

**ROCKFISH RECRUITMENT AND TROPHIC DYNAMICS ON THE WEST COAST
OF VANCOUVER ISLAND: FISHING, OCEAN CLIMATE, AND SEA OTTERS**

by

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Abstract

Fundamental questions in marine ecology concern processes that underlie the replenishment of marine populations and the cascading effects of large marine predators. My dissertation describes three studies in which I investigated the recruitment and trophic dynamics of nearshore Pacific rockfishes in the context of these two themes.

In the first study, my collaborators and I investigated spatial variation in rockfish recruitment success in the context of the effectiveness of Rockfish Conservation Areas (RCAs). We show that although rockfish recruitment is highly variable throughout nearshore seascapes, spatial patterns of recruitment success are generally consistent from year to year. We identify characteristics of locations that contribute to spatially recruitment patterns, including fetch, distance to open coast, tidal velocity, and sea surface temperature. Because most high-value areas with respect to rockfish recruitment fall outside of the RCA considered in this study, we propose that this protected area may be vulnerable to reduced long-term effectiveness.

Next, I investigated how interannual variation in the timing and magnitude of coastal upwelling affects the recruitment success of two groups of nearshore rockfishes. I used otolith microstructure analyses to compare birth and settlement dates, pelagic durations, and growth rates of rockfishes in years of contrasting recruitment success and upwelling dynamics. I found that although growth rates of both rockfish groups responded positively to ocean temperature, the highest recruitment success I observed over a six-year period corresponded to strong and prolonged upwelling that favored onshore transportation of pelagic larvae, but not pre-settlement growth and survival.

In the final study, I examined how the indirect effects of sea otters on kelp forest habitat size and productivity affect rockfish recruitment dynamics and post-settlement trophic dynamics. I tested the effects of sea otters on kelp forest size, and concomitant effects on rockfish recruitment success. I used stable isotopes and otolith microstructure analyses to compare rockfish trophic position and kelp-derived carbon content, and their relative effects on juvenile growth rates, between regions with and without sea otters. I show that kelp forests are larger in the presence of sea otters and associated with higher rockfish recruitment; however, higher kelp

productivity does not translate to rockfishes having higher kelp-derived carbon contents. Instead, in the presence of sea otters, adult rockfishes had higher mean trophic levels, indicating that these populations consume higher proportions of relatively high trophic level prey, i.e. fish.

These studies contribute broadly to understanding marine population dynamics, and hold important implications for predicting responses of species and ecosystems to marine protected areas, climate change, and the indirect effects of predator loss and reintroduction.

Preface

The research presented in Chapter 2 is the result of collaboration with Clifford L.K. Robinson (Parks Canada Agency, Western and Northern Service Centre) and Katie E. Lotterhos (Biological Sciences, Florida State University). C.L.K.R designed and Parks Canada Agency staff performed all fieldwork concerning rockfish recruitment in eelgrass meadows. R.W.M designed the kelp forest study and R.W.M. and K.E.L. jointly conducted all sampling in kelp forests. All authors contributed to the analyses and R.W.M wrote the manuscript.

All parts of Chapters 3 and 4, including design, data collection, analyses, and writing, were performed by R.W.M.

Table of Contents

Abstract.....	ii
Preface	iv
Table of Contents	v
List of Tables	vii
List of Figures.....	viii
Acknowledgements	x
Dedication	xii
1. Introduction.....	I
1.1 Effects of overfishing on marine ecosystems.....	I
1.2 Replenishment of marine populations	3
1.3 Study systems	6
1.4 Overview of dissertation.....	12
2 Spatially consistent patterns of temperate reef fish recruitment inform marine protected area design and effectiveness.....	15
2.1 Synopsis	15
2.2 Introduction	16
2.3 Methods	18
2.4 Results	28
2.5 Discussion.....	32
3 Effects of variable upwelling dynamics on the recruitment success of nearshore Pacific rockfishes (Genus <i>Sebastodes</i>)	40
3.1 Synopsis	40
3.2 Introduction	41
3.3 Methods	46
3.4 Results	52
3.5 Discussion.....	64
4 Indirect effects of sea otters on recruitment, trophic position and growth of kelp-associated rockfishes (Genus <i>Sebastodes</i>).....	72
4.1 Synopsis	72
4.2 Introduction	73
4.3 Methods	77
4.4 Results	85
4.5 Discussion.....	95
5 Conclusions.....	104
5.1 Effects of coastal upwelling dynamics and nearshore topography on temporal and spatial patterns of rockfish recruitment success	104

5.2 Collateral effects of the otter-urchin-kelp trophic cascade on rockfish recruitment and trophic dynamics	106
5.3 Future directions for rockfish recruitment and trophic dynamics	108
Bibliography	112
APPENDIX A: Deploying SMURFs in kelp forests	130
APPENDIX B: Supplementary figures	133

List of Tables

Table 2.1	Effects of species and year on black and CQB complex rockfish recruitment.....	30
Table 2.2	Cumulative % variance explained by PCA	34
Table 3.1	Early life history attributes of black and CQB complex rockfish.....	54
Table 4.1	Results comparing rockfish % kelp-carbon contents and trophic levels	91
Table 4.2	Effects of kelp-carbon and trophic level on juvenile rockfish growth.....	98

List of Figures

Figure 2.1	Map showing kelp forest and eelgrass sites in Barkley Sound.....	20
Figure 2.2	Annual recruitments of CQB and black rockfish	24
Figure 2.3	Map showing spatial patterns of black rockfish recruitment in Barkley Sound.....	27
Figure 2.4	CQB complex rockfish recruitment in July and August 2005	28
Figure 2.5	Black rockfish recruitment at five sites throughout Barkley	29
Figure 2.6	Black rockfish recruitment at eelgrass meadows with distance from coast.....	32
Figure 2.7	Pair-wise comparisons of annual black rockfish recruitment.....	33
Figure 2.8	Relationships between PCI values and black rockfish recruitment	36
Figure 3.1	Conceptual model depicting effects of upwelling on rockfish settlement rates	43
Figure 3.2	Annual black and CQB complex rockfish recruitment 2005-2010.....	44
Figure 3.3	Otolith increment width and variance preceding and following settlement.....	53
Figure 3.4	Cohort-specific oceanographic conditions in 2005 and 2006	56
Figure 3.5	Upwelling and sea surface temperature anomalies between 1977 and 2010	57
Figure 3.6	Juvenile rockfish birth and settlement in relation to upwelling events	58
Figure 3.7	Growth rates of juvenile black and CQB complex rockfishes in 2005 and 2006.....	59
Figure 3.8	Longitudinal growth profiles of juvenile black and CQB complex rockfishes.....	60
Figure 3.9	Ocean conditions and juvenile black rockfish early life history attributes	61
Figure 3.10	Ocean conditions and juvenile CQB rockfish early life history attributes.....	62
Figure 4.1	Map showing study regions on the west coast of Vancouver Island	80
Figure 4.2	Sea urchin densities and kelp forest depth and size	86
Figure 4.3	Black rockfish recruitment using SMURFs and visual surveys.....	87
Figure 4.4	Juvenile black rockfish pre- and post-settlement growth.....	88
Figure 4.5	$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of producers and consumers.....	90
Figure 4.6	Adult black and copper rockfish trophic niche space	92
Figure 4.7	Adult black and copper rockfish ontogenetic niche shifts	93

Figure 4.8	Juvenile black and CQB complex rockfish ontogenetic niche shifts	94
Figure 4.9	Juvenile black rockfish body condition, kelp-carbon, and trophic level	95
Figure 4.10	Effects of kelp-carbon and trophic level on juvenile rockfish growth.....	97
Figure A1	Length-frequency distributions of juvenile rockfish from SMURFs	131
Figure B1	Otolith length to body length relationships of juvenile rockfish.....	133
Figure B2	Back-calculated growth profiles of juvenile black and CQB rockfish.....	134

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Just months after I started this degree a young undergraduate student visited my office. He explained that he had heard that I was looking for a field assistant, and that he knew how to fish. Little did I know that over the next six years Stefan Dick and I would accomplish incredible amounts of field and lab work, and share a lifetime of adventures and friendship along the way.

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Dedication

I grew up on the BC coast at a time when mooching with live-herring and limiting out on salmon was the norm, and catching ‘rockcod’ was what you did for fun in the afternoon. My brother and I spent untold time observing the mysterious lives of perches through planks on the docks, snorkeling, and jigging up strange fishes, and inspired and haunted by stories of ‘monster’ lingcod, giant octopuses, sharks, and secret ‘cod holes’ where the prized red snappers lived. The place names alone inspired adventure...Buccaneer Bay, Merry Island, Secret Cove, Pirates Rock, Welcome Pass, Princess Louisa. We canned salmon on the beach with my mother and grandmother, and listened to their stories of the coast, of their trips to Duncanby Landing, and of my grandfather and uncle trolling for salmon, finding glass balls, and of that strange animal in the fog that “definitely wasn’t a whale”. I remember vividly the first time our little boat was surrounded by killer whales, and later being under-the-sea, with my father, seeing a bull kelp forest for the first time, streaming in the current with shafts of sunlight spotlighting rockfishes, and neon-blue basket stars. And then there will always be our six-gill shark encounter. These stories, experiences, memories, and adventures continue to shape who I am, what I do, and where.

To my family

I. Introduction

I.I Effects of overfishing on marine ecosystems

Humans have reduced the abundance and diversity of large marine vertebrates over vast areas of the earth's oceans (Jackson et al. 2001, Myers & Worm 2003, Baum & Myers 2004, Jackson 2008, Estes et al. 2011). In their landmark paper, Jackson et al. (2001) argued that historical overfishing has caused the ecological extinction, or complete extinction, of taxa ranging from Steller's sea cow, sea otters, sea lions, and the great whales, to sharks, groupers, giant sea bass, and tunas, to name a few. As a result, the structure and functioning of coastal marine ecosystems have been fundamentally altered worldwide. Because large vertebrate consumers have the potential to alter nutrient and energy cycles through cascading trophic interactions, the tremendous scale and extent of overfishing may influence ecosystem processes globally. However, the ecosystem-level consequences of overfishing are only recently being described and quantified (Botsford et al. 1997, Tegner & Dayton 2000, Jackson et al. 2001, Pauly et al. 2002, Frank et al. 2005, Worm et al. 2006). Pauly et al. (2002) review the impacts of fisheries on ecosystems and conclude that the result of 'fishing down food webs' (Pauly et al. 1998) is reduction of the number and length of pathways linking food fishes to primary producers, and therefore simplification of food webs. However, removal of top predators and serial depletion of trophic levels can also invoke strong indirect effects on food web structure, energy flow and ecosystem productivity in the form of "trophic cascades" (Paine 1980, Carpenter et al. 1985).

Trophic cascades involve alternating and inverse patterns of abundance or biomass across two or more links in a food web driven by the abundance of top predators (Pace et al. 1999). For example, in a three-level food web, predators may reduce abundance of herbivores, and therefore indirectly increase the abundance of plants. While some ecologists argue that trophic cascades are overly simplified and not generally applicable to complex food webs typically found in nature (Strong 1992, Polis & Strong 1996), the concept of trophic cascades has "radiated through ecology and become the focus of theoretical analysis, field studies and management applications" (Pace et al. 1999). Indeed, increasing numbers of investigations are demonstrating

that trophic cascades are a common and widespread outcome of removal of top predators in terrestrial, marine, and aquatic ecosystems (Shurin et al. 2002, Shurin & Seabloom 2005, Terborgh & Estes 2010, Estes et al. 2011).

The effects of trophic cascades, however, may continue well beyond impacted primary producers. Classic examples of terrestrial trophic cascades involve reintroduced wolf (*Canis lupis*) populations reducing the abundance of elk and deer, and thereby facilitating recovery of hardwood forests (Beschta & Ripple 2009). In marine ecosystems, the most well known trophic cascade was revealed following recovery of sea otter (*Enhydra lutris*) populations. By consuming herbivorous sea urchins, sea otters indirectly increase the abundance of macroalgae populations especially the kelps (Estes & Palmisano 1974). In both examples, impacted primary producers not only provide energy to local food webs through photosynthesis, but they also provide critical structural habitat that supports diverse and productive and food webs. Berger et al. (2001) describe a trophic cascade wherein grizzly bears (*Ursus arctos*) and gray wolves (*Canis lupis*) reduce moose (*Alces alces*) populations, which in turn affect riparian vegetation richness and, subsequently, nest densities of neo-tropical migrating birds. Thus, trophic cascades *per se* do not define the full range of predator effects on food webs or ecosystem processes. Reisewitz et al. (2006) conclude that few studies have focused on the associated effects of trophic cascades because they are often difficult to demonstrate. Yet, understanding the entire range of effects of large vertebrate loss and reintroduction, and the spatial scales over which they occur, is critical for understanding species' responses to human-induced impacts, and for predicting outcomes of management initiatives on food web structure and dynamics.

The concepts of “food webs” and “niche” are deeply rooted in ecology (Elton 1927, Lindeman 1942, Odum & Odum 1955, Hutchinson 1957, 1959) and provide key frameworks for investigations of processes determining the abundance, diversity, and distribution of species in space and time, and the impacts of human activities. Charles Elton (1927) defined a species’ niche as the sum of all interactions, especially trophic, resulting in the prey consumed by individuals and, therefore, the individuals themselves. Recognition that species’ niches change (i.e. expand, contract, or shift) in response to environmental change and food web structure underlies the concept of trophic “niche space” (Hutchinson 1957, MacArthur et al. 1972, Bearhop et al. 2004). Food webs are conceptual models that depict ecologists’ understanding of the energy sources and trophic interactions structuring communities and ecosystems. The structure of food webs

determines the number and nature of trophic interactions experienced by individuals, and thereby the quality and quantity of prey consumed by individuals. In other words, food webs represent the landscape of niche space available for individuals and populations. Critically, because the quantity and quality of prey consumed by individuals determines rates of growth, survival, and reproduction (i.e. fitness), species-specific responses to changes in food web structure are expressed as changes in these key demographic rates that underlie population sizes and distributions (Hutchinson 1957). Knowledge of the processes determining the nature and magnitude of species' responses to loss or reintroduction of large marine vertebrates (i.e. food web structure) is critical for understanding corresponding changes in ecosystem properties such as productivity, diversity, and resilience (Carr et al. 2002, Beisner et al. 2003, Folke et al. 2004, Duffy et al. 2007).

The first broad objective of the research described in this dissertation is to advance knowledge of the effects of overfishing on coastal ecosystems necessary for development of effective conservation and management strategies.

1.2 Replenishment of marine populations

Most marine organisms have complex “bipartite” life cycles with pelagic (open-ocean) eggs and larvae that have profound consequences for population dynamics and persistence (Roughgarden et al. 1985, Roughgarden et al. 1988, Caley et al. 1996). In the preceding section, I described how food web structure influences the growth and survival rates of individuals, and therefore the dynamics of associated populations. However, these processes take place in nearshore benthic (seafloor) habitats and adult populations, and may depend strongly upon the frequency and magnitude of eggs and larvae received from upstream adult populations (i.e. “replenishment”). That is, local population dynamics also influence food web dynamics. Populations persist when births + immigration equal or exceed deaths + emigration. Pelagic eggs and larvae effectively emigrate from local adult populations when they are released into the water column and transported downstream by prevailing ocean currents. Following pelagic durations lasting from days to several months, and dispersal distances from 10's to 100's of km (Shanks 2009), juveniles eventually settle into downstream benthic habitats and adult populations (but see Shanks & Eckert 2005). In this way, population birth rates decoupled from the reproductive output of local

adult populations are the basis of the paradigm of “open” marine populations (Roughgarden et al. 1985). However, evidence indicating that ocean circulation patterns and larval behaviour interact to retain or return eggs and larvae to their natal populations increasingly suggests that some marine populations may be more “closed” than previously thought (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Thorrold et al. 2001, Sponaugle et al. 2002, Swearer et al. 2002, Kinlan et al. 2005, Almany et al. 2007). Population persistence, therefore, is fundamentally linked to rates of “connectivity” among local populations through exchange, or retention, of eggs and larvae (Palumbi 2003, Sale 2004, Pineda et al. 2007, Cowen & Sponaugle 2009).

Patterns and processes underlying the degree of connectivity among local populations within regional “metapopulations” (Kritzer & Sale 2006), underlie fundamental questions in marine ecology (Warner et al. 2000, Warner & Cowen 2002). What is the geographic source of juveniles arriving in local populations, and where do eggs and larvae produced in a local population go? What proportion of young arriving into local populations, if any, are products of local production? What are the oceanographic processes and larval behaviours that facilitate or inhibit larval delivery to local populations? These questions highlight the importance of knowledge of processes determining spatial patterns of larval supply necessary to understand marine population dynamics. For example, ocean currents transporting eggs and larvae are spatially structured and, therefore, not all locations are equal with respect to probabilities of receiving larvae from, or contributing larvae to, neighbouring subpopulations (Gaines et al. 2003). In addition to variation in the degree of connectivity resulting from patterns of ocean currents, because populations differ in size and reproductive output, some local populations may be important “sources” (i.e. they export more larvae than they receive) while others become net demographic “sinks” (i.e. they export less than they receive) (Pulliam 1988, Crowder et al. 2000). Unfortunately, few empirical estimates of connectivity within marine metapopulations exist because the technologies required to directly determine larval dispersal routes and distances are not yet available (but see Thorrold et al. 2002, Palumbi et al. 2003, Selkoe et al. 2008).

Population replenishment and connectivity are critical for informing fisheries management, in particular the design of marine protected areas (Gaines et al. 2010a). Marine protected areas (MPAs) are spatial management tools for maintaining and restoring marine fisheries, ecosystems, and biodiversity, and are increasingly being implemented worldwide (Lubchenco et al. 2003, Botsford et al. 2009). The premise for MPAs is that areas closed to fishing reduce fishing-induced

mortality, increase local population sizes and density-dependent emigration, and increase production and export of eggs and larvae (i.e. they create source populations) (Kellner et al. 2007, Pelc et al. 2010). Because MPAs are typically small relative to dispersal distances, long-term population persistence within MPAs is likely to depend upon receiving eggs and larvae from upstream populations (Gaines et al. 2003). MPA “networks”, therefore, comprise multiple MPAs separated by distances intended to match dispersal distances of target species (Gaines et al. 2010b). However, because dispersal distances and source-sink dynamics are poorly known, failure of MPAs to receive adequate larval supply may undermine achieving the objectives for which they were established.

Investigations of marine population dynamics focus heavily on processes underlying spatially and temporally variable patterns of larval settlement in local populations and habitats (Carr 1994, Doherty & Fowler 1994, Anderson et al. 2007, Johnson 2007, Morgan et al. 2009). Although the origins of larvae settling into local populations remain largely unknown, larval settlement rates allow comparison of the magnitude of population replenishment in space and time. In turn, spatial and temporal patterns of settlement rates are used as the basis for investigations of processes influencing variation in the frequency and magnitude of larval delivery. Settlement occurs when late-stage pelagic larvae or juveniles “settle” into benthic habitats, adult populations, and food webs (Carr & Syms 2006). However, high mortality rates associated with settlement may substantially modify patterns observed by ecologists weeks or months later (Caley et al. 1996). For this reason, the term “recruitment” is typically used to describe the number of individuals that have settled and survived to accumulate in local populations at the end of annual recruitment seasons (Carr & Syms 2006).

The second broad objective of the research described in this dissertation is to advance understanding of processes underlying marine population replenishment in the context of inter-relationships between population and food web dynamics, and informing the design and effectiveness of MPAs.

I.3 Study systems

I.3.1 The “otter-urchin-kelp” trophic cascade

“I can only compare these great aquatic forests . . . with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp. Amidst the leaves of this plant numerous species of fish live, which nowhere else could find food or shelter; with their destruction the many cormorants and other fishing birds, the otters, seals, and porpoise, would soon perish also; and lastly, the Fuegian[s] . . . would . . . decrease in numbers and perhaps cease to exist.”

Charles Darwin, 1 June 1834, Tierra del Fuego, Chile

(Darwin 1909, pp. 256-257)

The near extinction of sea otters as a result of the North Pacific maritime fur trade (Busch & Gough 1997, Dick 2005), is arguably one of the most dramatic examples of human-induced impacts to the trophic structure and functioning of nearshore marine ecosystems (Estes et al. 1998, Jackson et al. 2001). Kelp forests are among the most diverse and productive ecosystems on the planet (Mann 1973, Dayton 1985, Steneck et al. 2002), and support a wide range of services valued by human societies past and present (Erlandson et al. 2007, Palumbi et al. 2009). In the absence of sea otters, however, kelp forests ecosystems are vulnerable to widespread deforestation by unregulated sea urchin populations (Estes & Palmisano 1974, Estes & Duggins 1995, Tegner & Dayton 2000). The time-scales over which sea otters, and other important kelp forest consumers have been reduced, extirpated, or hunted to extinction underline the phenomena of “sliding baselines” (Dayton et al. 1998). Because no baseline data are available, the indirect effects of reducing or removing these consumers from kelp forest ecosystems are largely unknown (Tegner & Dayton 2000, Steneck et al. 2004).

Sea otters are small marine carnivores (Family Mustelidae) that once ranged from northern Japan to central Baja California. Prized for their lush pelts sea otters were extirpated or ecologically extinct throughout most of their range by the mid to late 1800’s (Estes et al. 1989). Fewer than 1000 animals are estimated to have survived in 11 remnant populations the in Kuril, Commander and Aleutian Islands, and central California (Kenyon 1969). Estes and Palmisano (1974) studied recovering populations in the western Aleutian Islands and concluded that sea

otters are “keystone” predators” (sensu Paine 1966). They argued that otters play a disproportionate role in structuring nearshore rocky reef ecosystems of the western Aleutian Islands. Estes and Palmisano (1974) based their argument on comparisons they made between islands with and without sea otters. They found that at islands where sea otters were absent, benthic macroalgae (specifically “kelps”, Phaeophyta, Order Laminariales) were rare, and high densities of herbivorous sea urchins were evenly distributed between depths of 0-25 meters. However, islands with sea otters supported abundant kelp communities and sparse densities of small sea urchins found primarily at depths greater than 20-25 m. Estes and Palmisano (1974) deduced that dense populations of sea otters reduce sea urchins to sparse populations of small individuals through size-selective predation, and release from grazing pressure permitted substantial increases in the size and productivity of kelp communities. These authors further observed that islands with sea otters and abundant kelp communities also supported high abundances of fauna dependent upon nearshore marine productivity, including demersal fishes, seals, and eagles. Thus, Estes and Palmisano concluded that predation by sea otters, and high primary and secondary productivity resulting from high kelp biomass, has broad implications for the structure and dynamics of nearshore marine food webs and ecosystems.

The high productivity, diversity, and complex trophic interactions associated with kelp forest ecosystems (Steneck et al. 2002), result from kelp populations providing complex habitat, modifying local hydrodynamic regimes, and enhancing secondary productivity through production of kelp-derived biomass and detritus (Duggins 1988). Estimates of kelp-derived carbon content of some kelp-associated consumers are as high as 100% (Dunton & Schell 1987, Duggins et al. 1989, Bustamante & Branch 1996, Fredriksen 2003, Page et al. 2008). However, relatively little kelp production is consumed by herbivores directly. Instead, kelp-derived productivity enters food webs when decaying tissues (i.e. “detritus”) are consumed by small detritivores (e.g. crustacean invertebrates) after being eroded and fragmented by waves and bacteria (Newell & Field 1983, Mann 1988, Mann 2000). Kelp-derived suspended particulate detritus is assimilated directly by some suspension feeders and may enhance consumer growth rates in regions where primary productivity is limiting (Duggins et al. 1989, Duggins & Eckman 1994, 1997, Salomon et al. 2008).

Kelps also enhance the abundance and diversity of nearshore organisms by producing a distinct and spatially complex physical environment (Duggins 1988, Graham 2003). Large canopy-forming kelps (especially the giant kelp *Macrocystis* spp. and the bull kelp *Nereocystis luetkeana*)

provide three-dimensional structure in an otherwise two-dimensional environment, often forming large expansive kelp forests (Dayton 1985). The vertical component of kelp canopies are partitioned by mid-water reef fishes (Hallacher & Roberts 1985, Ebeling & Laur 1988), and the horizontal nature of kelps forests form distinct ‘edge’ and ‘interior’ habitats (Duggins 1988). Kelps themselves provide primary substrate for many species of epifaunal, infaunal, sessile, mobile, planktivorous and detritivorous invertebrates (Graham et al. 2008a). Invertebrates specialized for living or feeding on kelp, and the presence or absence of chemical and structural attributes of kelp that defend against herbivores, indicate that otter-invertebrate-kelp interactions in the northeastern Pacific have evolved in close association over millions of years (Estes & Steinberg 1988, Steinberg et al. 1995). At regional scales, the size, shape, and distribution of kelp habitats may affect recruitment patterns of nearshore fishes and invertebrates (Eckman et al. 1989, Graham 2003, Carr & Syms 2006), and attenuate cross-reef current velocities and onshore wave exposure (Jackson 1998, Gaylord et al. 2007). Finally, the effects of kelp extend well beyond the footprints of individual kelp beds or forests through, for example, export of kelp-derived detritus to ‘recipient’ habitats and ecosystems (Polis & Hurd 1996, Kaehler et al. 2006), or reduction of propagules and prey to adjacent habitats and populations (Gaines & Roughgarden 1987).

The extensive literature concerning the ecology of kelp communities and the effects of sea otters broadly support the original contentions of Estes and Palmisano (but see Foster & Schiel 1988, Carter et al. 2007), and highlight the ecological, evolutionary, and cultural significance of sea otters in coastal marine ecosystems (Simenstad et al. 1978, Estes & Steinberg 1988, Estes & Duggins 1995, Steinberg et al. 1995, Estes et al. 1998, Reisewitz et al. 2006, Anthony et al. 2008). At the same time, during the 100+ year absence of sea otters, rapid growth of many benthic invertebrate populations (e.g. urchins, abalone, geoduck, and crabs) lead to development of numerous aboriginal, recreational, and commercial shellfish fisheries that are now economic mainstays of many coastal communities (Watson 2000). Declines in these fisheries following a series of otter reintroductions in the early 1970’s to southeast Alaska, British Columbia, Washington, and Oregon have fueled a heated controversy (Wendell 1994, Watson & Smith 1996, Watson 2000, Fanshawe et al. 2003). Largely absent from this debate has been empirical evidence of potentially compensatory indirect effects of sea otters on the dynamics of marine fish populations, and ecosystem properties such as diversity, productivity, and resilience (but see Watson & Estes 2011). The paucity of these data owe largely to the challenges associated with

studying ecosystems and processes that are not readily manipulated or replicated (Hargrove & Pickering 1992). As a result, many of the direct and indirect effects of sea otters on coastal ecosystem dynamics remain untested (Estes 2008).

1.3.2 Nearshore Pacific rockfishes (Genus *Sebastes*)

Rockfishes of the genus *Sebastes* (Family Scorpaenidae) comprise one of most ecologically and economically important groups marine fishes along the Pacific coast of North America (Love et al. 2002). With 102 species worldwide and at least 72 species in the northeastern Pacific, rockfishes are found in all coastal habitats where they can be the most abundant group of demersal (bottom-dwelling) and mid-water fishes. For management purposes rockfishes are broadly categorized as “nearshore”, “shelf” and “slope” complexes (Parker et al. 2000). For the purposes of this introduction I focus on nearshore rockfishes that are common inhabitants of rocky reef and kelp forest habitats and food webs.

Nearshore rockfishes can be further subdivided into “mid-water aggregating” and “solitary-benthic” complexes, comprised of species representing primarily two subgenera that differ remarkably in their morphology, ecology, and evolutionary histories (Hyde & Vetter 2007). Species within the subgenus *Sebastosomus*, are mid-water aggregating species (e.g. *S. flavidus*, *S. melanops*, *S. mystinus*, *S. serranoides*), generally associated with shallow semi-pelagic habitats, are darkly or drably coloured, and have elongated bodies with greatly reduced head spines (Hyde & Vetter 2007). In contrast, subgenus *Pteropodus* is comprised of solitary benthic species (e.g. *S. carnatus*, *S. caurinus*, *S. chrysomelas*, *S. maliger*, *S. nebulosus*, *S. rastrelliger*), that are generally associated with shallow high-relief habitats, have deep bodies, often with distinct coloration patterns, and strong head spination (Hyde & Vetter 2007). In their recent phylogenetic reconstruction of the genus *Sebastes*, Hyde & Vetter propose that elongate body plans and semi-pelagic lifestyles of mid-water aggregating species are derived characteristics closely associated with pronounced increases in upwelling and primary productivity in the western Pacific Ocean approximately nine million years ago.

Many rockfishes are remarkable for their extreme longevity, with maximum ages commonly between 50 and 100 years, and with some species attaining more than 200 years of age (Lea et al. 1999, Munk 2001). These long generation times of rockfishes may represent bet-hedging

strategies in response to the variable oceanographic conditions of the North Pacific Ocean, highly variable recruitment success, and low first year survival (Love et al. 2002). Elaborate courtship behaviours and copulation generally occurs in the fall, and females give birth to live young (a process called “parturition”) during the winter and early spring. The numbers and quality of larvae released increase with increasing female size and age (Berkeley et al. 2004). At full length adult females may release more than a million larvae that are approximately 3-7 mm long at parturition. Larvae develop into pelagic juveniles after one to two months (Love et al. 2002), and remain in the water column and offshore for additional weeks to months before moving to inshore settlement habitats and adult populations (Moser & Boehlert 1991). However, the oceanographic and behavioural processes that are responsible for delivery of rockfish larvae to nearshore habitats are poorly understood (Larson et al. 1994, Bjorkstedt et al. 2002).

Early post-settlement juvenile and adult rockfish life history stages are better known. Settlement habitats are often species-specific, and include kelp forests, eelgrass meadows, and rocky and soft-bottom habitats (Love et al. 1991, Johnson et al. 2001, Love et al. 2002). The effects of kelp density and ‘architecture’ have strong effects on rockfish settlement patterns and post-settlement mortality rates (Carr 1989, 1991, 1994, Johnson 2006, 2007). By late summer and early fall juveniles begin to migrate deeper to adult habitats. Little is known about juvenile habitat selection upon leaving settlement habitats, but most studies indicate that there is little horizontal post-settlement movement among habitats (Love et al. 1991, Byerly 2001, Nelson 2001). Small home ranges of adult rockfishes, particularly solitary-benthic species, hold important implications for spatial settlement patterns and the effectiveness of marine protected areas. For example, home ranges of copper rockfish (*S. caurinus*) [solitary-benthic complex] are usually $< 10 \text{ m}^2$ on high relief reefs (Matthews 1990b, a), while home ranges of blue (*S. mystinus*) and black (*S. melanops*) rockfishes [mid-water aggregating complex] have been estimated at 1350 m^2 (Jorgensen et al. 2006) and 5500 m^2 (Parker et al. 2007), respectively. At least some solitary-benthic species are territorial (Larson 1980), and exhibit strong homing behaviour when displaced (Matthews 1990a). In California kelp forests, diverse assemblages of rockfishes reduce competition by finely partitioning prey resources and benthic and pelagic habitats (Hallacher & Roberts 1985).

Solitary-benthic and mid-water aggregating rockfish consume similar prey as larvae and pelagic juveniles, but their diets begin to diverge shortly after settlement. Pelagic larvae and juveniles

consume primarily copepod nauplii, and eventually copepodite stages, adult copepods, and euphausiids (Moser & Boehlert 1991). Following settlement, juveniles consume open-water prey (copepods, crab zoea, and juvenile polychaetes), and substrate-associated prey (gammarid amphipods, mysids, isopods, and caridean shrimp) (Singer 1985). Sub-adult and adult rockfishes consume increasingly larger prey as they grow larger, with solitary-benthic species consuming primarily benthic invertebrates, and mid-water aggregating species consuming macro-zooplankton and kelp-associated invertebrates. All rockfishes are opportunistic piscivores and readily cannibalize juvenile rockfishes (Hallacher & Roberts 1985, Hobson et al. 2001). Other predators of juvenile rockfishes commonly include other reef fishes, salmon, and seabirds (Ainley et al. 1993, Love et al. 2002). As adults, rockfishes are consumed by lingcod, cabezon, halibut, seals and sea lions (Love et al. 2002).

Numerous life history attributes make rockfishes particularly vulnerable to overfishing (Leaman 1991, Lea et al. 1999, Parker et al. 2000, Love et al. 2002). Highly variable recruitment, slow growth, and delayed reproductive maturity underlie intrinsically low rates of population increase. Nearshore rockfish populations suffer high fishing-induced mortality because of their strong association with rocky habitats, the ease with which they are taken by hook-and-line, and because the nature of their swim bladders make them vulnerable to barotraumatic injuries (Jarvis & Lowe 2008). Rockfishes have deep histories of overexploitation, as evidenced by archaeological records on the west coast of Vancouver Island (McKechnie 2007). Historically, dramatic population declines from Alaska to California over the past four decades resulting from targeted commercial and recreational fishing, and as by-catch (Parker et al. 2000, Williams et al. 2010), have made rockfishes key targets for protection by marine reserves and other forms of MPAs. In British Columbia, in an effort to rebuild nearshore rockfish populations, 164 Rockfish Conservation Areas (RCAs) were established between 2004 and 2007, collectively encompassing 20% of all rockfish habitats in outside waters (Yamanaka & Logan 2010).

1.4 Overview of dissertation

In this dissertation I present three studies that address the following questions concerning rockfish recruitment and trophic dynamics, and the indirect effects of sea otter reintroduction, in rocky reef and kelp forest ecosystems on the west coast of Vancouver Island.

1.4.1 What are the factors underlying spatially variable patterns of rockfish recruitment and how do they influence the effectiveness of Rockfish Conservation Areas?

In Chapter 2, I describe a large-scale, multi-year and collaborative investigation of factors underlying spatial patterns of nearshore rockfish recruitment in kelp forest and eelgrass meadow habitats on the west coast of Vancouver. Over a four-year period my collaborators and I assessed spatial patterns of rockfish recruitment success inside and outside of a Rockfish Conservation Area (RCA), and tested whether the resulting patterns were consistent from year to year. We asked: do locations that experience relatively high recruitment do so year after year? Our results support the hypothesis that spatially consistent patterns of recruitment intensity result from consistent patterns of larval delivery caused by stable interactions between nearshore topography and physical oceanography. Because the effectiveness of RCAs and other forms of marine protected areas (MPAs) are likely to depend upon receiving larvae from upstream sources, the results of this study provide valuable insight with respect to MPA location and design.

