al. 2000), with few signs of recovery (King 2001). Thus, where there are more rockfish I expect lower abundances of rockfish prey species. I also examine community composition in relation to environmental variables and geographic location, which I expect to influence species composition and abundance.

Materials and Methods

Study regions and sites

I conducted scuba-based assessments of the abundance of various taxonomic groups (i.e., select fish and invertebrate species) within RCAs and at adjacent, ecologically equivalent unprotected sites in the Strait of Georgia, British Columbia, Canada. All sites were surveyed over a two-year period, between June and October in 2009 and 2010. A total of 15 RCAs and associated control (i.e., unprotected) sites were selected, five pairs

of sites in each of three regions (Howe Sound, Gulf Islands, Sechelt), primarily to maximize the range of RCA ages (see Figure 2.1 and Table 2.1).

At each site, I selected haphazardly two survey locations that were predicted to be in 'good' rockfish habitat using a habitat model developed by Parks Canada – the federal agency responsible for national parks. This model attempts to identify suitable rockfish habitat by combining select seafloor features (e.g. slopes, depressions and ridges) with areas of high rugosity using bathymetric data and the Benthic Terrain Modeling tool in ArcGIS (see Lundblad et al. 2006). By restricting site selection to those sites of potentially high habitat suitability, I attempted to minimize the influence of habitat type on community structure.

Fish and invertebrate surveys

At each site I performed a total of eight belt transects (25 m long x 4 m wide) (four transects in each of two locations per site) to survey fish at depths from 8 to 15 m (chart datum). I recorded the species and number of fish encountered along each transect. I quantified invertebrate abundance by counting all individuals observed in 1 m^2 quadrats placed at 15 random positions along each transect. The fish and invertebrates taxa recorded in this study were chosen based on their potential to interact with rockfish (and the prey of rockfish; Murie 1995; Love et al. 2002) and/or because they are easily identified and/or have economic importance (see Table 3.1). Taxonomic resolution was variable, ranging from species to groups of multiple, related genera. This was done for biological reasons (e.g., rockfish are unlikely to discern between similarly sized shrimp of different genera) and to help minimize the duration of each survey given limited dive time. To minimize the potential effects of varying fish detectability, water temperature, or visibility throughout the survey period, half of the surveys at each site were carried out in early summer (June – early August) and the remainder during early fall (late August – October). Water temperature ranged from 8 to 14 °C and visibility from 4 m to 25 m. Search effort during fish and invertebrate surveys was standardized by controlling swimming speed (3 – 4 m•min^{-1}) and search time per quadrat (< 2 min), respectively. The mean site-level rugosity (averaged within, then across transects), kelp cover (averaged within, then across transects) and boulder cover (averaged across transects) were also calculated and used in the analysis (see Methods in Chapter 2).

Table 3.1.   Species or groups of species/genera recorded during surveys of RCAs and unprotected sites.

Taxon	Species or genera included in taxon:
Fishes	
Black rockfish	*Sebastes melanops*
Brown rockfish	*Sebastes auriculatus*
Copper rockfish	*Sebastes caurinus*
Puget Sound rockfish	*Sebastes emphaeus*
Quillback rockfish	*Sebastes maliger*
Tiger rockfish*	*Sebastes nigrocinctus*
Vermillion rockfish*	*Sebastes miniatus*
Yelloweye rockfish	*Sebastes ruberrimus*
Yellowtail rockfish*	*Sebastes flavidus*
Young-of-year rockfish	Unidentified *Sebastes* spp (usually < 5 cm total length)
Lingcod	*Ophiodon elongatus*
Kelp greenling	*Hexagrammos decagrammus*
Whitespotted greenling	*Hexagrammos stelleri*
Spiny dogfish	*Squalus acanthias*
Kelp perch	*Brachyistius frenatus*
Pile perch	*Rhacochilus vacca*
Shiner perch	*Cymatogaster aggregata*
Grunt sculpin	*Rhamphocottus richardsonii*
Irish Lords	*Hemilepidotus hemilepidotus* and *H. spinosus*
Sailfin sculpin*	*Nautichthys oculofasciatus*
Sculpins	Several cottid species including: *Artedius harringtoni, Jordania zonope* and possibly others
Invertebrates	
Giant Pacific octopus	*Enteroctopus dofleini*
Northern abalone	*Haliotis kamtschatkana*
Dungeness crab**	*Cancer magister*
Red rock crab*	*Cancer productus*
Crabs	Several brachyuran genera including: *Cancer, Pugettia, Scyra Oregonia;* several anomurans, including lithode and hermit crabs
Spot prawn	*Pandalus platyceros*
Shrimps	Numerous genera including: Lebbeus, Eualus, Heptocarpus, *Pandalus* and possibly others
Squat lobster	*Munida quadrispina*
Green sea urchin	*Strongylocentrotus droebachiensis*
Red sea urchin	*Strongylocentrotus franciscanus*
White sea urchin	*Strongylocentrotus pallidus*
California sea cucumber	*Parastichupus californicus*
Sunflower star	*Pycnopodia heliathoides*

*Absent in the analysis of 'young' RCAs.
**Absent in the analysis of 'old' RCAs.

Data analysis

I conducted a permutational multivariate analysis of variance (PERMANOVA) to compare the community structure of RCAs and unprotected sites. Like traditional parametric multivariate analysis of variance (MANOVA), PERMANOVA is used to simultaneously test the response of multiple variables to factors, but it relaxes the assumption of a multivariate normal distribution, which is rarely met with ecological count data (Bolker et al. 2009; Sileshi et al. 2009; O'Hara and Kotze 2010). The method converts data to distance (similarity or dissimilarity) measures, calculates a distance-based pseudo-F statistic, and then generates a P-value based on permutations of the data (Anderson et al. 2008). Here, I used a two-way PERMANOVA based on a Bray-Curtis similarity matrix generated from square-root-transformed abundance data (summed across transects to obtain a total (site-level) count for each taxon) with 9999 permutations. All analyses were carried out using the software PRIMER v6.1.13 (PRIMER-E Ltd) with PERMANOVA+ for PRIMER. A two-way crossed design allowed me to evaluate the effects of protection (2 levels: RCA vs unprotected) and region (3 levels: Howe Sound, Gulf Islands, Sechelt) while simultaneously accounting for each factor's potential influence on community composition. Abundance data were square-root transformed prior to analyses to avoid over-emphasizing abundant or rare species. This transformation was appropriate since I included species that occurred at considerably different densities (and trophic levels). A more severe transformation (such as 4th root or log-transformation) would have placed more weight on rare species and might have been appropriate if a comparison of species richness was the main interest (Clarke and Warwick 2001).

PERMANOVA can detect differences between groups due to differences in community composition (i.e., the number of species present and their abundance, termed 'location'), multivariate variability in community composition (i.e., the spread of the community composition within a group, termed 'dispersion') and/or due to an interaction between the main factors examined (Anderson et al. 2008). I therefore also carried out a permutational dispersion analysis (PERMDISP) to test for homogeneity of multivariate dispersion between the different levels in each factor (i.e. RCA protection vs. unprotected and all two-way comparisons of the three regions). This additional test allowed me to determine what combinations of location (i.e., the number of species and

abundance), dispersion (between group variability in the number of species and abundance) or two-way interactions (differences in location that depend on the level of the two factors) were responsible for group differences. Rocky reef communities were visualized using non-metric multidimensional scaling (nMDS) plots.

To understand which taxa contributed most to any observed differences in community composition between protected and unprotected areas and among geographic regions, I used an analysis of similarity percentages (SIMPER) on square-root-transformed abundance data. This analysis partitions the Bray-Curtis dissimilarity value for each group being compared and assigns a corresponding percentage to each taxon in descending order. Top ranked taxa therefore contribute most to the observed dissimilarity between the groups. I deemed taxa to be important to group differences if their individual dissimilarity contribution was six percent or more, which is twice the expected value if dissimilarity were evenly partitioned among all taxa in the analysis (i.e. 100 percent divided by 34 taxa, multiplied by 2). I also considered the evenness of each taxon's dissimilarity contribution across sites by examining the 'consistency ratio' (CR). The CR ratio is calculated by dividing a species' average dissimilarity contribution by the standard deviation in dissimilarity values (of that species, for the groups being compared). A CR value greater than one indicates a taxon that contributed fairly equally across all samples (Terlizzi et al. 2005). The SIMPER routine also produces within-group similarity values, which can be used to identify which species make a group unique. The Bray-Curtis within-group similarity value is partitioned much the same way dissimilarity is when evaluating between groups differences. I recorded as 'characteristic species' those species that contributed 10 percent or more to within-group similarity. Finally, the PERMANOVA, PERMDISP and SIMPER analyses as well as nMDS ordinations were replicated using subsets of the original data. More specifically, I contrasted the trends observed in 'young' RCAs (i.e. 2 – 3 year old RCAs) to those present in 'old' RCAs (i.e. 5 – 7 year old RCAs; see Table 2.1) to evaluate whether or not patterns might exist in 'old' RCAs, but that are not evident in the 'young' RCAs or whole data set.

I used distance-based linear modeling (DISTLM) to determine how much variation in the multivariate community data was explained by three habitat variables (rugosity, kelp cover, and boulder cover). Hence, given my objective, I examined the

marginal P-values (generated from 9999 permutations), which are not conditional on the order in which variables are evaluated (i.e., shared variation is not considered) (Anderson et al. 2008). Habitat variables were normalized and related to the Bray-Curtis similarity matrix generated from the taxon data following a square-root transformation.

I report exact P-values for all statistical tests, without correcting for multiple pairwise tests (e.g. the comparison between regions) following the logic and recommendations outlined in Perneger (1998). Although Bonferroni-type corrections for multiple hypothesis-testing can sometimes be useful (e.g., when identical tests are repeated on related data and if the 'universal null hypothesis' is of interest), because I am concerned with specific *a priori* comparisons, I feel that lowering the alpha level would be unnecessarily stringent.

Results

RCA protection

Protection did not significantly alter community composition on subtidal rocky reefs. Protected and non-protected sites did not differ in community composition and abundance (Pseudo-F = 1.22, P = 0.28; Figure 3.1), nor was there a difference in community dispersion between groups (Pseudo-F = 1.32, P = 0.26; Figure 3.1). Similarly, neither young nor old RCAs differed from their respective control areas in terms of community composition or dispersion (Table S3.1, Figures S3.2, and S3.3). The stress values for all nMDS plots were < 0.20, suggesting that they are fairly accurate representations of community differences (Clarke and Warwick 2001). Table 3.2 shows the contribution of the top fish and invertebrate taxa to dissimilarity in community composition between RCAs and unprotected sites.

