

THE EFFECTS OF SAN JUAN COUNTY, WASHINGTON, MARINE
PROTECTED AREAS ON LARVAL ROCKFISH PRODUCTION

Lucie Jean Weis

A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2004

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington
Graduate School

This is to certify that I have examined this copy of a master's thesis by

Lucie Jean Weis

and have found that it is complete and satisfactory in all respects, and that any and all
revisions required by the final examining committee have been made.

Committee Members:

Bruce S. Miller

Donald R. Gunderson

Arthur W. Kendall

Janet Duffy-Anderson

Date: _____

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Any other reproduction for any purposes or by any means shall not be allowed without my written permission.

Signature _____

Date _____

University of Washington

Abstract

The Effects of San Juan Marine Protected Areas on Larval Rockfish Production

Lucie Jean Weis

Chair of the Supervisory Committee:
Professor Bruce S. Miller
School of Aquatic and Fishery Sciences

Marine protected areas (MPAs) are becoming increasingly popular fisheries management tools for long-lived, late-maturing species with limited home ranges. North Puget Sound rockfish species have been recreationally overfished and are ideal candidates for MPAs. Two major assumptions underlying reserves are that a protected population produces more larvae, and that there is a spillover effect into depleted areas. Although larval export is a widely accepted mechanism, there is little empirical research in the literature. Ichthyoplankton samples were collected using a 0.5 m Tucker Trawl during spring 2002 in and around four MPAs around San Juan Island, WA. A Geographic Information System (GIS) application was used to investigate whether larval production is greater in MPAs as compared to unprotected areas and whether dispersal patterns from MPAs can be detected. Results suggest that rockfish larvae are heterogeneously distributed. MPAs had higher densities of rockfish larvae than non-reserve locations on the west side of San Juan Island while densities were actually lower within MPAs on the east side. Overall, spatial patterns indicate a high potential for larval linkages between sites. This study illustrates the difficulties associated with relating larval distribution patterns to potential areas of larval release.

Table of Contents

List of Figures	ii
List of Tables	iii
Introduction.....	1
Marine Protected Areas	1
Rockfishes.....	5
Gears	6
Oceanography in the San Juan Islands	8
Objectives	9
Materials and Methods	12
Gear	12
Sampling Design	12
Towing Methods.....	17
Sample Processing.....	18
Data Analysis	19
Results	22
Discussion.....	33
Conclusions.....	43
References.....	45
Appendix 1: The Kvichak Trawl.....	52
Appendix 2: Non-target Species Results (Tucker and Bongo).....	53

List of Figures

Figure 1. Study area.....	11
Figure 2. Tucker trawl diagram.....	13
Figure 3. Kvichak trawl diagram.....	14
Figure 4. Sampling design	16
Figure 5. Rockfish larval catch as a function of haul date.....	24
Figure 6. Lingcod, cabezon, and greenling catch values as a function of date.....	25
Figure 7. Rockfish larval standard lengths over time.....	27
Figure 8. Rockfish larval catch by depth	28
Figure 9. Plot of MPA and island side effects	30
Figure 10. Prediction map of larval rockfish for the east side of San Juan Island.....	31
Figure 11. Prediction map of larval rockfish for the west side of San Juan Island.....	32

List of Tables

Table 1. Observed spawning times for rockfishes in the northeast Pacific.	36
---	----

Acknowledgements

I would like to thank the Northwest Straits Commission (NWSC) for research funding and the School of Aquatic and Fishery Sciences for providing stipend and tuition support. My advisor, Bruce Miller, contributed an excellent balance of guidance and independence as well as knowledge and insight. Art Kendall, Don Gunderson, and Janet Duffy-Anderson formed the rest of my advisory committee and gave generously of their time and attention. Lyle Britt deserves special thanks, as he was critical to the success of my field season. Julia Fulmer was an exceptional field assistant in frequently inclement weather. Dennis Willows, Craig Staude, David Duggins, and many of the FHL staff kindly supported my technical needs. I am very appreciative to Dan Cooper and Jake Gregg for their diving assistance. In addition, I would like to thank Wayne Palsson, Bob Pacunski, Pat Halpin, Morgan Busby, Brooke Martin, Laura LaFrance, Ted Pietsch, Loveday Conquest, and Dale Gombert for helping in many important ways. This thesis would not have been completed without the support and encouragement of family and friends. I am particularly grateful to my husband, Elliott Hazen.

Introduction

Contrary to long-held beliefs, the ocean's living resources are now recognized as limited and vulnerable to overexploitation (Roberts and Hawkins 1999). Large, predatory fish (e.g. sharks, billfish, and rays) biomass is estimated at about 10% today of what it was before industrial fishing efforts (Myers and Worm 2003). Managers have implemented many different fisheries management strategies, but populations have failed to recover or continued to decline in areas throughout the world (Pauly et al. 2002). As of 2001, only 22 percent of federally managed fisheries in the U.S. were being harvested sustainably (Pew Oceans Commission 2003). Habitat destruction and high bycatch are also consequences of intense fishing efforts.

Marine Protected Areas

Traditional strategies have failed repeatedly to sustainably manage marine resources and habitat. As an alternative, marine protected areas (MPAs) are increasingly at the forefront of marine resource conservation and management. Researchers have identified a ubiquitous failure to acknowledge scientific uncertainty as the primary obstacle to successful fisheries management (Lauk et al. 1998). They conclude that MPAs provide the simplest and best approach to implement the precautionary principle and to achieve sustainability. As part of a precautionary approach, MPAs can be invaluable in the rehabilitation of depleted marine populations (Lauk et al. 1998) and are strongly supported by many scientists (Allison et al. 1998; Halpern 2003; Lubchenco et al. 2003). Creating a network of MPAs in the world's marine areas would be a major step

toward ecosystem protection and recovery of diminishing ocean stocks. Research has demonstrated that MPAs can be useful management and conservation tools (Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) 2002; Halpern 2003).

It is important to define the terminology. The most generally accepted definition of an MPA is that adopted by the World Conservation Union (IUCN) in 1988, which defines it as: *Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment.* Whether part or the entire enclosed environment is protected depends on objectives, which differ considerably from single-species to ecosystem level protection.