1.4.2 How does variable ocean climate affect recruitment success of nearshore rockfishes?

In Chapter 3, I build upon the results of Chapter 2 in which I detected high recruitment success of solitary-benthic and mid-water aggregating rockfishes in years of strongly contrasting oceanographic conditions. I ask: what were the oceanographic conditions responsible for the recruitment success, or failure, of rockfishes in these years, and during which pre-settlement

stages did they occur? To address this question I examined relationships between coastal upwelling events and rockfish early life history attributes. By analyzing rockfish otoliths (ear bones) I determined birth and settlement dates, pelagic durations, and pre- and post-settlement growth rates of juvenile rockfishes. I examined how changes in these attributes correspond to the intensity of coastal upwelling and associated changes in sea surface temperature and primary productivity. I reveal that although warm ocean temperatures enhance growth rates and decrease pelagic durations of both rockfish complexes, oceanographic processes underlying onshore delivery rates may be the primary determinant of mid-water aggregating rockfish recruitment success. The findings presented in this chapter provide insight into the specific responses of different rockfishes that will contribute to predictive models of recruitment success and fisheries management.

1.4.3 What are the indirect effects of sea otter reintroduction on rockfish population dynamics?

In Chapter 4, I integrate my investigations of processes underlying rockfish recruitment success with investigation of the indirect effects of recovering sea otter populations and kelp forest habitats. To do this, I first undertake a large-scale comparison of the extent to which kelp forest habitats increase in depth and size following sea otter recovery on the west coast of Vancouver Island. I then ask: what is the effect of kelp forest habitat size on rockfish recruitment success? In other words, following sea otter recovery, do larger kelp forests intercept and accumulate higher numbers of late-stage pelagic juvenile rockfishes? If this is the case, then sea otter reintroduction may hold broad implications for nearshore reef fish recruitment dynamics.

Following settlement, the size and productivity of kelp forest habitats and food webs are also likely to have important consequences for the diets (i.e. trophic niche space) and growth rates of juvenile and adult rockfishes. I test these predictions in the following ways. By analyzing the abundance of naturally occurring stable isotopes, I compare the kelp-carbon contents and trophic positions (i.e. trophic niche space) of adult rockfishes collected from areas with and without sea otters. I also contrast relationships between juvenile and adult rockfish body size, kelp-carbon content, and trophic position to compare the rates at which individuals “shift” their niche space with changes in body size in food webs with and without otters. Finally, because the results

indicate that rockfishes consume higher proportions of fish in the presence of sea otters, I ask: what are the relative effects of variable kelp-carbon content and trophic position on individual juvenile rockfish growth rates?

Through these questions and approaches I reveal how characteristics of kelp forest habitats, driven by sea otters, may affect rockfish recruitment success, and how rockfish diets and growth rates are intimately related to habitat size and productivity. More broadly, I show that the trophic and non-trophic indirect effects of sea otters extend well beyond sea urchins and kelp.

2. Spatially consistent patterns of temperate reef fish recruitment inform marine protected area design and effectiveness

2.1 Synopsis

Processes responsible for the spatial distribution and intensity of larval supply and recruitment of marine organisms are key determinants of rates of population replenishment and the effectiveness of Marine Protected Areas (MPAs). Working in the vicinity of a 46 km² Rockfish Conservation Area (RCA) on the west coast of Vancouver Island, Canada, we assessed spatial patterns of recruitment intensity of inshore Pacific rockfishes (*Sebastes* spp.) in kelp forest (*Macrocystis pyrifera*) and eelgrass meadow (*Zostera marina*) habitats. Kelp forests were distributed over approximately 156 km² and sampled bi-weekly between May and August for four years. We deployed Standard Monitoring Units for the Recruitment of Fish (SMURFs) in kelp forests to assess recruitment intensity. Eelgrass meadows were distributed over approximately 81 km² and sampled annually for seven years using beach seines. We evaluated relationships between black rockfish (*S. melanops*) recruitment intensity and location-specific measures of distance to the open coast, cumulative fetch, tidal velocity, and sea surface temperature to investigate processes underlying spatial patterns of recruitment intensity. Recruitment intensity was consistently highest at kelp and eelgrass locations that were short distances from the open coast, had high fetch, high tidal velocity, and low sea surface temperature. Kelp and eelgrass locations within the RCA experienced consistently low recruitment, even during an exceptionally strong black rockfish recruitment event in 2006. In contrast, we identified a 4.28 km² recruitment ‘hotspot’ located a short distance beyond the RCA boundaries. We propose that rockfish populations encompassed by the RCA examined here may fall largely within a recruitment ‘shadow’ created by outer coast (upstream) islands intercepting the majority of larvae moving onshore and insufficient tidal velocity to facilitate larval movement into the RCA.

2.2 Introduction

Knowledge of the processes underlying variation in the magnitude and frequency of the addition of new individuals to local populations (i.e. “replenishment”), and the exchange of individuals between local populations (i.e. “connectivity”), are critical to understanding marine population dynamics and the effectiveness of marine protected areas (MPAs) (Roberts 1998, Palumbi 2003, Fogarty & Botsford 2007, Botsford et al. 2009, Cowen & Sponaugle 2009). Many marine fishes and invertebrates have complex life histories (Roughgarden et al. 1988) that include pelagic larvae or eggs that may last several months and be transported hundreds of kilometers (Shanks et al. 2003, Pineda et al. 2007). Although interactions between larval behaviour and physical oceanographic processes may facilitate retention or return of larvae to natal populations (Jones et al. 1999, Swearer et al. 1999, Sponaugle et al. 2002, Warner & Cowen 2002), the numbers of pelagic juveniles arriving in benthic populations (i.e. “settlement”) may be largely decoupled from local production of eggs and larvae (Roughgarden et al. 1985). Settlement is rarely observed, and is associated with high mortality rates that may obscure spatial and temporal patterns of larval supply (Caley et al. 1996). For this reason “recruitment” in marine reef fish ecology is commonly used to describe interannual variation in the number of individuals that have settled and persisted to accumulate at the end of annual recruitment seasons (Carr and Syms 2006). Recruitment intensity can influence rates of local population replenishment (Caley et al. 1996, Armsworth 2002, Doherty 2002, Cowen & Sponaugle 2009), and therefore knowledge of processes underlying recruitment variability is critical to understanding of marine population dynamics. In this study we investigate spatial patterns of recruitment intensity of nearshore Pacific rockfishes (Genus *Sebastodes*) and consider their implications for the design and effectiveness of MPAs.

Marine protected areas (MPAs) are spatial management tools for maintaining and restoring marine fisheries, ecosystems, and biodiversity, and are increasingly being implemented worldwide (Botsford et al. 2009). Broadly defined as “areas of the ocean designated to enhance conservation of marine resources”, the level of protection conveyed by MPAs varies widely (Lubchenco et al. 2003). Common ecological and fisheries management objectives of MPAs include reduction or elimination of fishing-induced mortality to increase population-level characteristics such as total biomass or density, as well as the longevity and size of individuals. The reduction of fishing-induced mortality alone, however, is insufficient to guarantee population recovery and

persistence (Gaines et al. 2003, Fogarty & Botsford 2007, Gaines et al. 2010b). Build-up of biomass within MPAs is expected to protect spawning-stock biomass and enhance fisheries yields in two ways: density-dependent movement of juvenile and adults stages of mobile species across MPA boundaries (i.e. “spillover effects”; Botsford et al. 2003), and increased production and export of eggs and larvae to downstream regions (i.e. “recruitment-subsidy effects”; Russ 2002, Botsford et al. 2003, but see Walters et al. 2007).

Recovery and persistence of populations within MPAs, therefore, are the underpinnings of objectives related to fisheries management and conservation. However, MPAs are typically small relative to estimates of larval dispersal distances (Shanks 2009), and therefore the majority of eggs and larvae produced by local adult populations are likely to be exported beyond MPA boundaries and contribute little to local recruitment (Gaines et al. 2003, Gaines et al. 2010b). Owing to low adult immigration rates and low internal birth rates, the persistence of populations within MPAs is likely to depend on receiving externally-produced larvae (Roberts 1998, Warner et al. 2000, Gaines et al. 2003, Fogarty & Botsford 2007). For this reason, maximizing the likelihood that populations receive adequate recruitment through strategic configuration of MPAs (i.e. placement, size, shape, spacing) is a central goal of MPA design principles (Botsford et al. 2001, Sale et al. 2005).

Placement of MPAs and the topographic and oceanographic features they encompass are important determinants of larval delivery, recruitment rates, population growth rates, and ultimately, MPA effectiveness (Crowder et al. 2000, Warner et al. 2000, Gaines et al. 2003, Carr et al. in press). In particular, in nearshore environments dominant current regimes interact with local topography (i.e. headlands, islands, bays and reefs), to produce complex secondary flows that can aggregate and accumulate eggs and larvae, and therefore drive subsequent spatial patterns of recruitment intensity (see review by Wolanski & Hamner 1988). Thus, not all locations within nearshore seascapes are equivalent with respect to the probability of receiving eggs and larvae (Gaines et al. 2003). Numerous studies of marine fishes and invertebrates have reported consistent spatial patterns of recruitment intensity at scales relevant to the effectiveness of MPAs (Graham & Largier 1997, Tolimieri et al. 1998, Booth et al. 2000, Wing et al. 2003, Hamilton et al. 2006, White & Caselle 2008). For example, Hamilton et al. (2006) identified consistent spatial patterns of blue head wrasse (*Thalassoma bifasciatum*) recruitment at their sites in the US Virgin Islands over a twelve-year period. Identifying the characteristics of

areas experiencing consistently high or low recruitment can ensure MPAs are located so as to maximize the likelihood of recruitment rates adequate for connectivity, growth, and persistence of local populations.

Here we examine spatial patterns of rockfish recruitment intensity and their association with local topography and oceanography near a Rockfish Conservation Area (RCA) on the west coast of Vancouver Island, British Columbia. Using recruitment data collected in eelgrass meadow and kelp forest habitats over seven and four years, respectively, we describe and contrast spatial patterns of rockfish recruitment intensity between areas inside and outside of a recently established RCA. We investigate spatial patterns of recruitment by evaluating relationships between recruitment intensity and location-specific measures of distance to the open coast, fetch, tidal velocity and sea surface temperature. Our results support the hypothesis that spatially consistent patterns of rockfish recruitment result from predictable patterns of larval delivery caused by stable interactions between nearshore topography and physical oceanography. These findings suggest that the RCA considered here encompasses an area of generally low rockfish recruitment and, to the extent that recruitment rates influence local population sizes, indicate that this and other RCAs would benefit from consideration of spatial patterns of recruitment variability during their design.

2.3 Methods

2.3.1 Study species

Pacific rockfishes are among the most ecologically and economically important fishes on the west coast of North America. Following elaborate courtships and internal fertilization rockfishes give birth to live young. Larvae and pelagic juveniles typically remain in the water column for approximately 30-150 days (Love et al. 2002), and the few available estimates of dispersal distances range from 10-120 km (Buonaccorsi et al. 2004, Miller & Shanks 2004). Settlement of inshore species occurs in shallow nearshore habitats including kelp forests, eelgrass meadows, and rocky and soft-bottom habitats (Love et al. 1991, Carr 1994, Johnson et al. 2001, Love et al. 2002). Following settlement juveniles migrate deeper to adult habitats. Adult site fidelity is

generally high and there is little horizontal post-settlement movement among habitat types (Love et al. 1991, Byerly 2001, Nelson 2001). Nearshore species are strongly associated with rocky reef habitats where they prey upon a variety of invertebrates and fishes, and they are the targets of intense recreational and commercial fisheries. Rockfishes possess numerous life history characteristics that make them particularly vulnerable to over-fishing, including slow growth rates, delayed reproductive maturity, and high site fidelity (Lea et al. 1999, Munk 2001, Love et al. 2002). Dramatic population declines from Alaska to California over the past four decades (Parker et al. 2000, Williams et al. 2010) have made rockfishes key targets for protection by marine reserves and other forms of MPAs

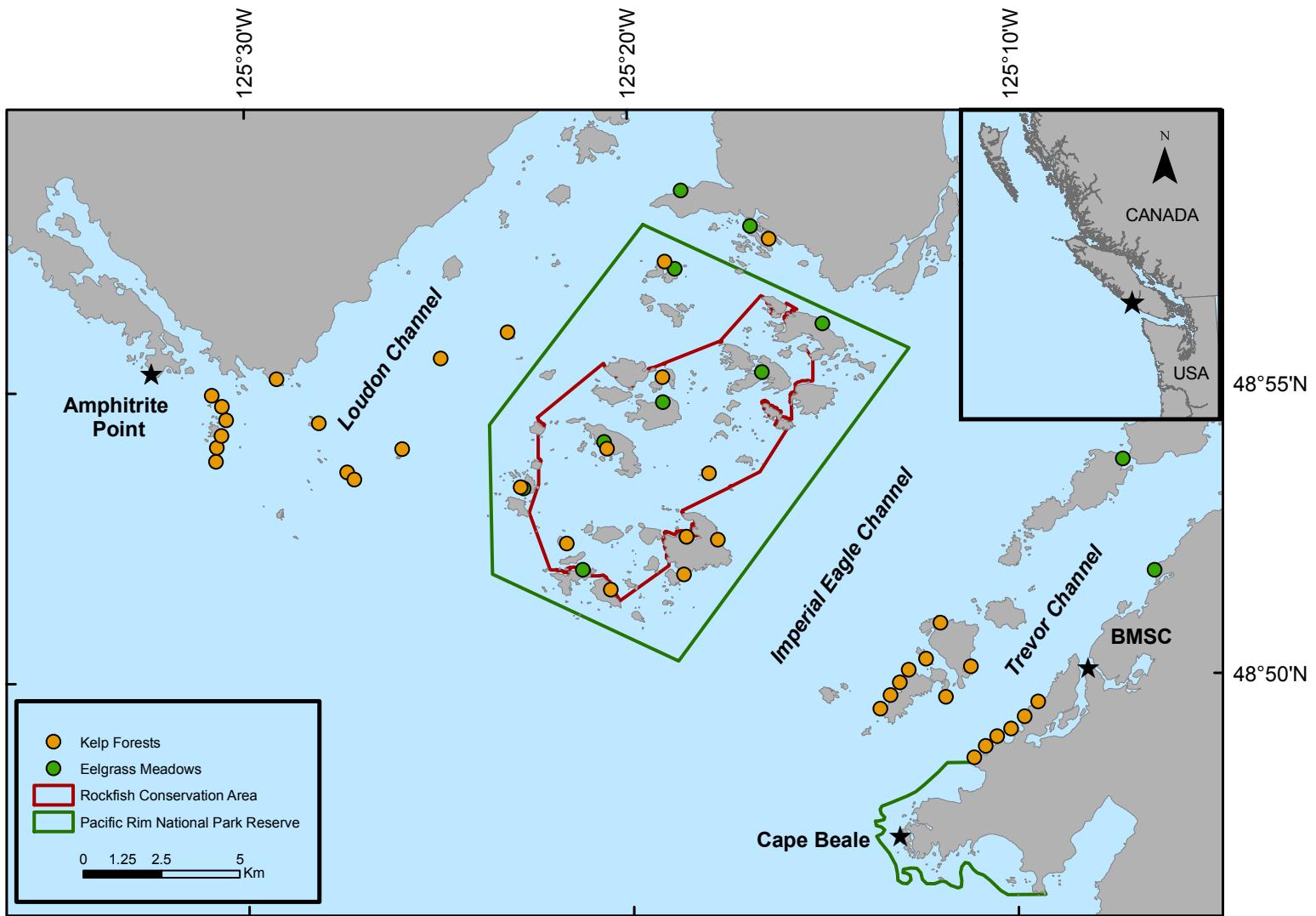


Figure 2.1. Eelgrass (*Z. marina*) and kelp forest (*M. pyrifera*) sampling locations in Barkley Sound (2005-2008)

2.3.2 Study system

In response to mounting conservation concern for inshore rockfish populations, Canada's federal agency responsible for fisheries management and protection (Fisheries and Oceans Canada) created an unprecedented system of Rockfish Conservation Areas (RCAs) (reviewed by Yamanaka & Logan 2010). Between 2004 and 2007, 164 RCAs were established that collectively encompass approximately 30% of inshore rockfish habitat within inside waters (i.e. east of Vancouver Island), and approximately 20% within the outside waters of coastal British Columbia. RCAs are intended to significantly reduce fishing-induced mortality by excluding all commercial and recreational fishing using hook and line and commercial bottom trawling. However, RCAs were not designed considering the connectivity or replenishment of local populations within regional meta-populations (i.e. marine reserve networks; Gaines et al. 2010). Instead, rockfish habitat was identified using a model that integrated benthic habitat complexity (measured as the second derivative of the slope) and commercial rockfish catch (catch-per-unit-effort density). RCA placement and precise boundaries were ultimately determined following an extensive stakeholder consultation process to address socioeconomic concerns, such as accommodating salmon troll fisheries and recreational fishing lodges (Yamanaka and Logan 2010).

This research was conducted in Barkley Sound ($48^{\circ} 50.0'N$, $125^{\circ} 22.0'W$) on the southwest coast of Vancouver Island (Fig. 2.1). In contrast to the relatively uniform coastline from California to Washington, the British Columbia coast is complex and characterized by myriad of island-studded sounds, inlets and fjords. The result of this complexity is a wide range of wave exposure, tidal velocities, substratum types, and disturbance regimes that support high habitat diversity over small spatial scales. Barkley Sound encompasses an area of approximately 500 km^2 and contains the Broken Group Islands (BGI), an archipelago of approximately 110 islands covering an area of approximately 100 km^2 . The BGI comprise one of three units of the Pacific Rim National Park Reserve of Canada. The Broken Group Islands RCA (46 km^2) was established in 2004 and falls within the boundaries of the National Park Reserve.

2.3.3 Spatial and temporal patterns of recruitment

We assessed spatial and temporal patterns of rockfish recruitment intensity in *Zostera marina* eelgrass meadows (hereafter “*Zostera*”) and *Macrocystis pyrifera* kelp forests (hereafter “*Macrocystis*”) throughout Barkley Sound. Eight to 12 eelgrass meadows accessible during low tides were sampled within the BGI each July between 2002 and 2008. Meadows ranged in size from 600-2200 m². At each meadow two or three beach seine sets were completed using a 9.2 m long seine having a 3.1 m drop in the centre tapering to 1.1 m at the wings with 4.0 mm black stretch mesh. Seining was conducted during a two-hour window before and after the early morning lowest low tide (tidal height < 0.6 m Canadian chart datum). The maximum total area of each eelgrass meadow sampled after three beach seines was approximately 300 m². Young-of-the-year (YOY) rockfishes were weighed, measured (total length, TL), and identified on the basis of size, body shape and pigment patterns (Matarese et al. 1989, Kendall 1991). Closely related black (*Sebastes melanops*) and yellowtail (*S. flavidus*) rockfish were differentiated on the basis of pigment patterns and timing of recruitment. Copper (*S. caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfishes were grouped as “CQB complex” rockfishes because of difficulty distinguishing early post-settlement juveniles. Rockfish recruitment in eelgrass meadows is reported as the number of rockfish per set.

We assessed rockfish recruitment in *Macrocystis* forests between 2005 and 2008. *Macrocystis* forests in this region are typically found on the leeward side of outer coast islands and headlands on rocky bottoms in areas of moderate wave exposure. *Macrocystis* forests ranged in size from 100-1600 m². To assess rockfish recruitment in kelp forest habitats we employed Standard Monitoring Units for Recruitment of Fishes (SMURFS; Ammann 2004). SMURFs permit assessment and comparison of coastal fish settlement by providing standardized units of artificial habitat. Each SMURF consists of a 1.0 m x 0.35 m cylinder of plastic garden fencing material (2.5 cm x 2.5 cm mesh), stuffed with strips of plastic snow fence material. We deployed SMURFs at six locations nested within five sites throughout Barkley Sound: George Fraser Islands (GF), Loudoun Channel (LC), Broken Group Islands (BGI), Edward King Island (EK), and Prasexe (PE) (Fig. 2.1). In 2005 the site BGI was not included in this sampling regime and just four SMURFs were deployed per site. SMURFs were moored at the seaward edge and in physical contact with *Macrocystis* forests, suspended horizontally 1.5 m below the surface, and anchored using 20 liter

plastic buckets filled with cement. For a description of the utility of deploying SMURFs in kelp forests as opposed to open water refer to Appendix A. Kelp forest locations were sampled approximately every two weeks between June and August. A Benthic Ichthyofaunal Net for Coral/Kelp Environments (BINCKE; Anderson & Carr 1998) was used with snorkeling equipment to capture all fish occupying SMURFs on each sampling date. Rockfish recruitment in kelp forests is reported as the number of rockfish per SMURF.

2.3.4 Data analyses: patterns among years

We compared rockfish recruitment between species and years within habitat types (eelgrass and kelp), but not between habitats due to gear type differences. To calculate mean recruitment in eelgrass meadows for each year we averaged catches across locations for each rockfish species or species complex. We sampled kelp forest locations multiple times each year, and because most recruitment occurred between June and August, we limited analyses to these months. To calculate mean recruitment in kelp forests for each year, we first averaged recruitment at each location across sampling dates within years, and then across locations within years. We calculated grand means of recruitment for all eelgrass and kelp locations by averaging location means across all years, 2005-2008.

To test for differences in recruitment intensity between species and years within each habitat we constructed negative binomial general linear models (R package ‘MASS’) fit with log link functions and minimum residual deviance (Crawley 2007). We treated species and year as fixed effects because annual differences in oceanographic conditions are key drivers of mean rockfish recruitment intensity (Caselle et al. 2010a). We limited subsequent analyses to black rockfish recruitment because CQB complex recruitment was weak and variable after 2005. We compared black rockfish recruitment intensity between the five kelp forest sites ($n = 6$ SMURFs/site), using the approach described above, treating both site and year as fixed factors.

To assess whether the rank order of location-specific recruitment intensity was consistent between years we used Kendall’s coefficient of concordance (W), a non-parametric statistic that represents the probability that variables are in the same order. We used all pair-wise combinations of black rockfish mean annual recruitment (2005-2008) in all eelgrass and kelp

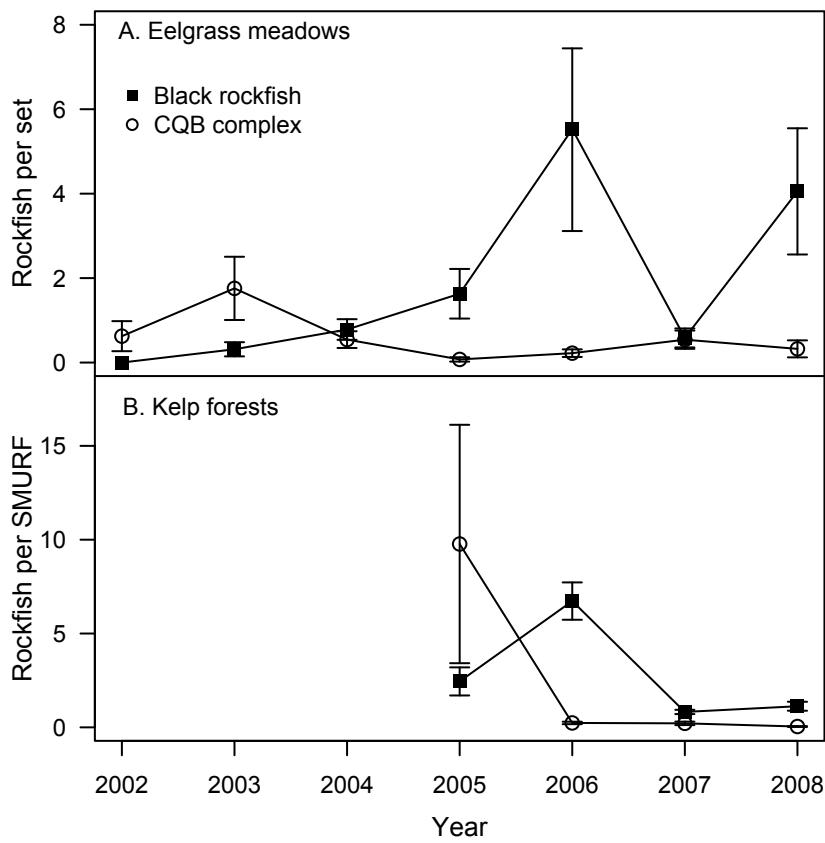


Figure 2.2. Annual recruitment of CQB complex (*S. caurinus*, *S. maliger*, *S. auriculatus*) and black (*S. melanops*) rockfishes in: (a) eelgrass meadows ($n = 9, 9, 11, 9, 12, 8, 12$, 2002-2008, respectively), mean no. rockfish /set \pm SE; and (b) kelp forests ($n = 16, 30, 30, 30$, 2005-2008, respectively), mean no. rockfish /SMURF \pm SE.

forest locations. Sample sizes differed somewhat between years because of small annual differences in sampling effort in both eelgrass and kelp habitats.

2.3.5 Data analysis: topographic and oceanographic drivers of spatial recruitment patterns

We used principal component analysis (PCA) to relate variables associated with topographic and oceanographic variability with areas of generally high and low recruitment intensity. We included the following variables in the PCA: distance to open coast (km), cumulative fetch (km), tidal velocity (m/s), and sea surface temperature (°C). We measured distance to the open coast by drawing a line perpendicular to the entrance of Barkley Sound (demarcated as a line between Cape Beale and Amphitrite Point, Fig. 2.1), inshore to each kelp and eelgrass location. Fetch is an estimate of the exposure of a site to ocean swell that is integrated over time. We estimated fetch for each location by extending and measuring radiating lines every ten degrees to the nearest landmass using the navigational software Nobletech (v.4.1). Where lines extended into the offshore region we assigned a maximum distance of 185 km (100 nautical miles). Fetch was recorded as the summed length of all lines for each location. We predicted that locations with short distances from the open coast and high fetch should have the lowest potential for “recruitment shadow” effects (*sensu* Jones 1997), and experience generally higher recruitment than interior areas with low fetch. We assigned all eelgrass and kelp forest locations single values of tidal velocity using the modeled estimates produced by Stronach et al. (1993). We predicted that high tidal velocity should be associated with high larval delivery and therefore recruitment. Sea surface temperature (SST) was measured on each sampling date and then averaged over months and years to provide an average value for each location. Because rockfish larvae are associated with upwelling fronts (Larson et al. 1988, Yoklavich et al. 1996, Bjorkstedt et al. 2002), we hypothesized that lower SST would be associated with the transport of recently upwelled water onshore, and therefore larval transport. Accordingly, we predicted SST would be correlated negatively with recruitment.

To examine the relationship between black rockfish recruitment and the first PCA axis of site features, we regressed the grand mean of black rockfish recruitment (2005-2008) at each eelgrass and kelp location onto their corresponding principal component axis values. Because the first

principal components axis (PC1) explained 65% of the variation, we confined analysis to this axis. We examined the direction and magnitude of the relationship between recruitment and PC1 in kelp and eelgrass habitats using simple linear regression. All analyses were performed using R (R Core Development Team 2011).

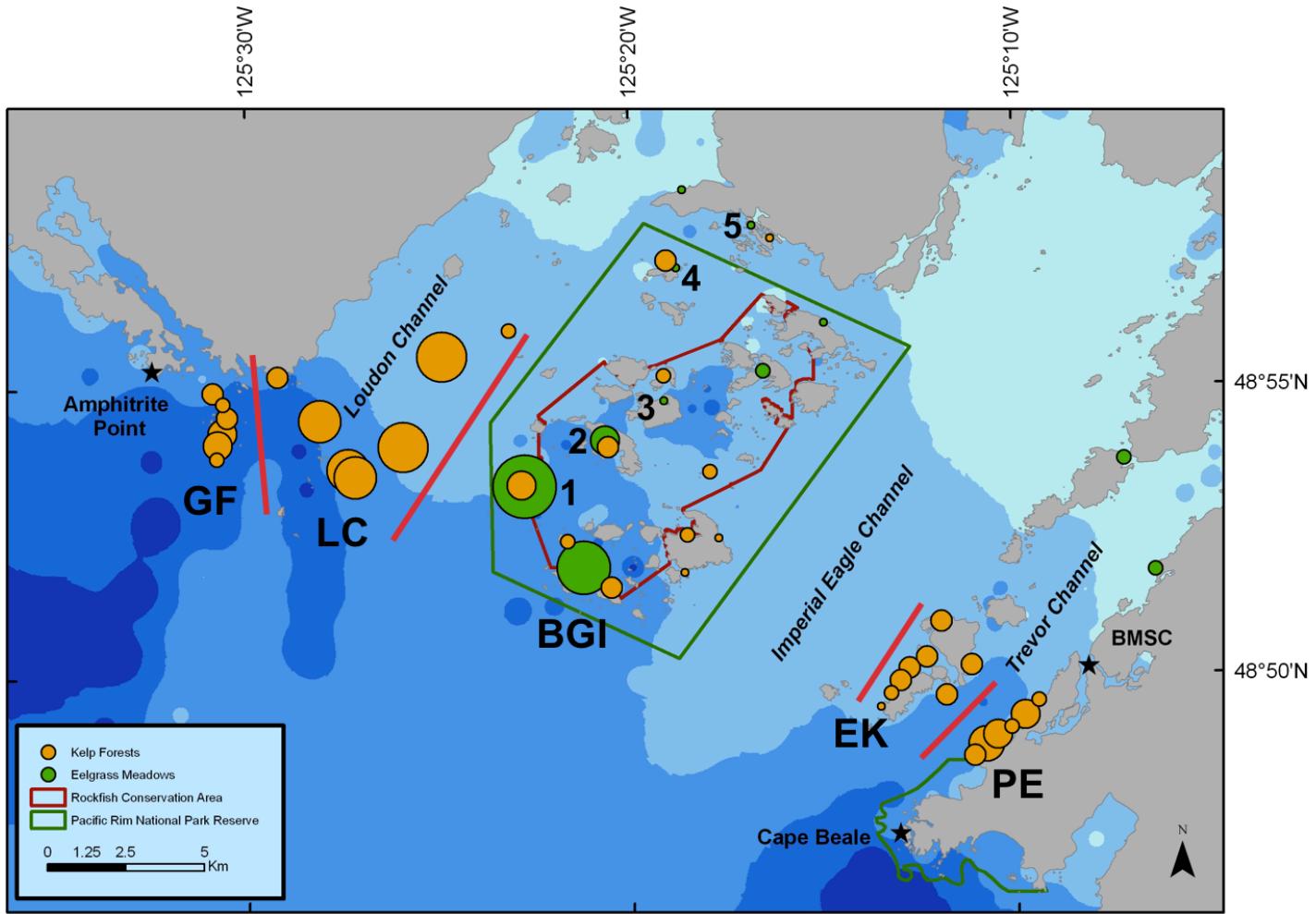


Figure 2.3. Mean black rockfish (*S. melanops*) recruitment (no./set or SMURF) at eelgrass meadow and kelp forest locations between 2005 and 2008. Bubble sizes indicate recruitment ranging from 0 (smallest) to 13 (largest). Red bars delineate sites with replicate kelp forest locations corresponding to Fig. 2.5, including George Fraser Is. (GF), Loudoun Channel (LC), Broken Group Is. (BG), Edward King Is. (EK), and PrasExe (PE). Numbers 1-5 indicate eelgrass meadow locations corresponding to Fig. 2.6. Shaded contours depict modeled tidal velocities (Stronach et al. 1993) and range from 0.001 m/s (light blue) to 0.292 m/s (dark blue).

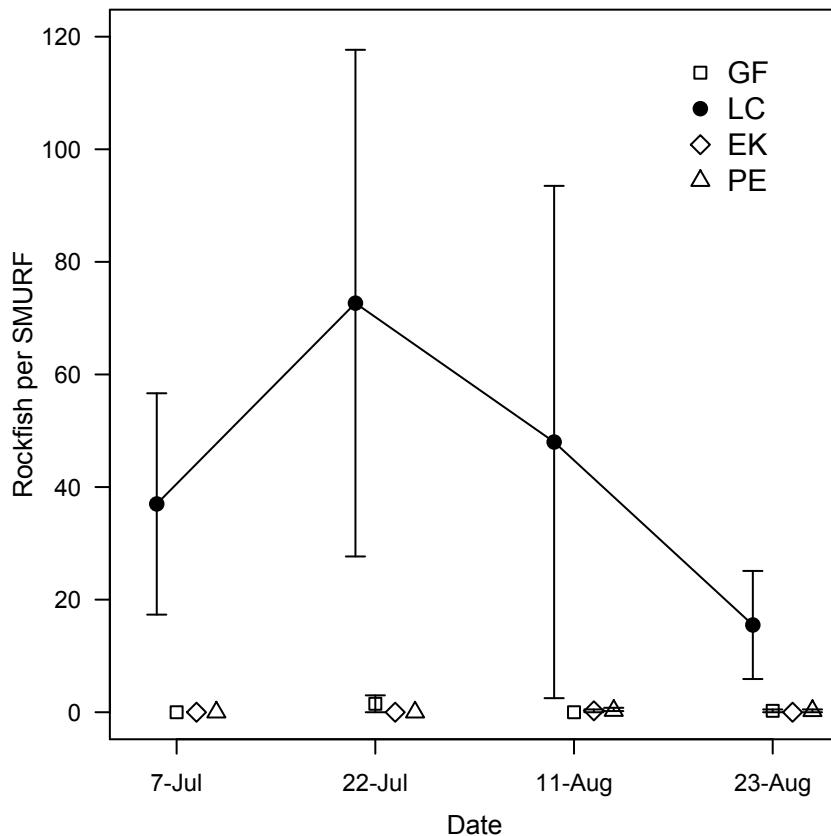


Figure 2.4. CQB complex rockfishes (*S. caurinus*, *S. maliger*, *S. auriculatus*) recruitment (mean no. rockfish/SMURF/site \pm SE) at four kelp forest sites ($n = 4$ SMURFs/site) during July and August 2005. Data markers are offset for clarity.

2.4 Results

2.4.1 Spatial and temporal patterns of rockfish recruitment

Rockfish recruitment varied widely over the course of the study. We found significant differences between species and among years of recruitment intensity within eelgrass meadow and kelp forest habitats (Table 2.1a,b). Black rockfish recruitment was exceptionally high in 2006

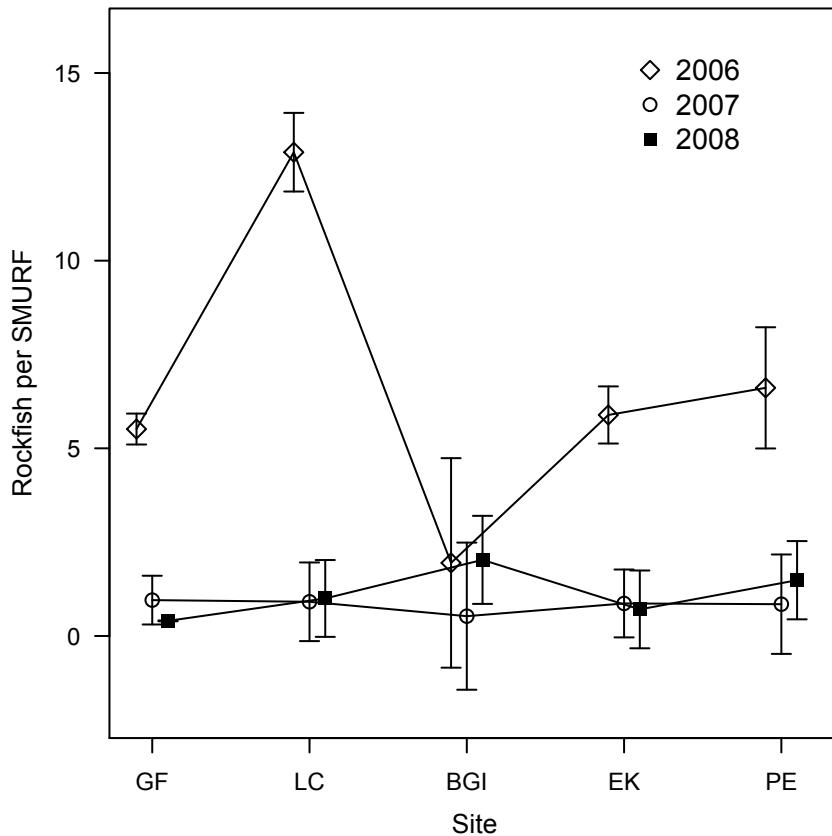


Figure 2.5. Black rockfish (*S. melanops*) recruitment (mean no. rockfish/SMURF \pm SE) within five sites ($n = 6$ kelp forest locations/site) throughout Barkley Sound (refer Figure to 2.3).

in kelp and eelgrass habitats (Fig. 2.2a), and CQB complex rockfish recruitment was exceptionally high in 2005 in kelp forests (Fig. 2.2b). Significant species*year interactions indicate that black and CQB rockfish recruitment intensity responds differently to interannual variation in environmental conditions.