Table 3.2. *Contributions of fish and invertebrate taxa to dissimilarity in community structure between RCAs and unprotected sites. Only taxa contributing 6% or more of total between-group dissimilarity are shown. Consistency ratios > 1 (highlighted in bold) indicate taxa that contributed consistently to dissimilarity across all samples. Abundance is expressed as the square-root of the number of individuals per 800 m^2 for fish and 60 m^2 for invertebrates (and sculpins). Standard errors are shown in brackets.*

Taxon	Protected Average abundance	Unprotected Average abundance	Percent contribution to between-group dissimilarity	Consistency ratio
1. Shiner perch	9.93 (3.0)	4.67 (2.6)	19.20	0.95
2. Shrimps	10.52 (2.1)	10.7 (2.1)	9.07	**1.15**
3. Green sea urchin	4.68 (1.3)	3.17 (0.9)	8.07	0.96
4. Crabs	5.99 (1.1)	7.47 (1.3)	7.38	**1.03**
5. Spot prawn	1.47 (0.5)	3.26 (1.3)	6.47	0.60
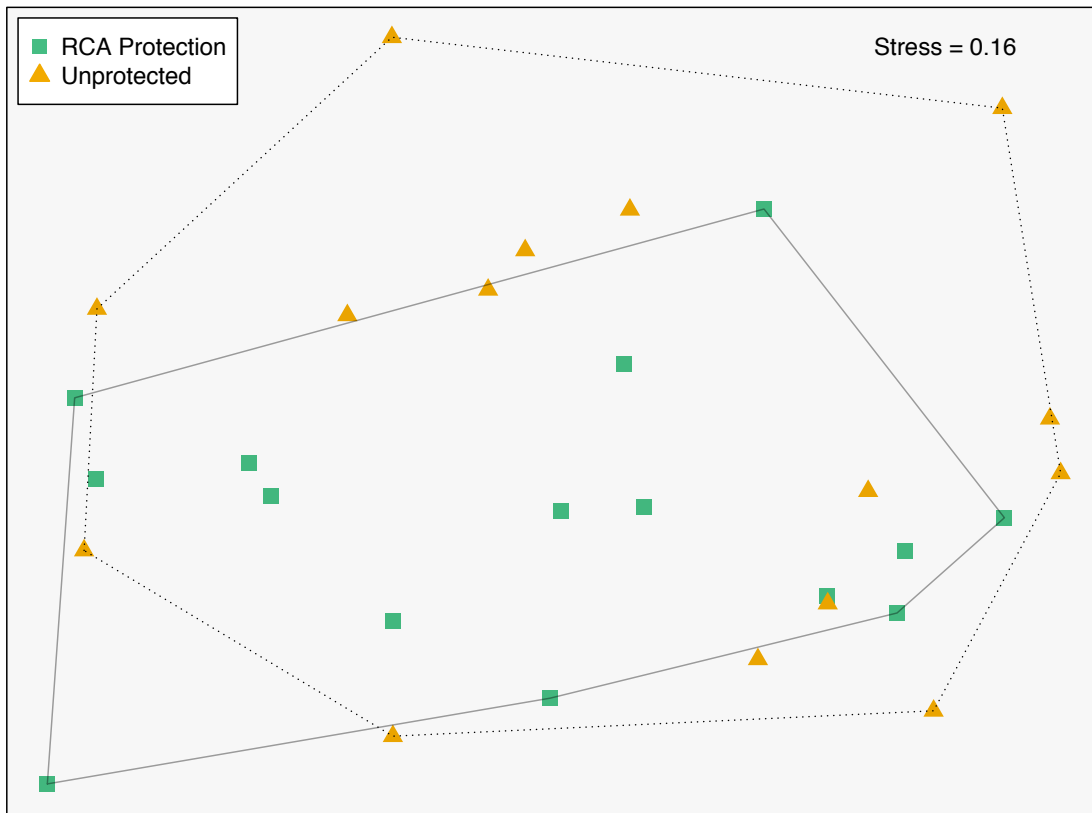
Figure 3.1.   Non-metric multidimensional scaling ordination (nMDS) of fish and invertebrate communities on rocky reefs of the Strait of Georgia, BC. Green square and orange triangle symbols represent Rockfish Conservation Areas (protected) and unprotected sites, respectively. Outer sites in each group are joined to form a polygon.

Geographic region

There were significant regional differences in community composition of subtidal rocky reefs. Pairwise comparisons (using PERMANOVA) indicated that all three regions differed from each other in their community compositions (Howe Sound – Gulf Islands: Pseudo-F = 2.41, P = 0.0003; Howe Sound – Sechelt: Pseudo-F = 1.96, P = 0.002; Sechelt – Gulf Islands: Pseudo-F = 3.80, P = 0.0002; Figure 3.2). I also detected significant differences in community dispersion between regions. Pairwise comparisons (using PERMDISP) revealed that the dispersion of sites in Howe Sound is larger than those of Sechelt and the Gulf Islands (Howe Sound–Gulf Islands: Pseudo-F = 3.80, P =

0.009; Howe Sound – Sechelt: Pseudo-F = 2.01, P = 0.05). However, the dispersion of sites in Sechelt and the Gulf Islands were not different from each other (Sechelt – Gulf Islands: Pseudo-F = 1.75, P = 0.10; Figure 3.2). There was no significant interaction between protection and region (Full data set: Pseudo-F = 0.44, P = 0.97; Young RCAs: Pseudo-F = 0.36, P = 0.97; Old RCAs: Pseudo-F = 1.09, P = 0.36), suggesting that the effect of RCA protection does not vary by region and that the observed differences in multivariate dispersion are real.

Table 3.3. *Contributions of fish and invertebrate taxa to dissimilarity in* *community structure of rocky reefs between regions*: **(a) Howe Sound vs Gulf Islands, (b) Howe Sound vs Sechelt, and (c) Sechelt vs Gulf Islands.** *Only taxa contributing 6% or more of total between-group dissimilarity are shown. Consistency ratios > 1 (highlighted in bold) indicate taxa that contributed consistently to dissimilarity across all samples. Abundance is expressed as the square-root of the number of individuals per 800 m^2 for fish and 60 m^2 for invertebrates (and sculpins). Standard errors are shown in brackets.*

a)

Taxon	Howe Sound Average abundance	Gulf Islands Average abundance	Percent contribution to between-group dissimilarity	Consistency ratio
1. Shrimps	7.91 (1.1)	19.83 (2.2)	19.21	**1.57**
2. Shiner perch	6.92 (3.2)	1.45 (1.3)	10.90	0.68
3. Crabs	5.24 (1.3)	11.20 (1.3)	10.89	**1.46**
4. Spot prawn	2.83 (2.0)	2.59 (0.8)	6.32	0.77

b)

Taxon	Howe Sound Average abundance	Sechelt Average abundance	Percent contribution to between-group dissimilarity	Consistency ratio
1. Shiner perch	6.92 (3.2)	13.52 (4.4)	19.24	**1.18**
2. Green sea urchin	4.61 (1.3)	5.67 (1.8)	7.62	**1.16**
3. Shrimps	7.91 (1.1)	4.11 (0.7)	7.12	**1.55**
4. Pile perch	0.42 (0.3)	4.32 (1.2)	6.28	**1.20**

c)

Taxon	Sechelt Average abundance	Gulf Islands Average abundance	Percent contribution to between-group dissimilarity	Consistency ratio
1. Shrimps	4.11 (0.7)	19.83 (2.2)	19.29	**2.20**
2. Shiner perch	13.52 (4.4)	1.45 (1.3)	13.90	**1.02**
3. Crabs	3.74 (0.5)	11.20 (1.3)	9.33	**1.59**
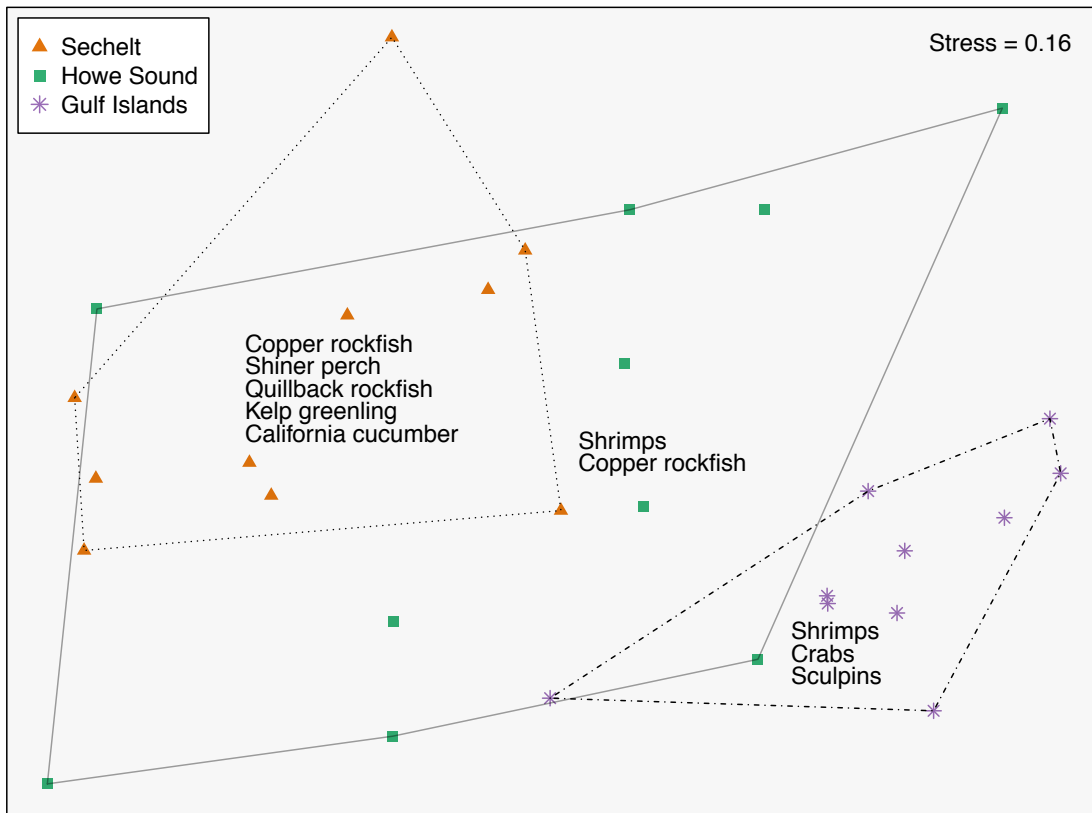
Figure 3.2.   Non-metric multidimensional scaling ordination (nMDS) of fish and invertebrate communities on rocky reefs of the Strait of Georgia, BC. Orange triangles = Sechelt, green squares = Howe Sound, purple asterisks = Gulf Islands. Outer sites in each group are joined to form a polygon. Listed species are 'characteristic' for the region, i.e., those species which contributed > 10% to within-group similarity (see Methods).

The species responsible for differences in subtidal rocky reef community composition varied by region. Four species were identified as being 'important' contributors to the overall dissimilarity between the communities of Howe Sound and the Gulf Islands. Shrimps, shiner perch and crabs accounted for more than 40% of the total dissimilarity between these two regions, with shrimps contributing almost twice as much as shiner perch or crabs. Shiner perch and spot prawns had a CR less than 1, indicating that their contributions to dissimilarity were variable between samples (Table 3.3). The overall dissimilarity between Howe Sound and Sechelt was also generated by four 'important' species. Shiner perch accounted for almost three times the total dissimilarity percentage of the next highest ranked species (Table 3.3). Finally, there were three

species identified as being 'important' contributors to the overall dissimilarity between Sechelt and the Gulf Islands. Shrimps and shiner perch accounted for over 30 percent of the dissimilarity between the two regions, with shrimps contributing approximately five percent more than shiner perch. Crabs were more abundant in the Gulf Islands and contributed approximately 9 percent to the dissimilarity with Sechelt (Table 3.3).

Howe Sound had the lowest within-group similarity (i.e., individual communities spanned nearly the entire nMDS plot; Figure 3.2) of the three regions examined. Its communities are characterized by two species: shrimps and copper rockfish. The Gulf Islands and Sechelt are characterized by more species: shrimps, crabs, and sculpins represent the Gulf Islands while copper rockfish, shiner perch, quillback rockfish, kelp greenling and California sea cucumbers are characteristic of Sechelt (Table S3.4). Finally, a number of species were detected in a single region (Table S3.5). Most notably, Northern abalone, which are recommended for an endangered status in Canada (COSEWIC 2009) were only observed in Sechelt.

Environmental variables

Howe Sound had significantly lower rugosity, kelp cover and boulder cover than the other two regions (Table S3.6). However, the distance-based linear modeling (DISTLM) revealed that none of the measured habitat variables was responsible for a significant amount of variation in fish and invertebrate community composition (Table S3.7), thus the variability in these habitat variables is unlikely to have biased the analysis (which did not explicitly consider continuous habitat variables). The relationships between the three variables and community composition had low, and similar R^2 values ($R^2_{Rugosity}$ = 0.06, R^2_{kelp} = 0.05, $R^2_{boulder}$ = 0.06).

Discussion

Contrary to my predictions I found no evidence for changes in community composition based on RCA protection status in BC. I compared protected sites with adjacent unprotected areas to determine if rockfish populations enhanced by protection (Chapter 2) had induced detectable changes, consistent with cascading effects, in rocky reef communities. I did not detect rockfish-induced trophic cascades. There were,

however, significant differences in community types among geographic regions. Shiner perch and shrimps were two of the top species driving regional differences. More generally, a number fish species were representative of communities in Sechelt while invertebrates characterized Gulf Island communities.