MPAs serve multiple functions simultaneously while simplifying management and enforcement costs. Benefits include the protection of ecosystem structure and function (Murray et al. 1999) and enhancement of adjacent fisheries (Guénette et al. 1998; Roberts et al. 2001). Lauk et al. (1998) lists six additional advantages:

- Biodiversity conservation
- Protection of essential life stages of commercial and recreationally important species
- Protection and enhancement of productivity
- Protection of artisanal and community fisheries
- Enhancement of public education
- Provision of marine research opportunities.

Two major assumptions underlying the use of reserves for enhancing productivity are that a protected population is more productive and that there is a spillover effect into

unprotected areas. A population with net emigration is called a source population while a population with net immigration is called a sink population. 'Leakage' from source populations could be in the form of larval, juveniles and adult stages. Adult movement across reserve boundaries is well-documented for many species (Russ and Alcala 1996). There is a significant body of evidence of increased abundance, length and weight frequency of adults in protected areas (Martell et al. 2000; Roberts et al. 2001; Eisenhardt 2002; Halpern and Warner 2002). Fishes targeted for protection were 3.7 times more abundant inside than outside reserves in an extensive meta-analysis (Mosquera et al. 2000). In a review of 89 studies, Halpern (2003) found consistently significant positive effects of reserves, with increases in density, biomass, organism size and diversity for nearly all functional groups in marine fish communities. Evidence of fishery benefits outside protected areas are less common. Five small reserves in St. Lucia increased catches by 46-90% for artisanal fishers within five years of creation, dependent on gear type (Roberts et al. 2001). It is important to recognize that effects of marine reserves are not consistently positive. Several studies reveal few differences between protected and unprotected areas. No significant changes were observed in species number or mean size of individuals of three species between reserve and non-reserve sites in Tasmania (Edgar and Barrett 1997). A model comparing traditional effort control to a marine reserve indicated that they could result in identical fishery yields (Hastings and Botsford 1999). Negative effects have been observed in some cases as well. Total fish landings decreased by 35% following the creation of a marine park in a Kenyan coral reef (McClanahan and Kaunda-Arara 1996).

Larger, more abundant and fecund individuals should theoretically increase local larval supply, within and outside the MPA (the “seeding effect”). Adult abundance relies on larval production, larval survival, and juvenile settlement rates. It is important to note that production of larvae alone may not translate into increases in adult biomass. Nonetheless, the effective design of MPAs depends critically on knowledge of larval dispersal patterns and population connectivity (Botsford et al. 2001). For MPAs to be successful, they must maintain high larval production of target species and augment harvested populations (Carr and Reed 1993).

Although larval export is a widely accepted “spillover” mechanism, there is little empirical research in the literature. Enhancement of downstream populations through larval export was observed for reserves in the Bahamas (Stoner and Ray 1996). Larval fish abundance was consistently greater in a (non-adjacent) fished area than a marine reserve in St. Lucia, West Indies (Valles et al. 2001). These results suggest larval spillover or that the protected area may not be ideally placed. Most research on larval production and dispersal to date has been theoretical. Models of larval export and fishery enhancement generally yield positive results (Black et al. 1991; Morgan and Botsford 1998).

The vast majority of marine reserve studies have been conducted in sub-tropical or tropical coral reefs and islands or along temperate, continental coastlines. Few have occurred in inland temperate waters. The San Juan Islands (SJIs), Washington, USA, are geographically unique, highly influenced by certain oceanic processes and major river systems yet buffered from both by distance. They are not necessarily subject to the same

types of hydrographic forces as oceanic islands. Studies off the coasts of California and Oregon generally focus on large-scale circulation or upwelling events (Richardson and Pearcy 1977; Shenker 1988; Yoklavich and Loeb 1996), neither of which pertain to the SJIs. Temperate rocky reef dynamics may not be analogous to tropical coral reefs. Studies in central California's marine reserves are among the most directly comparable (Starr et al. 2002).

Rockfishes

Rockfishes (*Sebastes* species) are generally long-lived, late-maturing live-bearers with limited home ranges. They are a diverse genus of 102 species, most of which occur in the northeast Pacific. Ten that occur in the San Juan Islands are copper rockfish (*Sebastes caurinus*), quillback rockfish (*Sebastes maliger*), black rockfish (*Sebastes melanops*), tiger rockfish (*Sebastes nigrocinctus*), yelloweye rockfish (*Sebastes ruberrimus*), yellowtail rockfish (*Sebastes flavidus*), brown rockfish (*Sebastes auriculatus*), China rockfish (*Sebastes nebulosus*), splitnose rockfish (*Sebastes diploproa*) and Puget Sound rockfish (*Sebastes emphaeus*) (Pacunski personal communication December 16th, 2003). Among these species, yelloweye rockfish are among the longest-lived, reaching 118 years and maturing at 19-22 years (Love et al. 2002). Larger, older rockfishes have the highest fecundity and their loss due to fishing pressure is the most detrimental to populations (Haldorson and Love 1991). Home ranges vary interspecifically and intraspecifically, but most rockfishes seem to remain within particular areas. Tagging studies of copper and quillback rockfish indicate high site fidelity with restricted movement, particularly in high relief areas (Matthews 1990)

while black rockfish are far more mobile. One black rockfish tagged off central Oregon was recaptured 619 km away in Puget Sound (Love et al. 2002).

After parturition rockfish larvae are pelagic for 3-12 months after which they settle as juveniles to different habitats. The larval phase for copper rockfish lasts approximately 1-2 months (Kendall and Picquelle 2003), although details of larval duration for most species are unknown. Newborn individuals have functional eyes, jaws and guts and are swimmers capable of capturing prey (Dygert and Gunderson 1991). However, they are smaller and less well developed at age than larvae of many other fish (Matarese et al. 1989). Because they are not morphologically distinct at small sizes, differentiating among larval rockfish species is difficult without using genetic techniques. It is not known whether rockfish larvae are completely passive or if they are capable of active transport. Passive dispersal has long been assumed for most fish larvae although evidence exists that some reef fishes exhibit nearshore (Marliave 1986) or near reef (Brogan 1994; Jones et al. 1999) retention patterns.

Due to their relatively sedentary nature, late-maturation, and longevity, rockfishes are among the species likely to benefit from MPAs (Soh et al. 2001). MPAs can successfully produce larger, more fecund rockfish than surrounding fished areas (Paddack and Estes 2000). Yield per recruit or stock-recruitment models that work for shorter-lived species are not appropriate (Leaman 1991). Their long life spans require long-term management plans tailored to their unique life histories.