Rockfish recruitment intensity was not spatially uniform throughout Barkley Sound (Fig. 2.3). In kelp forests, high CQB rockfish recruitment in 2005 was limited to a small number of locations within Loudoun Channel (Fig. 2.4). Similarly, in 2006 black rockfish recruitment in LC kelp forests was approximately 2 times higher than in GF, EK, and PE, and 6.6 times higher than those within BGI (Fig. 2.5). We found significant differences in recruitment among sites and years, which were not consistent (i.e. significant site*year interaction) (Table 2.1c), indicating that spatial differences in recruitment intensity became more prominent during years of high recruitment.

Eelgrass meadows were situated almost exclusively within the BGI (Figs. 2.1 and 2.3), and in 2006 they also experienced exceptionally high black rockfish recruitment (Fig. 2.2a). In 2006, however, just three of the 12 eelgrass locations sampled in 2006 received 85% of all new recruits captured in 2006, and one location just outside the RCA (Clarke Island) accounted for 43% of all new recruits. To visualize this relationship, we plotted the annual recruitment of only eelgrass meadow locations that were sampled every year between 2005 and 2008 ($n = 5$) against their corresponding distances to the open coast (Fig. 2.6). Clarke Island (1), followed by Turret Island (2) consistently experienced the highest recruitment intensities, despite large fluctuations among

Table 2.1. Effects of species and year, and their interaction, on rockfish recruitment in (a) eelgrass meadows (*Z. marina*), and (b) kelp forests (*M. pyrifera*), and (c) the effects of Site and Year on black rockfish (*S. melanops*) recruitment throughout Barkley Sound.

Models	Effects	DF	Deviance	DF Residual Deviance	Residual Deviance	P(> Chi)
Eelgrass meadows	Null			139	186.517	
Rockfish recruitment	Species	1	20.550	138	165.966	<0.0001
Negative binomial	Year	6	18.027	132	147.939	0.0062
Log Link Function	Species*Year	6	48.694	126	99.245	0.0002
Kelp forests	Null			203	501.23	
Rockfish recruitment	Species	1	202.783	202	298.45	<0.0001
Negative binomial	Year	3	109.216	199	189.23	<0.0001
Log Link Function	Species*Year	3	12.058	196	177.17	0.0072
Spatial comparison	Null			88	281.871	
Rockfish recruitment	Site	4	28.951	84	252.921	<0.0001
Negative binomial	Year	2	143.988	82	108.933	0.0001
Log Link Function	Site*Year	8	21.647	74	87.285	0.0056

years. Wouwer Island on the seaward edge of the BGI was not included here because it was not sampled in all years; however in 2006 this location was intermediate in recruitment to Clarke and Turret. The three remaining eelgrass locations in the interior of the BGI and up to 7.5 km from the open coast, Turtle (3), Hand (4), Pinkerton (5), received few recruits during the 2006 black rockfish recruitment event.

The concordance analysis, incorporating all kelp and eelgrass locations, shows that the rank order of location-specific recruitment was consistent for all pair-wise comparisons of annual recruitment between 2005 and 2008 (Fig. 2.7). This indicates that despite high variation in the magnitudes of annual recruitment, locations that have high rockfish recruitment tend to do so year after year (Fig 2.3). This pattern, however, was not apparent when locations were pooled within sites (Fig. 2.5). Recruitment intensities at five paired kelp and eelgrass locations in 2006 were highly concordant ($W = 0.987$, $P = 0.002$), and years ranked by annual recruitment in kelp and eelgrass habitats approached concordance despite low sample size ($W = 0.90$, $P = 0.10$, $n = 4$). Intra- and interannual concordance between habitats suggests that annual recruitment intensity in one habitat type is likely to represent recruitment success in the other.

2.4.2 Processes underlying spatially consistent recruitment

Principal component analysis revealed that 64.3% of the variability in topographic and oceanographic features was explained by the first eigenvector (PC1) (Table 2.2). PC1 was characterized by the contrast between high tidal velocity and high fetch vs. increasing distance to open coast and high SST. The second eigenvector (PC2) explained 24.9% of the variability and was associated with fetch. The third eigenvector (PC3) explained only 8.6% of the variability and was associated with low SST and high fetch. Black rockfish recruitment in both eelgrass meadows and kelp forests decreased with increasing PC1 values (Fig. 2.8). The strength of this relationship was stronger, and the slope steeper, in eelgrass meadows ($R^2 = 0.77$, $P = 0.0002$), than in kelp forests ($R^2 = 0.114$, $P = 0.05$), due to the higher number of eelgrass meadow locations occurring at greater distances from the open coast. These results indicate that areas of high black rockfish recruitment generally occur in outer coast areas that have relatively high fetch, high tidal velocity, and low sea surface temperatures.

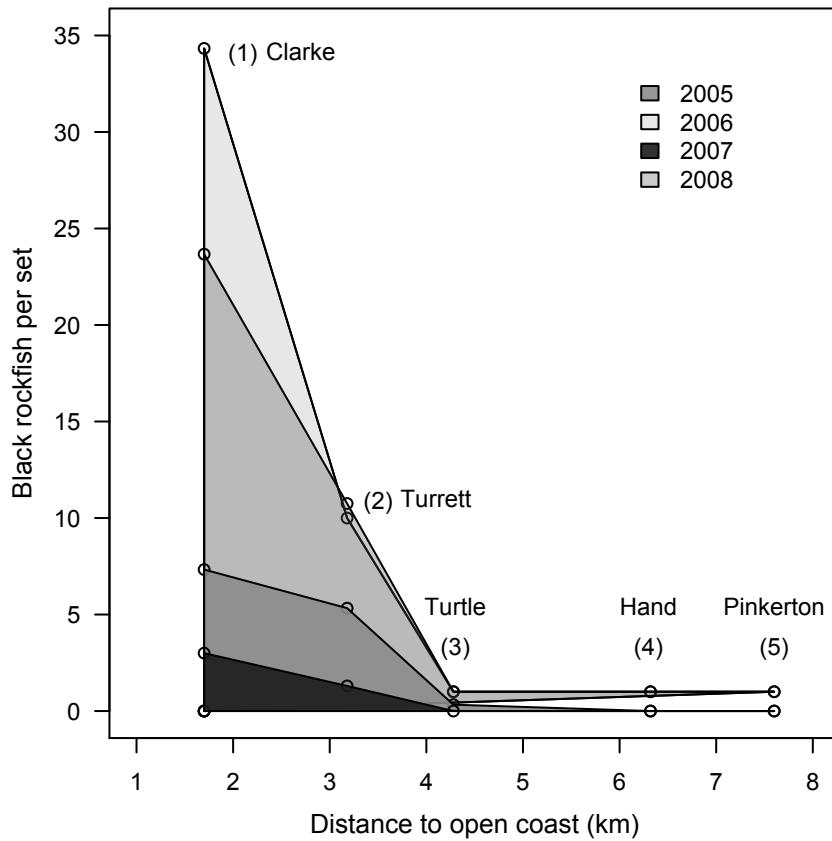


Figure 2.6. Black rockfish (*S. melanops*) recruitment (mean no. rockfish/set/location, 2005-2008) at five eelgrass meadow locations varying in distance from the open coast (refer to Fig. 2.3)

2.5 Discussion

2.5.1 Topography and oceanography underlie spatial differences in recruitment intensity

We found consistent spatial patterns of recruitment intensity of black (*S. melanops*) rockfish throughout Barkley Sound. By comparing among locations of similar habitat types we removed potentially confounding habitat effects. These results support the view that local topography and physical oceanography interact in consistent ways to produce predictable patterns of larval

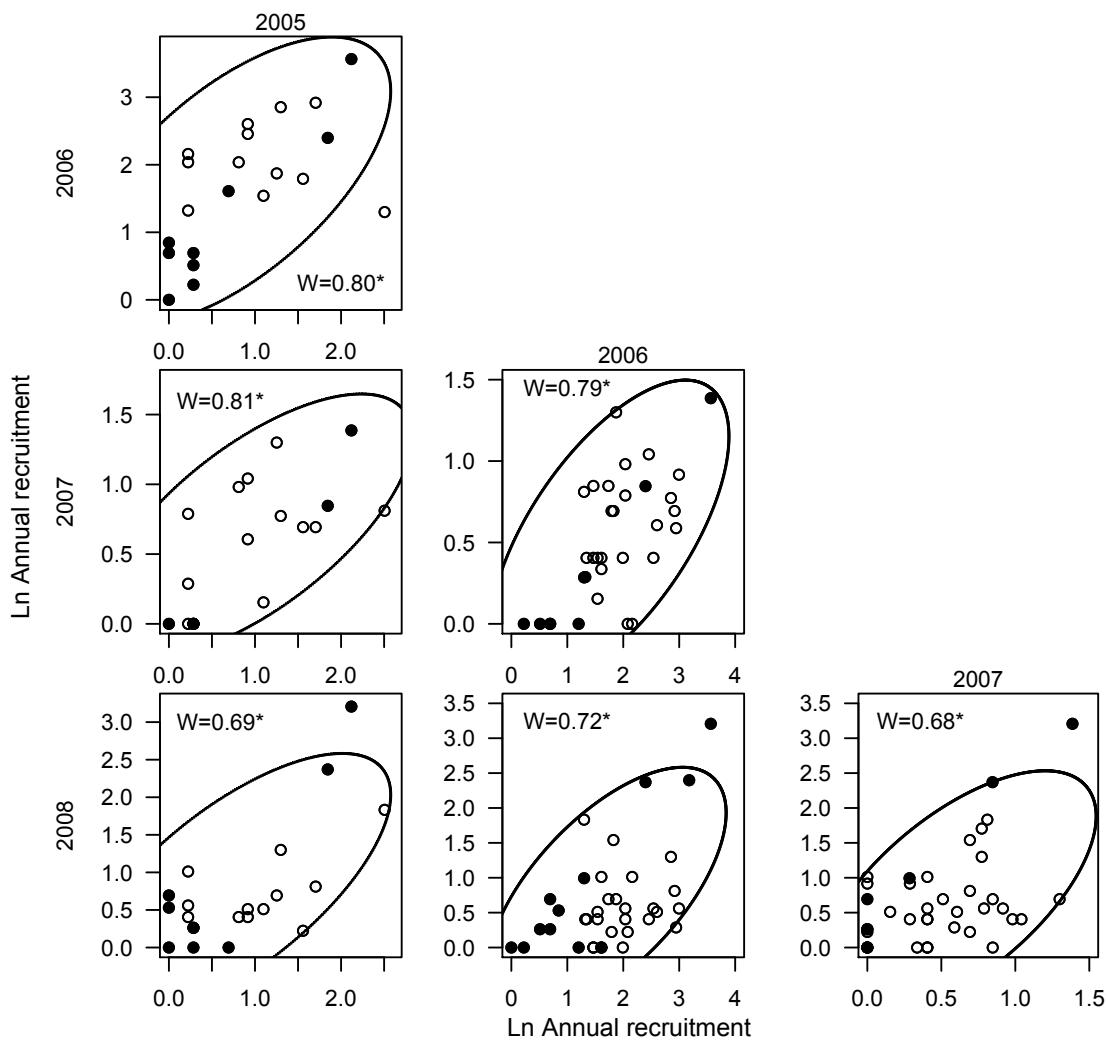


Figure 2.7. Pair-wise comparison of black rockfish (*S. melanops*) recruitment (mean no. rockfish/set or SMURF/location) between years for each eelgrass meadow (solid circle) and kelp forest (open circle) using scatter plots with 95% bivariate normal density ellipses and Kendall's coefficient of concordance (W); (*) denotes $p < 0.05$.

delivery and recruitment intensity (Doherty & Fowler 1994, Booth et al. 2000, Hamilton et al. 2006), and operate at spatial scales relevant to MPA design and effectiveness. Here we discuss several lines of evidence supporting the hypothesis that spatial differences in rockfish recruitment intensity are driven by location-specific differences in larval supply. This explanation contrasts

with the alternative hypothesis that homogenous larval supply and differential post-settlement mortality underlie these patterns.

Recent evidence suggests that cohorts of marine reef fish larvae are transported within common water masses (Selkoe et al. 2006), or aggregated by physical oceanographic features (e.g. upwelling fronts, Bjorkstedt et al. 2002), before being transported or moving to inshore settlement habitats. Subsequently, encounter rates between aggregations of larvae and settlement habitats are functions of the size and density of larval aggregations, the physical oceanographic and behavioural processes regulating their movements, and the size, distribution and orientation of settlement habitats (Carr & Syms 2006). Despite the potential for density-dependent post-settlement mortality to reduce the abundance of new recruits (Caley et al. 1996, Hixon & Webster 2002), locations experiencing high recruitment must receive high larval supply. In our study, kelp forest and eelgrass meadow locations with generally high rockfish recruitment intensity were located at the entrance to Loudoun Channel and the seaward edge of the Broken Group Islands. Black and CQB rockfishes first appear at seaward locations in or bordering Loudoun Channel. Consequently, Loudoun Channel appears to be a rockfish recruitment “hotspot” (e.g. Booth et al. 2000) and may be disproportionately valuable with respect to local

Table 2.2. Cumulative % variance explained by PCA axes and eigenvectors of eelgrass meadow and kelp forest site-specific measures of PCA variables: distance to open coast, fetch, tidal velocity, and SST.

	PC1	PC2	PC3
Cumulative % variance	64.25	89.19	97.82
Tidal velocity	-0.45	-0.63	0.43
Distance inshore	0.60	0.14	-0.02
SST	0.55	-0.17	0.73
Fetch	-0.37	0.75	0.53

population persistence if high recruitment translates to higher adult abundance and larval production (i.e. "sources" rather than "sinks"; Warner et al. 2000).

Black rockfish recruitment intensity was highest at locations closest to the open coast; areas with high fetch, high tidal velocity, and low sea surface temperature. Proximity to the open coast and cumulative fetch each contribute substantially to encounter rates between settlement habitats and aggregations of larvae. Despite evidence that larval behaviour can facilitate nearshore retention and self-recruitment (Sponaugle et al. 2002), larval transport is to some extent a passive process. Therefore, exposed coastlines and reefs have higher probabilities of intercepting aggregations of larvae moving alongshore or onshore (e.g. Jones 1997, Jenkins 1997). Cumulative fetch reflects the extent to which different locations are exposed to local current regimes and pathways of larval delivery. In Barkley Sound, we expect outer coast locations that are open to dominant flow regimes from the southwest during winter and early spring (i.e. Vancouver Island Coastal Current and Davidson Current; Crawford & Thomson 1991) to experience high rates of larval delivery and subsequent recruitment. However, neither *Macrocystis* forests nor *Zostera* meadows are found in the most wave-exposed and high-fetch areas throughout Barkley Sound. *Macrocystis* forests in this region are most abundant near the outer coast, but require protection from direct wave exposure and typically occur in the shelter of reefs, islands, and headlands. *Zostera* does not tolerate direct wave exposure and requires fine sediment to establish rhizomes. The scales at which aggregations of larvae are able to select settlement habitats remain unknown. Bell and Westoby (1988), report that characteristics of eelgrass meadows (e.g. size, shape, leaf height and leaf density), are not correlated with the abundance of juvenile fishes. Rather, these authors propose the "settle-and-stay" hypothesis, arguing that larvae are likely to settle in the first place they encounter, and that meadow location and the availability of competent larvae are the primary determinants of juvenile fish abundance. The fact that settling rockfishes commonly reach kelp and eelgrass meadow habitats suggests that upon encountering exposed shorelines aggregations of larvae continue to move alongshore until they encounter appropriate settlement habitats. Indeed, experimental manipulations of kelp forest habitat indicate that recruitment of young rockfishes varies markedly between adjacent sites depending on the habitat larvae encounter (Carr 1991, 1994).

In contrast to the high rockfish recruitment observed in Loudoun Channel and the seaward edge of the Broken Group Islands (BGI), we found exceptionally low recruitment at most kelp

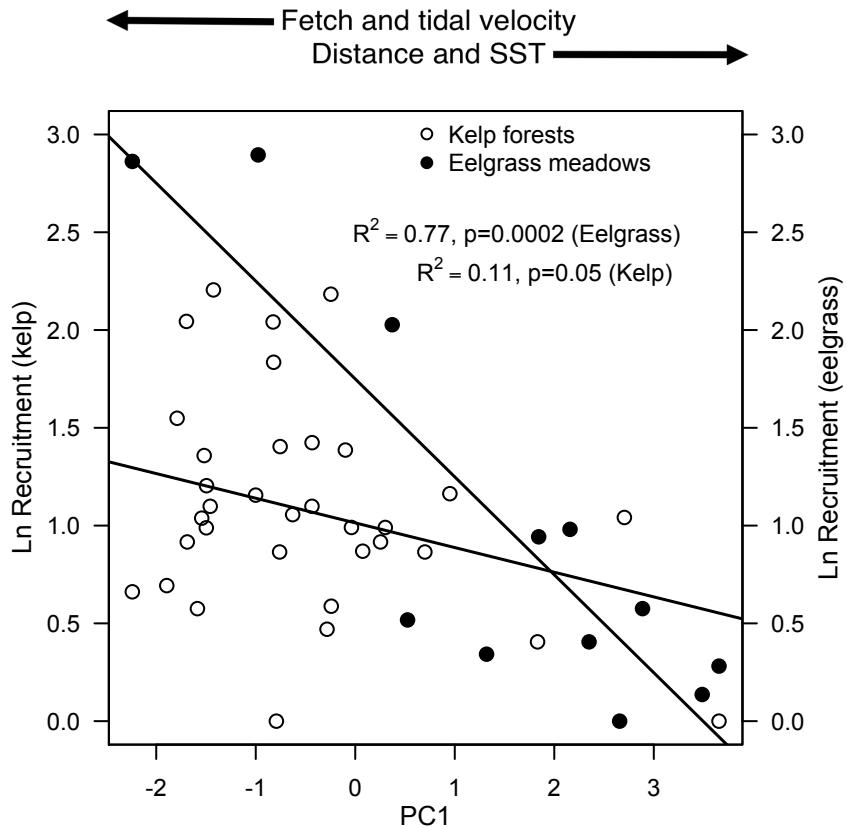


Figure 2.8. Relationships between PC1 values and black rockfish (*S. melanops*) recruitment (mean no. rockfish/set or SMURF/location, 2005-2008) in eelgrass meadows (left axis; open circles) and kelp forests (right axis; filled circles).

and eelgrass locations within the Broken Group Islands. Black rockfish recruitment intensity at eelgrass meadows within the BGI dropped sharply with increasing distance from the open coast. Three outer coast eelgrass locations sampled annually between 2005 and 2008 consistently accounted for nearly all new recruits collected each year. Strikingly, in 2006 when black rockfish recruitment was exceptionally high at nearly all kelp forest locations throughout Barkley Sound, recruitment rates within the BGI remained low. The corollary to high encounter rates between larvae and settlement habitat along exposed/upstream shores is the serial depletion of the size and number of larval aggregations moving downstream or away from the open coast. Consequently, downstream and inshore areas are vulnerable to low larval encounter rates due to

their position within local seascapes and current regimes (i.e. recruitment shadows; Jones 1997).

In addition to potential recruitment shadow effects, we found that variation in tidal velocity was a strong predictor of black rockfish recruitment intensity. Current regimes driven by tidal exchange are important mechanisms for aggregating and transporting marine fish larvae into settlement and nursery habitats (e.g. Yamashita et al. 2000). Jenkins et al. (1997) report that fish recruitment to their seagrass locations in Australia demonstrated interannual consistency, and concluded that although larval supply is variable in time it may be spatially predictable given that larvae are carried by geographically consistent tidal currents. Tidal velocities are generally low in the interior of the Broken Group Islands RCA, and tidal exchange may be insufficient to move pelagic juvenile rockfishes to settlement habitats inside the BGI. The dominant NE-SW tidal flows through the main channels in Barkley Sound may explain why the highest rockfish recruitment occurs in southwest Loudoun Channel and the seaward edge of the Broken Group Islands.

2.5.2 Implications for MPA design and effectiveness

Our study highlights the necessity of understanding what site characteristics enhance recruitment, and incorporating this understanding into MPA planning and evaluation processes. Gaines et al. (2003) emphasized that even simple current regimes can create spatially structured environments in which some locations receive more larvae than others. The results of our study suggest that most of the Broken Group Islands RCA may fall within a recruitment shadow created by the outer coast islands that intercept the majority of larval aggregations moving onshore, and tidal velocities that are insufficient to move larvae to interior settlement habitats. The fact that most locations within the BGI RCA failed to receive appreciable numbers of new recruits during the exceptional black rockfish recruitment event in 2006 suggests that these local populations may be vulnerable to “recruitment limitation” as a result of low larval delivery rates (Armsworth 2002, Doherty 2002). In recruitment-limited populations, abundance varies as a function of settlement rates, rather than post-settlement processes (i.e. competition and predation; Doherty & Fowler 1994). When included within MPAs, areas of consistently high recruitment may facilitate rapid increases in population sizes, and support fisheries goals by enhancing local catches beyond MPA borders (Hamilton et al. 2006, Gaines et al. 2010b).

Conversely, MPAs encompassing areas of chronically low recruitment may fail to achieve the objectives for which they were established.

The utility of spatially stable patterns of recruitment to MPA design and effectiveness depends upon the scales at which they occur, the size of MPAs, and the post-settlement survival and movements of target species. Field and Ralston (2005) report that rockfish recruitment and year-class strength is spatially synchronous at scales of 500-1000 km, and argue that large-scale (1000s of kilometers) physical forcing mechanisms are likely more important than local-scale processes (10s of kilometers) in controlling recruitment intensity. In the current study, however, we found spatially different yet temporally consistent patterns of rockfish recruitment occurring at scales that are directly relevant to the size of most MPAs (10s of kilometers). Kelp forest locations were distributed over approximately 156 km², and eelgrass meadow locations were confined primarily to the Broken Group Islands (81 km²) and the RCA nested within (46 km²). The islands comprising the Loudoun Channel recruitment hotspot are limited to an area of just 4.28 km², and the BGI eelgrass meadow location (Clarke Island) that consistently received high recruitment relative to all other eelgrass meadow locations has an area of just 2100 m². These results demonstrate that areas of consistently high recruitment can be very small relative to the size of MPAs and, conversely, areas of chronically low recruitment may extend over large spatial scales relative to the size of MPAs. As is typical of most studies of marine fish recruitment, the extent to which post-settlement movement patterns of juvenile and adult rockfishes reinforce or mitigate spatial recruitment patterns in this study is unknown. However, estimates of home range sizes for CQB complex (30-1500 m²; Matthews 1990b) and black rockfishes (0.55 km²; Parker et al. 2007) suggest that post-settlement movements of these species are unlikely to subsidize population replenishment significantly in low recruitment areas.

These results contribute to a growing understanding of the characteristics of areas likely to experience relatively high or low rockfish recruitment, and may be applicable to other species whose larval supply is driven by oceanographic processes. This study further demonstrates that very small differences in the placement of boundaries can have large implications for recruitment rates and subsequent rates of population growth and recovery. In general, to maximize the frequency and magnitude of rockfish recruitment, MPA boundaries should encompass areas close to open coasts that have high fetch, high tidal velocity and other oceanographic features that deliver or accumulate larvae. Planners should be aware of the potential for large-scale

recruitment shadows to negatively affect MPA performance, particularly along topographically complex coastlines such as those of British Columbia. Our results highlight the importance of managing MPAs adaptively (i.e. modification of design, regulations, and placement), by using ecological and oceanographic data to identify processes driving MPA effectiveness (Carr et al. in press).

Rockfish Conservation Areas in British Columbia represent a globally unprecedented management and conservation initiative, in terms of the area protected and the speed with which they were established. Consultation and planning processes often involve tradeoffs that may only become apparent retrospectively. For instance, outer coast areas of the Broken Group Island were excluded from the RCA to avoid conflicts with the recreational salmon fishery. In doing so, nearly all areas identified in this study as having high potential for rockfish recruitment were also excluded, and this trade-off may reduce the long-term effectiveness of this RCA. While some authors have advocated for the benefits of establishing MPAs where and when opportunities present rather than delaying for protracted scientific investigation (Roberts 2000), others have warned of the potentially harmful effects of establishing MPAs that do not work (Carr & Reed 1993). Studies such as ours that predict high-value areas with respect to population replenishment can provide guidance during MPA planning processes to facilitate long-term effectiveness.

3. Effects of variable upwelling dynamics on the recruitment success of nearshore Pacific rockfishes (Genus *Sebastes*)

3.1 Synopsis

Knowledge of processes underlying variable replenishment rates is critical for understanding marine population dynamics and the responses of species to variable ocean climate. I investigated relationships among of coastal upwelling dynamics and early life history attributes of black rockfish (*Sebastes melanops*) and CQB rockfishes (*S. caurinus*, *S. maliger*, *S. auriculatus*) during years of high and low recruitment on the west coast of Vancouver Island, Canada. I used otolith microstructure analyses to determine birth and settlement dates, pelagic durations, and pre- and post-settlement growth rates. I used the Modified-Fry back-calculation model to construct individual growth profiles and estimates of body size-at-settlement. High CQB rockfish recruitment in 2005 was associated with prolonged downwelling and unusually warm ocean temperatures, late birth dates, high pre-settlement growth rates, short pelagic durations, and small size-at-settlement. In contrast, high black rockfish recruitment in 2006 was associated with cool ocean temperatures, low pre-settlement growth rates, protracted pelagic durations, and settlement dates during an exceptionally strong upwelling event. Pre-settlement growth rates of black and CQB rockfishes increased with sea surface temperatures, but not chlorophyll-a concentrations. Pelagic durations decreased with increasing growth rates and increased with the strength of upwelling experienced during the 30 days prior to settlement. In contrast to studies demonstrating positive correlations between ocean conditions favouring pre-settlement growth rates, the results of this study show that high pre-settlement growth rates and reduced pelagic durations of marine fish larvae are not pre-conditions necessary for recruitment success.

3.2 Introduction

Variation in the frequency and magnitude of recruitment has strong effects on marine population sizes, persistence, and connectivity (Doherty & Williams 1988, Caley et al. 1996, Armsworth 2002, Cowen & Sponaugle 2009). Recruitment rates of marine fishes are typically highly variable, and few years of exceptionally strong recruitment are often separated by many years of weak recruitment (Houde 2009). In turn, strong year-classes can be disproportionately important with respect to future recruitment events and year-class strength (Hjort 1914). Because many years can pass between years of strong recruitment, future recruitment events are ‘stored’ in adult populations with generation times that match or exceed intervals between episodic years of strong recruitment (Secor 2007). Warner and Chesson (1985) proposed the ‘storage effect’ as a model to explain stable species coexistence in systems where recruitment is limited by juvenile habitat (Sale 1977). The storage effect also promotes population resiliency through interaction among overlapping generations by maintaining populations through long periods of environmental conditions unfavorable for recruitment (Secor 2007). Thus, understanding processes underlying strong recruitment events and year-class strength is critical to predicting population and community responses to exploitation, climate change, and conservation and management strategies.

Recruitment rates may closely reflect life history stages subject to the highest variability in cumulative mortality (Pepin 1991). In marine fish populations these stages are pelagic eggs and larvae (Pepin & Myers 1991, Leggett & Deblois 1994). Most marine fish and invertebrates have complex bipartite life histories in which birth rates of local populations are effectively decoupled from local production by widely dispersed pelagic eggs and larvae (Roughgarden et al. 1988). Following pelagic stages lasting from days to several months and dispersal distances from 10’s to 100’s of km (Shanks 2009), juveniles settle into benthic habitats and local adult populations (Roughgarden et al. 1985). High and strongly density-dependent mortality rates associated with settlement may obscure local settlement rates (Caley et al. 1996, Hixon & Webster 2002). Therefore, ‘recruitment’ is commonly used to describe the number of individuals that have settled and survived to the end of annual recruitment seasons (Carr & Syms 2006). Despite the potential for post-settlement processes to strongly reduce variation in recruitment rates, the magnitude of recruitment fluctuations and synchronous recruitment patterns among species with

similar life history attributes strongly suggest that ocean conditions affecting larval mortality rates are primary drivers of annual recruitment success (Houde 1989, Pepin 1991, Doherty & Fowler 1994, Field & Ralston 2005, Jenkins & King 2006). Because high adult fecundity and larval production rates of marine populations are associated with high mortality rates of pelagic eggs and larvae, processes causing very small changes in larval mortality rates can have order-of-magnitude effects on subsequent recruitment rates (Houde 1989). Infrequent spatial and temporal alignment of ocean conditions favouring larval growth and survival are likely to create narrow windows of reproductive opportunity and success (Lasker 1975, Cury & Roy 1989, Cushing 1990, Hedgecock 1994, Agostini & Bakun 2002).

Years of particularly strong recruitment are likely to result from ocean conditions favouring larval growth and/or survival (e.g. Bergenius et al. 2002, Jenkins & King 2006), and high rates of larval delivery (Bertness et al. 1992). Although adult body condition and larval production vary in response to changes in ecosystem productivity (Lenarz & Echeverria 1986, Woodbury 1999), the magnitude of variability in interannual larval production generally does not match the magnitude of variability in recruitment (Carr & Syms 2006). Larval fish mortality is size-dependent, decreasing rapidly with increasing body size; therefore, factors affecting growth rates also strongly affect mortality rates (Houde 1989, Pepin 1991, Hare & Cowen 1997, Otterlei et al. 1999). Cumulative larval mortality is a function of daily mortality (i.e. losses to starvation and predation) and the number of days over which mortality accrues (Leggett & Deblois 1994, Houde 2009), giving pelagic duration a strong influence on cumulative mortality and recruitment strength (Pepin & Myers 1991). The oceanographic processes affecting larval growth, pelagic duration, and onshore transport (i.e. delivery or retention; Warner & Cowen 2002), are therefore critical to shaping the population dynamics of marine species.

The fundamental objective of this study was to understand how oceanographic conditions and early life history characteristics influence the recruitment success of nearshore Pacific rockfishes (Genus *Sebastodes*). Rockfishes are important components of rocky reef ecosystems on the west coast of North America and the focus of recreational and commercial fisheries (Love et al. 2002). Extreme longevity (100-200 years in some species; Munk 2001), low reproductive rates, and

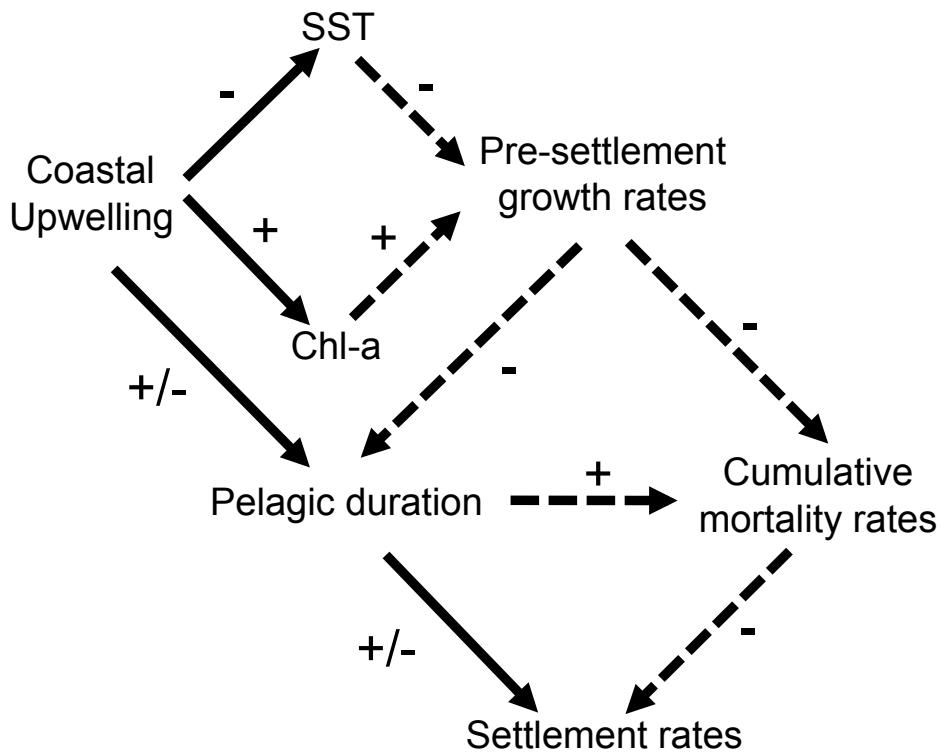


Figure 3.1. A conceptual model depicting the direct (solid lines) and indirect (dashed lines) effects of coastal upwelling on pelagic larval fish. By regulating sea surface temperature (SST) and primary productivity (Chl-a) coastal upwelling has indirect negative or positive effects on larval growth rates, depending on which factor is most limiting. As a result of size-specific predation rates, pre-settlement growth rates directly and indirectly impact pelagic-stage cumulative mortality rates, and therefore settlement rates. By regulating cross-shelf flow regimes coastal upwelling increases or decreases pelagic durations, and therefore settlement rates, by inhibiting or facilitating movement of larvae to nearshore settlement habitats and adult populations.

stochastic recruitment make rockfishes vulnerable to over-exploitation (Leaman 1991, Parker et al. 2000, Williams et al. 2010). As a result, rockfish populations are increasingly the focus of protection by marine protected areas and catch restrictions (e.g. Yamanaka & Logan 2010). However, because local population persistence depends upon population replenishment (Cowen & Sponaugle 2009), understanding processes that regulate the frequency, magnitude, and spatial

scales of interannual recruitment variability is key to marine protected area efficacy (Carr & Reed 1993, Gaines et al. 2003). Finally, growing empirical evidence that juvenile rockfish abundance can be an indicator of year-class strength in subsequent fisheries (Mearns et al. 1980, Ralston & Howard 1995, Mason 1998, Laidig et al. 2007), argues strongly for the importance of understanding processes driving rockfish recruitment success.