Rockfish-induced cascades undetected

Rockfish are a prominent group of demersal fishes found in rocky reef ecosystems. Because they have broad diets, are relatively sedentary, and exist in a human-altered ecosystem where lingcod (the formerly dominant rocky reef predator) have been severely depleted (Martell et al. 2000), I predicted that rockfish may a strong influence on community composition. It is therefore of interest to understand why their increased abundance in RCAs (Chapter 2) has not triggered detectable community shifts. It is possible that I did not detect rockfish-induced community shifts because they do not exist. Since rockfish are relatively scarce predators that have a generalist diet (Murie 1995) and live in a complex food web, the interactions between them and any particular species may be too weak to generate cascading effects (Hunter and Price 1992; Strong 1992; Polis et al. 2000; Baum and Worm 2009; O'Gorman and Emerson 2009). Moreover, rockfish may have ecological equivalents (e.g. kelp greenling, which are found in similar habitats and eat many of the same prey; Nemeth 1997; Murie 1995) that could also reduce their functional importance for prey populations (Jackson et al. 2001). In addition, other processes such as variability in the recruitment of fish and invertebrates could naturally override the effects of interspecific interactions involving rockfish (Fogarty et al. 1991; Pinnegar et al. 2000; Caley et al. 1996). For example, variation in recruitment (i.e. cohort survival) for some benthic fish can lead to marked differences in population abundance that can have long-lasting effects (e.g., cod, plaice, sole, whiting, and rockfish; see Myers and Cadigan 1993; Yamanaka et al. 2006).

Alternatively, trophic cascades may have gone undetected because they have not yet developed. The differences in rockfish density between protected and unprotected sites (Chapter 2) may not yet be large enough to generate different community responses. It is possible that cascading responses are triggered only beyond threshold abundances of higher-level consumers. For example, if rockfish have a type III functional response (i.e., the relationship between the number of prey

consumed and prey density is a sigmoidal curve), then small changes in their abundance are unlikely to elicit large changes in prey densities (i.e., if changes in predator density are far away from the threshold density; Holling and Buckingham 1976). Furthermore, predators may not be effective until they reach a certain size (Babcock et al. 2010). Many of the rockfish observed in RCAs were small (see Figure S2.6 for size frequency distribution), thus both their low absolute densities (see Chapter 2 Introduction for more details) and small sizes within MPAs may currently be insufficient to alter community assemblages.

In addition, the time required for indirect effects to appear once a threshold density is reached may be long. While there is little evidence for any time delays between the onset of direct and indirect effects in temperate intertidal communities (Menge 1997), the average time for indirect effects to appear in temperate and tropical marine reserves is approximately 13 years (Babcock et al. 2010). This difference in response times might be explained if prey alter their behaviour in response to predators, thereby reducing prey mortality rates and increasing the time needed for declines in prey abundance to become pronounced (avoidance strategies may also be enhanced by complex habitats, such as those in rocky reef ecosystems, which provide ample refugia for prey; Salomon et al. 2009; Baum and Worm 2009; Babcock et al. 2010). Such behaviourally-mediated traits (BMTs) are more likely to be displayed by mobile prey species (such as those reviewed by Babcock et al. (2010), and rockfish in this study) than by sessile prey (e.g. those in Menge1997) since mobility affords a suite of predator avoidance options. Thus, the detection of indirect effects in RCAs may be longer than the period of protection thus far, and because responses of prey to increased predator abundance are unlikely to be simple.

Lastly, a wide range of species was considered in this analysis, some of which may not interact strongly with rockfish. Furthermore, different rockfish species may be involved in interactions with different species, or may interact differently with the same species. Unfortunately, focusing on a smaller subset of taxa, with which rockfish do interact strongly and that are known to have strong influences on other species, could not be justified *a priori* due to a lack of knowledge surrounding rockfish feeding ecology and primarily, the feeding ecology of the other species involved. For these reasons I decided to investigate community composition using a broad sample of species with the

goal to describe community composition and possibly generate new hypotheses about specific pathways by which rockfish may induce trophic cascades. For example, this study suggests that several species that are preyed upon by rockfish (e.g., shrimps, crabs, and pile perch) are less abundant in RCAs. The demonstration of trophic cascades in Pacific rocky reef ecosystems may be possible by including these species, along with specific prey items for each (once data become available) in future studies. Furthermore, expanding the species list to include all large benthic rocky reef predators (i.e., lingcod and kelp greenling), all major pelagic fishes (i.e., herring, tubesnout), and zooplankton into three distinct functional groups where cascades can be evaluated on a large scale may yield different results. This approach would be similar to that used by Frank et al. (2005, 2011), who demonstrated a top-down cascade off the east coast of Canada, which begins with Atlantic cod and several other large benthic fish as the dominant predators.

Regional differences in community composition

The strongest effect of rocky reef community structure was linked to geography. This is perhaps not surprising given the marked variation in currents and upwelling, primary productivity and annual freshwater input among the three study regions (Yin et al. 1997; Masson and Peña 2009; see Chapter 2), although it is interesting that fish and invertebrate community composition was not linked to smaller-scale habitat features, such as rugosity, kelp and boulder cover. Perhaps few species in this study have strong relationships with any of the habitat variables measured. Alternatively, sample size (N = 30) may have limited my ability to detect patterns in the multivariate data.

Community dispersion, which describes how dissimilar sites are to each other within a region (see Methods), was greatest in Howe Sound. Greater dissimilarity among communities in Howe Sound might be explained by increased habitat variability or disturbances (Brown 1984; Warwick and Clarke 1993). It is possible that Howe Sound exhibits more environmental heterogeneity than the other two regions, and that my sample of sites reflects this. It was beyond the scope of this study to measure environmental heterogeneity at the regional scale. Alternatively, large community dispersion may reflect disturbance levels (Warwick and Clarke 1993). Strong disturbances (e.g., hurricanes, fires, droughts and pollution) can result in heavy mortality

of disturbance-sensitive species (Caswell and Cohen 1991), and at high frequency and large scales can result in homogenization of community structure across sites (Palmer et al. 1996). However, smaller, less frequent disturbance events can alter species composition in a more patchy fashion and lead to enhanced differences in community assemblages among sites (Palmer et al. 1996). This may be the case for Howe Sound, which has been impacted on very local scales by various industries, such as pulp mills (Stockner et al. 1977; Syvitski and Macdonald 1982; Macdonald et al. 1992), by coastal development, and by the freshwater discharges of various rivers, including the Squamish which empties directly into Howe Sound carrying heavy glacial silt and large amounts of freshwater (Stockner et al. 1977; Syvitski and Macdonald 1982). However, linking anthropogenic and natural disturbances to variation in marine community dispersion remains speculative at the moment.

In conclusion, this study is the first to demonstrate that after 2 – 7 years of establishment, RCA protection has not significantly altered subtidal rocky reef community composition despite higher densities of rockfish within their boundaries. It is possible that protected and unprotected communities have not diverged because rockfish are relatively scare predators that interact weakly with the species in this study. Alternatively, threshold densities and time lags may have hindered the detection of trophic cascades and ensuing community shifts; future studies may find that rockfish are in fact keystone species. Community composition and dispersion were significantly different among the three geographical regions surveyed. These differences may be linked to large-scale habitat heterogeneity and variable history of human-induced and natural disturbances; however, these hypotheses remain speculative at the moment.

Chapter 4.

General discussion

Marine species have always, to some degree, been affected by human activities, but in recent times modern fishing practices have had profound consequences on the marine environment and the ecosystems they contain (Jennings and Kaiser 1998; Jackson 2001; Halpern et al. 2008). For this reason, marine protected areas, from which fishing is greatly reduced or completely eliminated, are perceived as one of the most effective tools to reverse the effects of fishing (Alcala and Russ 1990; Polunin and Roberts 1993; Russ and Alcala 1996; Bohnsack 1998; Mosqueira et al. 2000; Côté et al. 2001; Gell and Roberts 2003; Harmelin-Vivien et al. 2008; Molloy et al. 2009). However, spatial protection needs to be accompanied by a reduction in total allowable catches, otherwise fishing effort can simply shift elsewhere and thus may not be effective at mitigating overall impacts (Allison et al. 1998; Salomon et al. 2002). In this thesis I evaluated the direct and indirect effects of marine protection using Rockfish Conservation Areas in the Strait of Georgia, British Columbia, Canada, as a case study. In Chapter 2, I found that rockfish densities were 1.6 times greater in protected than in unprotected areas. Although it remains unclear whether this difference is due to an increase in rockfish density within RCA boundaries or a continued depletion of unprotected rockfishes, this finding suggests a direct benefit of RCA protection and provided the impetus for assessing the indirect impacts that restored predator abundance may have on community structure (Pace et al. 1999; Pinnegar et al. 2000; Shurin et al. 2002; Dulvy et al. 2004; Salomon et al. 2009), especially since lingcod biomass has been substantially reduced in recent times (Martell et al. 2000). In Chapter 3, I examined whether increases in the relative density of rockfishes had altered community composition or induced any effects consistent with trophic cascades. This analysis revealed that, at present, marine communities are similar between protected and unprotected areas and that no cascading effects are evident. The latter is perhaps due to the fact that rockfish are scarce predators that have a generalist diet (Murie 1995) and live in a complex food

41

web, hence the interactions between them and any particular species are too weak to generate cascading effects (Hunter and Price 1992; Strong 1992; Polis et al. 2000; Baum and Worm 2009; O'Gorman and Emerson 2009). Alternatively, predator-induced cascades may only be triggered beyond threshold abundances of rockfish, which may not yet exist within RCAs (Salomon et al. 2009; Babcock et al. 2010). Overall, the research contained in this thesis provides BC's marine managers with the first comprehensive estimates of the effects of RCAs, which come after years of planning and nearly a decade of implementation.

Implications for management

I believe that my study provides five insights for Canadian marine managers, and particularly for those responsible for RCAs.

First, MPA design and implementation can be effective despite the existence of trade-offs between socio-economic constraints and biological needs so long as compromises are well thought out and consistent with the biology of the target species. This idea stems directly from the results obtained in Chapter 2, where I showed increased densities of rockfishes in RCAs, despite the known trade-offs that influenced RCA placement, size and number (Yamanaka and Logan 2010). The creation of RCAs received strong opposition from various sectors of industry (e.g., commercial and charter boat fishers), recreational anglers, and other members of the public at large, which undoubtedly had consequences on the RCA establishment process. However, despite these complications, the end result was the development of a set of MPAs that seem to be working.

Second, monitoring programs should be initiated pre- and post-RCA establishment in order to provide the most dependable estimates of the effects of management actions (both direct and indirect) on the marine environment. Without these initiatives, evaluating the extent to which management objectives are being met could remain equivocal (Osenberg et al. 2006; Lison De Loma et al. 2008). For instance, had pre-establishment data existed, I could have identified the specific mechanism(s) responsible for the higher densities of rockfish in than out of RCAs and precisely controlled for spatial and temporal variation that may have permeated the current study.

Moreover, the identification of thresholds and time lags at which indirect effects appear (if any) during rockfish recovery would be facilitated by the existence of time series data.

Third, new research should incorporate advanced technologies (e.g., remotely operated vehicles or ROVs) and make use of enforcement/illegal fishing data, which would complement the understanding of RCA performance. The use of ROVs will greatly increase the depths that can be surveyed in and out of RCAs, which should be of interest given that many rockfish are more common below 20 m, the maximum depth of this study (Love et al. 2002; Yamanaka et al. 2006). In addition, quantifying the prevalence of illegal fishing (e.g., through the use of infraction data or other means), the intensity of fishing adjacent to, and the enforcement effort associated with RCAs would aid in the interpretation of the effects of marine protection. RCAs may be doing exactly what they are intended to do; however, without accounting for poaching in RCAs, fishing pressure in control sites, and a more complete depth range, the effect of RCAs determined from this study may be incomplete.