Gears

While many sampling gears are suitable for ichthyoplankton, there are four primary types. Light traps catch larvae by attracting and confining them to an illuminated container. They work well for passively collecting larvae of phototactic species, but do not seem to attract nearshore rockfish larvae. Circular bridled plankton nets of various diameters are the most commonly employed gear type. They are easily deployed but the bridles impede water flow and generate vibrations that larvae can sense, thus decreasing efficiency. A bongo net is a pair of circular nets on a single weighted frame such that no bridles are needed (Gunderson 1993). It samples more effectively than a single bridled net but requires a larger vessel and usually cannot sample discrete depths. Tucker trawls are square frames that consist of three separate, unbridled nets that can be opened and closed at depth. A 0.5 m Tucker trawl frame can be deployed from a small vessel and three discrete samples can be collected with each haul (one from a discrete depth and two oblique or three obliques).

The distribution and small size of larval fish makes ichthyoplankton sampling difficult. Plankton assemblages are highly variable spatially and temporally and ichthyoplankton often exist in patches (North and Houde 2000). Nets with large mesh could miss the smaller larvae while small mesh could create a wake allowing larvae to escape. Further, the large oceanographic scale limits sampling to a small fraction of the total survey area.

Oceanography in the San Juan Islands

Larval fish ecology is inextricably linked to physical oceanography. The major driving forces in the San Juan Islands are oceanic inflow via tides and estuarine outflow from the Fraser River (Klinger 2000). Currents in the San Juan Islands are strong, swift and highly variable across scales. Water masses are generally well mixed or weakly stratified during most of the year between the islands due to converging water masses and high relief topography (Zamon 2002). By contrast, Haro, Rosario and Juan de Fuca Straits are characterized by stratification during summer months (Thomson 1981). The prevailing circulation pattern around the archipelago is counter-clockwise with a high degree of connectivity that potentially allows for substantial larval exchange between sites (Klinger 2000).

Although few unifying principles for MPA networks exist, it is generally agreed that high levels of linkage between protected and unprotected populations are important. Isolated MPAs have little impact on populations if they do not supply larvae to other areas. In fact, scientists generally agree that a system of interconnected MPAs will be most effective.

Monitoring and enforcement are important components to the long-term success of MPAs as a fisheries management tool and are often overlooked. The eight San Juan County MPAs are all voluntary no-take for bottomfish recovery with protection targeting rockfishes (*Sebastes* species), lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*), and greenling species (*Hexagrammos decagrammus*, and *H. stelleri*; *Hexagrammos spp.* will be designated as greenling even though lingcod are in the same

family). Enforcement relies on educated anglers acting out of goodwill. There are also three University of Washington research reserves in the SJIs that are mandatory no-take for all but recreational salmon and herring hook and line fishing. The reserves still require self-policing by anglers and researchers.

Objectives

My research objective was to use larval fish collections to examine connectivity at a set of sites in the San Juan Islands, Washington (Figure 1), and produce an ichthyoplankton monitoring protocol for use by marine resource management agencies. Specifically I am interested in whether larval production is greater in MPAs as compared to unprotected areas and whether dispersal patterns from MPAs are detectable. I conducted an extensive ichthyoplankton survey, incorporating depth and distance from shore to gain a better understanding of larval fish production, distribution and dispersal patterns.

This study focuses on rockfishes, an ecologically and recreationally important group whose life history makes them susceptible to overexploitation and good candidates for MPA management. Currently many of these populations are significantly depressed and in need of rebuilding (PFMC 2002). Copper, quillback, black and brown rockfishes in the Puget Sound region are considered “vulnerable” to extinction by the American Fisheries Society (Musik et al. 2000). Despite sharp declines, in 2001 the National Marine Fisheries Service (NMFS) determined that listing these species as endangered was not warranted. The decision was based on the inclusion of Puget Sound populations

as part of the entire Pacific coast populations, which as a whole are not declining (Puget Sound Action Team 2002).