Rockfish recruitment dynamics are associated with variation in coastal upwelling (Ainley et al. 1993, Larson et al. 1994, Lenarz et al. 1995, Ralston & Howard 1995, Rau et al. 2001, Bjorkstedt et al. 2002, Laidig et al. 2007, Wilson et al. 2008, Caselle et al. 2010a). Upwelling occurs seasonally along eastern boundaries of ocean basins during spring and summer months when northerly winds push the low-density surface Ekman layer offshore and cause a drop in nearshore sea level. As a result, cold and nutrient-rich deep water flows inshore and upwells into the euphotic zone where it fuels high primary production (Cury & Roy 1989). Cross-shelf flows during upwelling may transport pelagic larvae offshore or onshore, depending on the location of larvae relative to the thermocline (Shanks & Brink 2005, Mace & Morgan 2006). Conversely,

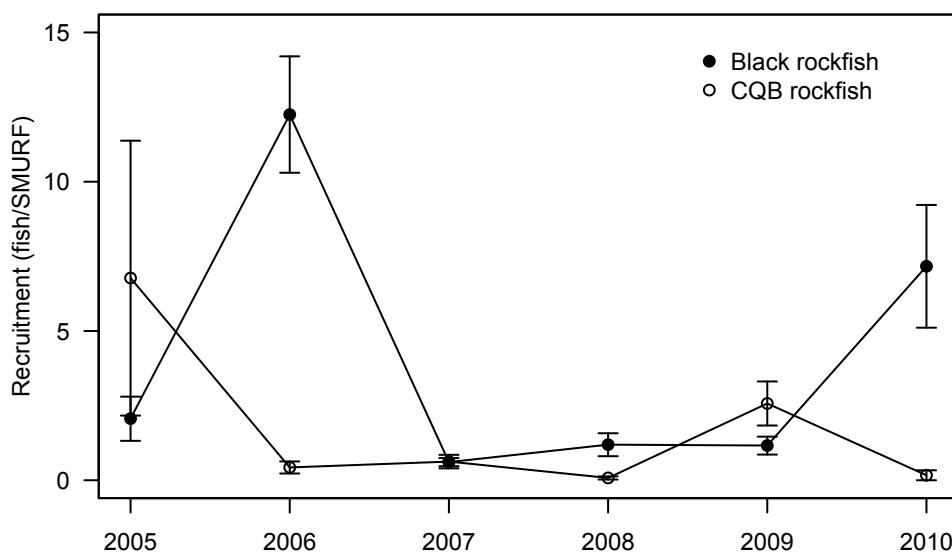


Figure 3.2. Annual recruitment (rockfish per SMURF; mean \pm SE) in August between 2005 and 2010. The number of SMURFs deployed varied annually: 2005 (n=16), 2006-2009 (n=30), 2010 (n=6).

onshore movement of late-stage pelagic juveniles may be facilitated by downwelling or intermittent ‘relaxation events’ during which cessation of equator-ward winds allow the surface layer to flow back onshore (Roughgarden et al. 1988, Farrell et al. 1991).

Coastal upwelling may influence rockfish recruitment dynamics in two key ways: indirectly by regulating ocean temperature and primary productivity and therefore pre-settlement growth rates, and directly by inhibiting or facilitating nearshore retention or onshore movement of larvae and pelagic juveniles (Fig. 3.1). The indirect effects of upwelling on larval growth and survival may be either positive (via increased primary production) or negative (via low temperature), while the direct effects are likely to be negative if they result in offshore advection of larvae. Caselle et al. (2010a) found that coastal upwelling was the best predictor of delivery rates of pelagic juvenile rockfishes to nearshore adult populations among many oceanographic variables. However, the effects of upwelling on recruitment success are equivocal (Shanks and Brink 2005), and attempts to relate interannual recruitment variation to the timing and magnitude of upwelling have met with mixed success (e.g. Laidig et al. 2007, Wilson et al. 2008, Caselle et al. 2010a,b). Because little is known about processes through which upwelling affects recruitment (Bjorkstedt et al. 2002), knowledge of the effects of oceanographic conditions on early life history events may contribute substantially to refining predictive models of population dynamics.

During an on-going investigation of rockfish recruitment dynamics on the west coast of Vancouver Island, British Columbia, I observed two exceptionally strong rockfish recruitment events between 2005 and 2010 (Fig. 3.2). Recruitment of copper (*S. caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfishes (“CQB complex”) was exceptionally high in 2005 and, with the exception of 2009, remained low in all subsequent years. Black rockfish (*S. melanops*) experienced high recruitment in 2006, and to a lesser extent in 2010. These recruitment events provided the opportunity to investigate how the timing and magnitude of coastal upwelling differentially affect early life history attributes and recruitment success of rockfishes with contrasting life history strategies. I compared oceanographic conditions in these years with juvenile rockfish life history parameters. I used otolith microstructure analysis to determine birth and settlement dates, pelagic durations, and pre- and post-settlement growth rates of black and CQB rockfishes in 2005 and 2006. I assessed the relative effects of upwelling intensity, ocean temperature, and primary productivity on these early life history attributes and corresponding recruitment success. I found that ocean temperature had similar effects on growth

and pelagic duration of black and CQB rockfishes; however, these groups responded differently to upwelling. In contrast to studies reporting that pre-settlement growth rates are effective predictors of recruitment success (Bergenius et al. 2002, Wilson & Meekan 2002, Jenkins & King 2006), I show that upwelling events facilitating onshore transport alone may result in exceptional black rockfish recruitment and year-class strength.

3.3 Methods

3.3.1 Study system

This study was conducted in Barkley Sound ($48^{\circ} 50.0'N$, $125^{\circ} 22.0'W$) on the southwest coast of Vancouver Island, British Columbia, situated at the northern-most origins of the California Current Large Marine Ecosystem. This region conforms to the seasonal transitions between upwelling-favourable northwest winds (spring/summer) and downwelling-favourable southerly winds (fall/winter) characteristic of the California Current System (Shanks and Eckert 2005). The Vancouver Island Coastal Current (VICC) is a narrow current (5-25 km) driven primarily by buoyancy flux from coastal runoff exiting the Strait of Georgia via the Strait of Juan de Fuca (Hickey et al. 1991). Following the spring transition the VICC continues in a narrow reduced band flowing northward towards Brooks Peninsula (Hickey et al. 1991, Thomson & Ware 1996).

I used Standard Monitoring Units for the Recruitment of Fishes (SMURFs; Ammann 2004) to assess rockfish recruitment between 2005 and 2010. I deployed SMURFs at the seaward edge of kelp forests (*Macrocystis pyrifera*) where they were moored horizontally 1.5 meters below the surface and anchored using 20L plastic buckets filled with cement. I used a Benthic Ichthyofaunal Net for Coral/Kelp Environments (BINCKE; Anderson & Carr 1998) and snorkelling equipment to collect all fish within SMURFs on each sampling date. All young-of-the-year (YOY) rockfishes were identified, weighed, measured (total length). Copper (*Sebastes caurinus*), quillback (*S. maliger*), and brown (*S. auriculatus*) rockfishes were grouped as “CQB” rockfishes because of difficulty distinguishing early post-settlement juveniles. Beginning in 2010, I reduced the number of SMURFs deployed annually from 30 locations in five sites to six locations in one site (“Prasexe”), and sampling took place only in August. I report the average number of rockfish per SMURF in August between 2005 and 2010 (Fig. 3.2).

3.3.2 Age and birth date determination

I used otolith microstructure analysis to determine birth dates, settlement dates, and pelagic durations of juvenile black and CQB complex rockfishes collected in 2005 and 2006. Deposition of daily increments by juvenile rockfishes has been validated previously for numerous early post-settlement rockfishes (Yoklavich & Boehlert 1987, Laidig et al. 1991, Woodbury & Ralston 1991, Kokita & Omori 1999, Plaza et al. 2001). I did not conduct additional validation experiments and assumed for both groups that each increment represents one day of growth, and that the total number of increments corresponds to the number of days between parturition and capture (i.e. age). To ensure representation of all sizes and ages I pooled black and CQB rockfishes collected in 2005 and 2006 over all sampling dates and randomly selected individuals from 10 mm size classes. I mounted right sagittal otoliths on glass slides in clear Crystalbond 509 thermoplastic epoxy with the sulcus facing downward and the anti-rostral end angled downward approximately 30-40 degrees from horizontal. I measured otolith lengths (the longest distance across the sagittae) using a digital image of the entire otolith. All digital images were obtained using a JVC 3-CCD camera mounted on a dissecting microscope or a inverted transmission light microscope. I used the digital imagery software Auto-Montage Pro (version 5.03, Syncroscopy, Beacon House, Cambridge) for image capture and otolith microstructure measurements.

I exposed daily growth increments using 3M 30 μ m and 3 μ m lapping paper and viewed them at 40x-1000x magnification. I did not use otoliths if the primordium or large sections of increments were not visible. Dark checks at the edge of the nuclear radius of numerous *Sebastodes* species have been identified as extrusion or parturition checks (Laidig & Ralston 1995, Ralston et al. 1996, Plaza et al. 2001, Miller & Shanks 2004). Consistent with these studies, I found checks at median nuclear radii of 11.77 μ m for *S. melanops* and 12.55 μ m for CQB rockfishes. When visible I measured increment widths from the primordium to parturition checks, and subsequently between each increment along a straight line to the most distal portion of the anti-rostral end. In most cases parturition checks were not observed and increments closest to the primordium were not visible. Instead, I started counts and measurements where increments first became continuously visible to a maximum distance of 25 μ m from the core, after which otoliths were rejected. I estimated the number of increments between the first measurement and the nuclear

radius at parturition by subtracting the median radii of parturition checks (above) and dividing the difference by the mean width of the first five increments measured.

3.3.3 Settlement date determination

Settlement marks on the otoliths of early post-settlement rockfishes have been identified and validated previously (Amdur 1991, Pasten et al. 2003, Gallagher 2007). I determined settlement dates using the transition-centered method (Wilson & McCormick 1997, 1999, Pasten et al. 2003). This method uses longitudinal profiles of daily increment width to identify a distinct transition from slow and consistent pre-settlement growth to fast and variable post-settlement growth associated with settlement of reef fishes. In addition, I constructed longitudinal profiles of increment width variance calculated over 5-day intervals and plotted these as 5-day moving averages. Using both types of plot I designated settlement (and corresponding age and date) as the increment immediately preceding a distinct transition to persistently rapid and variable growth. To visualize these relationships for each species and cohort, I centered increment width and variance profiles on designated settlement increments and plotted resulting mean increment widths and variances for the 20 days (increments) preceding and following settlement. I determined settlement dates twice independently and averaged the two readings. I determined pelagic duration by subtracting birth dates from settlement dates.

Finally, I compared the timing of births and settlements in 2005 and 2006 to the timing of specific oceanographic events. I focused these comparisons on time periods when the majority of birth and settlements occurred each year by using the 1st and 3rd quartiles of birth and settlement date distributions to define birth and settlement intervals for each rockfish group and year. I defined pelagic intervals as the time period between birth and settlement intervals.

3.3.4 Annual and inter-annual oceanographic variability

I obtained daily upwelling index estimates of Ekman transport ($m^3 s^{-1} 100m^{-1}$ of coastline) for position 48°N/125°W from the Pacific Fisheries Environmental Lab (<http://www.pfeg.noaa.gov>). Upwelling index values are modelled from recorded wind direction, velocity, and duration.

Positive values indicate upwelling-favourable winds and offshore transport of the shallow low-density Ekman layer, and negative values indicate downwelling-favourable winds and onshore transport of the Ekman layer. I obtained daily sea surface temperature (SST) data collected from Amphitrite Point Lighthouse, located at the northwest corner of Barkley Sound from Fisheries and Oceans Canada (<http://www.pac.dfo-mpo.gc.ca>). I obtained satellite-derived estimates of daily chlorophyll concentrations (mg m^{-3}) from Aqua MODIS sensors (<http://oceancolor.gsfc.nasa.gov/seadas>). I used the SeaDAS Level 3 browser to sample an 11x11 matrix of 4x4 km pixels ($1,936 \text{ km}^2$) situated at the entrance to Barkley Sound and centered at $48.649^\circ\text{N}/125.559^\circ\text{W}$. Due to cloud cover data were not available for all days, or for all pixels on each day. I derived daily estimates by averaging across pixels on each day and using an 11-day moving average to smooth trends and minimize data gaps.

I compared the average ocean conditions experienced by black and CQB rockfish cohorts in 2005 and 2006 during their pelagic phases. To control for differences in pelagic duration I limited analyses to the first 40 days and 60 days of the pelagic durations of individual CQB and black rockfishes, respectively. I selected these intervals on the basis of maximizing interval length and sample sizes. I aligned intervals of all individuals and calculated daily averages of upwelling index values, SST, and chlorophyll-a concentrations.

To examine oceanographic events in 2005 and 2006 in the context of long-term oceanographic variability I compared average upwelling and SST anomaly values for birth, pelagic, and settlement windows calculated for 2005 and 2006 to the same time periods for all years between 1977 and 2010. That is, since the last major North Pacific Ocean regime shift (Minobe 2000, Beamish et al. 2004). To do this I calculated daily upwelling and SST anomalies by subtracting corresponding long-term averages. I compared oceanographic variability within these windows among years for which I have recruitment data, and the benchmark El Niño years of 1983, 1993, and 1997, by plotting SST anomaly values against upwelling anomalies. To represent the long-term variability corresponding to these time periods I calculated and overlaid 95% confidence ellipses (R package ‘ellipse’).

I compared the timing of black and CQB rockfish birth, settlement and pelagic intervals, in 2005 and 2006, as well as the timing, magnitude, and duration of intra-annual upwelling events, and associated changes in SST and chlorophyll levels, by overlaying these data series.

3.3.5 Pre- and post-settlement growth rates

I compared daily growth rates of black and CQB rockfish in 2005 and 2006 by testing for differences in slopes of length-at-age relationships using simple linear regression and ANCOVA. In addition, I constructed longitudinal profiles of average pre- and post-settlement daily increment width. For each annual cohort and rockfish group, I centered individual longitudinal profiles on increments corresponding to settlement dates, and then calculated mean increment width for each increment (day) preceding and following settlement. Finally, I used individual longitudinal profiles of otolith increment width to model individual length-at-age profiles from parturition to collection. This approach allowed me to fit growth models representing each cohort and to estimate the body lengths of individual rockfish at the time of settlement (i.e. size-at-settlement).

I used the Modified-Fry back-calculation model to estimate body length for each incremental increase in otolith radius (Vigliola et al. 2000, Wilson et al. 2009). This model (Eq. 1) assumes non-linearity between otolith and somatic growth (i.e. age and growth effects) and constrains an allometric body length-otolith radius function through a biologically meaningful intercept:

$$L_i = a + \exp \left(\left(\ln(L_{0p} - a) + (\ln(L_{cpt} - a) - \ln(L_{0p} - a)) * \frac{(\ln(R_i) - \ln(R_{0p}))}{(\ln(R_{cpt}) - \ln(R_{0p}))} \right) \right) \quad (\text{Eq. 1})$$

where L_i is the length of the i^{th} fish at capture, L_{0p} is mean fish body length at first increment (parturition), R_i is otolith radius, R_{0p} is mean otolith radius at first increment (parturition), and R_{cpt} is otolith radius at capture, and where $a = L_{0p} - bR_{0p}^c$. The parameters b and c were obtained by fitting a non-linear regression (Eq. 2) to the relationship between fish length and otolith radius:

$$L_{cpt} = L_{0p} - bR_{0p}^c + bR_{cpt}^c \quad (\text{Eq. 2})$$

where L_{cpt} is fish body length at capture, b is the slope of the L-R relationship, and c is the coefficient of allometry. I constructed individual length-at-age profiles by plotting modeled estimates of body length for each daily growth increment from parturition to capture. To

represent average growth profiles of each cohort I fit a single growth model to the individual growth profiles comprising each cohort. I compared Von Bertalanffy, Logistic, Gompertz, and Schnute-Richards growth models using Akaike's Information Criterion (AIC) and found that the Logistic growth model most closely represented the sigmoidal growth trajectories of juvenile rockfishes in this study (Eq. 3).

$$L_i = \frac{a}{1 + b * \exp(-c * age)} \quad (\text{Eq. 3})$$

where L_i is fish length, a is the asymptotic fish length, b is the inflection point, and c is a relative growth coefficient (Bates & Watts 1988).

3.3.6 Data analyses

All analyses were performed using R (R Core Development Team 2011). I fit logistic growth models to modeled length-at-age profiles of annual black and CQB rockfish cohorts using nonlinear least squares approximation (R package 'nls'). To test for inter-annual differences in birth dates, settlement dates, pelagic durations, and size-at-settlement I used Student's t-tests.

I used simple linear regression to assess the effects of SST ($^{\circ}\text{C}$) and Chl-a (mg m^{-3}) on pre-settlement growth rates ($\mu\text{m/d}$) of individuals, and the effects of growth rates (i.e. developmental rates and swimming abilities) and upwelling (i.e. onshore/offshore transport) on pelagic duration. Because increment width increases with body length and otolith length, and because pelagic durations vary widely among individuals, I restricted analyses to growth profiles corresponding to 5-40 days and 5-60 days following parturition, for CQB and black rockfishes, respectively. I calculated mean upwelling index, SST, and chlorophyll concentrations over dates corresponding to individual growth profiles.

I estimated the independent effects of these explanatory variables on growth rates and pelagic durations using hierarchical variance partitioning (R package 'hier.part'). Hierarchical partitioning is a form of multiple regression that determines the contribution of each predictor to the total explained variance of a regression model, both independently and in conjunction with the other

predictors, for all possible candidate regression models. Hierarchical partitioning alleviates the problems of multicollinearity associated with traditional multiple regression approaches (Mac Nally 2002, Mac Nally & Walsh 2004).

3.4 Results

3.4.1 Birth, settlement, and pelagic duration

Longitudinal profiles of otolith daily increment width and variance were effective for determining settlement dates of both black and CQB rockfishes (Fig. 3.3). Pre-settlement growth was clearly differentiated from post-settlement growth by an abrupt transition from small and invariable to large and variable increment widths. Black rockfish birth dates did not differ between 2005 and 2006, but pelagic durations were on average nine days shorter, and settlement dates 11 days earlier, in 2005 (Table 3.1a). Back-calculated estimates of black rockfish size-at-settlement did not differ between years. In 2005, CQB rockfish birth dates were on average 28 days later, pelagic durations 12 days shorter, and settlement dates 16 days later, than in 2006. CQB rockfish were significantly smaller at settlement in 2005 than in 2006 (Table 3.1b).

Black rockfish birth and settlement windows based on 1st and 3rd quartiles were: births 2005 (11-February to 24-February), births 2006 (13-February to 1-March), settlement 2005 (17-April to 9-May), and settlement 2006 (27-April to 14-May). CQB rockfish windows were: births 2005 (9-April to 29-April), births 2006 (11-March to 8-April), settlement 2005 (23-May to 2-June), and settlement 2006 (16-May to 29-May).

I defined birth and settlement windows for black and CQB rockfish by combining birth and settlement dates from both years and calculating using the 1st and 3rd quartiles of the resulting distributions. The black rockfish windows were: births (11-February to 26-February) and settlement (23-April to 14-May). The combined CQB rockfish windows were: births (22-March to 13-April) and settlement (19-May to 15-June). I defined ‘pelagic’ windows for each group as the interval between birth and settlement windows.

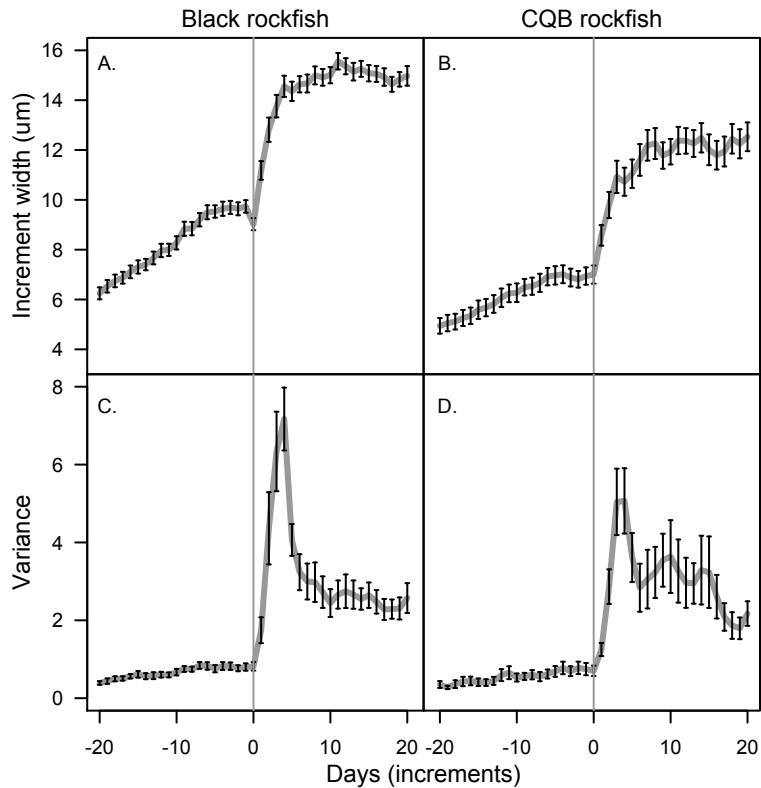


Figure 3.3. Comparison of black rockfish ($n = 68$) and CQB rockfish ($n = 42$) otolith daily growth increment width and variance (mean \pm SE) corresponding to the 20 days preceding and following increments designated as the day on which settlement occurred.

3.4.2 Cohort-specific oceanographic conditions

Ocean conditions experienced by pelagic larvae and juveniles of black and CQB rockfishes differed markedly between 2005 and 2006. Pre-settlement black rockfish in 2005 experienced downwelling-favourable conditions (i.e. negative upwelling index values), warm temperatures, and low primary productivity (Fig. 3.4 a,c,e). Upwelling consistently increased in 2006 beginning

Table 3.1. Comparison of early life history attributes of black and CQB rockfishes between 2005 and 2006

A. Black rockfish				
	2005 (n = 27)	2006 (n = 40)	T value	P>T
Birth date	17-Feb ± 2.5 d	19-Feb ± 1.8 d	0.78	0.4404
Settlement date	25-Apr ± 3.0	6-May ± 1.8 d	3.25	0.0022
Pelagic duration	67 d ± 1.7 d	76 d ± 1.4 d	4.04	0.0002
Size-at-settlement	19.85 mm ± 0.73	19.95 mm ± 0.54	0.11	0.9117

B. CQB rockfish				
	2005 (n = 20)	2006 (n = 19)	T value	P>T
Parturition	16-Apr ± 3.0	19-Mar ± 3.7	5.70	<0.0001
Settlement	6-Jun ± 3.3 d	21-May ± 4.0 d	2.89	0.0065
Pelagic duration	51 d ± 2.6 d,	63 d ± 2.7 d	3.37	0.0018
Size-at-settlement	11.83 mm ± 0.9	14.09 mm ± 0.90	2.17	0.0355

approximately 50 days prior to black rockfish settlement. Approximately 20 days prior to settlement upwelling index values became positive, marking the onset of a strong upwelling event that began in mid April and produced increasing chlorophyll-a levels.

Differences in ocean conditions experienced by CQB rockfishes in 2005 and 2006 were magnified both by parturition dates occurring later than black rockfish in both years, and because birth dates in 2005 occurred a month later than in 2006. In 2005, pre-settlement CQB rockfish experienced unusually warm and downwelling-favourable ocean conditions during the 40 days prior to settlement. In contrast, pelagic larvae and juveniles in 2006 experienced strong upwelling and cool ocean temperatures (Fig 3.4 b,d,f).

3.4.3 Long-term variability in stage-specific ocean conditions

Strong black rockfish recruitment occurred in 2006 and 2010, however, these cohorts experienced very different ocean conditions at the time of parturition. In all years for which I have recruitment data except 2010, black rockfish births corresponded to periods of above average upwelling and below average SST. Sea surface temperature at birth was notably low in 2006, and 2010 was notable for low upwelling and warm SST (Fig. 5a). Upwelling and SST during

the pelagic phase did not differ between years of high or low black rockfish recruitment (Fig. 3.5c); however, ocean conditions at settlement in 2006 and 2010 were remarkably similar (Fig. 3.5e). In these years of high black rockfish recruitment, settlement corresponded to periods of exceptionally strong upwelling.

High CQB rockfish recruitment occurred in 2005 and, to a lesser extent, in 2009. As for black rockfish, ocean conditions corresponding to the CQB births were very different between these two years. Ocean conditions during CQB rockfish births in 2005 were virtually identical to those during the El Niño conditions of 1993 (Fig. 3.5b) and to 2010. In 2009, births corresponded to high upwelling and low SST. The years 2005 and 2009 were most similar oceanographically during the pelagic phases of CQB rockfishes, with both years experiencing downwelling-favourable winds. In 2005, conditions were exceptional in this regard, mirroring the warm and downwelling-favourable ocean conditions of the 1993 and 1997 El Niño events (Fig. 3.5d). All years of low CQB rockfish recruitment corresponded to above average upwelling during the pelagic phase. Upwelling was still exceptionally low at the time of CQB settlement in 2005, but was slightly positive in 2009. Remarkably, ocean conditions during CQB settlement in 2005 and 2006 were nearly identical (Fig. 5f).

3.4.4 Ocean conditions during birth and settlement intervals

Black rockfish births occurred in mid-late February in both 2005 and 2006 during short periods of high upwelling, low SST, and high chlorophyll-a concentrations (Fig. 3.6 a,c,e). Black rockfish settlement in both years corresponded to periods of strong upwelling. High black rockfish recruitment in 2006 occurred during the peak and declining phase of an exceptionally strong upwelling event that occurred through late April and early May.

CQB rockfish births and settlements in 2005 occurred at the end of periods of exceptionally low upwelling and increasing SST and chlorophyll-a levels (Fig. 3.6 b,d,f). In 2006, CQB births occurred nearly a month earlier than in 2005 and immediately before upwelling increased in early April and remained above average until mid May.

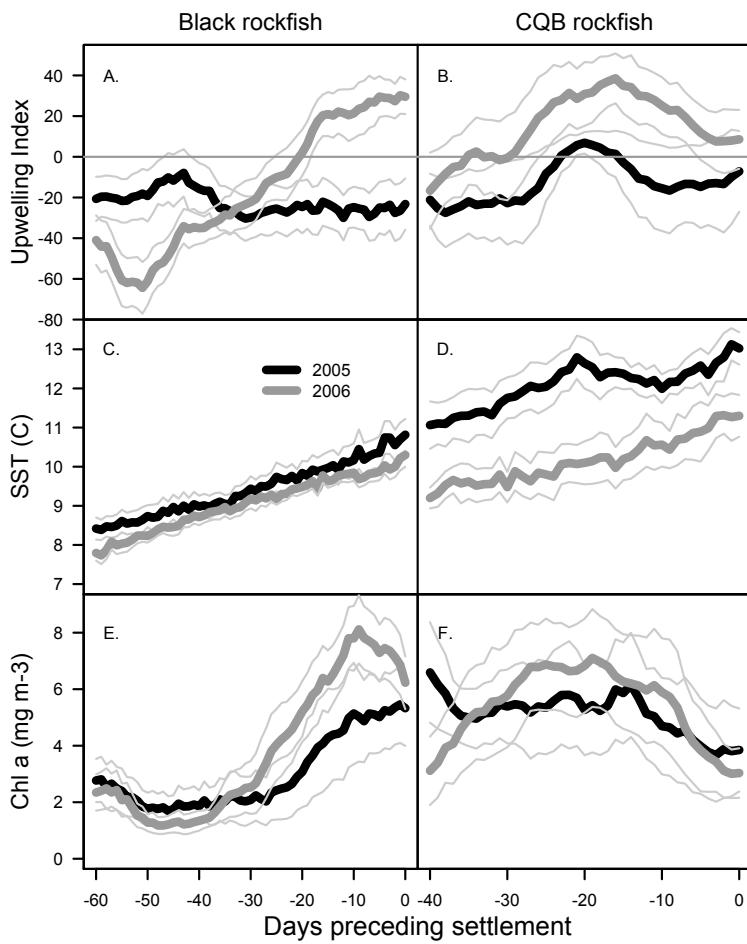


Figure 3.4. Cohort-specific oceanographic conditions experienced by pre-settlement black rockfish (2005, n = 27, 2006, n = 39) and CQB rockfishes (2005, n = 22, 2006, n = 19). Thick lines represent daily averages of oceanographic metrics corresponding to the 60 days (black rockfish) and 40 days (CQB rockfish) prior to settlement of individuals comprising each cohort. Thin lines represent 95% confidence intervals around daily means.

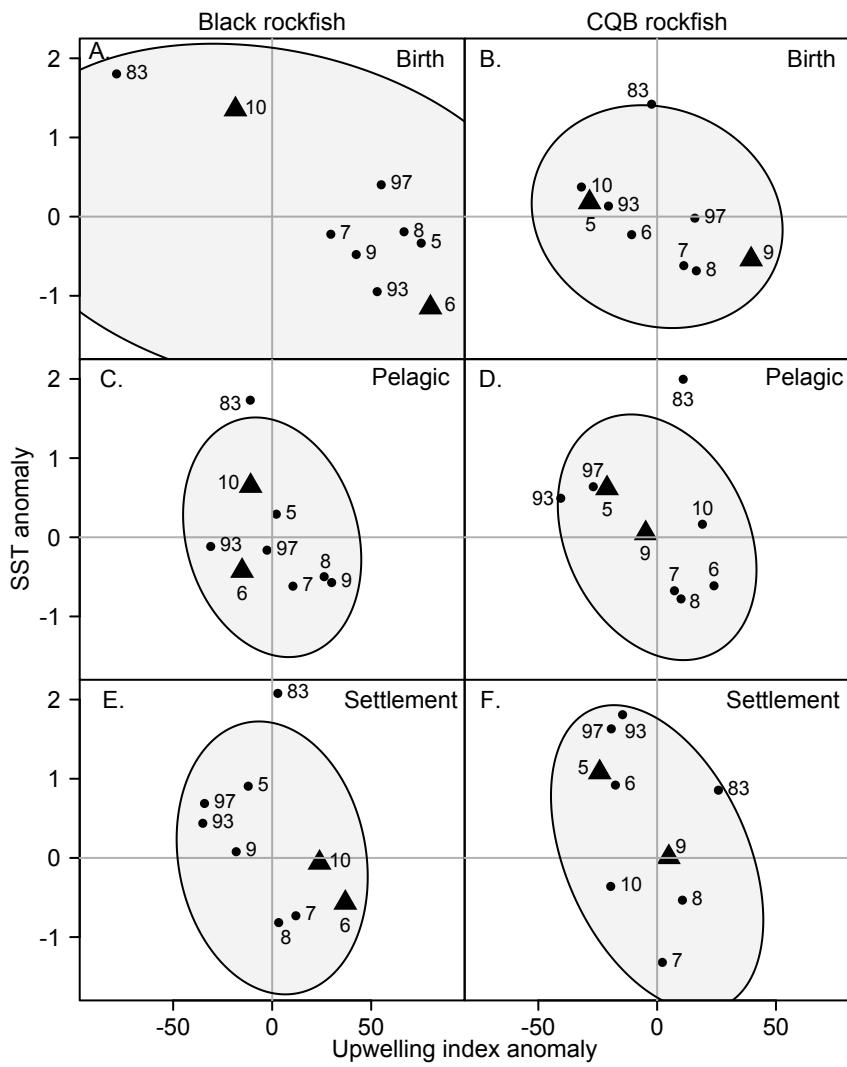


Figure 3.5. Annual upwelling and sea surface temperature (SST) anomalies corresponding to birth, pelagic, and settlement intervals of black and CQB rockfishes. Anomaly values represent differences from long-term averages between 1977 and 2010. Numbers represent years with corresponding recruitment data, as well as benchmark El Niño years. Blue triangles highlight years with high recruitment success. Shaded ovals are 95% confidence ellipses representing long-term oceanographic variability.

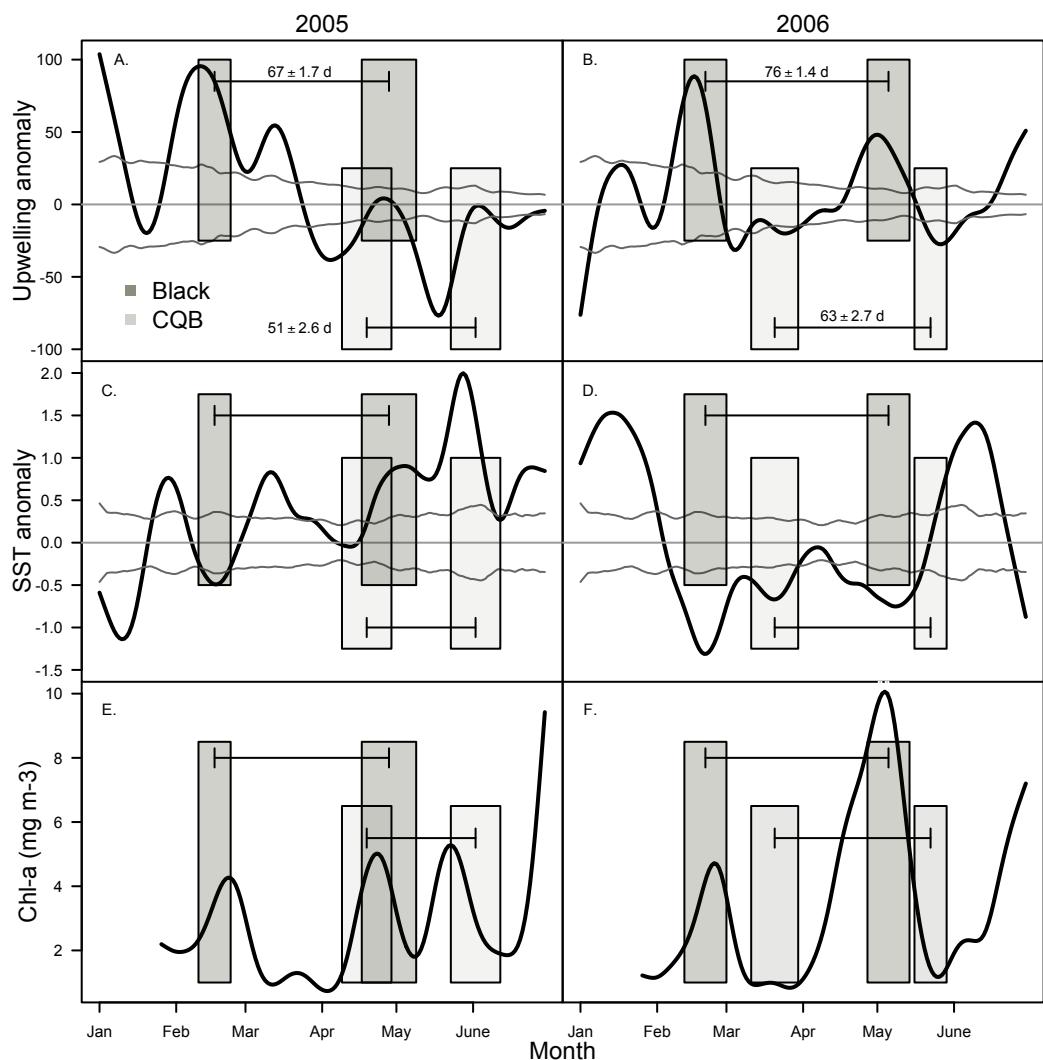


Figure 3.6. Black and CQB rockfish birth and settlement intervals in 2005 and 2006 in relation to daily upwelling index anomalies, sea surface temperature (SST) anomalies, and chlorophyll-a levels. Anomaly values are differences from daily averages between 1977 and 2010. Thin lines represent 95% confidence intervals around daily means.