Fourth, a thorough rockfish habitat model assessment should be done in order to inform managers as to the coverage and quality of habitat contained in RCAs. At present, RCAs capture ~ 18% of all DFO predicted rockfish habitat along the coast of BC (i.e., 2560.35 km^2/14,087.57 km^2 = ~ 18%; data taken from Table 4, Yamanaka and Logan 2010). However, these numbers are theoretical and the accuracy and reliability of the model upon which they are based have never been verified, despite the importance of this model for identifying potential RCA locations and being used as a 'meter stick' against which the rockfish conservation strategy targets are measured (Yamanaka and Logan 2010). A preliminary evaluation of a similar model (i.e., Parks Canada's), used here to select survey sites, revealed that indeed many sites predicted to be good rockfish habitat were in fact unsuitable for rockfish (i.e., they were composed of sand, shell, and mud; R.Cloutier, unpublished data). Hence, the absolute coverage of RCAs may be much less than anticipated and may not be adequate given the goals of the rockfish recovery strategy if the DFO model performs in a similarly poor fashion.

Finally, the underwater methodology used to survey rocky reef ecosystems should be standardized between agencies in order to foster collaboration and so that data are easily compared or assimilated. During the course of this research I have

collaborated with three agencies (i.e., Parks Canada, the Vancouver Aquarium, and DFO) who are all active in rockfish conservation and found that the methodologies used for monitoring benthic fishes and invertebrates vary substantially. For example, scientists at the Vancouver Aquarium use a roving-diver technique, which yields an index of abundance (number of rockfish-per-minute) rather than a true density estimate; scientists at Parks Canada use belt transects but choose sites non-randomly for monitoring purposes; DFO uses only ROV transects while my study used belt transects to survey sites selected in a random-stratified manner. These differences in methodologies will limit data comparisons and their use in multi-regional analyses (e.g. meta-analyses). Refinements in communication and standardization should help to remedy this issue and improve collaboration between these agencies.

Future work

The implications for management outlined above lead to two methodological issues that should be addressed in future work on the effectiveness of RCAs. First, as explained above, shallow-water SCUBA surveys of rockfishes (and other organisms) in and out of RCAs should be combined with deeper-water surveys by ROVs. There is, however, an urgent need to examine the extent to which these two methods generate density estimates that are comparable (e.g., fish may respond differently to stimulus associated with each method; Marchesan et al. 2005; Lorence and Trenkel 2006; Stoner et al. 2008). To achieve this, ROV and diver transects could be paired to survey the same transects. However, since 'true' natural rockfish density on these transects would not be known, the extent to which either method is biased would be unmeasurable. The solution would be to survey with both methods experimental areas with known numbers of rockfish (for example, by placing realistic rockfish models in realistic positions in natural habitat). This study would produce correction factors that could be applied to increase the comparability and accuracy of SCUBA- and ROV-derived density estimates in rocky reef ecosystems (or confirm the lack of need for such a correction).

Second, there is an equally important need to develop a standardized non-invasive rapid assessment for rocky reef communities, and in particular for RCAs. This is in part because subtidal-monitoring efforts often involve working in or around sensitive

habitats and species (e.g., some rockfish species are recommended for a threatened status in Canada; see Table S2.1), hence using non-destructive sampling techniques is essential. In addition, underwater surveys can be extremely labour intensive and may require special equipment such as SCUBA or ROVs (and associated support). While detailed and thorough monitoring should be encouraged, it would be both logistically and financially unrealistic to carry out such surveys in all 164 RCAs present on the BC coast. However, detailed monitoring of some 'flagship' RCAs could be complemented by quick and simple assessments at other sites (Molloy et al. 2010). For example, the creation of a streamlined survey, similar to the one used in this study, could be adapted to identify what proportion of RCAs meet or exceed target rockfish abundances. This information could provide marine managers with an updated RCA-performance trajectory when repeated annually. Recent evidence suggests that rapid-assessment surveys in which fewer transects are performed and that focused on a subset of easily identifiable species continued to maintain a high probability of detecting overall population trends (Molloy et al. 2010), and thus provides motivation for these types of surveys to be applied to RCAs. The effectiveness of this approach will depend on the identification of biologically meaningful targets of abundance (e.g., based on historical or ecological knowledge) and on the trade-off that exists between the simplicity and reliability of assessments at detecting important changes. Hence, it is critical that the survey design match the intended goals and that the data are not over-extended (i.e., the data may have limited application depending on the survey design). The overarching intent is that surveys should be simple enough to be easily repeated (i.e., they are cost-effective) yet provide managers with accurate information on the general trends of rockfish populations in and out of RCAs.

References

Adger, W. N., Hughes, T. P., Folke, C., Carpenter, S. R., & Rockström, J. (2005). Social-ecological resilience to coastal disasters. Science, 309, 1036-1039.

Alcala, A. C., & Russ, G. R. (1990). A direct test of the effects of protective management on abundance and yield of tropical marine resources. ICES Journal of Marine Science, 46, 40-47.

Allison, G. W., Lubchenco, J., & Carr, M. H. (1998). Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications, 8, 79-92.

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society of Biological Sciences, 276, 3019-3025.

Anderson, D. M., Glibert, P. M., & Burkholder, J. M. (2002). Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. Estuaries, 25, 704-726.

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E: Plymouth, UK.

Anderson, D. R. (2008). Model based inference in the life sciences: A primer on evidence. New York: Springer.

Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W., & Willis, T. J. (1999). Changes in community structure in temperate marine reserves. Marine Ecology Progress Series, 189, 125-134.

Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., McClanahan, T. R., Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences of the United States of America, 107, 18256-18261.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78, 699-714.

Beaudreau, A., & Essington, T. (2007). Spatial, temporal, and ontogenetic patterns of predation on rockfishes by lingcod. Transactions of the American Fisheries Society, 136, 1438-1452.

Bohnsack, J. A. (1998). Application of marine reserves to reef fisheries management. Australian Journal of Ecology, 23, 298-304.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. Trends in ecology & evolution, 24, 127-35.

Branch, T. A., Watson, R., Fulton, E. A., Jennings, S., McGilliard, C. R., Pablico, G. T., Ricard, D., Tracey, S. R. (2010). The trophic fingerprint of marine fisheries. Nature, 468, 431-5.

Browman, H. I., & Stergiou, K. I. (2004). Perspectives on ecosystem-based approaches to the management of marine resources. Marine Ecology Progress Series, 274, 269-303.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. The American Naturalist, 124, 255-279.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information theoretics approach. Springer.

COSEWIC. 2009. COSEWIC assessment and update status report on the Northern Abalone Haliotis kamtschatkana in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 48 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

COSEWIC. 2009. COSEWIC assessment and status report on the Quillback rockfish Sebastes maliger in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 71 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

COSEWIC. 2010. Canadian Wildlife Species at Risk. Committee on the Status of Endangered Wildlife in Canada. Web site: http://www.cosewic.gc.ca/eng/sct0/rpt/rpt_csar_e.cfm [accessed 4 October 2010].

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., & Menge, B. A. (1996). Recruitment and the Local Dynamics of Open Marine Populations. Annual Review of Ecology and Systematics, 27, 477-500.

Carpenter, S. R., Kitchell, J. F., & Hodgson, J. R. (1985). Cascading trophic interactions and lake productivity. BioScience, 35, 634-639.

Caswell, H., & Cohen, J. (1991). Communities in patchy environments: A model of disturbance, competition, and heterogeneity. Ecological Heterogeneity, Chapter 6, 97-122. Springer-Verleg, New York.

Clarke, R.K., & Gorley, R. (2006). PRIMER v6: User Manual/Tutorial. PRIMER-E: Plymouth.

Clarke, R.K., & Warwick, R. (2001). Change in marine communities: An approach to statistical analysis and interpretation, 2nd edition. PRIMER-E: Plymouth.

Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., Garcia-Charton, J. A., Perez-Ruzafa, A., Badalamenti, F., Bayle- Sempere, J., Brito, A., Bulleri, F., Culioli, J-M., Dimech, M., Falco J. M., Guala, I., Milazzo, M., Sanchez-Meca, J., Somerfield, P.J., Stobart, B., Vandeperre, F., Valle, C., Planes, S. (2008). Marine reserves: Size and age do matter. Ecology, 11, 481-489.

Collicutt, L. D. and T. F. Shardlow. 1992. Strait of Georgia sport fishery creel survey statistics for salmon and groundfish, 1990. Canadian Manuscript Report of Fisheries and Aquatics Sciences. 2109: 76 p. + vii.

Côté, I. M., Mosqueira, I., & Reynolds, J. D. (2001). Effects of marine reserve characteristics on the protection of fish populations : A meta-analysis. Journal of Fish Biology, 59, 178-189.

Danovaro, R., Corinaldesi, C., Dell'Anno, A., Fuhrman, J. A., Middelburg, J. J., Noble, R. T., & Suttle, C. A. (2011). Marine viruses and global climate change. FEMS Microbiology Reviews, 35, 993-1034.

DFO. (2000). Inshore Rockfish. Science Stock Status Report, A6-15, 2000.

DFO. (2002). Toward an inshore rockfish conservation plan. A structure for continued consultation. Consultation discussion document, March 05, 2002.

DFO. (2007). Rockfish conservation areas: Protecting British Columbia's rockfish. The Department of Fisheries and Oceans Canada.

Dudley, N. (editor) (2008). Guidelines for applying protected area management categories. Gland, Switzerland: IUCN. X + 86pp.

Dulvy, N. K., Freckleton, R. P., & Polunin, N. V. C. (2004). Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters, 7, 410-416.

Dulvy, N. K., Sadovy, Y., & Reynolds, J.D. (2003). Extinction vulnerability in marine populations. Fish and Fisheries, 4, 25-64.

Essington, T. E., Beaudreau, A. H., & Wiedenmann, J. (2006). Fishing through marine food webs. Proceedings of the National Academy of Sciences, 103, 3171-3175.

Estes, J. A., & Palmisano, J. F. (1974). Nearshore communities sea otters : Their role in structuring nearshore communities. Science, 185, 1058-1060.

Fraser, G. A. (2008). A preliminary review of the groundfish integration pilot program. Fraser and Associates. Victoria, B.C.

Fogarty, M. J., Sissenwine, M. P., & Cohen, E. B. (1991). Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology & Evolution, 6, 241-246.

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. Science, 308, 1621-1623.

Frank, K. T., Petrie, B., Fisher, J. A. D., & Leggett, W. C. (2011). Transient dynamics of an altered large marine ecosystem. Nature, 477, 86-91.

Frid, A., & Marliave, J. (2010). Predatory fishes affect trophic cascades and apparent competition in temperate reefs. Biology Letters, 6, 533-536.

Gell, F. R., & Roberts, C. M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution, 18, 448-455.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine, 23, 2865-2873.

Goñi, R., Quetglas, A., & Reñones, O. (2006). Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. Marine Ecology Progress Series, 308, 207-219.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., Polti, S., et al. (2008). Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. Marine Ecology Progress Series, 366, 159-174.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. Journal of Evolutionary Biology, 24, 699-711.

Haggarty, D. R., & King, J. R. (2004). Hook and line survey of lincod (Ophiodon elongatus) and rockfish (Sebastes sp.) stocks in the southern Strait of Georgia (statistical areas 17, 18, 19). Canadian Technical Report of Fisheries and Aquatic Sciences, 2533: 38p.

Harmelin-Vivien, M., Le Direach, L., Bayle-Sempere, J., Charbonnel, E., Garcia-Charton, J., Ody, D., Perez-Ruzafa, A., Renones, O., Sanchez-Jerez, P., Valle, C. (2008). Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological Conservation, 141, 1829-1839.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., Watson, R. (2008). A global map of human impact on marine ecosystems. Science, 319, 948-952.

Hixon, M. A., Tissot, B. A., & Pearcy, W. G. (1991). Fish assemblages of the rocky banks of the Pacific northwest. U.S. Department of the Interior Minerals Management Service: Pacific OCS Region.

Holling, C., & Buckingham, S. (1976). A behavioral model of predator-prey functional responses. Behavioral Science, 21, 183-195.

Holmlund, C. M., & Hammer, M. (1999). Ecosystem services generated by fish populations. Ecological Economics, 29, 253-268.