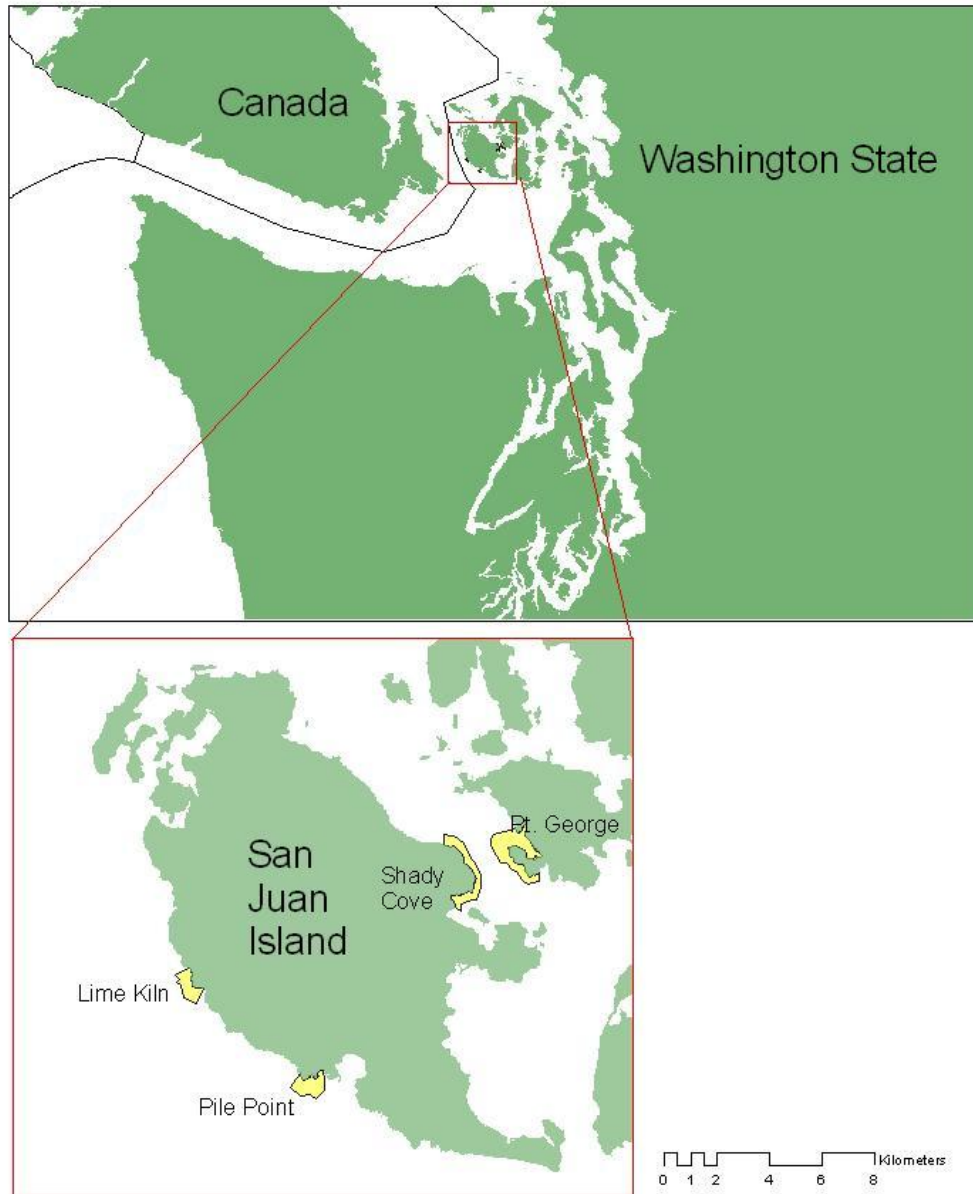


Figure 1. The Northwest Straits Region including the San Juan Archipelago of Washington State. The study area around San Juan Island is shown as an inset with arrows representing the general current patterns during ebb tide (reversed during flood tide).

Materials and Methods

Gear

A 0.5 m Tucker trawl (Figure 2) and a 0.62 m bongo net were used to collect fish larvae. A Kvichak trawl with a mouth opening of 3.6 m² and mesh decreasing from mouth to codend (Figure 3) was also used as a second, exploratory method to attempt to catch larger larvae that may have avoided the Tucker trawl. The Kvichak trawl is a midwater frame trawl with weighted horizontal spreader bars, more commonly used to sample juvenile salmonids. It was used in this study to sample for juvenile target fishes.

A Wildlife Computers, Inc., sensor (model MK7) monitoring depth, light and temperature every five seconds was attached to the net frame and those data were downloaded at the end of each day to determine actual net depths. Volumes of water strained were determined using General Oceanics flowmeters, which were calibrated by pulling them a fixed distance multiple times and at different rates, to get average revolutions per meter for each flowmeter. Flowmeters were suspended in the mouths of each Tucker trawl and bongo net and attached to the upper spreader bar on the Kvichak trawl.

Sampling Design

A pilot study sampled the channel on the east side of San Juan Island in the spring of 2000. As part of an undergraduate research course, I collected 100 ichthyoplankton samples for a larval rockfish project. These data are referred to for comparison with results from my 2002 thesis research.

To determine which piece of gear would be more efficient a net comparison experiment was conducted. Thirty-four oblique hauls were conducted at 17 stations to

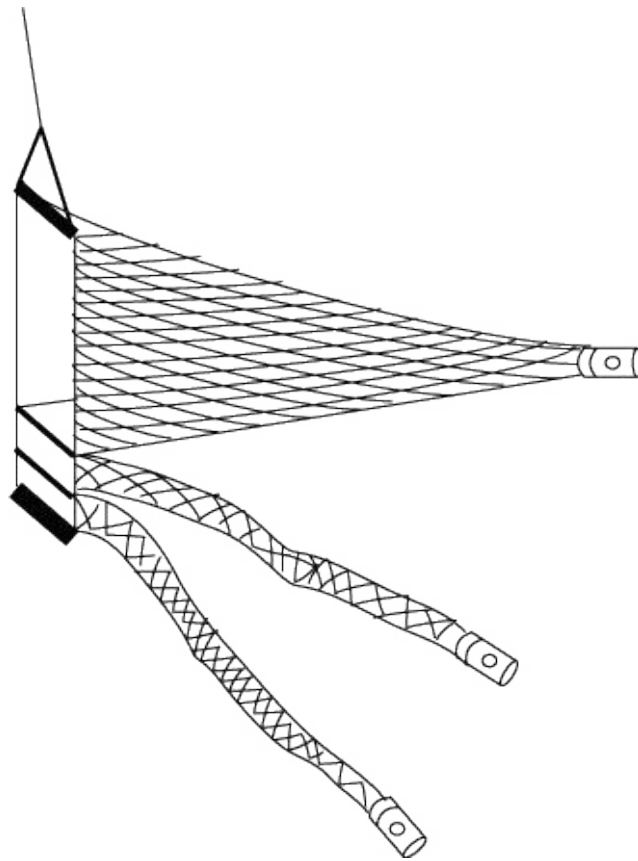


Figure 2. Tucker trawl with three separate nets that can be opened and closed at depth.

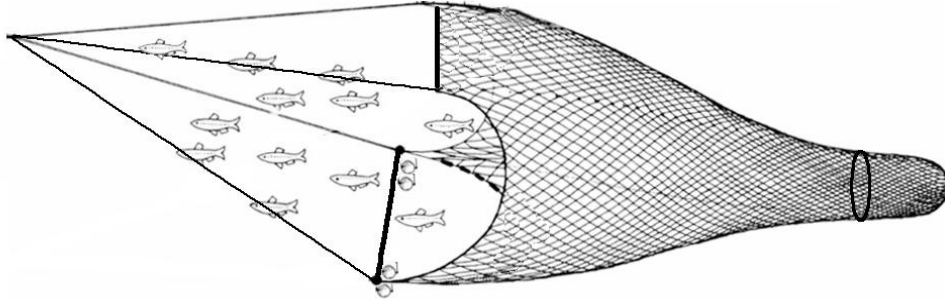


Figure 3. Kvichak Trawl, a midwater frame trawl designed for sampling juvenile fish.

compare the catch efficiencies of a 0.5 m Tucker trawl and a 0.62 m bongo net. One Tucker trawl net and both bongo nets were used for this experiment; each net had 500 μm mesh. Each Tucker trawl sample and one randomly selected bongo net sample was processed and compared pair-wise. In addition, samples were collected during the day and night to test for differences in catch values with time of day and depth.