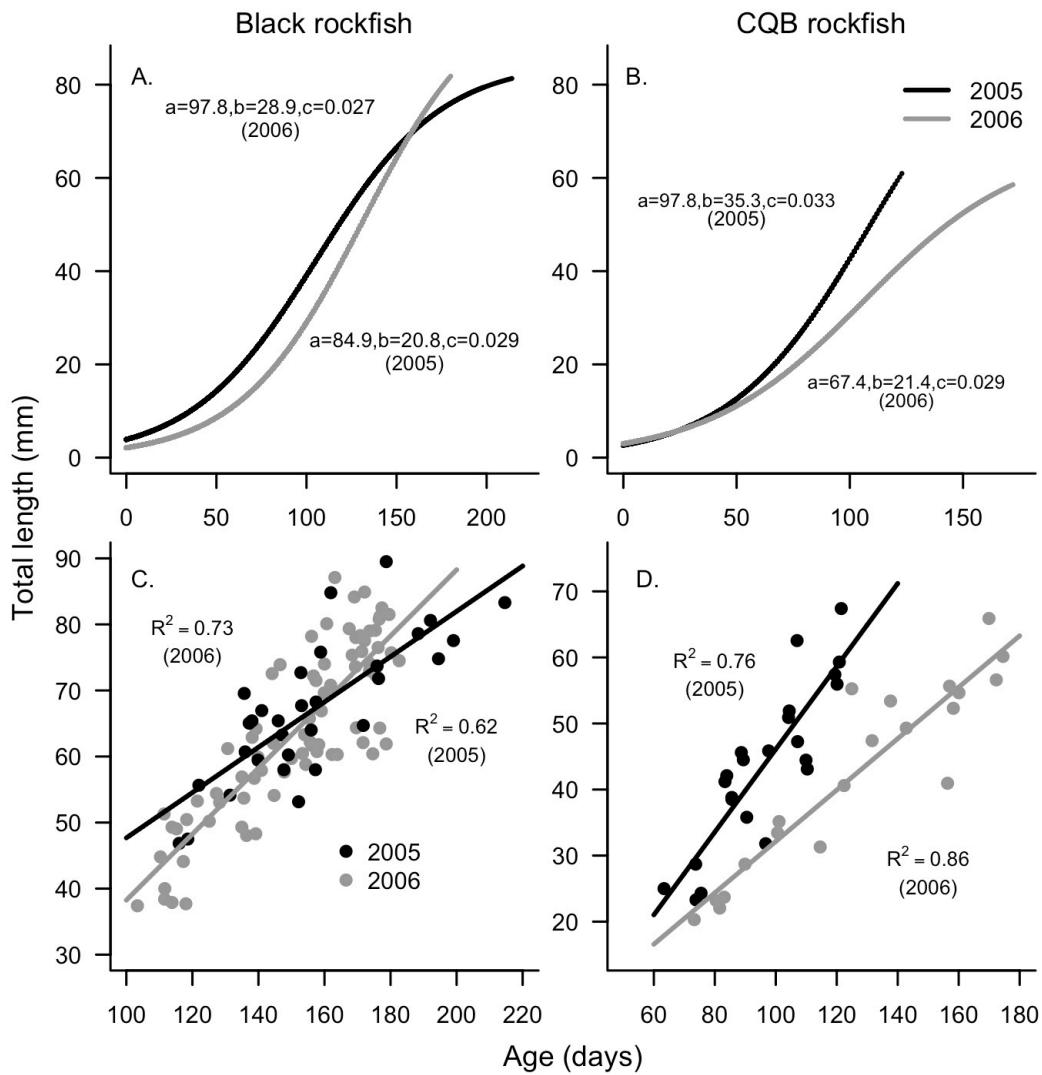


Figure 3.7. Growth rates of black and CQB rockfishes in 2005 and 2006. Growth curves (A and B) are logistic growth models fitted to back-calculated growth trajectories of individuals comprising each cohort. Length-at-age relationships (C and D) represent length (total length) and age (days) at capture.

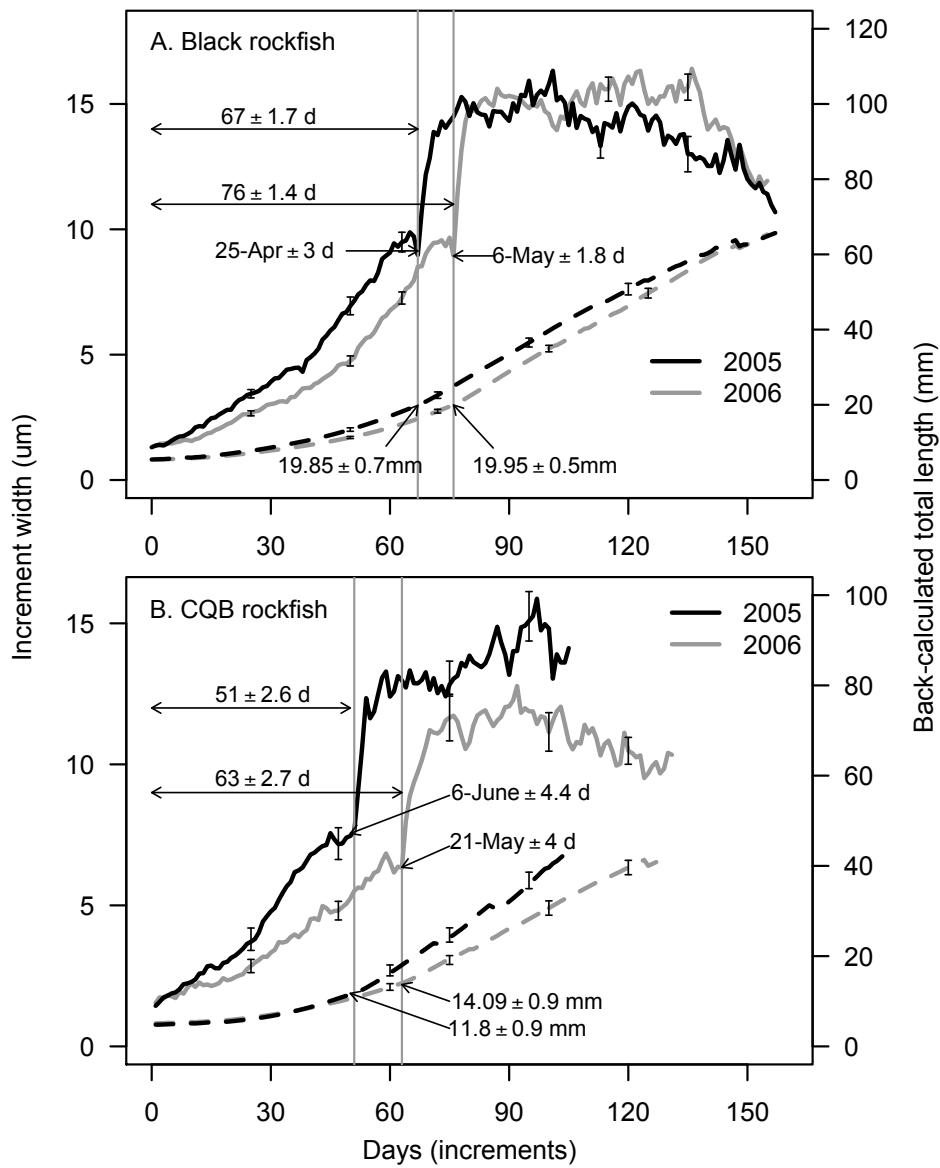


Figure 3.8. Longitudinal growth profiles of black and CQB rockfishes based on mean otolith daily growth increment width (solid lines, left y-axis) and back-calculated (Modified-Fry model) length-at-age (dashed lines, right y-axis). Daily means (\pm SE) were calculated by centering individual growth profiles on settlement increments/day (vertical lines). Settlement dates and pelagic durations are set to annual means of each cohort.

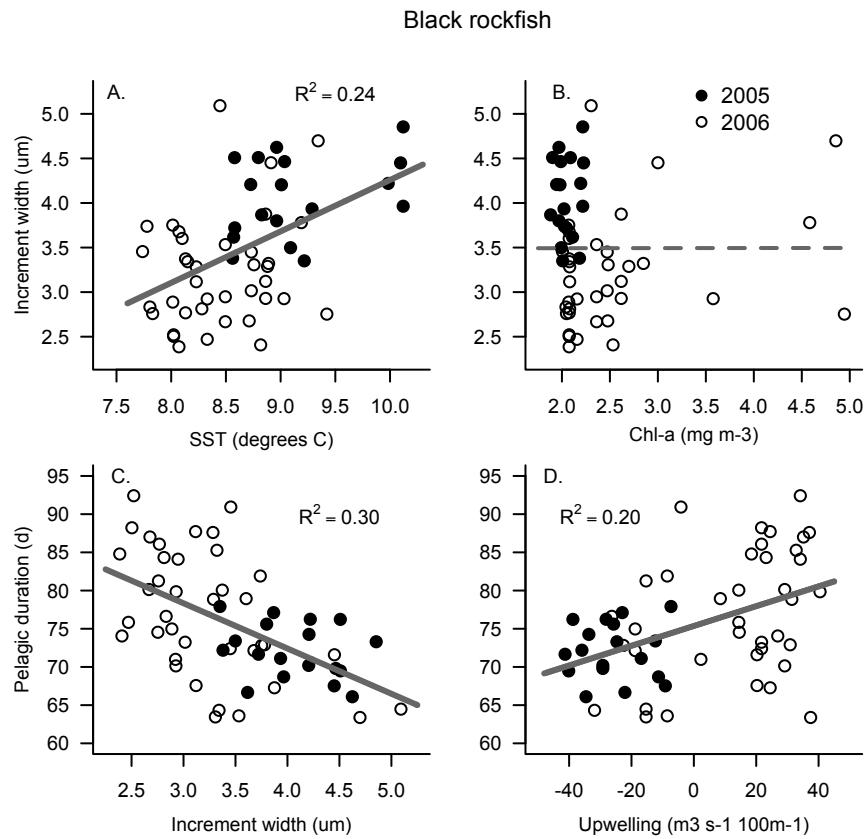


Figure 3.9. Effects of sea surface temperature (SST), chlorophyll-a (Chl-a), and upwelling (Upwelling Index) on black rockfish pre-settlement growth (A and B) and pelagic duration (C and D). Values of growth, SST, and Chl-a are averages for the 60 days following birth. Values of upwelling are averages for the 30 days prior to settlement.

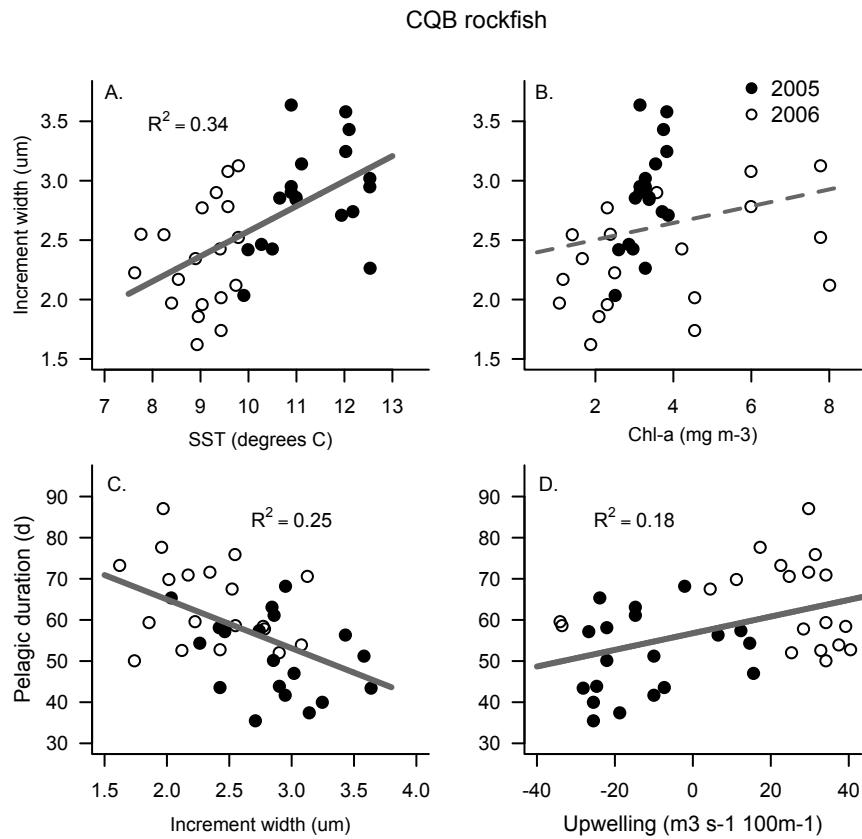


Figure 3.10. Effects of sea surface temperature (SST), chlorophyll-a (Chl-a), and upwelling (Upwelling Index) on CQB rockfish pre-settlement growth (A and B) and pelagic duration (C and D). Values of growth, SST, and Chl-a are averages for the 40 days following birth. Values of upwelling are averages for the 30 days prior to settlement.

3.4.5 Pre- and post-settlement growth

Juvenile black and CQB rockfish otolith lengths increased closely with increasing body lengths (Appendix B, Fig. B1). This relationship formed the basis for modeling individual length-at-age profiles using the Modified-Fry back-calculation model (Appendix B, Fig. B2). Logistic growth models fitted to back-calculated length-at-age profiles indicate that black rockfish growth rates were initially slightly higher in 2005 than 2006; however, in 2005 post-settlement growth slowed at approximately 150 days after which 2006 growth rates were faster (Fig. 3.7a). Fitted growth models for CQB rockfish show faster growth in 2005 compared to 2006 (Fig. 3.7b). Length-at-age relationships closely mirrored the modeled comparison of pre-and post-settlement growth. Black rockfish growth was slightly higher in 2006 (Fig. 3.7c; ANCOVA, length*year, $F = 6.49, P = 0.0123$), and CQB rockfish length-at-age was markedly higher in 2005 (Fig. 3.7d; ANCOVA, length*year, $F = 8.19, P = 0.0067$).

Comparison of average daily increment width profiles reinforced these patterns. Black rockfish grew faster pre-settlement in 2005 than in 2006, but post-settlement growth was faster in 2006 (Fig. 3.8a). Black rockfish size-at-settlement was similar in 2005 and 2006, despite the trend towards higher pre-settlement growth in 2005 (Fig. 3.8a, Table 3.1). CQB rockfish pre-settlement increments were consistently wider in 2005 than in 2006, and this trend continued post-settlement (Fig. 3.8b). Higher CQB rockfish growth rates (logistic models, length-at-age, and increment width-at-age) in 2005 corresponded to significantly smaller sizes-at-settlement (Fig. 3.8b, Table 3.1).

3.3.7 Relationships between ocean conditions, growth rates, and pelagic duration

I found strong and consistent relationships between black (Fig. 3.9) and CQB (Fig. 3.10) rockfish pre-settlement growth rates, pelagic duration, SST, upwelling (Fig 3.9). Growth rates increased significantly with increasing SST (black rockfish, $R^2 = 0.2369, F_{1,54} = 16.76, P = 0.00014$; CQB rockfish, $R^2 = 0.3377, F_{1,36} = 18.36, P = 0.00013$), but not chlorophyll concentrations (black rockfish, $R^2 < 0, F_{1,54} < 0, P = 0.9950$; CQB rockfish $R^2 = 0.0555, F_{1,36} = 2.11, P = 0.1547$). Pelagic durations decreased with increasing growth rates (black rockfish, $R^2 = 0.2993, F_{1,54} = 23.07, P < 0.0001$; CQB rockfish, $R^2 = 0.2506, F_{1,36} = 12.04, P = 0.0014$), and increased with upwelling

experienced during the 30 days prior to settlement (black rockfish, $R^2 = 0.1996$, $F_{1,54} = 13.47$, $P = 0.0006$; CQB rockfish, $R^2 = 0.1784$, $F_{1,36} = 7.82$, $P = 0.0082$).

Hierarchical variance partitioning demonstrated that growth rates of black and CQB rockfishes are primarily associated with the independent effects of SST (black rockfish = 87.7%; CQB rockfish = 89.8%) but not chlorophyll levels (black rockfish = 12.3%; CQB rockfish = 10.2%). Pelagic durations of rockfishes were strongly affected by the independent effects of pre-settlement growth rates (black rockfish = 45.4%; CQB rockfish 61.2%) and the magnitude of upwelling prior to settlement (black rockfish = 54.6%; CQB rockfish = 38.8%).

3.5 Discussion

This research contributes insight into the responses of nearshore Pacific rockfishes to coastal upwelling. Black and CQB rockfish showed large interannual variability in early life history attributes (i.e. birth and settlement dates, growth rates and pelagic durations) corresponding closely, but differently, to specific upwelling events. High CQB rockfish recruitment was associated with prolonged downwelling, warm ocean temperatures, late birth dates, high growth rates, and short pelagic durations. In contrast, exceptionally strong black rockfish recruitment was associated with near opposite conditions; strong upwelling, cool ocean temperatures, slow growth rates, and long pelagic durations. These results provide evidence that high larval growth rates and reduced pelagic durations are not necessary conditions for strong black rockfish recruitment success. Rather, oceanographic processes facilitating onshore delivery of late-stage pelagic juveniles may be the primary determinant of recruitment success.

3.5.1 Contrasting oceanographic conditions in 2005 and 2006

Ocean conditions differed remarkably between 2005 and 2006 on the west coast of Vancouver Island and throughout the northern California Current Large Marine Ecosystem (CCLME). In 2005 the spring transition to upwelling-favourable winds that normally occurs in mid April was delayed by 2-3 months by atmospheric-blocking of the jet stream (Schwing et al. 2006). Prolonged downwelling-favourable winds resulted in vertically-stable ocean conditions, unusually warm sea surface temperatures (Kosro et al. 2006) and low primary productivity (Thomas &

Brickley 2006). Poleward and onshore displacement of numerous taxa were detected reflecting the lack of cross-shelf offshore flow that usually occurs at this time of year (Brodeur et al. 2006). Ecosystem-level effects associated with this event included altered zooplankton community composition (Mackas et al. 2006), recruitment failures of intertidal invertebrates (Barth et al. 2007), seabird breeding failure (Sydeman et al. 2006), and changes in marine mammal foraging behaviour (Newell & Cowles 2006, Weise et al. 2006). In contrast, in 2006 the west coast of Vancouver Island experienced above average upwelling-favourable winds through the spring and summer (DFO 2007). In the same year, intense and prolonged upwelling off the coast of Oregon resulted in the oxygen minimum zone being pulled up onto the continental shelf and causing a large-scale anoxia event that resulted in mass mortalities of benthic invertebrates and displacement of demersal fishes (Chan et al. 2008). Thus, upwelling dynamics in 2005 and 2006 likely represent opposite ends of a continuum of oceanographic variability occurring throughout the CCLME and their corresponding effects on nearshore Pacific rockfish recruitment dynamics.

3.5.2 Long-term oceanographic context

My research focuses primarily on the strong recruitment events of CQB and black rockfishes in relation to exceptional upwelling in 2005 and 2006. Yet, just how exceptional were these years relative to other years for which recruitment data are available, and within the context of long-term oceanographic variability? Further, during what early life history stages were years of successful recruitment most similar? I addressed these questions by comparing upwelling and SST anomalies calculated for black and CQB rockfish birth, pelagic, and settlement windows for all years between 1977 and 2010.

Warm ocean temperatures and fast growth during the pelagic phase are apparently major factors promoting recruitment of CQB rockfishes. The warm ocean temperatures that occurred during the large CQB rockfish recruitment of 2005 were above average but within the range of long-term oceanographic variability. However, 2005 was the only year for which I have recruitment data when SST was above average during the birth window; all subsequent years of low CQB rockfish recruitment (2006-2010) experienced below average SST at the time of parturition. During the 2005 CQB rockfish pelagic interval, warm ocean temperatures and strong downwelling conditions mirrored the El Niño years of 1993 and 1997 when high recruitment of

these and other solitary benthic rockfishes was observed in central and northern California (Lenarz et al. 1995, Carr & Syms 2006).

CQB rockfish settlement in 2005 and 2006 occurred during virtually identical conditions, despite the large differences in upwelling dynamics and recruitment success in these years. In both years most settlement occurred during below average upwelling and above average SST. The upwelling anomaly corresponding to the 2005 CQB settlement interval was the third lowest since 1977 after 1988 and 1990. The only other year besides 2005 to experience significant CQB rockfish recruitment was 2009. These years were most similar during the pelagic interval when the 2009 upwelling anomaly became slightly negative. Closer inspection revealed an 18 day period during which upwelling was deeply negative during the 2009 pelagic window (mean = -36.29, n = 18), exceeding anomaly values in 1997 (mean = -26.87, n = 35) and 2005 (mean = -21.09, n = 35). However, because this 18 d period of strongly downwelling-favourable conditions was bracketed by above average upwelling, the average for this 35 d window was near normal (mean = -4.81, n = 35). This result highlights the potential importance of brief oceanographic events in annual recruitment success. This long-term perspective demonstrates that high CQB rockfish recruitment in 2005 corresponded to unusually warm ocean temperatures and downwelling-favourable winds.

In contrast to CQB rockfish, black rockfish births in all years except 2010 occurred during periods of above average upwelling and below average SST. In 2006 ocean conditions at birth were marked by colder SST than the other five years for which I have recruitment data, and the third coldest since 1977 after 1979 and 1989. Upwelling was strong and SST was low during the pelagic stage of low black rockfish recruitment years (2007, 2008, and 2009). Years of high black rockfish recruitment (2006 and 2010) experienced below average upwelling through this period. However, 2006 and 2010 experienced periods of strong upwelling at the time of settlement. The upwelling anomaly during black rockfish settlement in 2006 was the second highest after 1990 since 1977.

These results show that black rockfish recruitment success is associated with strong upwelling at the time of settlement, and indicate that upwelling facilitates onshore delivery of late stage pelagic juveniles. Conditions for growth and survival at birth and through the pelagic durations were very different from those at recruitment. Sea surface temperature was unusually cold at birth in 2006 and unusually warm in 2010, corresponding to above and below average upwelling,

respectively. These results suggest two possible explanations for high black rockfish recruitment success in these years. The first is that recruitment strength was set during different life history stages (i.e. near the time of parturition in 2010, and at settlement in 2006). A second possibility is that recruitment success in both years was determined around the time of settlement, and therefore, for black rockfish, ocean conditions regulating larval growth and mortality rates may be of secondary importance to processes regulating delivery to nearshore adult populations.

3.5.3 Effects of upwelling on growth

By regulating nearshore ocean temperatures and primary productivity, variable coastal upwelling dynamics may increase or decrease pre-settlement growth rates, and therefore affect size-dependent vulnerability to predation, pelagic durations, and cumulative mortality. Larval growth and development rates increase with ocean temperature and are highest near larval thermal tolerance maxima (Pepin 1991, Houde 2009). In turn, high developmental rates associated with increasing growth rates can reduce pelagic duration by decreasing the age at which metamorphosis occurs and larval competency is reached (Francis 1994). In contrast, upwelling, which lowers SST, provides nutrients that fuel primary productivity and may enhance the resources available to developing juvenile rockfishes. Therefore, the effects of upwelling on larval growth and mortality depend on whether larval growth is more constrained by ocean temperature or productivity.

I found higher pre-settlement growth rates in both black and CQB rockfishes during the warm ocean temperatures of 2005. Furthermore, growth rates varied strongly with SST but not Chl-a, and pelagic durations of both groups were inversely related to growth rates. The highest growth rates and shortest pelagic durations were closely associated with the warm ocean conditions of 2005. High growth rates and short pelagic durations of CQB rockfishes were also associated with significantly smaller body sizes (total length) at settlement in 2005. These results support the idea that intense upwelling and low ocean temperatures lead to low pre-settlement growth rates, increased pelagic durations and, by extension, relatively high pelagic-stage cumulative mortality. Although years of high CQB rockfish recruitment coincide with fast pre-settlement growth, black rockfish demonstrated the opposite pattern: the highest recruitment was preceded by slow pre-settlement growth rates and protracted pelagic durations. These contrasting relationships

indicate that black and CQB rockfish life histories differ fundamentally with respect to the relative importance of processes affecting larval growth and mortality vs. those affecting larval transport.

3.5.4 Birth and settlement in relation to upwelling events

Coastal upwelling may affect pelagic duration and mortality rates of rockfishes if cross-shelf flows inhibit or facilitate movement of pelagic juveniles to adult habitats. I found that CQB rockfish birth and settlement intervals in 2005 and 2006 were associated with periods of downwelling-favourable winds (i.e. onshore advection of the surface layer). Short pelagic durations and high recruitment in 2005 occurred when upwelling intensity remained low throughout the pelagic stage. Long pelagic durations and low recruitment in 2006 occurred when upwelling intensity remained above average throughout the pelagic duration. Thus, these patterns support the ‘upwelling-relaxation’ hypothesis (Roughgarden et al. 1988, Cury & Roy 1989, Farrell et al. 1991, Shanks & Brink 2005), and suggest that downwelling-favourable winds and onshore advection of the surface layer reduce pelagic durations and facilitate nearshore retention or onshore movement of CQB rockfish larvae and pelagic juveniles. Importantly, birth and settlement dates associated with downwelling events suggest that CQB rockfish larvae and pelagic juveniles occupy shallow surface layers above the thermocline (Shanks & Brink 2005).

In contrast to CQB rockfish, black rockfish birth and settlement intervals in 2005 and 2006 were associated with periods of above average upwelling. Births in 2005 and 2006 occurred in mid February and corresponded closely to short but strong upwelling events that resulted in a rapid decrease in SST and increase in Chl-a. The extent to which these events contributed to recruitment in these years is unknown. One possibility is that high primary productivity coinciding with spawning may have increased very early larval growth and survival rates (Cury and Roy 1989). Most black rockfish settlement in 2006 occurred during the peak and declining phase of a strong upwelling event. In contrast to CQB rockfish, this pattern suggests that black rockfish pelagic juveniles occupy deep-water layers below the thermocline (Shanks & Brink 2005). Hierarchical variance partitioning revealed that although pre-settlement growth rates of both rockfish groups contribute substantially and independently to variable pelagic durations, the independent effects of upwelling intensity experienced in the 30 days prior to settlement was

higher for black rockfish than for CQB rockfish (55% and 39% respectively). These results demonstrate that ocean conditions favourable for high larval growth rates and survival are not necessary for high settlement and recruitment rates of black rockfish. Rather, exceptional oceanographic events favouring onshore movement of pelagic juveniles, in this case strong upwelling, may be primary determinants of black rockfish recruitment. However, persistently poor ocean conditions for larval production, growth, and survival are expected to underlie chronically low rockfish recruitment success, regardless of flow regimes that may inhibit or facilitate larval delivery (Cury & Roy 1989, Laidig et al. 2007, Caselle et al. 2010a). My results highlight the importance of episodic oceanographic events that have large effects on spatial and temporal patterns of recruitment success that differ among species or groups.

3.5.5 Contrasting black and CQB rockfish life histories

Synchronous recruitment across large spatial scales suggests that suites of oceanographic variables favour taxa with similar early life histories (Sponaugle & Cowen 1997, Field & Ralston 2005). My research adds to a growing number reporting distinct differences in recruitment patterns of two complexes of nearshore rockfishes. Lenarz et al. (1995) and Carr and Syms (2006) observed that during El Niño years (1992/1993 and 1997/1998), high recruitment of ‘solitary benthic’ rockfishes (including CQB rockfish) corresponded to above average ocean temperatures and weak upwelling that favoured onshore advection. In contrast, the ‘mid-water aggregating’ rockfishes (including black rockfish) recruited heavily during a La Niña event in 1999 which was associated with strong upwelling and cold ocean temperatures. My study contributes to the growing empirical evidence that rockfish groups may exhibit fundamentally different responses to coastal upwelling.

The most compelling explanation for the differential recruitment success of mid-water aggregating and solitary benthic species during upwelling vs. downwelling, respectively, is the differential use of deep vs. shallow depth strata. Recent studies have demonstrated that the effects of coastal upwelling on the pelagic stages of marine organisms are taxon-specific, and depend strongly on their vertical location in the water column relative to the thermocline (Shanks & Brink 2005, Mace & Morgan 2006). Lenarz et al. (1995) investigated this hypothesis and found that larvae of solitary benthic species were indeed more abundant higher in the water

column than mid-water aggregating species, and therefore more likely to benefit from onshore advection of surface waters during downwelling events. Conversely, mid-water aggregating rockfish larvae were more abundant in deep water and therefore more likely to benefit from onshore advection during upwelling.

Black rockfish occupation of deep water also implies tolerance, if not preference, for low ocean temperatures. Black rockfish and other mid-water aggregating species spawn in the early winter (January-March) and have pelagic durations lasting 2-4 months. CQB rockfish and other solitary benthic species spawn in early spring (March-May) and have pelagic durations of 1-2 months. I found that pre-settlement growth increased and pelagic durations decreased of black and CQB rockfishes with increasing ocean temperature. Therefore, as a result of their earlier parturition and protracted pelagic durations, black rockfish larvae experience lower seasonal ocean temperatures and are expected to be vulnerable to slow growth and high pelagic-stage cumulative mortality. However, the fact that recruitment success of black rockfish does not appear to depend upon high growth rates or short pelagic durations suggests that pelagic larvae and juveniles have physiological or behavioural attributes that offset this vulnerability. The difference in pelagic juvenile body sizes of black and CQB rockfish is likely a significant factor mitigating vulnerability to predation and processes affecting onshore movement. The smallest early post-settlement black rockfish that I collected in Barkley Sound are approximately 35-40 mm TL, whereas CQB rockfish are 20-25 mm TL. Because large body sizes are associated with enhanced swimming and foraging abilities (Pepin 1991, Green & Fisher 2004), black rockfish larvae and pelagic juveniles may compensate metabolically for low ocean temperatures by increasing prey intake rates.

3.5.6 Conclusions and Implications

The ecological and economic importance of Pacific rockfishes has fuelled extensive research focused on understanding relationships among physical oceanographic processes, recruitment success, and year-class strength (Laidig et al. 1991, Woodbury & Ralston 1991, Ralston & Howard 1995, Bjorkstedt et al. 2002, Field & Ralston 2005, Laidig et al. 2007, Wilson et al. 2008, Caselle et al. 2010a, Caselle et al. 2010b). My study adds to a growing understanding of the contrasting ways in which mid-water aggregating and solitary benthic rockfishes are affected by

upwelling dynamics. Using otolith microstructure analysis to reconstruct early life history attributes provided a detailed picture of the nature and magnitude of the responses of these rockfish groups to oceanographic events underlying recruitment success.

The distinct early life history attributes of mid-water aggregating and solitary benthic rockfishes suggest that these groups may differ markedly in terms of dispersal and population connectivity. Pelagic duration and recruitment success are fundamental determinants of population connectivity and persistence (Cowen & Sponaugle 2009). The long pelagic durations and higher average recruitment success of black rockfish and other mid-water aggregating species (Carr and Syms 2006), suggests relatively high potential for connectivity within regional meta-populations. In contrast, short pelagic durations and low recruitment rates of CQB rockfishes may indicate lower connectivity and threaten persistence of solitary benthic rockfish populations, and lead to slower responses to protection by marine protected areas (Fogarty & Botsford 2007, Lipcius et al. 2008).

My study also shows that species responses to climate variability depend greatly on life history traits, which suggests that ongoing climate change produces winners and losers among marine taxa (Harley et al. 2006). Climate change is predicted to increase the intensity of coastal upwelling (Bakun 1990, Snyder et al. 2003, McGregor et al. 2007), with potentially dramatic effects on coastal ecosystems (e.g. Chan et al. 2008). The results of my study suggest that whereas the frequency and magnitude of mid-water aggregating rockfish recruitment success may benefit from increasing upwelling intensity, rates of CQB rockfish population replenishment may decline. However, the specific timing and duration of these events are as important as their seasonal averages.

4. Indirect effects of sea otters on recruitment, trophic position and growth of kelp-associated rockfishes (Genus *Sebastes*)

4.1 Synopsis

Large vertebrate predators that indirectly affect the size and productivity of habitat-forming primary producers by consuming grazers may also have extensive trophic and non-trophic indirect effects on associated populations and food webs. I investigated the indirect effects of sea otter (*Enhydra lutris*) reintroduction on the west coast of Vancouver Island, Canada, on *Macrocystis* kelp forest size, and related effects on rockfish (*Sebastes* spp.) carbon supply and trophic position, growth and recruitment rates. At locations without otters, sea urchin (*Strongylocentrotus franciscanus*) densities were high (16.2 ± 1.72 [mean \pm se] /m²). At locations that sea otters had re-colonized sea urchins were rare and *Macrocystis* kelp forests extended 3.7 times deeper and surface areas were 18.8 times larger. High rates of rockfish recruitment in large kelp forests support the hypothesis that otters indirectly increase rockfish settlement rates by increasing the target size of settlement habitats. Despite order-of-magnitude increases in the size and productivity of kelp forests, diets of adult rockfishes in the presence and absence of sea otters contained similarly high (50-75%) contributions of kelp-derived carbon. In contrast, adult rockfish in the presence of sea otters fed at higher trophic positions, indicating that these populations consume higher proportions of energy-rich fish prey that use kelp as a refuge from piscivores. Contrasting relationships between adult rockfish body size and trophic positions suggest that low resource availability associated with sea otter absence and small kelp forests limit the ability of rockfish to maximize growth rates by feeding at higher trophic positions. I tested for associations between kelp-carbon content and trophic position on daily growth rates of juvenile black rockfish (*S. melanops*); growth was more strongly affected by changes in trophic position than kelp-carbon content. These results indicate that by indirectly increasing the size and

productivity of kelp forest habitats and food webs, recovering sea otter populations hold substantial implications for the recruitment and trophic dynamics of nearshore Pacific rockfishes.