Hunter, M. D., & Price, P. W. (1992). Playing Chutes and Ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. America, 73, 724-732.

Jackson, J. B. (2001). What was natural in the coastal oceans? Proceedings of the National Academy of Sciences of the United States of America, 98, 5411-8.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke,R., Erlandson, J., Estes, J.A., Hughes, T. P., Kidwell, S., Lange, C.B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J., Warner, R. R. (2001). Historical overfishing and the recent collapse coastal ecosystems. Science, 293, 629-638.

Jennings, S., & Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. Advances in Marine Biology Vol 34. Academic Press Limited.

Jennings, S., Reynolds, J. D., & Mills, S. C. (1998). Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London Biological Sciences, 265, 333-339.

Jessen, S., Chan, K., Côté, I., Dearden, P., De Santo, E., Fortin, M. J., Guichard, F., Haider, W., Jamieson, G., Kramer, D.L., McCrea-Strub, A., Mulrennan, M., Montevecchi, W. A., Roff, J., Salomon, A., Gardner, J., Honka, L., Menafra, R., Woodley, A. (2011). Science-based guidelines for marine protected areas and MPA networks in Canada scientist authors. Wilderness. Vancouver: Canadian Parks and Wilderness Society. 58 pp.

Johnson, S. W., Murphy, M. L., & Csepp, D. J. (2003). Distribution, habitat, and behavior of rockfishes, Sebastes spp., in nearshore waters of southeastern Alaska: Observations from a remotely operated vehicle. Environmental Biology of Fishes, 66, 259-270.

King, J. R. (2001). Assessment of lingcod in the Strait of Georgia. Area. Canadian Science Advisory Secretariat Research Document, 2001/132.

King, J. R., & Withler, R. E. (2005). Male nest site fidelity and female serial polyandry in lingcod (Ophiodon elongatus, Hexagrammidae). Molecular Ecology, 14, 653-60.

Lai, H., & Helser, T. (2004). Linear mixed-effects models for weight-length relationships. Fisheries Research, 70, 377-387.

Lelieveld, J., Crutzen, P. J., Ramanathan, V., Andreae, M. O., Brenninkmeijer, C. M., Campos, T., Cass, G. R., Dickerson, R. R., Fischer, H., de Gouw, J. A., Hansel, A., Jefferson, A., Kley, D., de Laat, A. T., Lal, S., Lawrence, M. G., Lobert, J. M., Mayol-Bracero, O. L., Mitra, A. P., Novakov, T., Oltmans, S. J., Prather, K. A., Reiner, T., Rodhe, H., Scheeren, H. A., Sikka, D., Williams, J. (2001). The Indian ocean experiment: Widespread air pollution from south and southeast Asia. Science, 291, 1031-1036.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airamé, S., Warner, R. A. (2009). Biological effects within no-take marine reserves: A global synthesis. Marine Ecology Progress Series, 384, 33-46.

Levin, P. S., Fogarty, Michael J, Murawski, S. A., & Fluharty, David. (2009). Integrated ecosystem assessments: Developing the scientific basis for ecosystem-based management of the ocean. Public Library of Science: Biology, 7, 23-28.

Lison De Loma, T., Osenberg, C. W., Shima, J. S., Chancerelle, Y., Davies, N., Brooks, A. J., & Galzin, R. (2008). A Framework for Assessing Impacts of Marine Protected Areas in Moorea (French Polynesia). Pacific Science, 62, 431-441.

Lorance, P., & Trenkel, V. (2006). Variability in natural behaviour, and observed reactions to an ROV, by mid-slope fish species. Journal of Experimental Marine Biology and Ecology, 332, 106-119.

Love, M. S., Carr, M. H., & Haldorson, L. J. (1991). The ecology of substrate-associated juveniles of the genus Sebastes. Environmental Biology of Fishes, 30, 225-243.

Love, M.S., Yoklavich, M., Thorsteinson, L. (2002). The rockfishes of the northeast Pacific. Berkley, California: University of California Press.

Lundblad, E. R., Wright, D. J., Miller, J., Larkin, E. M., Rinehart, R., Naar, D. F., Donahue, B. T., Anderson, M. S., Battista, T. (2006). A benthic terrain classification scheme for american samoa. Marine Geodesy, 29, 89-111.

Macdonald, R. W., Cretney, W. J., Crewe, N., & Paton, D. (1992). A History of Octachlorodibenzo-p-dioxin, 2,3,7,8-Tetrachlorodibenzofuran, and 3,3',4,4'-Tetrachlorobiphenyl Contamination in Howe Sound, British Columbia. Environmental Science and Technology, 26, 1544-1550.

Marchesan, M., Spoto, M., Verginella, L., & Ferrero, E. A. (2005). Behavioural effects of artificial light on fish species of commercial interest. Fisheries Research, 73, 171-185.

Marliave, J, & Challenger, W. (2009). Monitoring and evaluating rockfish conservation areas in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences, 66, 995-1006.

Martell, S. J. D., Walters, C. J., & Wallace, S. S. (2000). The use of marine protected areas for conservation of lingcod (Ophiodon elongatus), 66, 729-743.

Masson, D., & Peña, A. (2009). Chlorophyll distribution in a temperate estuary: The Strait of Georgia and Juan de Fuca Strait. Estuarine Coastal and Shelf Science, 82, 19-28.

Matthews, K. R. (1990a). An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (Sebastes spp.). Environmental Biology of Fishes, 29, 161-178.

Matthews, K. R. (1990b). A telemetric study of the home ranges and homing routes of copper and quillback rockfishes on shallow rocky reefs. Canadian Journal of Zoology, 68, 2243-2250.

Menard, S. (2000). Coefficient of determination for multiple logistic regression. American Statistical Association, 54, 17-24.

Menge, B. A. (1997). Detection of direct versus indirect effects: were experiments long enough? The American Naturalist, 149, 801-823.

Mccann, K. (2007). Protecting biostructure. Nature, 446, 2007-2007.

Miller, J. A., & Shanks, A. L. (2004). Evidence for limited larval dispersal in black rockfish (Sebastes melanops): implications for population structure and marine-reserve design. Canadian Journal of Fisheries and Aquatic Sciences, 61, 1723-1735.

Mittlbock, M., & Schemper, M. (1997). Explained variation for logistic regression. Statistics in Medicine, 15, 1987-1997.

Molloy, P. P., McLean, I. B., & Côté, I. M. (2009). Effects of marine reserve age on fish populations: A global meta-analysis. Journal of Applied Ecology, 46, 743-751.

Moser, H. G., & Boehlert, G. W. (1991). Ecology of pelagic larvae and juveniles of the genus Sebastes. Environmental Biology of Fishes, 30, 203-224.

Mosqueira, I., Côté, I. M., Jennings, Simon, & Reynolds, John D. (2000). Conservation benefits of marine reserves for fish populations. Animal Conservation, 3, 321-332.

Murie, D. J. (1995). Comparative feeding ecology of two sympatric rockfish congeners, Sebastes caurinus (copper rockfish) and S. maliger (quillback rockfish). Marine Biology, 124, 341-353.

Murie, D. J., Parkyn, D. C., Clapp, B. G., & Krause, G. G. (1994). Observations on the distribution and activities of rockfish, Sebastes spp., in Saanich Inlet, British Columbia, from the Pisces IV submersible. Fishery Bulletin, 92, 313-323.

Murawski, S. A., Wigley, S. E., Fogarty, M. J., Rago, P. J., & Mountain, D. G. (2005). Effort distribution and catch patterns adjacent to temperate MPAs. ICES Journal of Marine Science, 62, 1150-1167.

Myers, R. A., & Cadigan, N. (1993). Density-dependent juvenile mortality in marine demersal fish. Canadian Data Report of Fisheries and Aquatic Sciences, 50, 1576-1590.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. Nature, 423, 280-283.

Nemeth, D. H. (1997). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, Hexagrammos decagrammus. Journal of Experimental Biology, 200, 2155-2164.

O'Gorman, E. J., & Emmerson, M. C. (2009). Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences, 106, 13393-13398.

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. Methods in Ecology and Evolution, 1, 118-122.

Obradovich, S. G., Yamanaka, K. L., Cooke, K., Lacko, L. C., and Dykstra, C. 2008. Summary of non-halibut catch from the Standardized Stock Assessment Survey conducted by the International Pacific Halibut Commission in British Columbia from June 4 to July 7, 2007. Canadian Technical Report of Fisheries and Aquatic Sciences. 2807: x + 83 p.

Osenberg, C. W., B. M. Bolker, J. S. White, C. St. Mary, and J. S. Shima. 2006. Statistical issues and study design in ecological restorations: Lessons learned from marine reserves. Pages 280–302 in D. A. Falk, M. A. Palmer, and J. B. Zedler. Foundations of restoration ecology. Island Press, Washington, D.C.

Pace, M., Cole, J., Carpenter, S., & Kitchell, J. (1999). Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution, 14, 483-488.

Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastrucure. Journal of Animal Ecology, 49, 667-685.

Palmer, M. A., Allan, J. D., & Butman, C. A. (1996). Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology & Evolution, 11, 322-6.

Parker, S. J., Berkeley, S. A., Golden, J. T., Gunderson, D. R., Heifetz, J., Hixon, M. A., Larson, R., Leaman, B. M., Love, M. S., Musick, J. A., O'Connell, V. M., Ralston, S., Weeks, H. J., Yoklavich, M. M. (2000). Management of Pacific Rockfish. Fisheries, 25, 22-30.

Pauly, D, Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. Science, 279, 860-863.

Perneger, T. V., & Journal, M. (1998). What's wrong with Bonferroni adjustments. British Medical Journal, 316, 1236-1238.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J., Sainsbury, K. J. (2004). Ecosystem-based fishery management. Science, 305, 346-347.

Piñeiro, G., Perelman, S., Guerschman, J. P., & Paruelo, J. M. (2008). How to evaluate models: Observed vs. predicted or predicted vs. observed? Ecological Modelling, 216, 316-322.

Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M-L., Hereu, B., Milazzo, M., Zabala, G., D'Anna, G., Pipitone, C. (2000). Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation, 27, 179-200.

Polis, G., Sears, A., Huxel, G., Strong, D., & Maron, J. (2000). When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution, 15, 473-475.

Polunin, N. V. C., & Roberts, C. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series, 100, 167-176.

Ralston, S., & Howard, D. F. (1995). On the development of year-Class strength and cohort variability in two northern California rockfishes. Fishery Bulletin, 93, 710-720.

Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., & Hutchings, J. A. (2005). Biology of extinction risk in marine fishes. Proceedings of the Royal Society of Biological Sciences, 272, 2337-2344.

Richards, L. J. (1987). Copper rockfish (Sebastes caurinus) and quillback rockfish (Sebastes maliger) habitat in the Strait of Georgia, British Columbia. Canadian Journal of Zoology, 65, 3188-3191.

Russ, G. R., & Alcala, A. C. (2003). Marine reserves: Rates and patterns of recovery and decline of predatory fish, 1983-2000. Ecological Applications, 13, 1553-1565.

Sala, E. (1997). The role of fishes in the organization of Mediteranean sublitoral community II: Epifaunal communities. Journal of Experimental Marine Biology and Ecology, 212, 45-60.

Salomon, A. K., Waller, N. P., Mcilhagga, C., Yung, R. L., & Walters, C. (2002). Modeling the trophic effects of marine protected area zoning policies: A case study. Aquatic Ecology, 85-95.

Salomon, A. K., Gaichas, S. K., Shears, N. T, Smith, J. E., Madin, E. M. P., & Gaines, S. D. (2009). Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology , 24, 382-94.

Shears, N. T., & Babcock, R. C. (2002). Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia, 132, 131-142.

Shears, N. T., & Babcock, R. C. (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. Marine Ecology Progress Series, 246, 1-16.

Shears, N. T., Babcock, R. C., & Salomon, A. K. (2008). Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecological Applications, 18, 1860-73.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., & Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters, 5, 785-791.

Sileshi, G., Hailu, G., & Nyadzi, G. I. (2009). Traditional occupancy–abundance models are inadequate for zero-inflated ecological count data. Ecological Modelling, 220, 1764-1775.