I collected ichthyoplankton samples from 28 March to 26 July 2002. The survey area covered the length of San Juan Channel and the west side of San Juan Island and included four MPAs, two on each side of the island (University of Washington's Point George and Shady Cove biological reserves on the east side; San Juan County's Pile Point and Lime Kiln bottomfish recovery areas on the west side). A stratified random sampling design was used (Figure 4). The area was stratified by "inside" or "outside" of an MPA and by distance from shore ("inside" was defined as 0.5 km from MPA boundaries, "outside" included all data collected outside those areas). Distance from shore categories were approximately 0.0-0.5 km, 0.5-1.0 km and 1.0-4.0 km offshore. Starting positions for all hauls were selected randomly from within equally spaced 0.25 km^2 grid squares to try to sample the entire survey area.

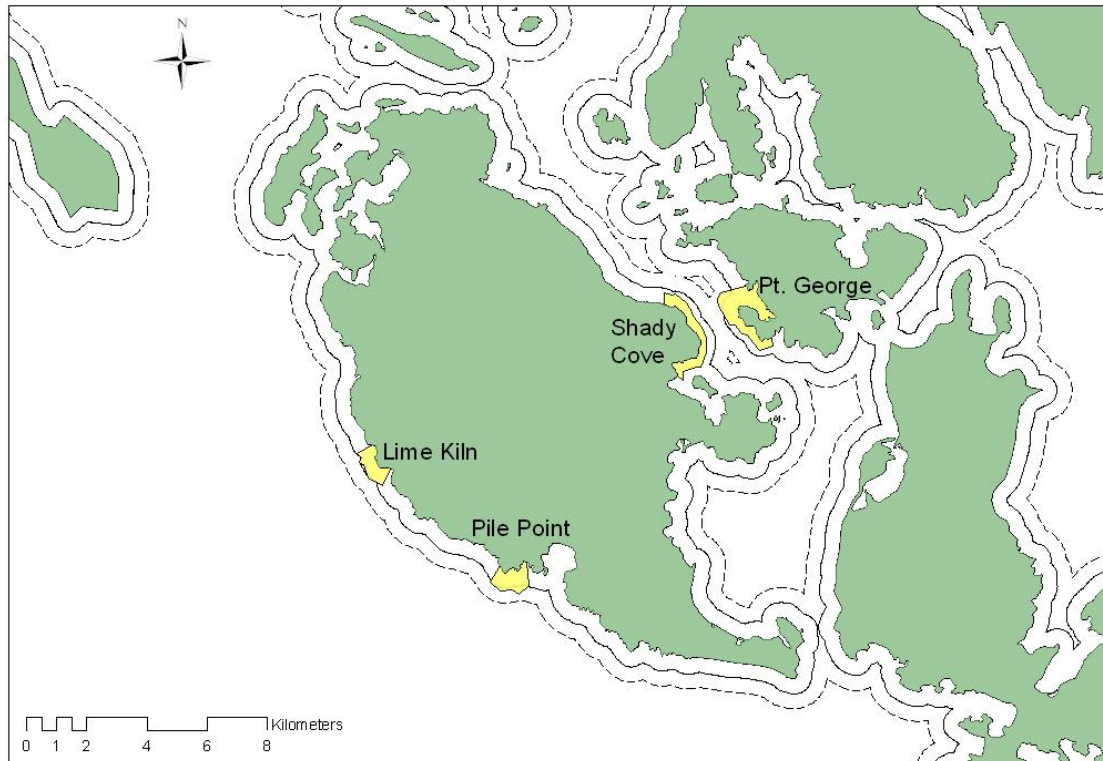


Figure 4. Stratified random sampling design. Haul positions were stratified by inside versus outside of an MPA and distance from shore. The four MPAs: Lime Kiln, Pile Point, Shady Cove and Point George, are outlined and shaded. Sampling was conducted in 0.25 km² grid squares throughout the entire study area and categorized by distance from shore. Distance from shore categories were from shore to 0.05 km (solid line), 0.5-1.0 km (dashed line), and greater than 1.0 km.

Towing Methods

Nearshore hauls were conducted as near and parallel to shore as possible. This was difficult because the Tucker trawl is relatively unwieldy and rocky outcroppings abound. All tows were made into the current when possible, and direction was determined by surface current patterns and tidal state. Once on station, the intended route was traversed, using the depth sounder to determine the bottom topography. Starting and ending positions were obtained using a hand-held GPS receiver. The minimum bottom depth minus 10 m was used as a maximum depth for the gear. When a maximum haul depth was determined and the boat was located at the starting point, position, time and flowmeter readings were recorded and the gear was submerged. Initially a few meters were let out quickly so the net cleared the propeller safely. Cable was then released one meter at a time in a stepped manner, with five seconds in between steps (only because the winch available did not allow continuous feeding out). When the maximum depth was reached, time and GPS coordinates were recorded again and the net was raised slowly and continuously. When making a discrete tow, a messenger was sent down the cable to close net 1 and open net 2 when the net reached desired depth and wire out. Discrete tows lasted five minutes after which the second messenger was sent (to close net 2 and open net 3) and the oblique tow was immediately resumed. Time and position were recorded every time a messenger was dropped. Depths for discrete tows were randomly selected from surface, 10, 20, and 30 m nearshore and surface, 10, 25, 50, 75 and 100 m for offshore stations as bottom depth permitted. Net depths were estimated based on wire

angles and meter wheel readings in the field. Kvichak sampling increased when Tucker catch rates declined (in late-May).

Sample Processing

At the completion of each haul, the nets and cod ends were rinsed from the outside and catches were transferred to 16 or 32 oz. plastic jars. Buffered formalin solution (37%) was then added to each jar to make a 5% solution.

In the lab, after a minimum of five days in formalin, samples were repeatedly rinsed with seawater (or freshwater if seawater unavailable) to remove as much formalin as possible. The plankton was then carefully sorted using a Bogoroff plankton sorting tray and a dissecting microscope. All fish larvae were counted and removed, and San Juan County bottomfish recovery species (rockfishes, lingcod, cabezon and greenlings) were individually separated. Standard lengths of rockfish were also digitally measured using a camera mounted on a dissecting scope and Image-Pro software. Processed larvae were all subsequently preserved in 70% ethanol.