4.2 Introduction

Mitigating the global loss of biodiversity and managing for ecosystem properties and societal values depends critically on understanding processes that underlie ecosystem change (Carpenter et al. 2009). Large vertebrate predators are typically the first group to disappear from food webs and landscapes (Duffy 2003), yet the effects of these removals are often poorly known. Hairston, Smith, and Slobokin (1960) introduced the idea that regulation of herbivores by predators maintains predominance of plant populations, and by extension, the food webs they support. Subsequently, natural and manipulative experiments removing predator and herbivore populations have demonstrated that large vertebrate consumers often exert strong influences on community structure and productivity in the form of trophic cascades (Estes & Palmisano 1974, Shurin et al. 2002, Beschta & Ripple 2009, Terborgh & Estes 2010). Much less well known are the collateral effects of trophic cascades on biodiversity and ecosystem properties, particularly when the affected primary producers provide both productivity and habitat to food webs across large spatial scales.

The ‘otter-urchin-kelp’ trophic cascade is a classic example of how a marine predator can have positive indirect effects on habitat-forming primary producers (Estes & Palmisano 1974). Hunted to near extinction during the North Pacific maritime fur trade (ca. 1778-1911), recovering and reintroduced sea otter (*Enhydra lutris*) populations have extensive direct and indirect effects on nearshore marine ecosystems (Simenstad et al. 1978, Duggins et al. 1989, Estes et al. 1998, Reisewitz et al. 2006, Anthony et al. 2008). By preying upon herbivores, sea otters reduce grazing pressure, and indirectly increase the abundance of large fleshy algae such as kelp in rocky reef ecosystems (Estes & Duggins 1995, Watson & Estes 2011). Kelp forests are among the most diverse and productive ecosystems and support a wide range of ecosystem services (Steneck et al. 2002). In the absence of sea otters, however, kelp forests are vulnerable to deforestation by unregulated populations of grazing sea urchins (previous references). These indirect effects of sea otters extend well beyond rocky reef ecosystems because kelp-derived productivity is exported and contributes substantially to the productivity of adjacent marine and terrestrial ecosystems

(Duggins et al. 1989, Bustamante et al. 1995, Polis & Hurd 1995, Kaehler et al. 2006). Furthermore, by moderating local hydrographic regimes (Jackson 1998, Gaylord et al. 2007), providing refuges from predators (Johnson 2007), and supporting abundant consumer populations (Gaines & Roughgarden 1987), kelp forests can also influence patterns of larval supply and recruitment of nearshore benthic invertebrates (Duggins et al. 1990, Eckman et al. 2003). Despite the ability of sea otters to regulate the size and productivity of kelp forest habitats, hypotheses regarding the indirect effects of this predator on marine population and food web dynamics remain largely untested (Estes 2008).

Rocky reef ecosystems with and without sea otters provide the opportunity to investigate relationships between habitat size, productivity, food web structure, and population dynamics. Larger habitats support higher species richness as a result of higher microhabitat diversity and colonization rates (Hutchinson 1959, MacArthur & Wilson 1967, MacArthur 1972). Larger habitats and ecosystems may also support longer food chains because total ecosystem productivity is closely related to ecosystem size (Pimm 1982, Schoener 1989). Others argue the higher species diversity, habitat availability and heterogeneity, associated with larger ecosystems, and not productivity, are better predictors of food-chain length (Post et al. 2000). Nevertheless, high productivity in systems such as kelp forests can increase detrital subsidies that create parallel food chains and support greater densities of high trophic level consumers (Polis & Hurd 1995, Jefferies 2000, Moore et al. 2004). The structural properties of food webs, including complexity and stability (Rooney et al. 2006), however, may depend more upon how habitats and ecosystems are distributed across regional landscapes and connected through the exchange of nutrients, prey, propagules, and genes (Flather & Bevers 2002, Fahrig 2003, Brudvig et al. 2009, Massol et al. 2011).

Kelp forests support abundant and diverse populations of temperate reef fishes that depend upon kelp-derived productivity and habitat during one or more life history stages (Holbrook et al. 1990). I investigated the indirect effects of sea otters on rocky reef fish population and food web dynamics. The structural complexity of kelp forest habitats play key roles in the success of reef fish recruitment by influencing processes during (Carr 1989, 1991, 1994) and following (Johnson 2006, 2007, White & Caselle 2008) settlement. Primary consumers of living and decaying kelp provide a critical prey base for food web structure and productivity (Davenport & Anderson 2007, Graham et al. 2008b). In this study, I tested the effects of sea otter recovery on (a) kelp

forest habitat size, (b) reef fish recruitment dynamics, and (c) reef fish trophic dynamics and (d) demographic rates. I investigated these effects using comparative studies, and provide insight into how top predators indirectly affect dynamics of populations and food webs associated with habitat-forming primary producers. I addressed the following questions:

(1) *How does kelp forest habitat size differ between sites with and without sea otters?* The distribution of kelp populations is determined by several factors including substratum and slope, grazing intensity, wave exposure, and light intensity (Dayton 1985). In the presence of sea otters and absence of high sea urchin grazing pressure, I predicted that kelp forest sizes increase by extending to deeper depths owing to reduction of urchin populations.

(2) *Do larger kelp forests experience higher rates of reef fish population replenishment?* Settlement and recruitment rates of reef fishes in kelp forests may reflect encounter rates resulting from spatial distributions of aggregations of larvae moving onshore, and the size, number, and distribution of settlement habitats (Carr & Syms 2006). Recruitment intensity is typically measured as within-habitat densities (i.e. individuals/m²). However, because kelp forest habitat size may have large effects on recruitment success, estimates of recruitment expanded to the area of recruitment habitats (i.e. individuals/kelp forest) may better represent local rates of population replenishment. Here, I employed both approaches, and predicted that kelp forests in regions with sea otters experience higher reef fish recruitment success owing to higher encounter rates between late-stage pelagic juveniles and larger kelp forest habitats.

I tested for potential effects of kelp forest size on the pelagic duration of larval rockfish by comparing juvenile rockfish birth and settlement date distributions, and pelagic durations, between regions with and without otters. Reduced pelagic durations in areas where sea otters and kelp forests have recovered would support the hypothesis that large kelp forests intercept more aggregations of rockfish pelagic juveniles moving onshore or alongshore. I tested for potential effects of kelp forest size on juvenile rockfish post-settlement growth rates by comparing pre-and post-settlement growth rates between regions with and without otters. I predicted that pre-settlement growth should be similar in both regions, and that enhanced growth in either region would be indicative of differences in resource availability or density-

effects. Conversely, differences in pre-settlement growth rates would indicate regional differences in offshore ocean temperature experienced during pelagic larval stages.

(3) *Do sea otters affect the structure and/or productivity of local food webs, and therefore the diets of reef fishes, through changes in kelp forest size and productivity?* Charles Elton's definition of a species' "niche" (Elton 1927) emphasized the significance of body size because body size influences what resources can be consumed and what predators are dangerous for a given organism (Leibold 1995). In this context, consumer diets reflect relationships among body size, growth rates, and resource availability resulting from local food web structure and productivity. Ratios of naturally occurring stable isotopes in an organism's tissues derive from all trophic pathways contributing to an individual's diet, and therefore can be used to quantify and compare trophic 'niche space' among species and habitats (Bearhop et al. 2004, Layman et al. 2007). Sea otters increase kelp community productivity through multiple inter-dependent processes (Duggins 1988). I predicted that higher kelp-derived and food web productivity associated with sea otter reintroduction should result in (a) higher kelp-carbon contents comprising reef fish tissues, and (b) enable reef fishes to shift to higher trophic positions at smaller body sizes (i.e. faster ontogenetic niche shifts; Werner & Gilliam 1984). Because large habitats support higher species richness and microhabitat diversity (MacArthur & Wilson 1967), I also predicted that the trophic niche space of reef fishes should increase following sea otter and kelp forest recovery.

(4) *Does variation in kelp-carbon content and trophic position affect consumer performance?* Many studies have used stable isotopes to detect changes in consumer trophic niche space in response to changes in food web structure (e.g. Vander Zanden et al. 1999), yet few have quantified their demographic consequences (but see Post 2003). Demographic rates are the critical connection between population dynamics and food web structure and productivity. Here, I tested for effects of kelp-carbon content and trophic level on daily growth rates of juvenile rockfishes. I predicted that growth rates should increase at higher kelp-carbon contents and higher trophic positions.

4.3 Methods

4.3.1 Study system

This research was conducted on the west coast of Vancouver Island, British Columbia, Canada (Fig. 4.1). This complex coastline spans approximately 470 km between 48° 18' N / 123° 32' W and 50° 48'N / 128 29' W, and is characterized by reef and island-studded sounds, inlets, and deep fjords. Historical records (Busch & Gough 1997), and modern estimates of habitat carrying capacity (Gregr et al. 2008), indicate that as many as 55,000 sea otters may have been harvested from British Columbia during the maritime fur trade. The last record of a sea otter being killed in British Columbia is from 1929 (Cowan & Guiguet 1960), and sea otters were extirpated until 89 Alaskan sea otters were reintroduced between 1969 and 1972 (Bigg & Macaskie 1978).

Subsequently, this population grew at ~15% year⁻¹ and by 2008 had increased to an estimated 4110 animals (Nichol et al. 2009). As in Alaska (Estes & Duggins 1995), range expansion of sea otters was followed by widespread transformation of rocky reef ecosystems to kelp forests (Morris et al. 1981, Breen et al. 1982, Watson 1993, Watson & Estes 2011). Where sea otters remain absent, abundant sea urchin populations maintain extensive urchin ‘barrens’ (Harrold & Pearse 1987) devoid of fleshy macroalgae.

The current research focuses on the habitat and productivity formed by the ‘giant’ kelp *Macrocystis pyrifera* (hereafter “*Macrocystis*”). In this region *Macrocystis* is found largely on hard bottoms in areas of moderate wave exposure, typically on the leeward side of outer coast islands, bays, and headlands. The kelp *Nereocystis luetkeana* seasonally also forms extensive forests in this region, generally in areas of higher wave exposure and less stable substrata compared to *Macrocystis*. Understory kelps here include *Pterygophora californica*, *Eisenia aborea*, and *Laminaria setchellii*.

This research focuses primarily on two species of nearshore kelp-associated Pacific rockfishes: black rockfish (*Sebastodes melanops*) and copper rockfish (*S. caurinus*). Black rockfish range from southern California to the western Aleutian Islands, and are most common to depths less than 55 m (Love et al. 2002). After a pelagic duration of approximately 80 days (Chapter 3), the young settle into shallow vegetated habitats; macroalgae on rocky reefs and seagrasses in shallow embayments (Love et al. 1991). Both juveniles and adults form aggregations in the water column

above rocky reefs. Copper rockfish range from central California to the northern Gulf of Alaska, and are most commonly found to depths of approximately 0-90 m (Love et al. 2002). After a pelagic duration of approximately 55 days (Chapter 3), the young settle into shallow macroalgal habitats on rocky reefs (Love et al. 1991). Juveniles and adults are solitary and demersal and have strong affinity for rocky habitat.

4.3.2 Experimental design

To investigate the effects of sea otter reintroduction on rockfish population and trophic dynamics I employed a ‘space-for-time-substitution’ approach (Pickett 1989), taking advantage of the natural experiment created by sea otter reintroduction and range expansion on the west coast of Vancouver Island. I delineated ‘otter-present’ (Kyuquot Sound to Nuchatlitz Inlet) and ‘otter-absent’ (Barkley Sound) regions that were separated by approximately 145 km. Within regions I randomly selected four sites that encompassed outer coast areas with *Macrocystis* forests representative of each region. Sites within regions were separated by approximately 2-15 km, and each site covered approximately 2 km of coastline. Within each site I established six permanent sampling locations by selecting *Macrocystis* forests that were the largest in each site and separated from adjacent forests by at least 250 m. All field sampling was conducted between May and August 2006.

Regional-comparative approaches like the one I employed in this investigation are necessary for studying ecological processes at large spatial scales, but unavoidably suffer from the inability to statistically infer cause-and-effect relationships as a result of spatial and temporal pseudoreplication (Hurlbert 1984, Hargrove & Pickering 1992). In this study, because sites with and without otters were not interspersed, the factor “otters” (present-absent) was spatially confounded. I acknowledge this limitation, and make the following points concerning similarities and differences between these regions with respect to factors that may contribute to differences in *Macrocystis* forest size or rockfish trophic dynamics: 1) the spatial extent of rocky habitat is similar or greater in the otter-absent region, and unlikely to constrain *Macrocystis* forest size; 2) exposure to ocean swell is equivalent or slightly lower in the otter-absent region, and also unlikely to drive differences in *Macrocystis* forest size; and 3) recreational fishing pressure is higher in the otter-absent region, and adult rockfish populations are presumed to be smaller but

were not quantified in this study. Finally, I emphasize that the 23-year investigation of Watson and Estes (2011), conducted in the same study regions, closely documented the transition of rocky reef habitats from urchin-dominated to kelp-dominated following sea otter range expansion.

4.3.3 Urchin density, kelp forest size, and rockfish recruitment

At each location I measured sea urchin (*Strongylocentrotus franciscanus*) densities, *Macrocystis* forest depth (m) and surface area (ha), and rockfish recruitment intensity. Urchin densities were estimated by counting all urchins within 50 x 50 cm quadrats placed at 10 random points along the seaward edge of each *Macrocystis* forest. I measured the depths to which *Macrocystis* forests extend into the subtidal (hereafter ‘perimeter depth’) using a digital depth sounder and by slowly maneuvering a small boat around the perimeter of each forest. Depths were recorded approximately every three meters and were converted to values below Canadian chart datum (mean lowest low tide). I measured *Macrocystis* forest surface areas using a hand-held GPS unit with an area calculator function, or in the case of very small forests where GPS-based estimates became unreliable, a 100 m tape. I tested for effects of sea otters on *Macrocystis* forest depth and surface area using REML-based linear mixed effects models (lme in R package ‘nlme’), using Otters (presence/absence) as a fixed effect nested within Site, and Site as a random effect. I assessed rockfish recruitment rates in two ways. I deployed Standard Monitoring Units for the Recruitment of Fish (SMURFs; Ammann 2004) at the seaward edge of each *Macrocystis* forest moored horizontally 1.5 meters below the surface, and anchored using a 20 liter plastic bucket filled with cement. I used a Benthic Ichthyofaunal Net for Coral and Kelp Environments (BINCKE; Anderson & Carr 1998) to collect all fish occupying SMURFs every 28 days from May through August. All fish collected were euthanized in the field, immediately stored on ice, and later identified, weighed, measured (total length, TL). Fish were stored frozen prior to isotope and growth analyses. I also visually estimated juvenile rockfish densities on each sampling date by using snorkeling equipment to survey an area of *Macrocystis* forests approximately 10 x 10 m. I estimated of the abundance of juvenile rockfish occupying each *Macrocystis* forest by scaling up

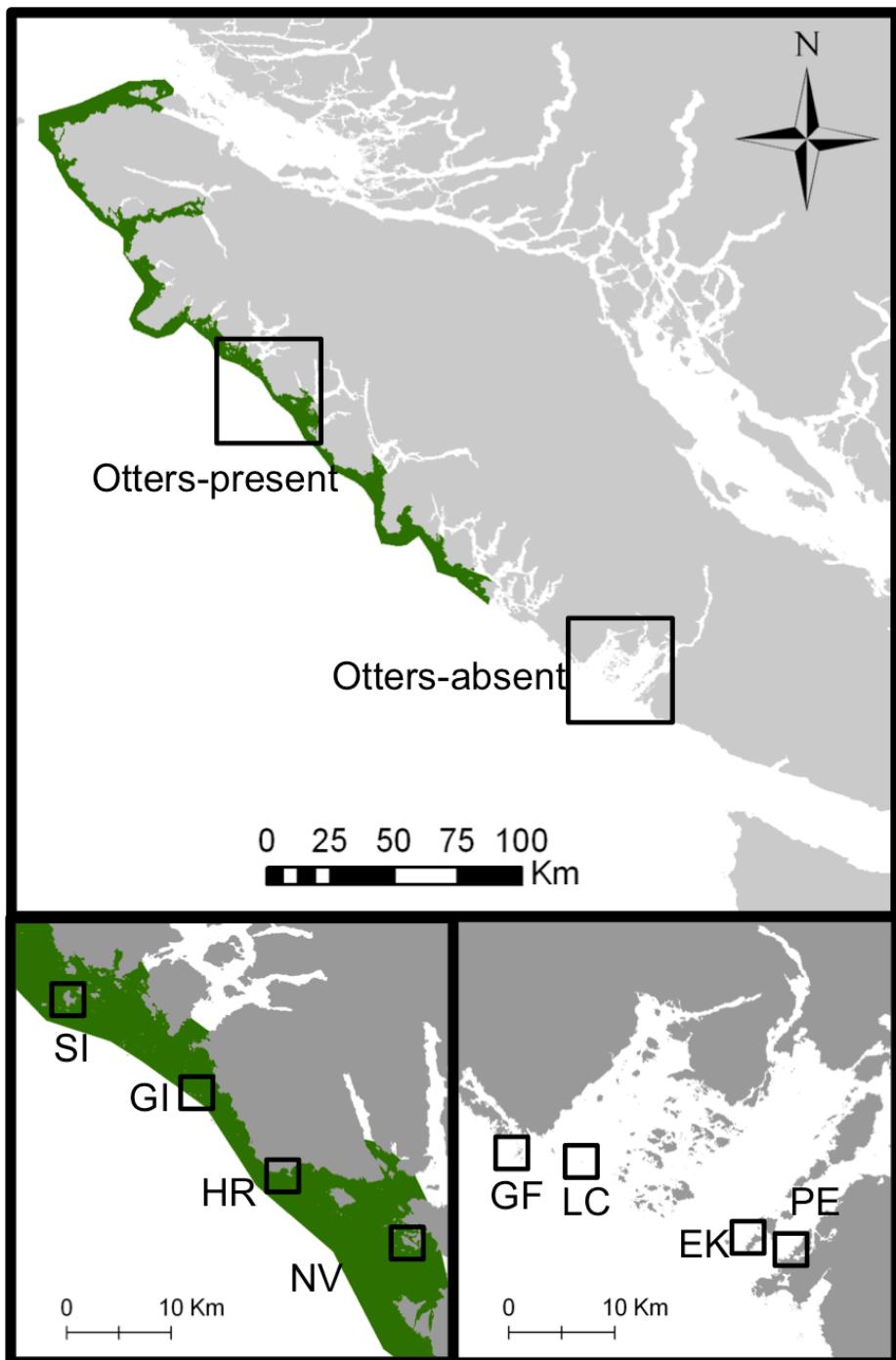


Figure 4.1. Otters-present and otters-absent regions along the west coast of Vancouver Island.

Green shading indicates current distribution of sea otter population (Nichol et al. 2009).

Boxes indicate sites nested within each region.

visual estimates of juvenile rockfish density (#/100 m²) to corresponding kelp forest areas (#/kelp forest). I tested for the effect of Region on both measures of recruitment by constructing general linear models with Poisson error distributions and log-link functions (glm in R package ‘stats’).

Methods for using otolith microstructure analysis to determine birth and settlement dates, and pelagic duration, and pre- and post-settlement growth are described for Chapter 3. I compared pre-settlement growth (5-60 days post-parturition) and post-settlement growth (days 5-70 post-settlement) between regions with and without otters. I used the Modified-Fry back-calculation model to estimate daily length-at-age for the same time periods (Vigliola et al. 2000, Wilson et al. 2009).

4.3.4 Adult and juvenile rockfish kelp-carbon content and trophic position

I collected approximately 25 adult black and copper rockfishes at the periphery of *Macrocystis* forests throughout each region using hook-and-line techniques. All fish were weighed (kg) and measured (total length, cm), and I collected dorsal muscle tissue samples for stable isotope analysis. I selected juvenile black rockfish for isotopic analysis by sub-sampling the total population of fish collected. I ensured replication across all body sizes by pooling collections within region and randomly selecting approximately 30 individuals from within each of the following size classes: <40, 40-50, 50-60, 60-70, 70-80, >80 mm.

I used naturally occurring stable carbon and nitrogen isotope ratios to compare population mean and variance of kelp-derived carbon contents and trophic positions of adult and juvenile rockfish from kelp forest habitats with and without sea otters. Stable carbon isotope ratios (¹³C/¹²C) vary among primary producers that use different photosynthetic pathways (i.e. macroalgae vs. phytoplankton and C3 vs. C4 plants), but change little during trophic transfers, and therefore can be used to determine ultimate sources of dietary carbon (Peterson & Fry 1987). In contrast, stable nitrogen isotopes ratios (¹⁵N/¹⁴N) exhibit predictable rates of enrichment with trophic transfers, and therefore can be used to estimate consumer trophic positions (Post 2002).

Stable isotope ratios are reported in the standard delta (δ) notation, where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ([R_{\text{sample}} / R_{\text{standard}}] - 1) \times 1000$, and $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Peterson & Fry 1987). I used the following simple two-source mixing model (Eq. 1) to estimate the relative contributions of

phytoplankton- vs. kelp-derived carbon (Mcconaughey & Mcroy 1979, Bustamante & Branch 1996):

$$\%C_{kelp-derived} = \frac{(\delta^{13}\text{C}_{consumer} - \delta^{13}\text{C}_{phytoplankton} - I)}{(\delta^{13}\text{C}_{kelp} - \delta^{13}\text{C}_{phytoplankton})} \times 100 \quad (\text{Eq. I})$$

where I is the average post-photosynthetic fractionation of $\delta^{13}\text{C}$ per trophic level. Based on the review of Post (2002) I used $I = 0.5$. To represent the kelp carbon signatures (Eq. I) I used mean *Macrocystis* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each region. To test whether fresh and decaying *Macrocystis* tissues differ in $\delta^{13}\text{C}$ values I collected two *Macrocystis* tissue types at each location: ‘fresh’ (blades dark in colour, firm and not decaying) and ‘decaying’ (tattered, pale, and senescent in appearance; collected from the distal ends of blades).

In contrast to kelp tissue, samples of naturally occurring phytoplankton are difficult to isolate because seawater samples contain mixtures of micro-zooplankton and suspended particulate detritus in addition to phytoplankton. For this reason, particulate organic matters (POM) samples collected offshore (i.e. with low probability of containing particulate marine benthic or terrestrial carbon sources) are typically used to represent phytoplankton isotopic signatures (Kaehler et al. 2000, Fredriksen 2003, Hill et al. 2006). To test whether POM samples collected inside and outside of kelp forests differ, I collected two types of POM samples: ‘in-kelp’ (collected within *Macrocystis* forests) and ‘out-kelp’ (collected 100-250m seaward of each forest). I obtained POM samples by filtering 1.0 liter of surface seawater through a 54 μm sieve onto pre-weighed 45 mm 1.2 μm Whatman GF/C filters. To represent phytoplankton isotopic signatures in calculation of kelp-carbon content and trophic level I used the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the 5% most carbon-depleted POM samples (regions and types combined). I tested for effects of State (‘fresh’ vs. ‘decaying’ kelp) and Location (‘in-kelp’ vs. ‘out-kelp’ POM) and Otters (presence/absence) on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Macrocystis* and POM, respectively, using State, Location, Otters, and their interaction as fixed effects nested within the random effect Site.

I calculated trophic positions of adult and juvenile rockfishes using the model developed by Post (2002):

$$TL = 1 + (\delta^{15}\text{N}_{sc} - [\delta^{15}\text{N}_{base1} \times \alpha + \delta^{15}\text{N}_{base2} \times (1-\alpha)]) / \Delta n \quad (\text{Eq. 2})$$

where TL is the trophic level of the consumer, $\delta^{15}\text{N}_{sc}$ is the $\delta^{15}\text{N}$ value of the secondary consumer (i.e. rockfish), $\delta^{15}\text{N}_{base1}$ is the average $\delta^{15}\text{N}$ of POM (i.e. as a proxy for phytoplankton signatures), $\delta^{15}\text{N}_{base2}$ is the average $\delta^{15}\text{N}$ value of *Macrocystis* (i.e. as proxy for kelp signatures), and Δ_n is the enrichment value of $\delta^{15}\text{N}$ per trophic level. Post (2002) reviewed 56 estimates of $\delta^{15}\text{N}$ from previous studies, and calculated a mean value of enrichment per trophic level of $\Delta_n = 3.4\text{‰}$; I used this value in the current study. The parameter α is the proportion of nitrogen in the consumer ultimately derived from the primary producers of each food web (Post 2002). This value is estimated using carbon isotopes (assuming that nitrogen moves through food web similarly to carbon) using Equation 3:

$$\alpha = \frac{(\delta^{13}\text{C}_{sc} - \delta^{13}\text{C}_{base2})}{(\delta^{13}\text{C}_{base1} - \delta^{13}\text{C}_{base2})} \quad (\text{Eq. 3})$$

Finally, to assess kelp-carbon contents of benthic invertebrates common to these kelp forest food webs and the trophic pathways by which kelp-carbon reaches higher rockfishes, I opportunistically collected various kelp-associated crustaceans (decapod crabs, amphipods, isopods, and shrimp) as well as a common gastropod (*Tegula pulligo*) and California mussels (*Mytilus californianus*). All tissue samples collected for isotope analyses were rinsed with de-ionized water and dried at 50°C for 48 hrs before being ground into a fine powder using a digital Touchpad Amalgamator (Henry Schien Inc). Samples were not acid-fumed or lipid extracted. All analyses were performed at the University of California-Davis Stable Isotope Facility using an elemental analyzer and a continuous flow isotope ratio mass spectrometer (IRMS).

4.3.5 Analyses of effects of kelp-carbon and trophic level

I performed all statistical and graphical analyses using R (R Core Development Team 2011). I tested for an effect of Region (otters-present or absent) on kelp-carbon content and trophic level

of adult rockfishes using Welch's two-sample *t*-test. I used *F* tests to test for homogeneity of variances and quantile-quantile plots to check for normal distribution of residual errors. I tested for regional differences in ontogenetic relationships (i.e. slope) between adult and juvenile rockfish between body size (length), kelp-carbon content, and trophic level by using analysis of covariance (ANCOVA).

I refer to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space in which species are plotted as 'niche space' (Bearhop et al. 2004) and used convex hull area (i.e. the minimum adequate polygon) to quantify and compare the trophic niche space occupied by all individuals in 2-dimensional isotopic space (Cornwell et al. 2006). This represents a measure of the total niche space occupied by a species and therefore serves as proxy for the total extent of trophic diversity among individuals in a given habitat type (Layman et al. 2007). I compared adult rockfish trophic niche space by plotting trophic positions against kelp-carbon content and using R functions 'chull' and 'polygon' (R package 'grDevices') to find and plot convex hull areas. I tested for regional differences in convex hull area ('convhulln' in R package 'geometry') by jackknifing trophic level~kelp-carbon matrices and comparing the resulting distributions using Welch's two-sample *t*-test.

I examined relationships between juvenile black rockfish body condition (Fulton's condition factor; Blackwell et al. 2000), kelp-carbon content and trophic level using linear, polynomial, and partial regression. I tested the effects of kelp-carbon content and trophic level on juvenile black rockfish growth rates by pairing these isotopically derived measures with measures of individual growth derived from otolith microstructure analysis. Methods for quantifying juvenile rockfish pre- and post-settlement growth are described for Chapter 2. For the purposes of this study I defined individual growth rate as the average width of daily growth increments from parturition to capture ($\mu\text{m}/\text{day}$). Because rockfish were only piscivorous in the otter-absent region (see Results), I tested for the effects of body size (length), kelp-carbon content, and trophic level on juvenile black rockfish growth rates within regions only. I used linear models (lm in R package 'stats') to test for the random effects of Length, Kelp, Trophic level, and their interactions, on juvenile black rockfish growth rates.

4.4 Results

4.4.1 Urchin density and kelp forest depth and surface area

In the absence of sea otters, sea urchin (*Strongylocentrotus franciscanus*) densities at the periphery of *Macrocystis* forests were high ($16.2 \pm 1.72 / m^2$ [mean \pm SE], $n = 22$), but in the presence of sea otters sea urchins were absent (Fig. 4.2a). Correspondingly, absence of sea otters and high sea urchin densities were associated with shallower ($F_{1,6} = 17.77$, $P = 0.0056$) *Macrocystis* forest perimeter depths (1.51 ± 0.15 m, $n = 22$), compared to areas where otters were present and perimeter depths were on average 3.7 times deeper (5.58 ± 0.35 m, $n = 21$) (Fig. 4.2b). *Macrocystis* forest surface areas on average were 18.8 times larger ($F_{1,6} = 101.61$, $P < 0.0001$) in the presence of otters ($11,290.72 \pm 1701.46$ m 2) than in the absence of otters (599.44 ± 100.23 m 2) (Fig. 4.2c).

4.4.2 Rockfish population replenishment

I limited analysis of the effects of sea otters on rockfish recruitment intensity to black rockfish (*Sebastodes melanops*) because in 2006 these species were abundant throughout both regions, whereas “CQB complex” rockfishes (*S. caurinus*, *S. maliger*, and *S. auriculatus*) were rare (Chapters 2 and 3). During visual surveys I observed low numbers of juvenile yellowtail rockfish (*S. flavidus*) in association with juvenile black rockfish. Because of the difficulty of distinguishing these species during visual surveys I included these with counts of black rockfish. I detected a significant effect of otters on rockfish recruitment using visual surveys (no. rockfish/100 m 2 ; Deviance $_{1,42} = 4.7233$, $P = 0.00023$) (Fig. 4.3b) but not using SMURFs (no. rockfish/SMURF; Deviance $_{1,46} = 0.00012$, $P = 0.9914$) (Fig. 4.3a). Scaled-up visual estimates of rockfish density (rockfish/100 m 2) to corresponding *Macrocystis* forest areas (i.e. recruit abundance) were on average 46 times higher (Fig. 4.3c) in the otter-present region ($30,859 \pm 6,439$ rockfish / forest, $n = 21$) than in the otter-absent region (668 ± 186 rockfish / forest, $n = 24$) as a result of both higher rockfish densities and larger kelp forest areas in the otter-present region.

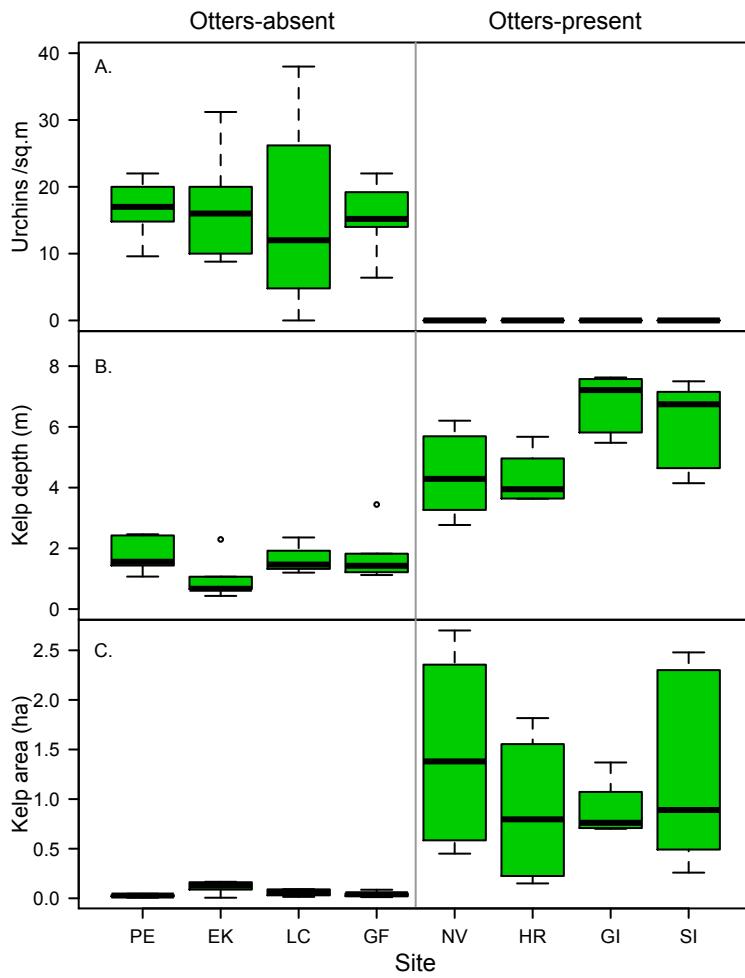


Figure 4.2. Box plots comparing (A) urchin densities; (B) *Macrocystis* forest perimeter depth; and, (C) *Macrocystis* forest surface area, between sites within regions with and without sea otters. *Macrocystis* forests were 3.7 times deeper ($F_{1,6} = 17.77, P = 0.0056$) and 18.8 times larger ($F_{1,6} = 101.61, P < 0.0001$) in the otter-present region.

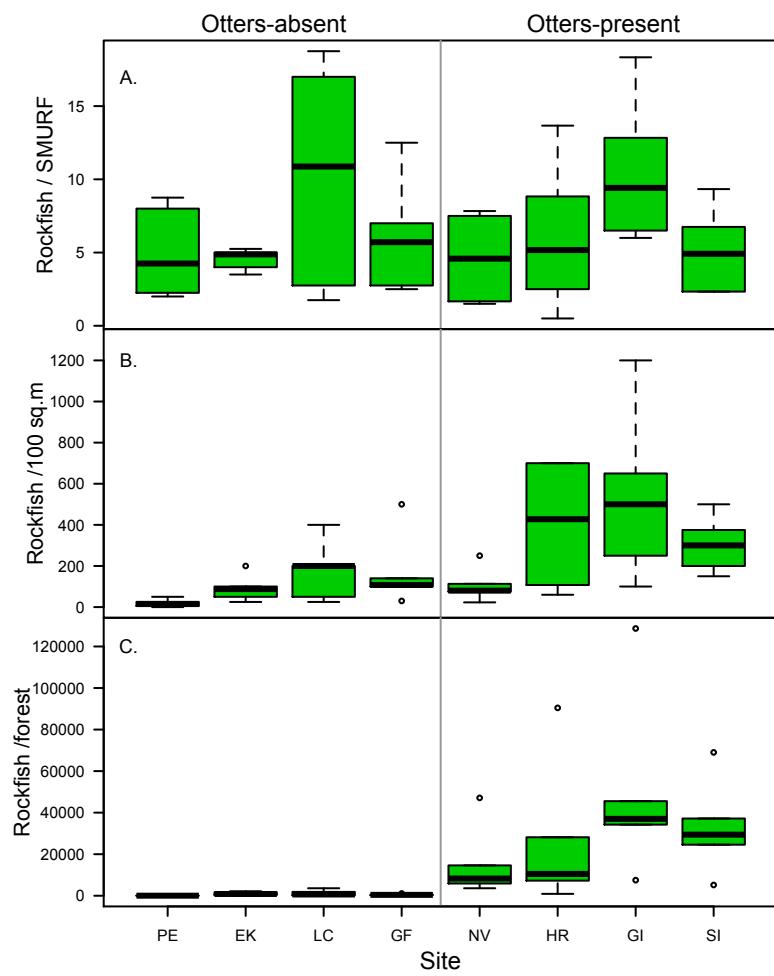


Figure 4.3. Box plots comparing (A) numbers of juvenile black rockfish per SMURF; (B) numbers of juvenile black rockfish per 100 m² of *Macrocystis* forest; and, (C) scaled-up estimates of juvenile black rockfish total abundance per *Macrocystis* forest, between sites within regions with and without sea otters. Juvenile densities were higher ($\text{Deviance}_{1,42} = 4.7233, P = 0.00023$) in the otter-present region, but numbers/SMURF were not ($\text{Deviance}_{1,46} = 0.00012, P = 0.9914$). The factor 'site' (random) was not included in general linear models fit with Poisson errors.