Spalding, M. D., Fish, L., & Wood, L. J. (2008). Toward representative protection of the world's coasts and oceans-progress, gaps, and opportunities. Conservation Letters, 00, 1-10.

Standish, J. D., White, J. W., & Warner, R. R. (2011). Spatial pattern of natal signatures in the otoliths of juvenile kelp rockfish along the Californian coast. Marine Ecology Progress Series, 437, 279-290.

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, 436-459.

Stockner, J., Cliff, D., & Buchanan, D. (1977). Phytoplankton production and distribution in Howe Sound , British Columbia : A coastal marine embayment-fjord under stress. Journal of the Fisheries Research Board of Canada, 34, 907-916.

Stoner, A. W., Ryer, C. H., Parker, S. J., Auster, P. J., & Wakefield, W. W. (2008). Evaluating the role of fish behavior in surveys conducted with underwater vehicles. Canadian Journal of Fisheries and Aquatic Sciences, 65, 1230-1243.

Strong, R. (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosytems. Ecology 73, 474-754.

Syvitski, P. M., & Macdonald, D. (1982). Sediment character and prevenance in a complex fjord; Howe Sound, British Columbia. Canadian Journal of Earth Sciences, 19, 1025–1044.

Terlizzi, A., Benedetti-cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P., & Anderson, M. J. (2005). Multivariate and univariate asymmetrical analyses in environmental impact assessment : A case study of Mediterranean subtidal sessile assemblages. Marine Ecology Progress Series, 289, 27-42.

Tetreault, I., & Ambrose, R. F. (2007). Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecological Applications, 17, 2251-67.

Tolimieri, N., Andrews, K., Williams, G., Katz, S., & Levin, P. (2009). Home range size and patterns of space use by lingcod, copper rockfish and quillback rockfish in relation to diel and tidal cycles. Marine Ecology Progress Series, 380, 229-243.

Tupper, M. H. (2007). Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. Fishery Bulletin, 105, 527-537.

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T. J. C., Fromentin, J-M., Hoegh-guldberg, O., Bairlein, F. (2002). change. Nature, 416, 389-395.

Ward, P., & Myers, Ransom. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology, 86, 835-847.

Ware, D. M., & Thomson, R. E. (2005). Bottom-up production in the northeast Pacific. Science, 308, 1280-1284.

Warwick, R. M., & Clarke, K. R. (1993). Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology, 172, 215-226.

Watson, D. L., Harvey, E. S., Kendrick, G. A, Nardi, K., & Anderson, M. J. (2007). Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. Marine Biology, 152, 1197-1206.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J. Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. Science, 314, 787-790.

Yamanaka, K L, & Lacko, L C. (2001). Inshore rockfish (Sebastes ruberrimus, S. maliger, S. caurinus, S. melanops, S. nigrocinctus, and S. nebulosus): Stock assessment for the west coast of Canada and recommendations for management. Canadian Science Advisory Secretariat, 2001/139.

Yamanaka, K. L., Lacko, L. C., Grandin, C., Lochead, J. K., Martin, J. C., Olsen, N., & Wallace, S. S. (2006). A review of quillback rockfish Sebastes maliger along the Pacific coast of Canada: biology, distribution and abundance trends. Canadian Science Advisory Secretariat, 2006/077.

Yamanaka, K. L., Lacko, L. C., Withler, R., Grandin, C., Lochead, J. K., Martin, J. C., Olsen, N., Wallace, S. S. (2006). A review of yelloweye rockfish (Sebastes ruberrimus) along the Pacific coast of Canada: biology, distribution and abundance trends. Canadian Science Advisory Secretariat, 2006/076.

Yamanaka, K. L., Lacko, L. C., Lochead, J. K., Martin, J., Haigh, R., Grandin, C., & West, K. (2004). Stock assessment framework for inshore rockfish. Canadian Science Adivisory Secretariat Research Document, 2004/068.

Yamanaka, K. L., and Lacko, L. C. 2008. 2004 Research catch and effort data on nearshore reef-fishes in British Columbia Statistical Area 12. Canadian Technical Report of Fisheries and Aquatic Sciences. 2803: ix + 45 p.

Yamanaka, K. L., & Logan, G. (2010). Developing British Columbia's inshore rockfish conservation strategy. American Fisheries Society, 2, 28-46.

Yin, K., Goldblatt, R., Harrison, P., St. John, M. A., Clifford, P., & Beamish, R. J. (1997). Importance of wind and river discharge in influencing nutrient dynamics and phytoplankton production in summer in the central Strait of Georgia. Marine Ecology Progress Series, 161, 173-183.

Zetterberg, P.R. and Carter, E.W., 2010. Strait of Georgia sport fishery creel survey statistics for salmon and groundfish, 2008. Canadian Manuscript Report of Fisheries and Aquatics Sciences. 2929: xiv + 123 p.

Zuur, A. F., Ieno, E. N., Walker, N. W., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R. Springer.

Supplements

Table S2.1.   The threat status for rockfish (Sebastes spp) according to the International Union for Conservation of Nature (IUCN), the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the Endangered Species Act (ESA). Note that not all Sebastes species have been assessed.

Listing agency	Threat status	Species	Assessment date	Notes on agencies
IUCN[1]	Critically endangered	Boccacio (*S. paucispinus*)	1996	The International Union for Conservation of Nature (IUCN) is a global conservation network that promotes the sustainable use of natural resources.
	Endangered	Redfish (*S. fasciatus*)	1996	
	Least concern	Cortez (*S. cortezi*)	2009	
	Least concern	Deepwater Redfish (*S. mentella*)	2009	
	Data deficient	No common name (*S. koreanus*)	2009	
	Data deficient	No common name (*S. nivosus*)	2009	
	Data deficient	No common name (*S. peduncularis*)	2009	
COSEWIC[2]	Endangered	Deepwater Redfish (*S. mentella*)	2010	The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a committee of experts whose aim is to identify species at risk of extinction in Canada. Its recommendations for protections may be implemented under the Canadian Species At Risk Act (SARA).
	Threatened	Boccacio (*S. paucispinus*)	2002	
	Threatened	Acadian Redfish (*S. fasciatus*)	2010	
	Threatened	Canary (*S. pinniger*)	2007	
	Threatened	Quillback (*S. maliger*)	2009	
	Threatened	Yellowmouth (*S. reedi*)	2010	
	Special concern	Rougheye I and II (*S. aleutianus*)	2007	
	Special concern	Darkblotched (*S. crameri*)	2009	
	Special concern	Yelloweye (*S. rubberimus*)	2008	
ESA[3]	Endangered	Boccacio (*S. paucispinus*)	2010	The Endangerd Species Act (ESA) is an act that aims to protect species at risk of extinction in the United States.
	Threatened	Canary (*S. pinniger*)	2010	
	Threatened	Yelloweye (*S. ruberrimus*)	2010	
	Special concern	Cowcod (*S. levis*)	2009	

[1] IUCN redlist listings accessed on Nov 1, 2011 (http://www.iucnredlist.org/)

[2] COSEWIC. 2010 (see references). The species at risk act (SARA) provides the legal protection of wildlife in Canada

[3] ESA listings accessed on Nov 1, 2011 (http://www.nmfs.noaa.gov/pr/species/esa/)

***Table S2.2.   Standardized model-averaged parameter estimates and
unconditional standard errors for all variables influencing a) the
presence/absence of rockfish along a transect and b) the density of rockfish, if
rockfish are present. The parameter values represent the magnitude of change in
rockfish (in cloglog space for rockfish presence or log space for rockfish density)
given a change of 2 SD from the mean. Parameters in bold have estimates shown
relative to the Gulf Islands. Protection status and duration were never
simultaneously present in a model but were evaluated in the same number and
combination of models.***

Parameter	a) Rockfish presence		b) Rockfish density	
	Estimate	Uncond.SE	Estimate	Uncond.SE
Intercept	0.45	0.19	1.71	0.19
Sechelt	155	5392	0.64	0.23
Howe Sound	0.07	0.34	-0.34	0.28
Rugosity	1.12	0.49	0.54	0.11
Boulder cover	-0.09	0.33	-0.01	0.08
Kelp cover	-0.14	0.29	-0.87	0.14
Depth	0.14	0.22	0.03	0.07
Young RCAs	0.34	0.29	0.47	0.24
Old RCAs	0.21	0.28	0.40	0.23
RCA protection	0.26	0.23	0.47	0.19
Sechelt*Rugosity	-0.16	0.78	-0.30	0.15
Howe Sound*Rugosity	0.89	0.83	0.11	0.24
Sechelt*Kelp	767	19083	0.92	0.18
Howe Sound*Kelp	0.27	0.88	-0.47	0.47
Sechelt*Boulder	0.80	0.87	0.03	0.13
Howe Sound*Boulder	0.56	0.74	-0.24	0.26
Rugosity*Kelp	0.75	0.69	-0.47	0.16
Rugosity*Boulder	0.30	0.64	-0.17	0.09
Boulder*Kelp	-0.74	0.53	-0.31	0.14
Young*Rugosity	-1.04	0.71	0.00	0.18
Old*Rugosity	-0.88	0.67	0.04	0.15
Sechelt*Young	0.07	0.78	-1.05	0.50
Sechelt*Old	2.63	4572	0.43	0.45
Howe Sound*Young	0.50	0.62	-0.34	0.49
Howe Sound*Old	-0.95	0.73	-0.22	0.53
Boulder*Young	0.79	0.93	0.09	0.18
Boulder*Old	0.46	0.65	0.19	0.13
Kelp*Young	-0.47	0.77	0.37	0.23
Kelp*Old	0.06	0.54	0.76	0.21
RCA*Rugosity	-1.00	0.58	0.04	0.13
Sechelt*RCA	0.30	0.68	-0.20	0.45
Howe Sound*RCA	-0.20	0.51	-0.17	0.47
Boulder*RCA	0.57	0.60	0.17	0.12
Kelp*RCA	-0.12	0.46	0.59	0.17
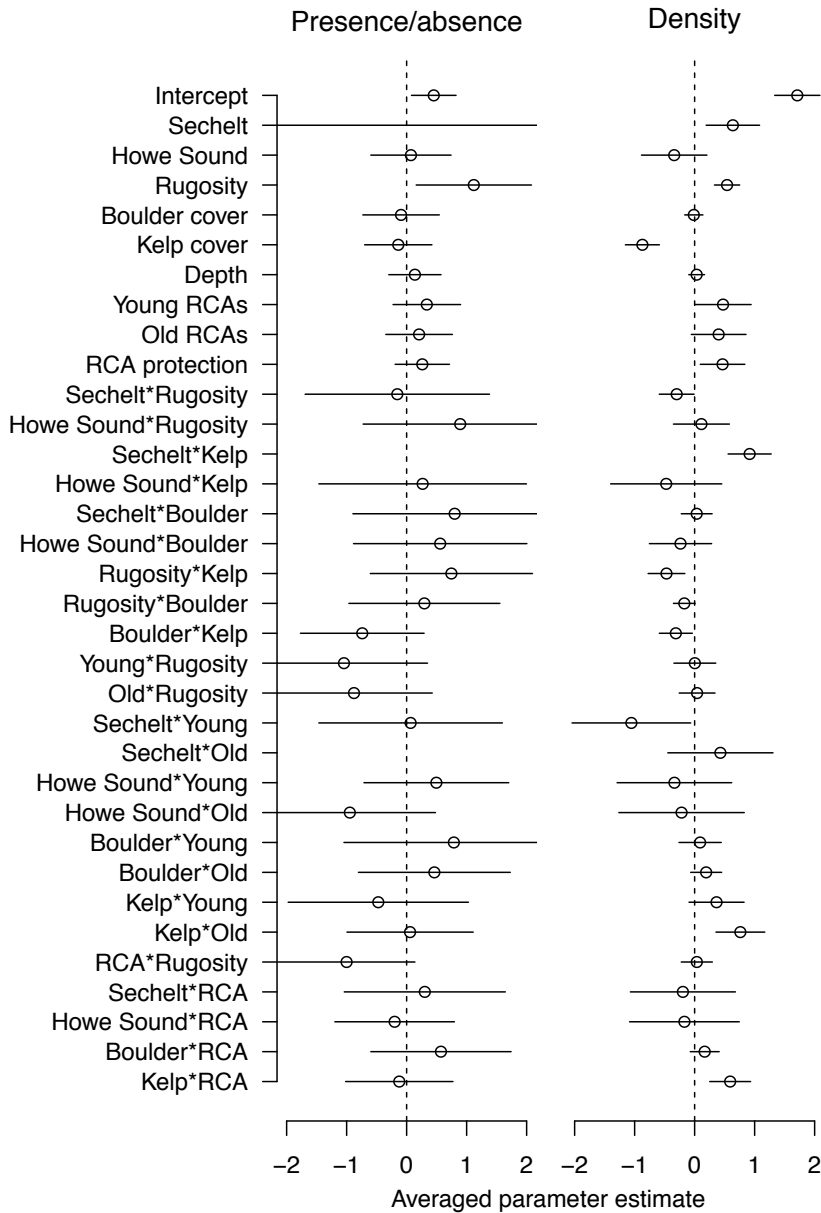
Figure S2.3.   Standardized model-averaged parameter estimates and unconditional 95% confidence intervals for models of rockfish presence/absence (left) and density (right). Black type indicates main effects; grey type indicates interactions. Parameters estimates represent the effect of each variable on the response going from -2SD to +2SD from the mean while all other variables are at their mean or baseline values (see Methods). Two parameter estimates were outside the scale shown; their values can be found in Table S2.2.