All larvae targeted for this study were separated from the 587 samples and non-target fishes were sorted out for future identification. Since rockfish larvae greatly outnumbered other target groups, data analyses focused on this genus. Identifying rockfish larvae to species requires genetic techniques that are beyond the scope of this study. However, the rockfish caught are assumed to consist primarily of copper and quillback rockfish, as they are by far the most common adults in the area (DeLacy et al. 1972).

Data Analysis

For the gear comparison, a parametric paired t-test was performed on 17 paired samples to compare the efficiency of the Tucker trawl and bongo net. Catch rates were calculated by dividing numbers of individuals by the volume of water strained through each net (number per 1000 m³). All (non-Kvichak) hauls are included in the data analysis (n=475).

Initially, exploratory data analyses were conducted to evaluate the structure of the dataset. S-Plus and ArcGIS software were used to examine the frequency distribution, variance, and spatial trends in the data. A normal Q-Q plot and standardized residuals were used to examine distribution and variance patterns. Because of the non-normal distribution and convention with larval fish catch data, the data were fourth-root ($x^{1/4}$) transformed (Field et al. 1982).

ArcGIS (Johnston et al. 2001) software was used for all spatial and geostatistical analyses. Catch rates of rockfish, lingcod, greenling and cabezon at all sampling stations were first mapped as circles with sizes proportional to their values. The World Geodetic Survey (WGS) 1984 geometric coordinates were projected into the Universal Transverse Mercator (UTM) zone 10 coordinates. The data were divided into two categories for all further analysis: east and west of San Juan Island. This was necessary because the island naturally separates the survey area such that hauls on either side were independent of each other. Distances to shore and the nearest MPA were calculated for every haul using the spatial analyst extension in ArcGIS. Linear regressions tested for correlation between catch rates and distance from shore, distance from the nearest MPA, and gear depth.

Dispersal was examined by testing for an effect of time and space on catch rates and mean SL measurements. Two-dimensional probability plots illustrating a continuous surface of relative abundance and distribution were generated using inverse distance weighted interpolation (IDW) methods. IDW values were calculated using equation 1 where Z is the value being predicted, s is the location of the value, and λ are the weights assigned to each measured point.

$$\hat{Z}(s_0) = \sum_{i=1}^N \lambda_i Z(s_i) \quad (1)$$

This deterministic technique derives predictions for unsampled areas from the measured values surrounding them, giving more weight to the nearby points than those farther away. An underlying assumption for this process is that autocorrelation is present, and that catch rates close together are more similar than rates farther apart. This feature differentiates geostatistics from classical statistics, in which observations are assumed to be independent (Johnston et al. 2001). Autocorrelation was investigated by using the empirical semivariogram and covariance functions in ArcGIS. The semivariogram/covariance tool elucidates spatial relationships between pairs of points. If autocorrelation exists, pairs of hauls that are close together have lower squared differences than pairs located farther apart. A spatial-dependence model was fit to the measured data to estimate values for unsampled areas, creating an interpolated raster grid surface from which questions about larval dispersal and connectivity could be investigated. Larval rockfish standard lengths and geographic distribution over time were examined to investigate larval dispersion.

To test for a depth effect, only catches for discrete depth hauls were included (n=150). A bias toward shallow sampling occurred due to the reduced depth in many nearshore areas resulting in unequal sampling of the water column. The depth distribution data were binned into 20 m depth intervals and were standardized by number of tows. Linear regression of abundance as a function of distance from MPA, distance from shore and island side investigated any correlations between larval distribution and these features. All hauls with a starting point within 0.5 km of the boundary were defined as “inside” the effects of a particular MPA. All other hauls were “outside” and allocated to the east or west side of the island for comparison.

Results

The Tucker trawl and bongo net were found to be equivalent for rockfish and total fish catch rates ($p>0.2$). This is consistent with a comparative gear efficiency study for walleye pollock (*Theragra chalcogramma*) (Shima and Bailey 1994). The Tucker trawl became the primary sampling gear because of the relative ease involved in deploying it (the bongo requires a larger vessel). The Kvichak trawl did not effectively sample larval or juvenile rockfish (only 38 individuals in 119 hauls). However, it was very effective at catching gadid species (7,116 individuals in 119 hauls). Due to low rockfish catches, Kvichak analysis is included in appendix 1 rather than being addressed in the text. A total of 587 hauls (459 Tucker, 17 bongo, 119 Kvichak) were conducted for a combination of 436 oblique and 151 discrete tows.

The complete tally was 4,123 target larvae (3,833 rockfish, 234 greenlings, 48 cabezon and 8 lingcod) and 44,486 non-target larvae (51,602 including 7,116 Gadidae individuals caught in the Kvichak trawl) for a total of 55,725. In the 2000 pilot study, rockfish catches were also larger than the other three target species (1462 rockfish, 61 greenlings, 7 cabezon, and 1 lingcod). The possible rockfish species include copper and quillback (most common), black and yellowtail (spotty occurrence), tiger (uncommon), brown, China, splitnose (rare), and yelloweye rockfish (status unknown but likely uncommon) (Pacunski, personal communication). Invertebrate larvae comprised the majority of the biomass for all samples although they were not quantified. The most common groups represented were adult copepods (*Calanus marshallae* and *C. pacificus*), crab zoea (e.g. *Cancer magister* and *C. productus*), mysids, euphausiids, chaetognaths and

cnidarians (jellyfishes). Asteroidea, octopus, molluscs and polychaetes were also present in fewer numbers. Abundant non-target fish families and species included Gadidae (*Theragra chalcogramma*, *Microgadus proximus*, and *Gadus macrocephalus*), Cottidae, Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), Pleuronectidae and Paralichthyidae.

A histogram of larval rockfish catches revealed a negative binomial distribution, a high frequency of low numbers and a long tail of larger values. A Q-Q plot confirmed the non-normal distribution. The standardized residuals revealed non-constant variance in the raw data. The fourth-root ($x^{1/4}$) transformation resulted in a more normal Q-Q plot with constant variance in standardized residuals.