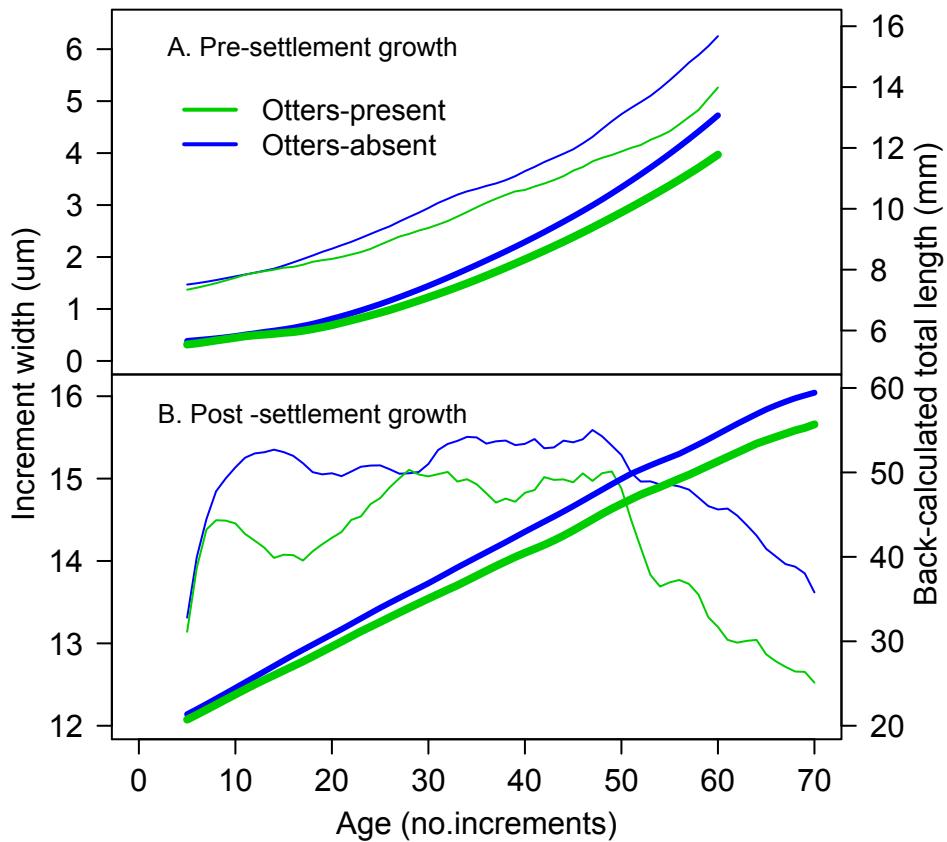


Figure 4.4. Comparison of (A) pre-settlement and (B) post-settlement growth rates of juvenile black rockfish between regions with and without sea otters. Thin lines indicate relationships between otolith-derived mean daily growth increment width and age, and thick lines indicate relationships between back-calculated (Modified-Fry model) total length at age.

Birth dates did not differ between regions ($t = 0.90, P = 0.3688$) with otters (21-Feb ± 1.58 d [mean \pm se], $n = 40$) and without otters (19-Feb ± 1.30 d, $n = 72$). Mean settlement dates were five days later ($t = 1.9755, P = 0.0518$) in the otter-present region (12-May ± 2.15 d, $n = 40$) than in the otter-absent region (7-May ± 1.52 d, $n = 72$). Pelagic durations did not differ between regions ($t = 1.5993, P = 0.1123$): otters-present (81 ± 1.7 d, $n = 72$) and otters-absent (77 ± 1.30 d, $n = 72$). Both pre- and post-settlement growth rates of juvenile black rockfish were slower in the otter-present region (Fig. 4.4).

4.4.3 Isotopic baselines

There was no effect of Otters ($F_{1,6} = 0.567, P = 0.48$) or State ($F_{1,6} = 0.02, P = 0.892$) on *Macrocystis* $\delta^{13}\text{C}$ values, therefore I pooled both ‘fresh’ and ‘decaying’ samples types. The mean *Macrocystis* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each region were: otters-present ($\delta^{13}\text{C} = -14.82 \pm 0.21$ and $\delta^{15}\text{N} = 6.53 \pm 0.27, n = 44$) and otters-absent ($\delta^{13}\text{C} = -14.41 \pm 0.33$, and $\delta^{15}\text{N} = 6.07 \pm 0.20, n = 45$) (Fig. 4.5).

There was no effect of Otters ($F_{1,6} = 2.924, P = 0.138$) or Location ($F_{1,6} = 0.994, P = 0.357$) on POM $\delta^{13}\text{C}$ values, therefore I averaged across ‘in-kelp’ and ‘out-kelp’ sample types. The mean POM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each region were: otters-present ($\delta^{13}\text{C} = -20.27 \pm 0.91$ and $\delta^{15}\text{N} = 6.93 \pm 0.93, n = 44$) and otters-absent ($\delta^{13}\text{C} = -19.60 \pm 0.53$, and $\delta^{15}\text{N}, 6.50 \pm 0.91, n = 43$). The average of the 5% most carbon-depleted POM samples used in mixing models were $\delta^{13}\text{C}$ (-22.93 $\pm 0.4, n = 4$) and $\delta^{15}\text{N}$ ($8.36 \pm 1.37, n = 4$) (Fig. 4.5).

4.4.4 Adult rockfish niche shifts and niche space

Kelp-carbon contents of adult black and copper rockfishes did not differ between regions with and without otters (Table 4.1; Fig. 4.6). In both regions % kelp-derived carbon ranged between approximately 60-70%. However, black and copper rockfishes in the otter-present region had significantly higher trophic levels than in the otter-absent region, indicating higher proportions of higher trophic level prey in the diets of these consumers (Table 4.1; Fig. 4.6). The convex hull area (i.e. trophic niche space) of adult black rockfish from the otter-present region was significantly ($W = 552, P < 0.0001$) higher ($41.09 \pm 2.34, n = 24$) than that of the otter-absent region ($32.22 \pm 1.56, n = 24$) (Fig. 4.6a). The convex hulls area of adult copper rockfish from the otter-present region was significantly ($W = 26, P < 0.0001$) smaller ($29.71 \pm 0.70, n = 26$) than from the otter-absent region ($33.44 \pm 1.7, n = 24$) (Fig. 4.6b).

I found strong evidence of ontogenetic niche shifts by adult black and copper rockfishes. There was no relationship between adult black rockfish body size and kelp-derived carbon content in either region (Fig. 4.7a); however, in the otter-present region trophic position increased significantly with increasing body size (Fig. 4.7c). I found significant but opposite relationships between copper rockfish body size and kelp-derived carbon content.

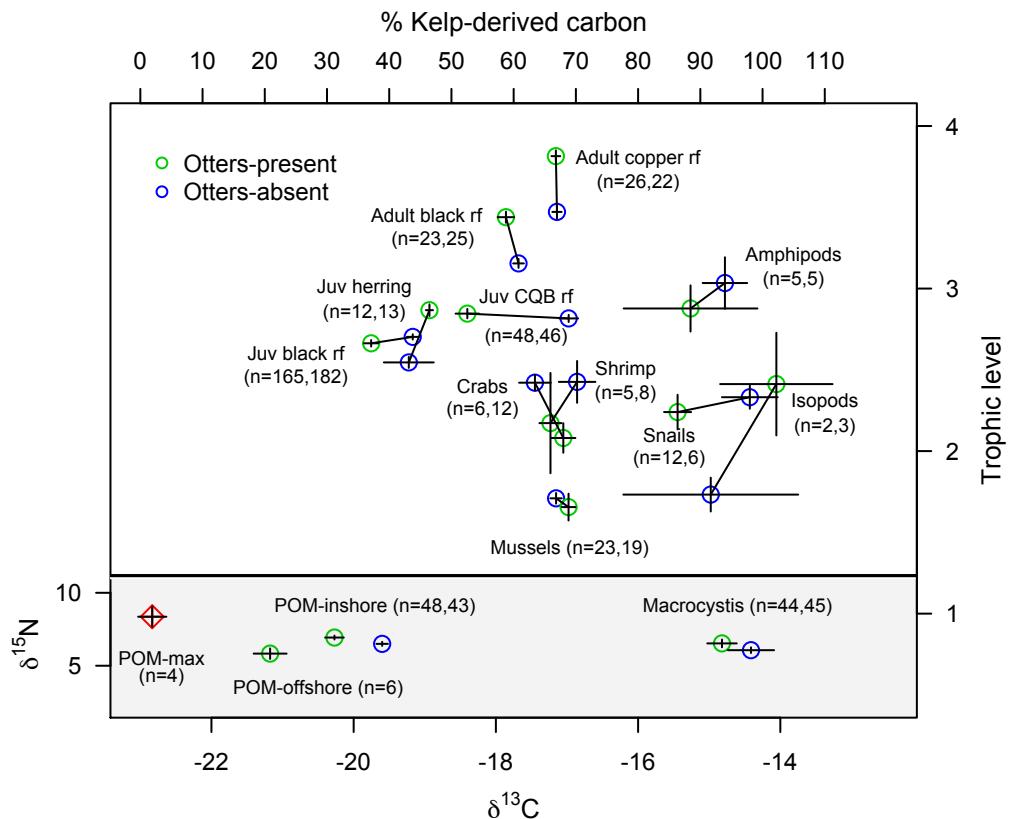


Figure 4.5. Between-region comparison of mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers (trophic level 1) illustrated in the shaded area. Upper plot shows between-region comparison of mean (\pm SE) % kelp-derived carbon vs. mean (\pm SE) trophic level of invertebrates and fish (“rf”=rockfish; and “pom-max” refers to the POM values used to calculate % kelp-derived carbon and trophic position).

In the otter-absent region, kelp-derived carbon content increased with increasing length, whereas in the otter-present region the largest individuals had the lowest kelp-carbon contents (Fig. 4.7b). In the otter-absent region copper rockfish trophic level increased with body size, whereas in the otter-present region all individuals had generally high trophic levels regardless of body size (Fig. 4.7d).

Table 4.1. Results from t-tests comparing mean % kelp-derived carbon (A) and trophic levels (B) of adult and juvenile rockfish from otters-present and otters-absent regions.

A. % Kelp-derived carbon						
Group/status	Otters-present		Otters-absent		<i>T</i>	<i>P</i>
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>		
Adult black rockfish	60.0 ± 0.86	24	61.33 ± 0.78	24	1.1434	0.2588
Adult copper rockfish	65.61 ± 0.76	26	67.11 ± 0.71	24	1.4386	0.1568
Juvenile black rockfish	40.53 ± 1.24	134	46.32 ± 0.88	157	3.792	0.0002
Juvenile CQB rockfish	51.85 ± 1.52	43	68.84 ± 1.52	46	7.9047	<0.0001

B. Trophic Level						
	Otters-present		Otters-absent		<i>T</i>	<i>P</i>
	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>		
Adult black rockfish	3.44 ± 0.03	24	3.14 ± 0.03	24	7.07	<0.0001
Adult copper rockfish	3.72 ± 0.05	26	3.38 ± 0.03	24	5.731	<0.0001
Juvenile black rockfish	2.63 ± 0.022	134	2.67 ± 0.015	157	1.3276	0.1855
Juvenile CQB rockfish	2.82 ± 0.025	43	2.82 ± 0.022	46	0.104	0.9174

4.4.5 Juvenile rockfish ontogenetic niche shifts

Juvenile black and CQB rockfishes demonstrated strong ontogenetic niche shifts. Early post-settlement juvenile black rockfish collected in early June (~35-50 mm TL) had generally low kelp-carbon contents (~10-20%) and low trophic positions (~2.1-2.4), reflecting predominance of phytoplankton-derived carbon sources during pelagic larval and juvenile stages (Fig. 4.8a). By early August most individuals had grown to ~70-85 mm TL, and had relatively high kelp-carbon contents (~45-65%) and high trophic levels of (~2.6-3.2) (Fig. 4.8c). The relationship between juvenile black rockfish body size and kelp-carbon content was asymptotic, with the largest individuals in the otter-absent region demonstrating a distinct decrease in kelp-carbon that corresponded to onset of consumption of juvenile Pacific herring that was not observed in the otter-present region. Trophic positions increased asymptotically with body size in the otter-absent region, and linearly in the otter-present region, with a small number of individuals feeding above trophic level 3.0.

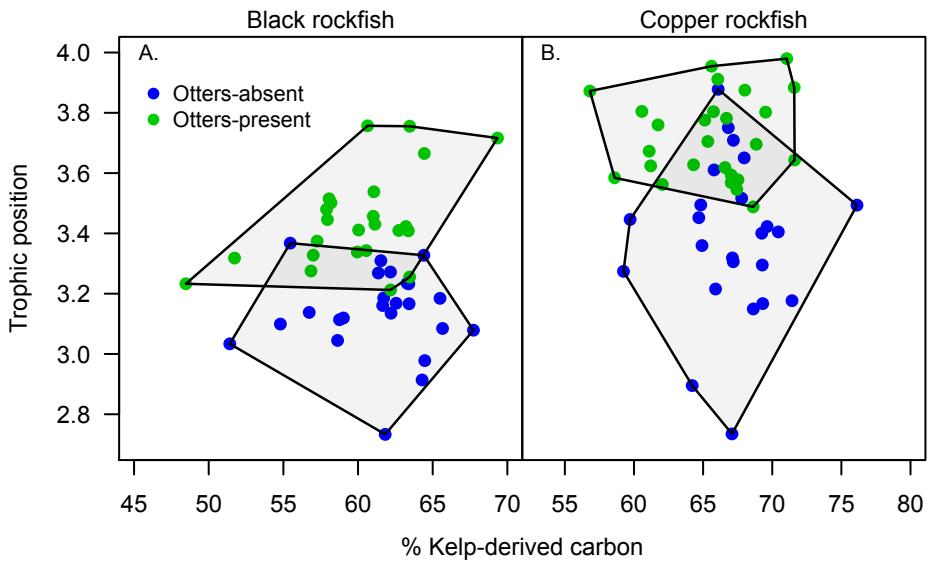


Figure 4.6. Comparison of trophic niche space (convex hull area) of adult black (A) and adult copper (B) rockfish between regions with and without sea otters.

Early post-settlement CQB complex rockfishes from the otter-present and otter-absent region differed markedly in kelp-carbon contents and trophic levels (Fig. 4.8b), because of large differences in body size distributions (otter-present, 28.9 ± 0.7 mm, $n = 43$; otters-absent, 53.3 ± 0.2 mm, $n = 46$, $T_{1,98} = 13.57$, $P < 0.0001$). By pooling individuals across regions (and excluding three distinct outliers) I found that CQB rockfish kelp-carbon content increased significantly with increasing body size, but trophic position did not (Fig. 4.8d).

4.4.6 Juvenile rockfish condition and growth

I detected strong relationships between juvenile black rockfish body condition, individual growth rates, kelp-derived carbon content, and trophic level. In the otter-present region juveniles demonstrated a significant U-shaped relationship between kelp-carbon content and Fulton's condition factor (Fig. 4.9a). Because kelp-carbon content increases with body size this

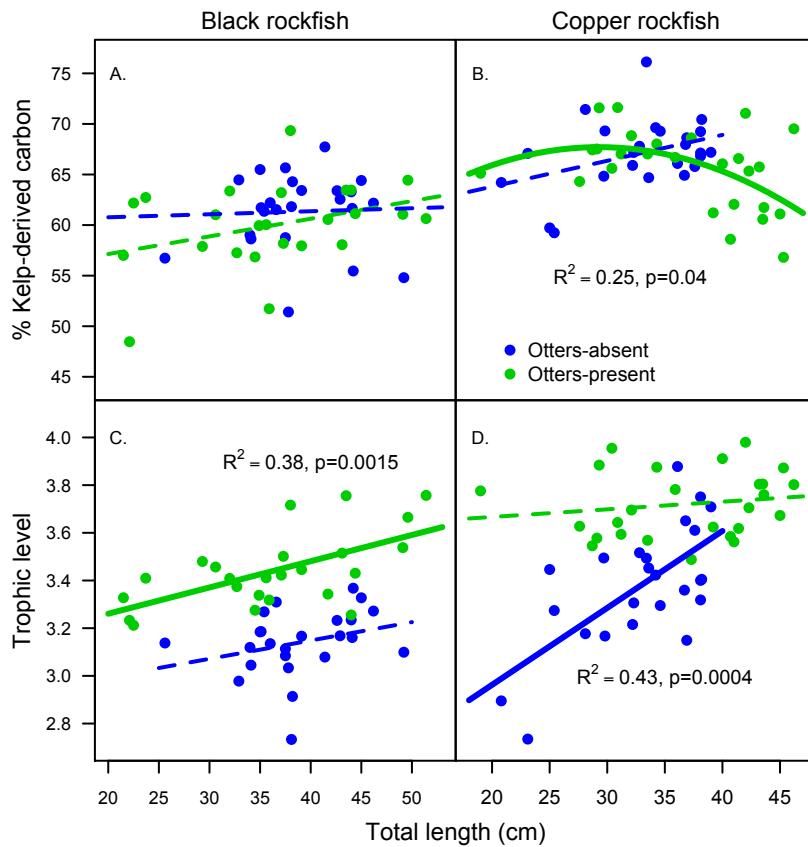


Figure 4.7. Comparison of the relationship between adult rockfish body size (total length in cm) and % kelp-derived carbon (A and B), and body size and trophic position (C and D), between regions with and without sea otters. Fitted lines indicated significant (solid) and insignificant (dashed) linear and polynomial regressions.

relationship reflects changes in both length-mass relationships (i.e. condition factor) and kelp-carbon content with increasing body size. In the otter-absent region, individuals followed a similar pattern until reaching ~65 mm TL (~50% kelp-carbon content) when an abrupt increase in condition factor and decrease in kelp-carbon content corresponded to the onset of consuming juvenile Pacific herring. Relationships between trophic position and condition factor mirrored these patterns: condition factor increased with trophic level (and therefore body size) in both regions until individuals in the otter-absent region rapidly increased in condition factor, corresponding to increasing trophic level, and decreasing kelp-carbon content, associated with consumption of juvenile Pacific herring (Fig. 4.9b).

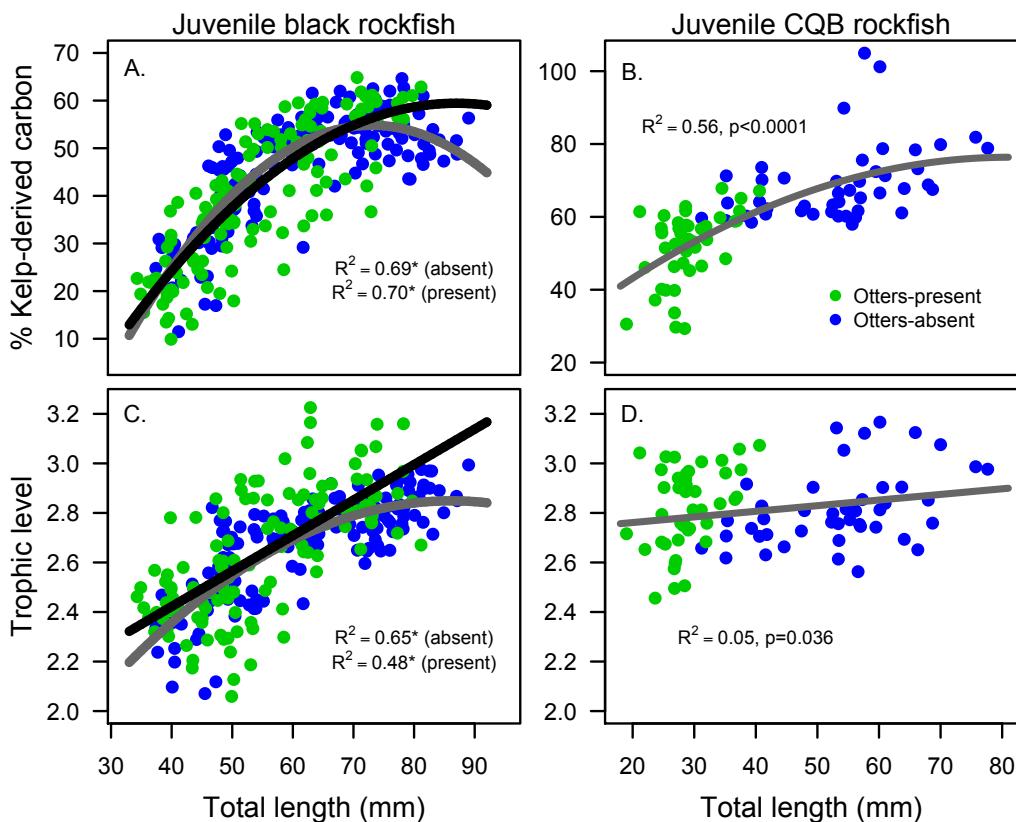


Figure 4.8. Comparison of the relationship between juvenile rockfish body size (total length in mm) and % kelp-derived carbon (A and B) and body size and trophic position (C and D) between regions with and without sea otters. Fitted lines indicated significant linear and polynomial regressions for juvenile black rockfish (black = otters-present; gray = otters-absent) and CQB rockfish (gray = regions combined).

Because the shift to piscivory occurred only in the otter-absent region, and higher pre- and post-settlement growth rates in the otter-absent region indicated possible regional differences in ocean temperature (Fig. 4.4), I tested for within-region effects of body size, kelp-carbon and trophic level on juvenile black rockfish daily growth rates. Variation in growth was driven primarily by changes in body size, and the importance of kelp-carbon content and trophic level differed between regions (Fig. 4.10). In the otter-present region (piscivory-absent) growth rates were driven primarily by differences in body length, but I found a significant interaction between body length and kelp-carbon content. There was no effect of trophic level on juvenile growth rates in the otter-present region. In contrast, in the otter-absent region (piscivory-present) I

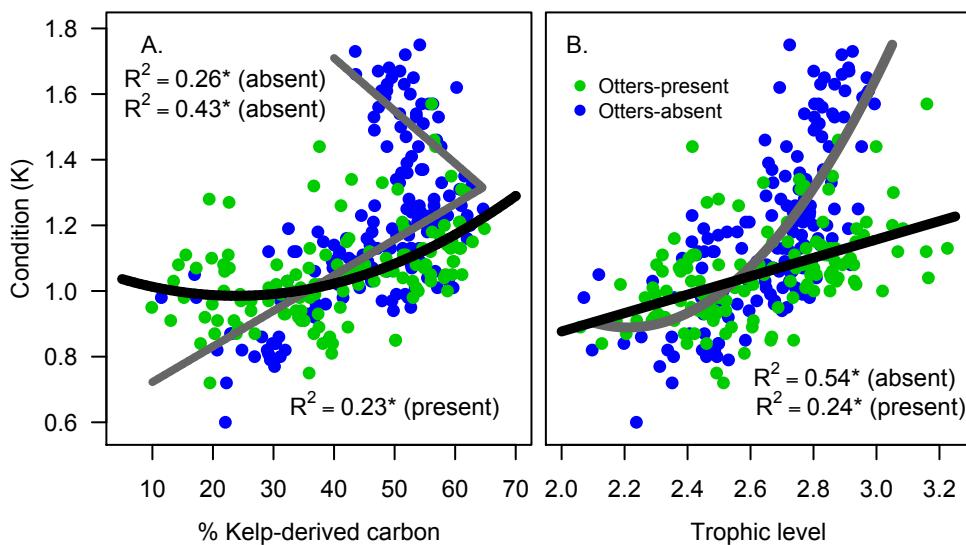


Figure 4.9. Comparison of the relationship between body condition (Fulton's condition factor) of juvenile black rockfish and % kelp-derived carbon (A) and trophic level (B) between regions with and without sea otters. Fitted lines indicated significant linear, partial, and polynomial regressions for the otter-present (black) and otter-absent (gray) regions.

found significant main effects of length and trophic level, as well as significant length*trophic level and length*kelp-carbon interactions (Table 4.2).

4.5 Discussion

4.5.1 Effects of sea otters on kelp forest size

The indirect effects of sea otters on *Macrocystis* forest depth and area were striking. Absence of sea otters was associated with high urchin densities and small *Macrocystis* forests often comprising only narrow sub-littoral fringes surrounded by extensive urchin barrens. In contrast, where sea otters were present, sea urchins were absent and *Macrocystis* forests extended 3.7 times deeper than in the otter-absent region. These results corroborate previous studies demonstrating strong negative effects of sea urchins on macroalgal populations through direct

manipulation (Duggins 1980), environmental catastrophe and disease (McLean 1962, Pearse & Hines 1979) and marine reserves that increase urchin predator populations (Salomon et al. 2008). In Barkley Sound, Pace (1981) found that kelp population densities increased and expanded downward in a single year following experimental removal of sea urchins. My results are also supported by the 23-year study of Watson and Estes (2011), conducted in the same study regions, showing that sea otter predation upon sea urchins maintains rocky reef ecosystems where urchins are rare and macroalgae populations are abundant.

In contrast, the effects of sea otters on the spatial extent of kelp forest habitat sizes have not been examined. As a consequence of maximum perimeter depths being 3.7 times deeper *Macrocystis* forest surface areas were on average 18.8 times larger in the otter-present region. Cumulatively, the *Macrocystis* forests sampled in this study occupied approximately 237,000 m² of seafloor in the otter-present region, compared to just 14,400 m² in the otter-absent region. The critical implication of these vast differences in area is that the structural habitat and productivity provided by *Macrocystis* forests are also ~18.8 times larger in the otter-present region. Although *Macrocystis* forests on the west coast of Vancouver Island are conspicuous for their large size and surface canopies, several understory kelp species are also abundant in this region, notably *Pterygophora californica* (Watson and Estes 2011), and these may contribute as much or more to ecosystem net primary productivity (NPP) as *Macrocystis* (Miller et al. 2011). Thus, landscape-level assessments of kelp-derived habitats and food webs are needed to understand more fully the effects of sea otter reintroduction on properties of nearshore ecosystems.

4.5.2 Effects of kelp forest size on rockfish recruitment

The high densities and abundance of juvenile black rockfish associated with large *Macrocystis* forests found in this study support the hypothesis that by increasing kelp abundance sea otters have positive indirect effects on recruitment of kelp-associated rockfish populations. Population sizes of marine organisms with pelagic larval stages may be determined by rates of larval supply and settlement, and processes determining post-settlement density-dependent and independent growth and survival (Doherty & Fowler 1994, Caley et al. 1996, Hixon et al. 2002). Previous studies have demonstrated strong effects of *Macrocystis* on temperate reef fish populations during

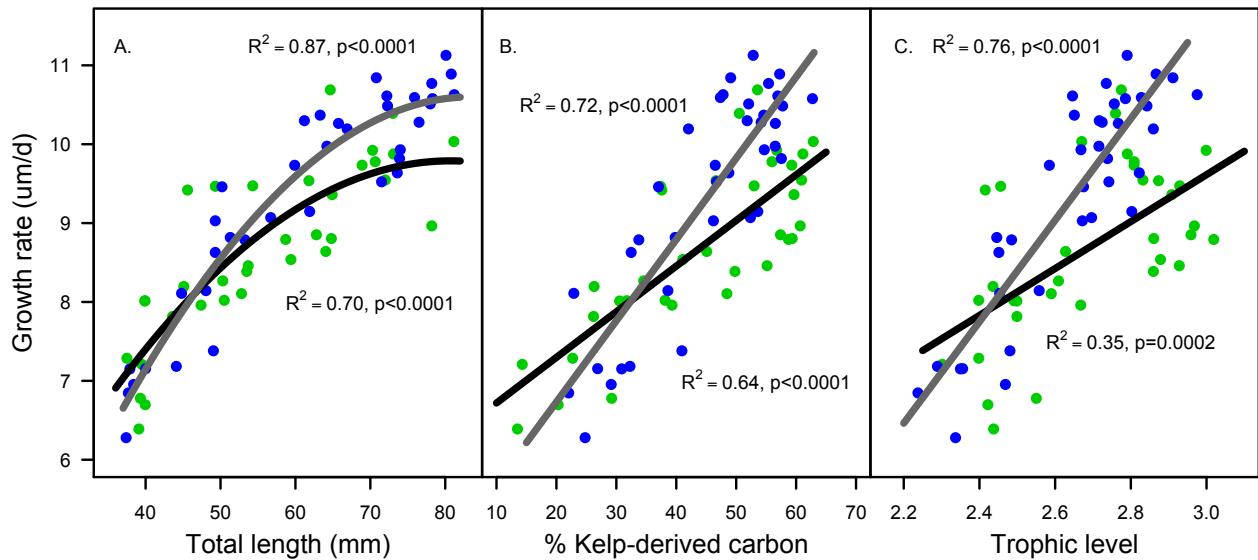


Figure 4.10. Comparisons of the effects of body size (A), % kelp-derived carbon (B), and trophic level (C) on daily growth rates of juvenile black rockfish between regions with (blue) and without (green) sea otters.

settlement and post-settlement life stages (Carr 1991, 1994, Johnson 2006, 2007, White & Caselle 2008, Deza & Anderson 2010). However, none have considered effects of changes in *Macrocystis* forest size driven by sea otter loss and reintroduction.

My findings that high rockfish recruitment is associated with large kelp forests surface areas support the seascape perspective of Carr and Syms (2006). These authors proposed that local recruitment intensities reflect encounter rates between habitats and larvae, and these are functions of the distribution and movement patterns of aggregations of larvae moving onshore or alongshore, and the size, shape, distribution, and orientation of settlement habitats. I found that birth and settlement dates, and pelagic durations, of juvenile black rockfish in the otter-present and absent regions were remarkably similar despite being separated by approximately 150 km. Although slower pre- and post-settlement growth rates in the otter-present region suggest that this region may experience cooler average ocean temperatures (Chapter 3), these early life history attributes indicate that pelagic juvenile black rockfish settling in both regions made similar

Table 4.2. Results from linear models testing the effects of body size (length in mm), % kelp-derived carbon, and trophic level on juvenile black rockfish growth (mean increment width) in regions with otters (A) and without otters (B).

A. Otters-present / Piscivory-absent					
	df	SS	MS	F	P
Length	1	0.3712	0.3712	89.3379	<0.0001*
Kelp-carbon	1	0.0107	0.0107	2.5836	0.1192
Trophic level	1	0.0118	0.0118	2.8392	0.10311
Length*Kelp-carbon	1	0.0230	0.0230	5.5434	0.0258*
Length*Trophic level	1	0.0086	0.0086	2.0580	0.16249
Residual error	28	0.1163	0.0042		

B. Otters-absent / Piscivory-present					
	df	SS	MS	F	P
Length	1	0.7912	0.7912	318.3332	<0.0001*
Kelp-carbon	1	0.0048	0.0048	1.9432	0.17324
Trophic level	1	0.0107	0.0107	4.2934	0.04667*
Length*Kelp-carbon	1	0.0102	0.0102	4.1115	0.05126*
Length*Trophic level	1	0.0105	0.0105	4.2357	0.04807*
Residual error	31	0.0771	0.0025		

ontogenetic movements from offshore pelagic environments to nearshore settlement habitats.

These results support the hypothesis that factors that increase encounter rates with settlement habitats (Chapter 1) are responsible for high recruitment rates in the otter-present region. *Macrocystis* forests more than an order-of-magnitude larger in the otter-present region may increase the ‘target size’ of settlement habitats and thereby increase rockfish settlement rates. A second effect of otter-driven differences in kelp forest size may be to attenuate alongshore-current velocities. Gaylord et al. (2007) found that *Macrocystis* forests in California needed to be more than ~100 m in length to significantly slow current velocities and increase particle residence times. Because none of the *Macrocystis* forests in the otter-absent region attain lengths of this kind, locally high current velocities over rocky reef habitats in the absence of sea otters may also reduce rockfish settlement rates.

By multiplying estimates of juvenile rockfish densities from visual surveys by areas of corresponding *Macrocystis* forests, I estimated the abundance of juvenile black rockfish occupying kelp forests to be 46 times higher on average in the otter-present region. This result highlights the importance of incorporating space into studies of population and food web dynamics (Polis et al. 1997, Massol et al. 2011). Although local-scale results may indicate factors driving post-settlement processes, these patterns may change when viewed at the scale of entire habitats or regions (White & Caselle 2008). The large differences in rockfish recruitment detected in my study strongly suggest that sea otter reintroduction may have important implications for patterns of black rockfish population connectivity and genetic diversity (Pulliam 1988, Palumbi 2003). High recruitment of juvenile rockfishes may also represent demographically significant trophic subsidies in local food webs (following sections).

4.5.3 Effects of sea otters on adult rockfish trophic niche space

Despite order-of-magnitude increases in kelp forest size and productivity associated with sea otter reintroduction, I found that adult rockfishes in areas with and without otters differed in terms of trophic position but not kelp-carbon content. Niche spaces of both rockfish species were centered around similar proportions of kelp-derived carbon in both regions (~50-75%), indicating that regardless of kelp forest sizes or kelp abundance these rockfishes directly or indirectly consume high abundances of prey that consume kelp. In contrast, the niche space of adult black and copper rockfishes in the otter-present region were centered around higher trophic positions than conspecifics in the otter-absent region, indicating that availability and consumption of high-trophic level prey differs between these habitats and food webs. While convex hull areas of adult black rockfish were similar in both regions, I found that adult copper rockfish in the otter-absent region occupied larger trophic niche space, indicating more diverse diets than conspecifics in the otter-present region. This pattern is supported by both theory and empirical evidence that high resource availability allows individuals to specialize on the most profitable prey, resulting in reduced trophic niche space (Bolnick et al. 2003, Newsome et al. 2009).

Fresh and decaying kelp supports abundant communities of benthic and kelp macro-invertebrates that, in turn, support abundant populations of small carnivorous reef fishes and

their predators (Horn & Ferry-Graham 2006). Rockfish prey can be broadly categorized as either ‘invertebrate’ or ‘fish’, and in terms of energetic profitability (i.e. lipid content and digestibility), fish are preferred over invertebrates. Black rockfish are a mid-water aggregating species with diets that include high proportions of pelagic prey (i.e. macro-zooplankton), while copper rockfish are a benthic solitary species with diets that include high proportions of benthic invertebrates, particularly crustaceans (i.e. crabs, shrimp, isopods). However, both species are opportunistic piscivores and consume high-value fish prey when available (Love & Ebeling 1978, Hobson et al. 2001, Love et al. 2002). Whereas the high kelp-carbon contents of benthic invertebrates that I found in my study can explain the high kelp-carbon signatures of adult rockfishes in both regions, high rockfish trophic positions in the otter-present region indicate more frequent consumption of other fishes.