Size frequency distribution
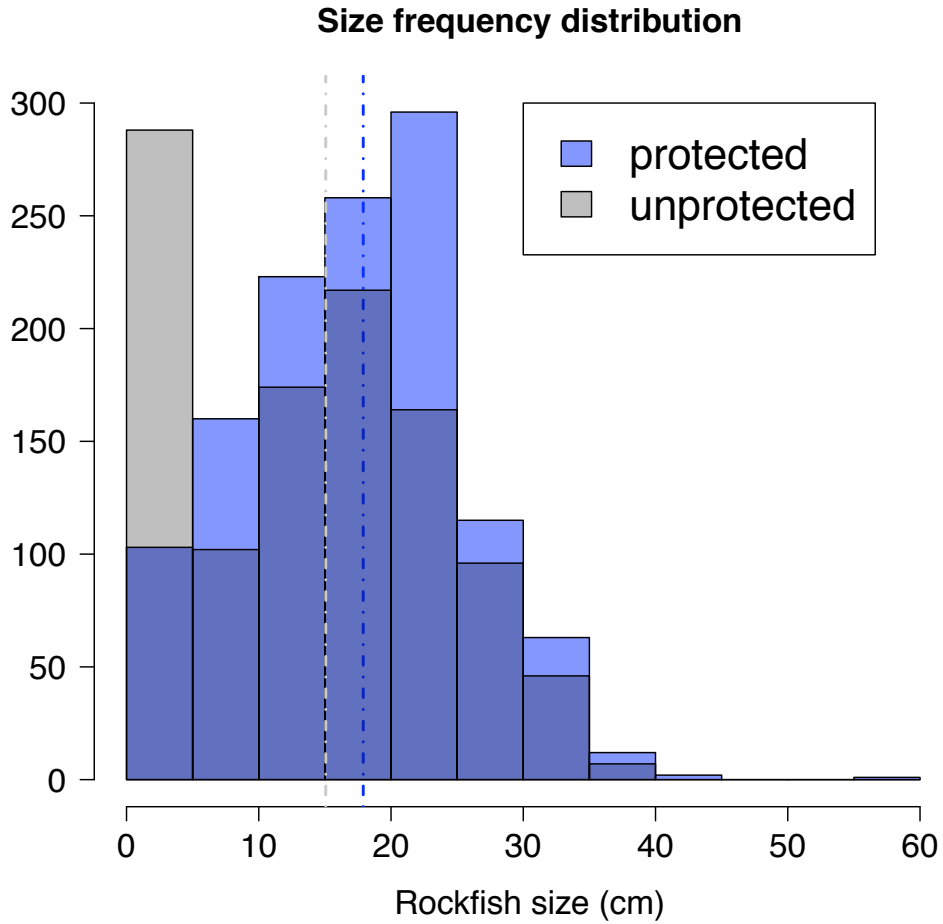
Figure S2.4. Size frequency distribution of rockfish (all species combined) at protected and unprotected sites. Each size category is right-closed (5 cm intervals). Light blue bars indicate frequency of rockfish observed in protected areas and grey bars for unprotected sites. Dark blue areas indicate regions of overlap between protected and unprotected categories. Blue and grey vertical dashed lines indicate the group mean sizes.

Table S2.5   Rockfish species used in presence/absence and density analyses.

Sebastes species	Number of observations	Comments
Black, *S. melanops*	65	55 black rockfish were observed in the Gulf Islands
Brown, *S. auriculatus*	18	16 Brown rockfish were observed in the Gulf Islands
Copper, *S. caurinus*	997	494 Copper rockfish were observed in Sechelt
Juvenile rockfish	411	Most juvenile rockfish were ~ < 5 cm total length and could not be reliably identified down to species
Puget sound, *S. emphaeus*	177	165 Puget sound rockfish were observed in the Gulf Islands
Quillback, *S. maliger*	645	461 Quillback were observed in Sechelt
Tiger, *S. nigrocintus*	1	Observed in Howe Sound
Vermillion, *S. miniatus*	1	Observed in Howe Sound
Yelloweye, *S. ruberrimus*	9	All individuals observed were juveniles ~ < 10 cm total length
Yellowtail, *S. flavidus*	23	23 were observed in the Gulf Islands

Table S2.6   Results of AICc analysis of models of rockfish presence/absence.
Models with weights adding to 0.20 are presented. Note that 483 models were
required to achieve a model weights sum of 0.95 for the presence/absence
analysis, thus only the top 12 models are shown. df = degrees of freedom, AIC =
Akaike information criterion, AICc = Akaike information criterion correted for small
sample size, ΔAICc = difference in AICc between each model and top ranked
model, wi = model weight, ER = evidence ratio.   Models (identified by their rank in
the top panel) are defined in the bottom panel.

Model rank	df	AIC	AICc	ΔAICc	wi	ER
1	5	166.41	166.73	0.00	0.04	1.00
2	7	166.77	167.38	0.65	0.03	1.38
3	10	166.75	167.96	1.23	0.02	1.85
4	9	167.00	167.99	1.26	0.02	1.88
5	8	167.58	168.36	1.63	0.02	2.26
6	6	168.06	168.52	1.79	0.01	2.44
7	6	168.22	168.67	1.94	0.01	2.64
8	4	168.49	168.70	1.97	0.01	2.68
9	6	168.39	168.85	2.12	0.01	2.88
10	9	168.10	169.09	2.36	0.01	3.25
11	3	169.10	169.23	2.50	0.01	3.49
12	8	168.50	169.28	2.55	0.01	3.58

Model rank	Model variables
1	Rugosity + RCA protection + Rugosity*RCA protection
2	Region + Rugosity + RCA protection + Rugosity*RCA protection
3	Region + Rugosity + Kelp + RCA protection + Kelp*Region + Rugosity*RCA protection
4	Region + Rugosity + Kelp + RCA protection + Kelp*Region
5	Region + Rugosity + Kelp + Kelp*Region
6	Rugosity + Depth + RCA protection + Rugosity*RCA protection
7	Rugosity + Kelp + RCA protection + Rugosity*RCA protection
8	Rugosity + RCA protection
9	Rugosity + Boulder + RCA protection + Rugosity*RCA protection
10	Region + Rugosity + Kelp + Kelp*Region + Rugosity*Kelp
11	Rugosity
12	Region + Rugosity + Depth + RCA protection + Rugosity*RCA protection

Table S2.7 ***Results of AICc analysis of models of rockfish density. Models with weights adding to 0.95 are presented. df = degrees of freedom, Pseudo-R² = approximation of coefficient of determination, AIC = Akaike information criterion, AICc = Akaike information criterion correted for small sample size, ΔAICc = difference in AICc between each model and top ranked model, wi = model weight, ER = evidence ratio. Models (identified by their rank in the top panel) are defined in the bottom panel.***

Model rank	df	Pseudo-R^2	AIC	AICc	ΔAICc	wi	ER
1	13	0.56	651.87	654.42	0.00	0.23	1.00
2	11	0.56	652.85	654.67	0.25	0.20	1.13
3	13	0.56	652.89	655.43	1.01	0.14	1.66
4	12	0.56	654.42	656.58	2.16	0.08	2.95
5	15	0.57	653.28	656.68	2.26	0.07	3.10
6	12	0.56	654.77	656.94	2.52	0.06	3.52
7	13	0.57	654.51	657.06	2.64	0.06	3.74
8	15	0.57	654.67	658.07	3.65	0.04	6.21
9	14	0.57	655.99	658.95	4.53	0.02	9.61
10	12	0.55	656.85	659.02	4.60	0.02	9.98
11	13	0.56	656.48	659.02	4.60	0.02	9.99
12	13	0.55	657.90	660.45	6.03	0.01	20.38

Model rank	Model variables
1	Region + Rugosity + Kelp + RCA protection + Rugosity*Region + Kelp*Region + Rugosity*Kelp + Kelp*RCA protection
2	Region + Rugosity + Kelp + RCA protection + Kelp*Region + Rugosity*Kelp + Kelp*RCA protection
3	Region + Rugosity + Boulder + Kelp + RCA protection + Kelp*Region + Rugosity*Kelp + Rugosity*Boulder + Kelp*RCA protection
4	Region + Rugosity + Boulder + Kelp + RCA protection + Kelp*Region + Rugosity*Kelp + Kelp*RCA protection
5	Region + Rugosity + Kelp + Duration of protection + Rugosity*Region + Kelp*Region + Rugosity*Kelp + Kelp*Duration of protection
6	Region + Rugosity + Kelp + RCA protection + Kelp*Region + Rugosity*Kelp + Rugosity*RCA protection + Kelp*RCA protection
7	Region + Rugosity + Kelp + Duration of protection + Kelp*Region + Rugosity*Kelp + Kelp*Duration of protection
8	Region + Rugosity + Boulder + Kelp + Duration of protection + Kelp*Region + Rugosity*Kelp + Rugosity*Boulder + Kelp*Duration of protection
9	Region + Rugosity + Boulder + Kelp + Duration of protection + Kelp*Region + Rugosity*Kelp + Kelp*Duration of protection
10	Region + Rugosity + Kelp + RCA protection + Rugosity*Region + Kelp*Region + Kelp*RCA protection
11	Region + Rugosity + Boulder + Kelp + RCA protection + Kelp*Region + Rugosity*Boulder + Kelp*Boulder + Kelp*RCA protection
12	Region + Rugosity + Boulder + Kelp + RCA protection +Rugosity*Region + Kelp*Region + Kelp*RCA protection

Table S3.1. ***Contributions of fish and invertebrate taxa to dissimilarity in community structure between protected and unprotected sites, grouped by young and old RCAs. Only taxa contributing 6% or more of total between-group dissimilarity are shown. Consistency ratios > 1 (highlighted in bold) indicate taxa that contributed consistently to dissimilarity across all samples. Abundance is expressed as the square-root of the number of individuals per 800 m^2 for fish and 60 m^2 for invertebrates (and sculpins). Standard errors shown in brackets. PERMANOVA and PERMDISP results indicate no difference in location or dispersion between age categories of RCAs and paired unprotected sites.***

a)

Taxon	Young RCAs Average abundance	Unprotected Average abundance	Percent contribution	Consistency ratio
1. Shiner perch	8.40 (3.0)	5.08 (2.7)	21.90	**1.10**
2. Crabs	5.85 (1.1)	7.35 (1.4)	9.47	**1.01**
3. Shrimps	10.35 (2.3)	10.42 (2.6)	9.07	0.99
4. Green sea urchin	5.61 (1.7)	2.58 (0.4)	8.98	0.85

b)