A bar graph of abundance over time with catches binned and averaged by week, shows a peak in rockfish larvae occurring in mid-April for 2000 and 2002, lasting three weeks (Figure 5). The abundance over time for lingcod, cabezon, and greenling is similar temporally but highly different in magnitude (Figure 6). Non-rockfish species were all caught in very low numbers (means for all three groups were <0.002 individuals per 1000 m^3). The timing of maximum catch rates for lingcod and greenling corresponded to the April peak for rockfishes; the occurrence of cabezon was extended, lasting from early April to mid-June. No further analyses were completed for non-rockfish groups because of the high occurrence of zero catches.

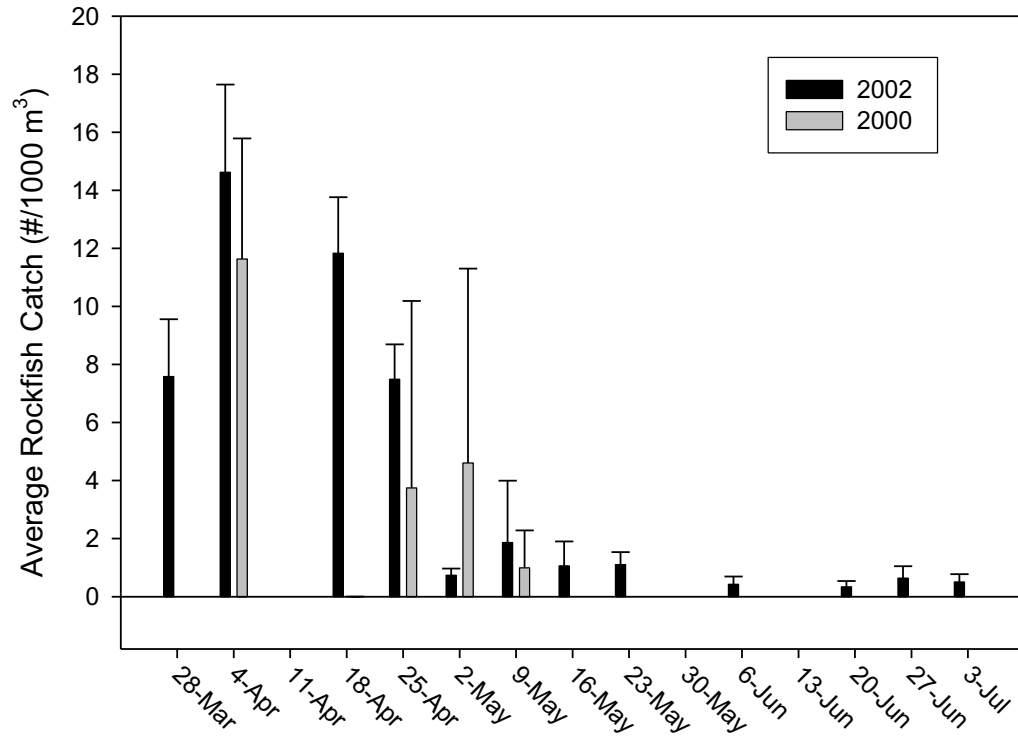


Figure 5. Rockfish larval catches shown as weekly averages (with standard error bars), as a function of haul date, for 2000 and 2002. Weeks without data indicates periods without hauls due to equipment failures or windy weather.

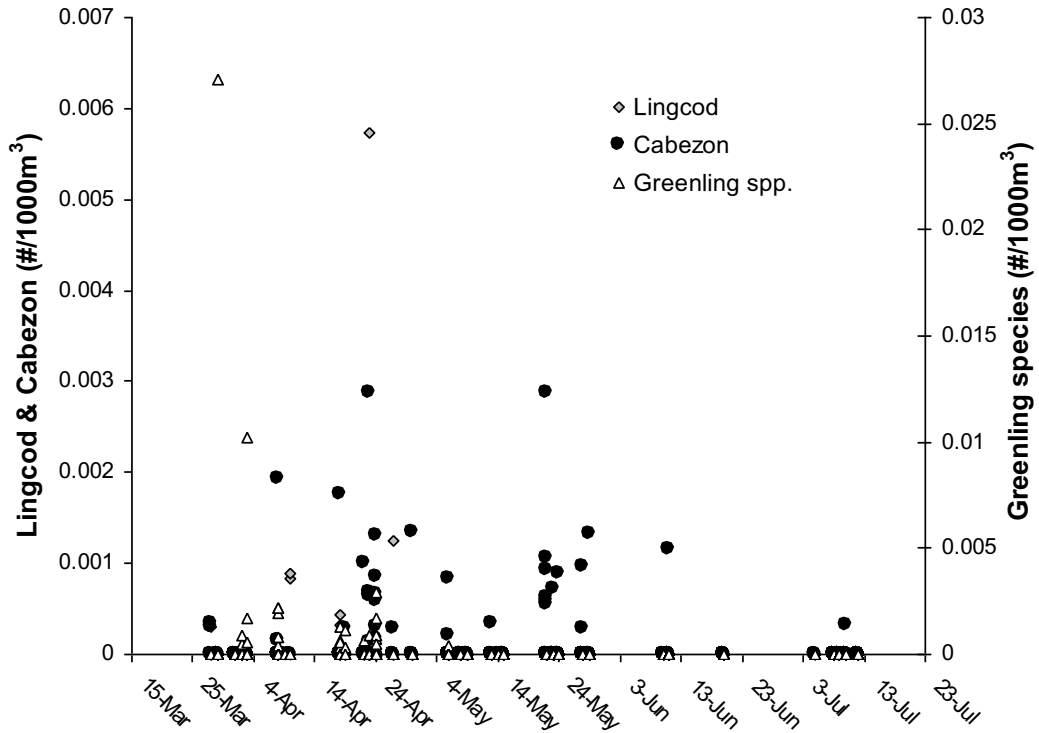


Figure 6. Lingcod, cabezon, and greenling catch values as a function of date. The highest catches for lingcod and greenling were in April while cabezon had a wider peak throughout April and May.

The spatiotemporal effect of MPAs on catch was difficult to examine. More than 98% of the larvae ranged in size from 4-6 mm SL throughout the survey period. The limited distribution of larval rockfish standard lengths over time precluded further analysis of dispersion. The size range indicates that larvae were recently extruded (Matarese et al. 1989). A linear regression revealed no effect of time on larval standard lengths ($p > 0.05$; $r^2 = 0$) and there was no apparent change in size ranges collected over the duration of the study (Figure 7).