Black rockfish trophic positions in the otter-present region increased steadily with body size while conspecifics in the otter-absent region remained at generally low trophic levels regardless of body size. Trophic positions of copper rockfish in the otter-absent region increased with body size, but only at the largest body sizes did these individuals attain trophic levels comparable to those in the otter-present region. Because predators shift between prey in response to fluctuating prey abundance and quality in order to maximize potential for individual growth and reproduction (Werner & Gilliam 1984), these results suggest that the rates at which rockfishes in the otter-absent region move to higher trophic positions is limited by lower availability of high trophic level prey. The net primary productivity available to support local food webs is a function of production rates and habitat size, and because energy loss occurs with each trophic transfer, consumers occupying higher trophic levels require disproportionately more habitat area to support them (Pimm 1982, Schoener 1989). The results of my study indicate that the sizes of *Macrocystis* forests in the otter-absent region are insufficient to support rockfish populations at higher trophic levels. Lower rates of piscivory by black and copper rockfishes in the otter-absent region may be accompanied by lower individual growth rates. In the final section of this chapter I assessed the association between variation in kelp-carbon content, trophic level, and demographic performance of juvenile black rockfish.

4.5.4 Effects of kelp-carbon and trophic level on juvenile rockfish performance

I examined the effects of variable carbon supply and trophic position on individual juvenile black rockfish condition and growth. In contrast to the results presented for adult rockfish, I detected higher rates of piscivory among juvenile black rockfish in the otter-absent region. Through late July and August I often observed juvenile Pacific herring in the stomachs, or extending from the mouths, of juvenile black rockfish greater than approximately 65 mm in the otter-absent region, but not the otter-present region. The otter-absent region (Barkley Sound) includes a major Pacific herring-spawning site, and therefore I do not expect this regional difference to be related to kelp forest size. Consumption of juvenile herring in the otter-absent region corresponded to abrupt increases in condition factor, and slowly decreasing kelp-carbon contents may reflect the depleted $\delta^{13}\text{C}$ values of juvenile Pacific herring (Fig. 5). However, the lack of individuals greater than ~75 mm from the otter-present region confound this interpretation.

I tested for effects of juvenile black rockfish body size, kelp-carbon content, and trophic level on daily growth rates within each region. Growth rates increased greatly with body size. In the absence of piscivory (otters-present) I found a significant interaction between body size and kelp-carbon content, but neither kelp-carbon nor trophic level had main effects on juvenile growth. In the presence of piscivory (otters-absent), however, I found main effects of body size and trophic level on juvenile black rockfish growth. These results indicate that access to energy-rich high-trophic level prey has strong positive effects on body condition and growth rates of juvenile black rockfish. In this study, that access may be provided largely by proximity to a major herring spawning area in the otter-absent region.

Understanding how variable food web structure and productivity impact the demographic performance of consumers is a fundamental question in community ecology, and key to predicting ecosystem responses to over-exploitation, habitat degradation, and climate change. My results provide empirical evidence that individuals feeding at higher trophic levels grow faster. As predation risk and mortality typically decrease with increasing body size (Pepin 1991), factors affecting growth rates also affect mortality rates and therefore may have strong effects on population dynamics (Werner & Gilliam 1984, Sponaugle & Pinkard 2004). In contrast to the positive effects of kelp-carbon content on growth rates reported for benthic invertebrate suspension feeders (e.g. Duggins et al. 1989), the demographic importance of kelp-derived carbon

for growth rates of higher consumers are obscured by concomitant shifts to higher trophic levels.

4.5.5 Summary

The ecological consequences of the near extinction and recovery of sea otters have figured prominently in the development of fundamental concepts in community ecology, including keystone predation (Estes & Palmisano 1974, Power et al. 1996), trophic cascades (Estes et al. 1998, Pace et al. 1999), interaction strength (Paine 1980), multiple or alternative stable states (Simenstad et al. 1978, Beisner et al. 2003) and ecosystem resilience (Folke et al. 2004). On the west coast of Vancouver Island, Watson and Estes (2011) found that algal and urchin-dominated phase states, in the presence and absence of otters, respectively, remained unchanged during the 23-years over which they were monitored, and propose that these phase states are globally-stable basins of attraction (Lewontin 1969). In this study, I have shown that trophic cascades resulting from sea otter over-exploitation and reintroduction have extensive collateral effects on food web structure and productivity, and consumer trophic and recruitment dynamics, at large spatial scales.

At high latitudes sea otter reintroduction dramatically transforms rocky reef habitats and food webs with consequences for the diets, performance, and recruitment rates of kelp-associated rockfish populations. Previous studies have described the direct negative impacts of sea otters on benthic invertebrate populations (e.g. Lowry & Pearse 1973, Watson 2000, Fanshawe et al. 2003), and their indirect positive effects on macroalgal populations (Estes & Palmisano 1974, Watson & Estes 2011). Although potential positive indirect effects of sea otters on rocky reef and kelp forest fish communities have long been suspected (Ebeling & Laur 1988), few studies have tested the mechanisms by which they may occur (but see Reisewitz et al. 2006). Here, I revealed previously unknown indirect effects of sea otters using measures of carbon supply and trophic position from stable isotopes, otolith-derived measures of daily growth, and recruitment dynamics at multiple spatial scales. The surprising and counterintuitive result, that higher kelp production in the presence of sea otters does not contribute more to fish tissues, but does change the food webs that support them, provides valuable insight towards understanding relationships between food web structure and key demographic rates. These results will guide

future integrative food web and spatial-ecological approaches aimed at understanding how the cumulative effects of sea otters scale-up to influence the productivity and resilience of nearshore marine ecosystems.

5. Conclusions

In the preceding chapters, I investigated processes underlying the recruitment success and trophic dynamics of nearshore Pacific rockfishes in the broad contexts of: 1) design and effectiveness of marine protected areas, 2) variable ocean climate, and 3) changes in habitat size and food web structure driven by the near-extinction and recovery of another marine vertebrate predator, the sea otter. I did this by examining multiple life history stages at multiple spatial scales. In this chapter, I attempt to synthesize the common themes and key findings of these investigations, and highlight how these studies have contributed to fundamental questions in ecology, as well as empirical evidence immediately relevant for ecosystem-based conservation and management. Finally, I conclude by commenting on valuable future research directions stemming from each investigation.

5.1 Effects of coastal upwelling dynamics and nearshore topography on temporal and spatial patterns of rockfish recruitment success

A long-standing debate in marine ecology concerns the relative importance of pre-settlement vs. post-settlement processes in determining the dynamics of marine populations (Caley et al. 1996). Pre-settlement (pelagic) growth and mortality rates, and delivery of juvenile to settlement habitats, strongly reflect large-scale oceanographic processes, and resulting patterns of larval supply and recruitment can be key drivers of population dynamics (Doherty 2002). In contrast, post-settlement (benthic) growth and mortality rates may strongly reflect local resource availability and abundances of competitors and predators (i.e. habitat, productivity, and food web dynamics); therefore, strong density-dependent mortality can obviate patterns of larval supply (Hixon & Webster 2002). Although increasingly pluralistic perspectives acknowledge that both kinds of processes are important, investigating these processes at the spatial and temporal scales over which they occur is a fundamental challenge in marine ecology.

In Chapters 2 and 3, I contributed primarily to the perspective that pre-settlement processes play large roles in determining recruitment success and population dynamics. Critical to this debate is the fact that high recruitment under any circumstances must result from high rates of larval delivery. Marine populations are rarely at equilibrium (Doherty & Williams 1988), and because the likelihood that the strength of density-dependent mortality increases linearly with density (i.e. exact compensation) is also low, it is unlikely that locally high recruitment rates do not result in the addition of new adults (Caley et al. 1996). For these reasons, I expect the recruitment patterns I detected reflect real differences in larval supply and have demographically significant effects on local populations. However, because I did not measure post-settlement survival rates I do not know the degree to which the strong recruitment events described in these chapters were preserved in the age structure of local populations.

In Chapter 2, I tested two hypotheses concerning the spatial distribution of rockfish settlement rates across nearshore seascapes. Based on the conclusions of Gaines et al. (2003), the first simply states that not all nearshore locations are equivalent with respect to the probability of intercepting aggregations of larvae moving onshore or along shore. The corollary to this hypothesis is that coastal currents regimes are spatially structured, in part because they interact with coastal topographic features (i.e. headlands, islands, submarine canyons, etc.). As a result, nearshore environments are mosaics of locations differing widely in terms of their exposures to prevailing wind and surface currents, current velocities, ocean temperatures, and habitat types. The second hypothesis follows from the first, and predicts that because coastal currents interact with coastal topography in consistent ways, to the extent that larval supply is a passive process, spatial patterns of recruitment should be relatively consistent among years.

I found that rockfish recruitment success does vary widely over small spatial scales, and that locations experiencing high recruitment tend to do so year-after-year. Most importantly, I demonstrated that spatial recruitment patterns were explained by seascapescale patterns of fetch, distance from the open coast, tidal velocity, and sea surface temperature. These patterns strongly support differential larval supply as the mechanism underlying spatial recruitment patterns. These are key findings in terms of understanding local-scale variability in rockfish population dynamics and the effectiveness of MPAs. Because MPAs are typically small relative to the dispersal distances of pelagic larvae, long-term persistence of populations within MPAs is likely to depend upon larval supply from beyond MPA borders (Gaines et al. 2003). Although

MPAs are increasingly being implemented to conserve and restore biodiversity and fisheries, these spatial management tools are still relatively new, and research has focused primarily on placement and design. Only recently, with increasing histories of MPAs are investigations turning to assessing factors underlying successes and failures.

In Chapter 3, I showed that pre-settlement (pelagic) rockfish growth rates respond more strongly to changes in ocean temperature than they do to primary productivity. Because factors that increase individual growth rates and pelagic durations also reduce daily and cumulative mortality rates, I expected higher larval survival rates, and therefore higher recruitment rates, in years of warm ocean temperatures. This was true of CQB rockfishes, but not black rockfish. Instead, high black rockfish recruitment corresponded to cool ocean temperatures, low pre-settlement growth rates, and protracted pelagic durations. This key finding runs contrary to our conventional understanding of processes underlying marine fish recruitment success, and indicates that oceanographic processes affecting larval transportation may be more important, or compensate for, poor conditions for larval growth and survival in determining the recruitment success of some species.

Thus, through the research presented Chapters 2 and 3, I have contributed significantly towards understanding (1) how large-scale oceanographic variability affects rockfish early life history attributes that are important determinants of recruitment success; and (2) processes that underlie the spatial distribution of larval delivery and recruitment success throughout nearshore habitats and populations. These results advance theoretical frameworks and contribute empirical evidence necessary for developing predictive models of marine population dynamics, and the design and effectiveness of marine protected areas.

5.2 Collateral effects of the otter-urchin-kelp trophic cascade on rockfish recruitment and trophic dynamics

In Chapter 4, I moved from large-scale patterns of oceanography (Chapter 3), and spatial distributions of nearshore settlement habitats (Chapter 2), to characteristics of settlement habitats that affect rockfish recruitment success, and post-settlement growth and trophic dynamics. While rockfishes themselves represent large marine vertebrates that have been widely overfished along the Pacific coast of North America, I placed this investigation the context of the

near-extinction and reintroduction of another predator in this system, the sea otter. Sea otters profoundly impact rocky reef ecosystems by regulating the abundance of herbivorous sea urchins, thereby maintaining abundant populations of kelps that provide critical habitat and productivity for reef fish populations.

I tested the hypothesis that sea otters indirectly increase nearshore rockfish recruitment by increasing the ‘target’ size of settlement habitats provided by *Macrocystis* kelp forests. My finding that rockfish recruitment was markedly higher in sites with sea otters and large kelp forests support this hypothesis. This result indicates that the otter-urchin-kelp trophic cascade has important collateral effects on the dynamics of associated populations and food webs. By increasing the structural habitat provided by kelp forests, sea otters indirectly increase the settlement and recruitment habitat available for juvenile rockfishes. In contrast, absence of otters and high densities of sea urchins dramatically reduce the size and productivity of kelp forest habitats. From a landscape ecological perspective, reduction of the size and number of kelp forest habitats is highly analogous to patterns of habitat loss and fragmentation described in terrestrial ecosystems. Similar effects may occur in other ecosystems in which consumers directly or indirectly impact the size and connectivity of critical habitats (e.g. seagrass meadows and coral reefs). Loss of connectivity among marine populations resulting from habitat loss is likely to have important, yet uninvestigated, consequences for metapopulation and food web dynamics.

In Chapter 4, I also revealed a critical relationship between kelp forest habitat size and food web structure and productivity. Using stable isotope techniques, I found that adult rockfishes from regions with and without sea otters did not differ, as I predicted, in terms of kelp-derived carbon content. Instead, I found that adult rockfishes in the otter-present region feed at higher mean trophic levels, indicating that their diets include higher proportions of fish. This result has two key implications. First, the ability of rockfishes to feed at higher trophic levels when otters are present indicates that food webs that include sea otters support more abundant fish populations. Additional investigation is needed to quantify and compare the abundance and diversity of fish communities, and their invertebrate prey, in kelp forests with and without sea otters. It is noteworthy, however, that juvenile rockfishes themselves constitute important prey for many reef fishes, particularly adult rockfishes. Therefore, higher rockfish recruitment in large kelp forests represents not only higher population replenishment, but also a valuable trophic subsidy. The second implication lies with the demographic consequences of consuming higher

proportions of fish (e.g. individual growth and survival). I examined this relationship further, and found that juvenile rockfishes with higher trophic positions also had higher growth rates. Because mortality rates of juvenile fishes depend strongly on body size, higher growth rates resulting from feeding at higher trophic positions are also expected to increase survival. Ultimately, I expect changes in rockfish settlement rates and post-settlement growth and survival rates resulting from sea otter reintroduction and increasing kelp forest habitat size to increase the abundance of nearshore rockfish populations.

Thus, through the research presented in Chapter 4, I have contributed to understanding (1) how loss and reintroduction of large marine predators may have trophic and non-trophic indirect effects that reach well beyond the herbivore populations they regulate; and (2) how changes in habitat size (and therefore productivity) have important consequences for population and food web dynamics. These findings contribute empirical evidence and new insight with respect to the debate concerning the ecological and social-economic effects of sea otters on coastal marine ecosystems.

5.3 Future directions for rockfish recruitment and trophic dynamics

With respect to Chapter 2, two key questions should guide future research directions. First, what is the relationship between spatially consistent patterns of rockfish recruitment and subsequent adult population dynamics? That is, do locations that experience high recruitment also support high adult populations? Answers to these questions are critical if the explanatory variables underlying spatial recruitment variability I identified in this study are to be informative for planning and assessing the effectiveness of MPAs. Determining the extent to which years of strong recruitment translates to year-class strength in local populations is critical (e.g. CQB rockfishes in 2005 and black rockfish in 2006). Approaches required to address these questions are challenging, laborious and expensive. One approach is to simply examine the nature of the relationship between local recruitment intensity and abundance of adult populations in general, and how these relationships change spatially and temporally. However, to elucidate process and relative effects, studies are needed that follow the fate of cohorts beginning in years of strong

recruitment, and compared among sites varying in recruitment intensity, adult population sizes, and habitat characteristics.

The second key question concerns the extent to which juvenile rockfishes move horizontally from settlement habitats. That is, how far do post-settlement juvenile rockfishes (particularly more mobile mid-water species) move among habitats, and what are the factors that influence movement? Again, these questions are critical for MPA effectiveness, both in terms of the importance that they encompass settlement and juvenile habitats, and for understanding the factors that influence movement of fishes beyond MPA borders (i.e. spillover) and thereby enhancement of fisheries. Radio-telemetry technology and increasingly smaller tags and batteries should soon make tracking juvenile rockfishes entirely feasible if it isn't already.

With respect to Chapter 3, I envision the following research directions. First, the results from this chapter indicate strong effects of ocean temperature on pelagic larval and juvenile rockfish growth rates, pelagic durations and, by extension, mortality rates. Variation in these demographic parameters is predicted to have strong effects on larval dispersal distances and population connectivity (O'Connor et al. 2007). Future research should strive to understand not only the effects of variable ocean climate on local and regional recruitment success, but also how oceanographic events such as delayed upwelling in 2005 affect patterns of larval retention or dispersal, and therefore interannual variation in marine metapopulation dynamics. Population genetics approaches allowing measures of genetic diversity, relatedness, and source-sink dynamics should be used to determine how parameters such as these vary with oceanographic events affecting larval mortality rates and dispersal distances.

The second direction I envision is closely related to that which I described for Chapter 2. Future investigations need to follow the effects of variable ocean climate events on rockfish recruitment success in local adult populations. For example, to what extent has the strong upwelling and resultant high black rockfish recruitment in 2006 been preserved in the age-structure of local populations? Because abundant rockfish populations may exhibit strong top-down control over invertebrate and fish populations, strong-year class strength resulting from oceanographic events may also have important consequences for food web structure and dynamics.

With respect to Chapter 4, there are several key directions for future research in the contexts of ecosystem-level effects of sea otters, and ecosystem ecology in general. In Chapter 4, I employed a regional-comparative approach to infer process from pattern. Unlike classical experimental ecological approaches in which replicated experimental units are manipulated at relatively small spatial scales, these tools are not available when working at the scale of ecosystem and regions. At these scales, pseudoreplication (Hurlbert 1984), is unavoidable and regional-comparative studies suffer from the inability to statistically infer cause-and-effect relationships (Hargrove & Pickering 1992). Instead, ecosystem ecologists must rely on developing multiple lines of evidence to support mechanistic models, supplemented by small-scale experiments when possible.

My results from Chapter 4 provide compelling evidence that recovery of sea otters and kelp forests have strong effects on food web structure and productivity, and the population dynamics of fishes associated with shallow rocky reef and kelp forest habitats. The productive-space hypothesis (Schoener 1989), is an excellent starting point for future investigation of relationships between kelp forest habitat size and productivity, and properties of food webs and ecosystems. Addressing the following questions will provide valuable future research directions. First, how does the distribution of biomass and productivity within food webs differ between ecosystems with and without sea otters? That is, does higher macroalgal productivity in the presence of sea otters support more biomass at higher trophic levels? If so, by which direct and indirect trophic pathways is biomass distributed and supported within these webs? These questions should be addressed by employing detailed quantitative assessments of community structure and population size structure in order to construct and compare biomass/productivity-specific food webs. A key question regarding sea otter and kelp forest ecosystem recovery, and reef fish population dynamics is, what are the demographic implications (i.e. individual growth, survival, and fecundity) of feeding at higher mean trophic levels? Future investigations could attempt to integrate quantitative assessments of population age or size structure, dietary analyses, and bioenergetic relationships, to model rockfish population dynamics under varying levels of food web structure and resource availability. In addition, this approach could be combined with analysis and comparison of food web structural properties (e.g. trophic height, linkage density, connectance, trophic chain length, fraction of biomass at higher and lower trophic levels, biomass-production

ratios, and robustness). Using dominator trees analyses to identify the linear pathways essential for energy delivery in these complex food webs (Allesina & Bodini 2004) would be one approach.

Finally, a critical next step in this work will be developing strategies for scaling-up small-scale measures (e.g. via quadrats and transects) to the areas of corresponding habitats. That is, moving from measures of density to spatially explicit measures of abundance. For example, in Chapter 4 I scaled-up visual estimates of juvenile rockfish densities (numbers/100m²) to the total area of corresponding kelp forests to estimate the total number of juvenile rockfish per kelp forest. Similar approaches are required to develop and compare spatially explicit estimates of food web and ecosystem properties at the scales of habitats and ecosystems (Polis et al. 1997, Massol et al. 2011). However, because species' distributions within habitats are not homogenous, convincing approaches will necessarily account for differential patterns of habitat use when attempting to investigate processes at these scales.

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APPENDIX A: Deploying SMURFs in kelp forests

Standard Monitoring Units for the Recruitment of Fishes (SMURFs; Ammann 2004) deployed over deep water and in the absence of other forms of structural habitat accumulate competent (i.e. ready to settle) pelagic juvenile fishes and provide relative measures of larval supply in the absence of internal factors such as habitat complexity, competitors and predators (e.g. Ammann 2004, Selkoe et al. 2006, White & Caselle 2008, Wilson et al. 2008). In natural habitats, however, spatial differences in larval supply and settlement rates may be modified by location-specific mortality rates (Caley et al. 1996), and resultant recruitment rates integrate spatially differential larval supply and early post-settlement losses (Sale 2004). In the current study I deployed SMURFs in *Macrocystis* kelp forests because my intention was to obtain small-scale estimates of rockfish recruitment, not larval supply, in kelp forest habitats. I also opted for the standardized methodology provided by SMURFs because visual estimates in this region can be unreliable due to poor underwater visibility (<3m) during summer months. However, avoidance or length-biased utilization of “in-kelp” SMURFs by post-settlement rockfishes could undermine the utility of this method to provide useful estimates of recruitment.

To compare the abundance and length-frequency distributions of juvenile rockfishes collected from in-kelp and out-kelp SMURFs I conducted the following experiment. In 2005 I deployed 16 pairs of SMURFs at four locations nested within four sites (32 SMURFs) throughout Barkley Sound (GF, LC, EK, and PE). At each location in-kelp SMURFs were deployed in physical contact with the seaward edge of *Macrocystis pyrifera* kelp forests, and out-kelp SMURFs were deployed over deep water (15-20m) and approximately 100 m seaward of in-kelp SMURFs. All SMURFs were deployed mid June 2005 and sampled at 14-day intervals through July and August. Low utilization of in-kelp SMURFs relative to out-kelp SMURFs would suggest that juvenile rockfish avoid SMURFs in kelp forests because they prefer natural kelp habitat. Conversely, high utilization of in-kelp SMURFs would reflect the relatively high densities of post-settlement juvenile rockfishes utilizing kelp forest habitats. I further predicted that if SMURFs accumulated juvenile rockfishes in proportion to their abundance within kelp forests, then length-frequency relationships would be normally distributed. Alternatively, skewed distributions would suggest size-specific predation or avoidance of SMURFs.

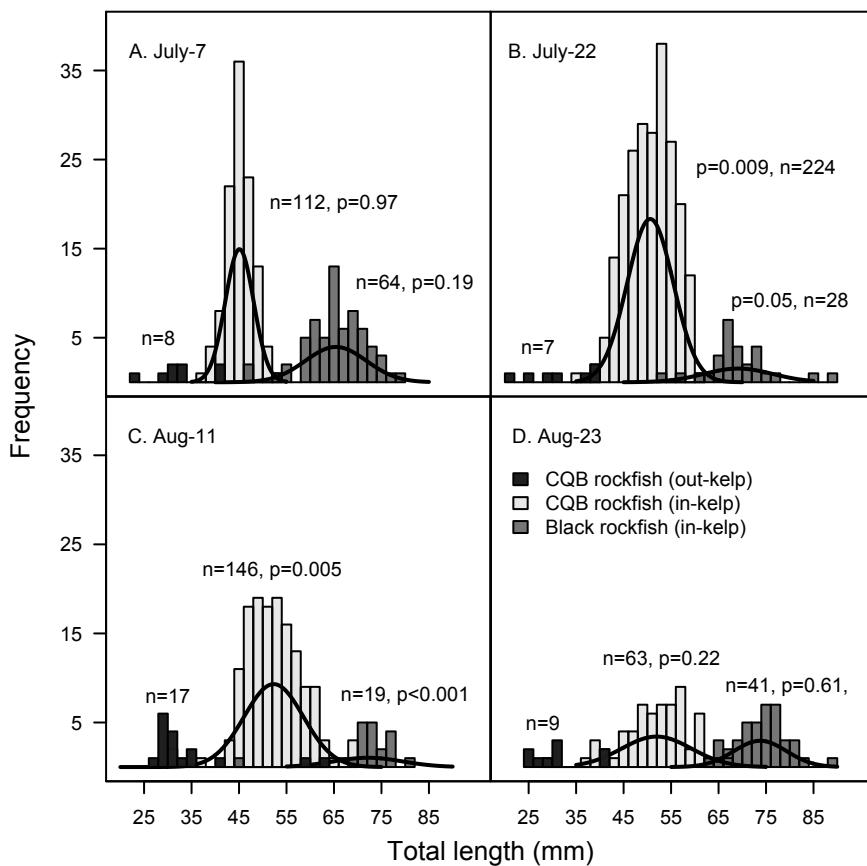


Figure A1. Rockfish length-frequency distributions from in-kelp ($n = 16$) and out-kelp ($n = 16$) SMURFs sampled bi-weekly through July and August 2005 and fitted with expected normal distributions. P-values < 0.05 indicate length-frequency distributions differing significantly from normal (Shapiro-Wilk normality test).

Over the eight weeks they were deployed in 2005, out-kelp SMURFs accumulated low numbers of pre-settlement CQB complex (*Sebastes caurinus*, *S. maliger*, *S. auriculatus*) rockfishes ($n = 37$, median = 30.10 mm TL, range = 21.10-41.80 mm TL), and in-kelp SMURFs accumulated large numbers of post-settlement CQB ($n = 545$, median = 49.70 mm TL, range = 28.70-69.90 mm TL), and black (*S. melanops*) ($n = 152$, median = 67.57 mm TL, range = 49.90-89.50 mm TL) rockfishes (Fig. A1). I assume that no black rockfish were collected from out-kelp SMURFs because this species had settled prior to SMURF deployment in late June (Ammann 2004).

Length-frequency distributions of post-settlement CQB and black rockfishes collected from in-kelp SMURFs were normally distributed ($p > 0.05$) on two of four sampling dates (Shapiro-Wilk normality test). All non-normal length-frequency distributions were significantly kurtotic (Anscombe-Glynn kurtosis test). Only black rockfish length-frequencies on Aug-11 were significantly skewed (D'Agostino skewness test), likely due to the low sample size on this date ($n = 19$).

In the same way that SMURFs deployed over deep-water provide relative measures of the abundance of larvae/pelagic juveniles moving onshore, I argue that SMURFs deployed in kelp forests provide relative measures of the abundance of post-settlement juvenile rockfishes utilizing kelp forest habitats. In-kelp SMURFs were occupied much more extensively by black and CQB rockfishes than out-kelp SMURFs, reflecting the high abundances of post-settlement rockfishes that seasonally accumulate in these habitats. Length-frequency distributions of black and CQB rockfishes were either normally distributed or over-distributed within distribution centers (kurtotic), but were not skewed. These results suggest that in-kelp SMURFs generally attract post-settlement rockfishes in proportion to their abundance in kelp forests. Length-specific avoidance of in-kelp SMURFs does not appear to hamper the ability of this method to provide relative estimates of rockfish recruitment intensity within kelp forest habitats. SMURFs deployed in kelp forests have the advantage of providing relative estimates of recruitment intensity that integrate variable larval supply and early post-settlement mortality. In addition, repeated sampling of post-settlement length-frequency distributions can provide location-specific estimates of post-settlement growth and survival.

APPENDIX B: Supplementary figures

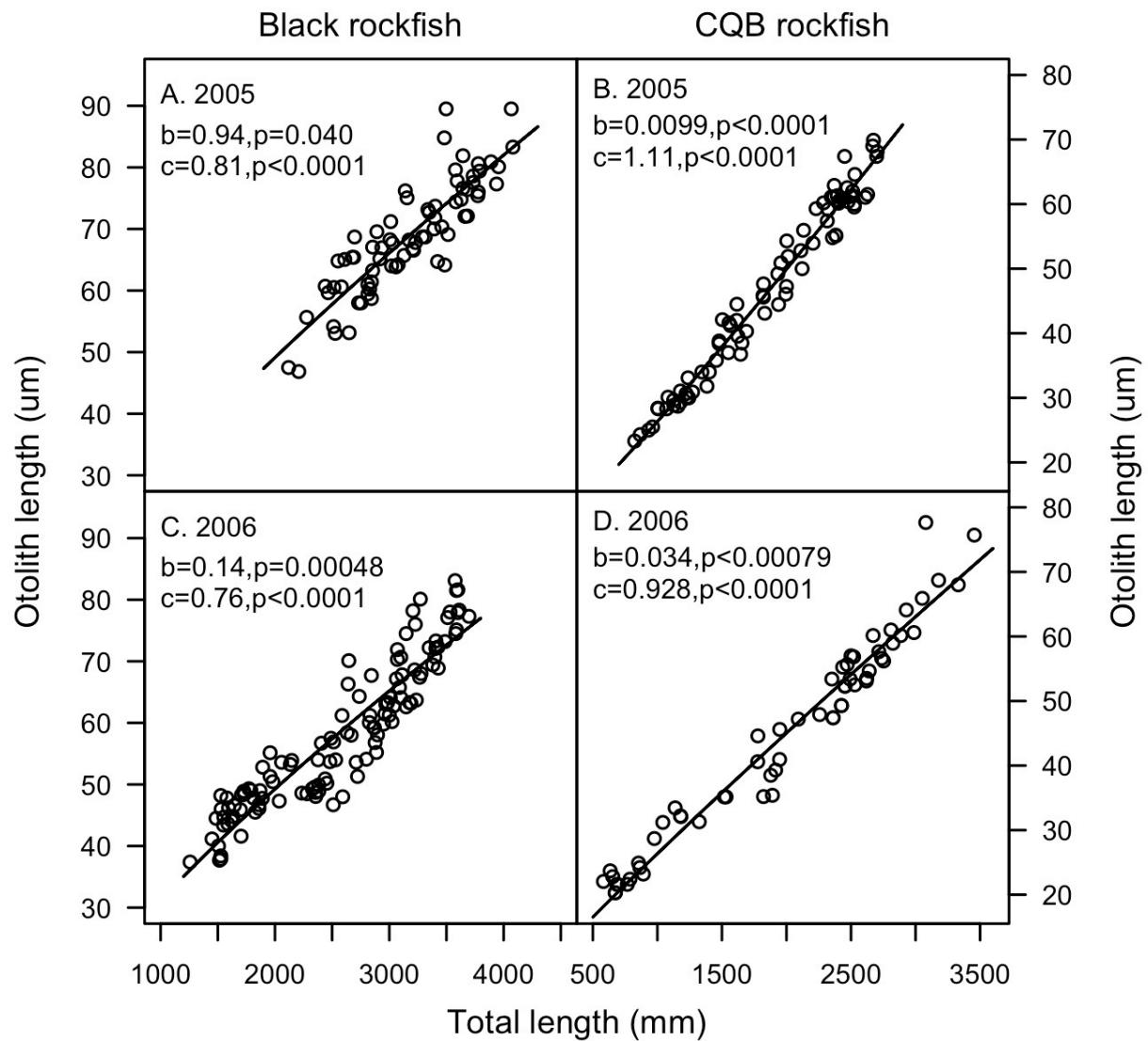


Figure B1. Non-linear regressions between otolith length and body length of black and CQB rockfishes used to back-calculate daily length-at-age in 2005 and 2006 using the Modified-Fry back-calculation model (Vigliola et al. 2000; Wilson et al. 2009); refer Equation 2, Chapter 3.

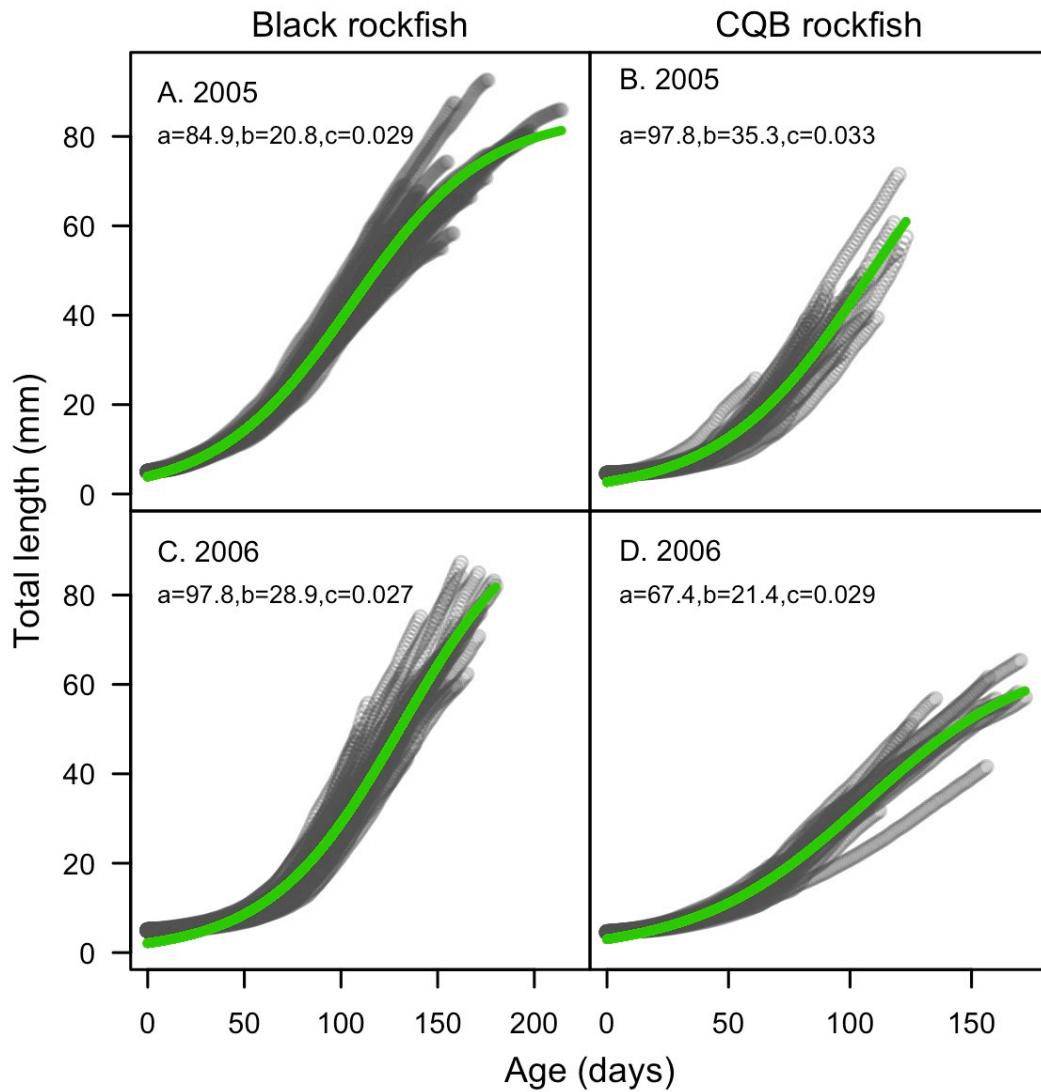


Figure B2. Individual growth profiles of black and CQB rockfishes in 2005 and 2006 constructed using the Modified-Fry back-calculation model (Vigliola et al. 2000; Wilson et al. 2009). Parameter values and green lines represent logistic growth models fit to growth profiles of annual cohorts.