Taxon	Old RCAs Average abundance	Unprotected Average abundance	Percent contribution	Consistency ratio
1. Shiner perch	11.26 (3.2)	4.31 (2.7)	16.96	0.81
2. Green sea urchin	3.86 (1.1)	3.69 (1.1)	8.71	0.99
3. Spot prawn	1.84 (0.5)	4.38 (1.7)	7.75	0.61
4. Shrimps	10.68 (2.2)	10.95 (1.9)	7.30	**1.17**
5. Crabs	6.10 (1.1)	7.58 (1.4)	6.44	**1.19**

a) PERMANOVA: Pseudo-F = 0.49, P = 0.81, PERMDISP: Pseudo-F = 1.09, P = 0.35
b) PERMANOVA: Pseudo-F = 1.39, P = 0.20, PERMDISP: Pseudo-F = 0.12, P = 0.72

Figure S3.2.   Non-metric multidimensional scaling ordination (nMDS) of fish and invertebrate communities on rocky reefs of the Strait of Georgia, BC. Green squares = young RCAs (i.e. protected sites 2-3 years old) and orange triangles = unprotected sites. Outer sites in each group are joined to form a polygon.
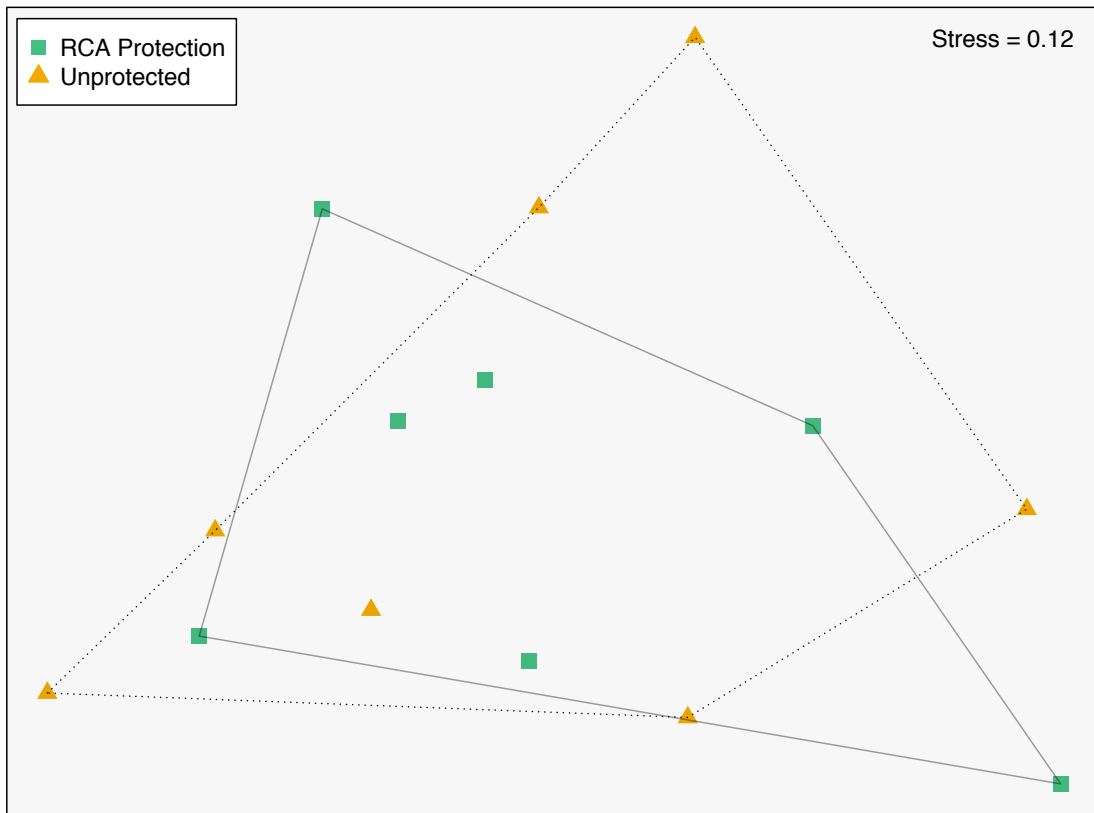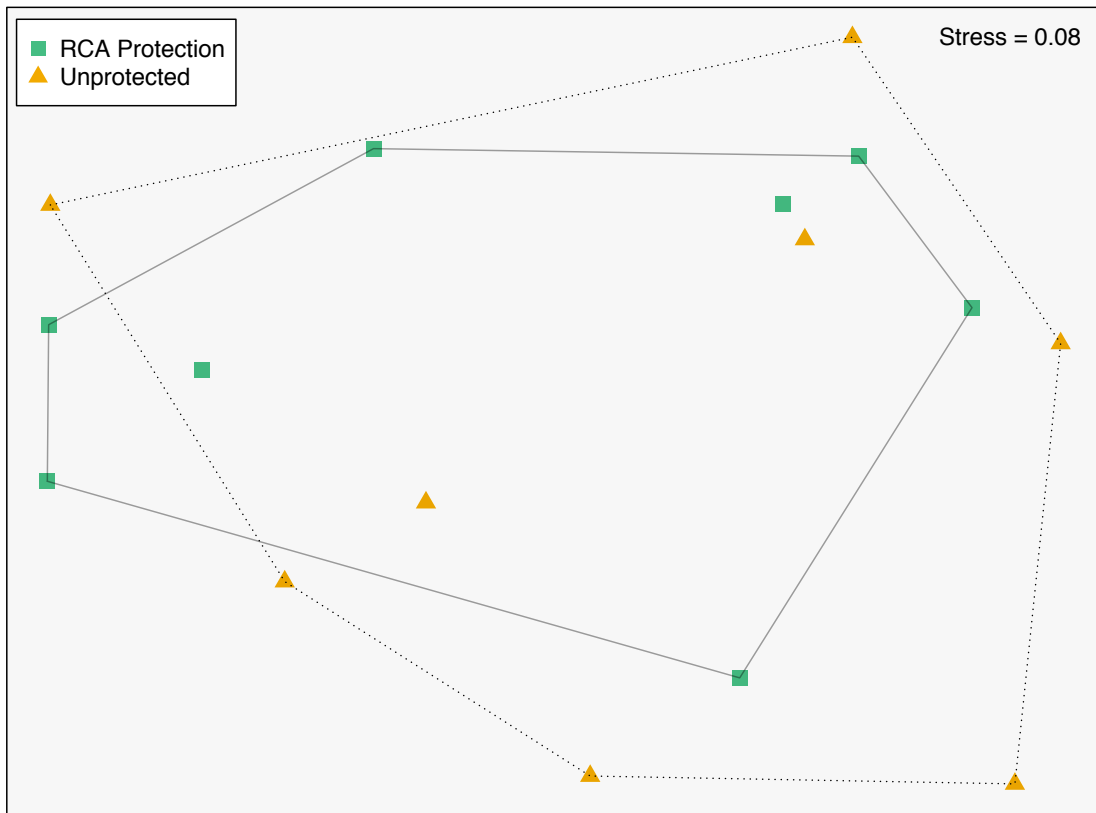
Figure S3.3. Non-metric multidimensional scaling ordination (nMDS) of fish and invertebrate communities on rocky reefs of the Strait of Georgia, BC. Green squares = old RCAs (i.e. protected sites 5-7 years old) and orange triangles = unprotected sites. Outer sites in each group are joined to form a polygon.

Table S3.4. ***Contributions of fish and invertebrate taxa to similarity in community structure of rocky reefs within regions. Only taxa contributing 10% or more of total within-group similarity are shown. Consistency ratios > 1 (highlighted in bold) indicate taxa that contributed consistently to similarity across all samples. Abundance is expressed as the square-root of the number of individuals per 800 m² for fish and 60m² for invertebrates (and sculpins). Standard errors shown in brackets. Within-group similarity (based on Bray-Curtis coefficient) also shown in brackets; larger numbers indicate sites within a group have more similar species composition and abundance.***

	Howe Sound (52.74)		
Taxon	Average abundance	Percent contribution	Consistency ratio
Shrimps	7.91 (1.1)	18.19	**2.17**
Copper rockfish	4.65 (0.7)	11.41	**1.76**

	Gulf Islands (67.55)		
Taxon	Average abundance	Percent contribution	Consistency ratio
Shrimps	19.83 (2.2)	31.14	**3.61**
Crabs	11.20 (1.3)	17.59	**2.91**
Sculpins	6.42 (0.5)	10.97	**6.54**

	Sechelt (62.62)		
Taxon	Average abundance	Percent contribution	Consistency ratio
Copper rockfish	6.86 (0.5)	12.29	**3.34**
Shiner perch	13.52 (4.4)	12.14	0.66
Quillback rockfish	6.51 (0.6)	11.25	**6.45**
Kelp greenling	6.01 (0.4)	10.91	**4.17**
California cucumber	5.61 (0.3)	10.81	**3.65**

Table S3.5. ***Unique (i.e., recorded in a single region) and absent fish and invertebrate taxa for each survey region.***

	Sechelt	Gulf Islands	Howe Sound
Unique species:	Northern abalone	Yellowtail rockfish Irish Lords	Dungeness crab Vermillion rockfish Grunt sculpin Sailfin sculpin
Absent species:	Dungeness crab Pacific octopus Black rockfish Puget Sound rockfish Tiger rockfish Vermillion rockfish Yellowtail rockfish Grunt sculpin Irish Lords Sailfin sculpin	Northern abalone Tiger rockfish Vermillion rockfish Yelloweye rockfish Pile perch	Northern abalone Brown rockfish Yellowtail rockfish Irish Lords Spiny dogfish

* see Table 2.1 for species' scientific names

Table S3.6.   Results of comparisons of mean habitat variables (and standard errors) between protected and unprotected sites (paired t-tests) and between pairs of regions (Student t-tests). Degrees of freedom (df), t-values, and associated P-values are given.   * = significant difference.

Variable	Protected Mean (Std.Err)	Unprotected Mean (Std.Err)	df	t-value	P-value
Rugosity	1.21 (0.02)	1.21 (0.02)	14	0.08	0.94
Kelp	18.17 (4.3)	19.39 (5.1)	14	0.43	0.68
Boulder	21.4 (3.9)	20.67 (4.7)	14	-0.13	0.89

Variable	Howe Sound Mean (Std.Err)	Sechelt Mean (Std.Err)	df	t-value	P-value
Rugosity	1.15 (0.02)	1.27 (0.03)	14.65	-4.49	0.0005*
Kelp	5.46 (1.6)	21.40 (5.7)	10.49	-2.69	0.02*
Boulder	9.08 (2.9)	33.64 (5.5)	13.67	-3.96	0.001*

Variable	Howe Sound Mean (Std.Err)	Gulf Islands Mean (Std.Err)	df	t-value	P-value
Rugosity	1.15 (0.02)	1.21 (0.02)	15.34	-2.54	0.02*
Kelp	5.46 (1.6)	29.48 (5.9)	10.37	-3.89	0.003*
Boulder	9.08 (2.9)	20.33 (3.7)	17.01	-2.39	0.03*

Variable	Sechelt Mean (Std.Err)	Gulf Islands Mean (Std.Err)	df	t-value	P-value
Rugosity	1.27 (0.03)	1.21 (0.02)	17.89	1.78	0.09
Kelp	21.40 (5.7)	29.48 (5.9)	17.96	-0.98	0.34
Boulder	33.64 (5.5)	20.33 (3.7)	15.82	2.01	0.06

Table S3.7. ***Results from distance-based redundancy analysis indicating that no habitat variable accounted for a significant portion of variation in community structure. Individual R² values are presented. Breakdown of variation explained by dbRDA axes is shown.***

Variable	R^2	Pseudo-F	P-value
Rugosity	0.0586	1.6567	0.1185
Boulder	0.0530	1.5679	0.1428
Kelp	0.0578	1.7182	0.1134

	Percentage of variation explained by individual axes			
	Fitted model		Total variation	
dbRDA axis	Individual	Cumulative	Individual	Cumulative
1	62.26	62.26	11.09	11.09
2	22.70	84.96	4.04	15.14
3	15.04	100.00	2.68	17.82