Vertically, rockfish larvae were distributed throughout the sampled water column (up to 122 m), although there appeared to be a modest trend toward greater numbers of rockfish larvae occurring in the top 60 m of the water column. Linear regressions of catches illustrate no relationship between depth and abundance ($p > 0.05$; $r^2 = 0.04$), and an ANOVA examining catch as a function of depth in 20 m bins was also non-significant ($p > 0.05$; Figure 8). No effect of sampling distance from bottom on rockfish catch was found because a linear regression yielded a slope not significantly different from zero ($p > 0.05$; $r^2 = 0$). No differences were found in depth distributions and catch rates of larval rockfish collected between night and day ($p > 0.05$), so data were pooled over time of day to lend greater power to the statistical examination.

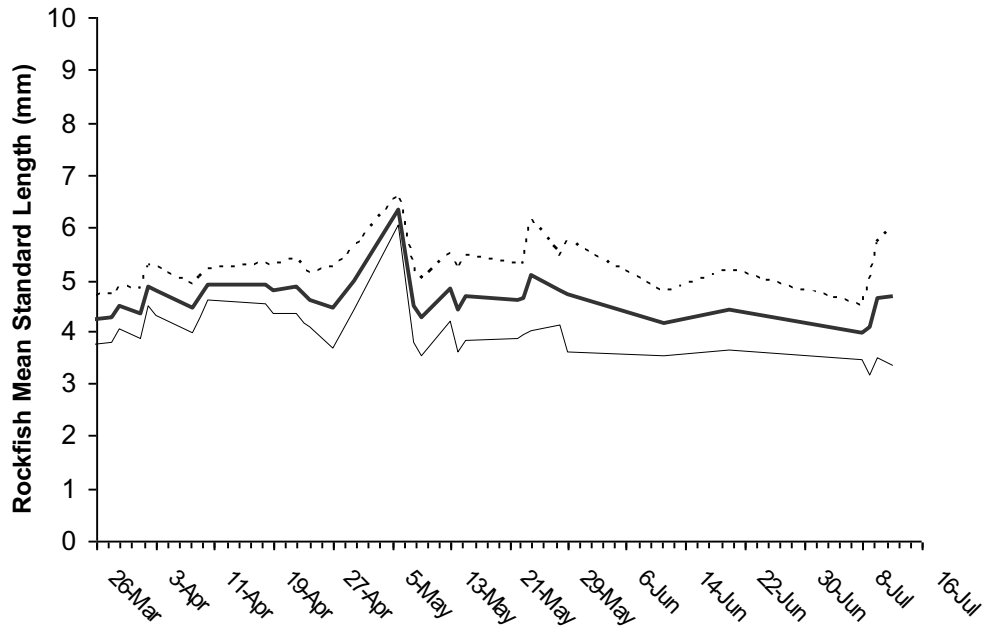


Figure 7. Mean rockfish standard lengths over time. The dashed lines represent one standard deviation above and below. The peak in standard lengths in early May is based on only three rockfish.

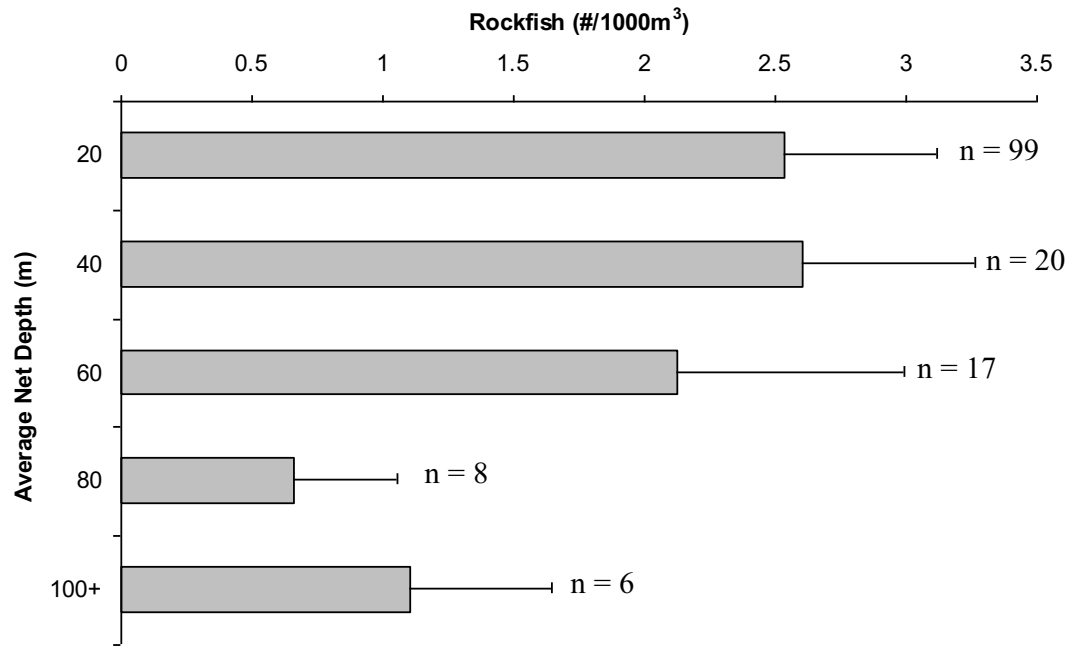


Figure 8. Rockfish catch is plotted on the x-axis with average net depth in 20 m intervals on the y-axis. Sample size and standard error bars are included. No significant stratification was found.

A two-way ANOVA revealed significant variation in catches from different sides of the island ($p < 0.05$). Catches were significantly higher on the west side. Proximity to MPAs was not a significant ($p > 0.05$) factor overall. Catches were significantly higher within 0.5 km of the boundary (“inside”) at Lime Kiln and significantly lower “inside” Pt. George and Shady Cove (Figure 9) resulting in a significant interaction effect between island side and MPA distance ($p < 0.05$). Since all MPAs are nearshore, effects of distance from MPA and distance from shore cannot be examined independently. Surface interpolation plots from IDW analysis (Figures 10, 11) show that densities were greater near MPAs on the west side. A shaded gradient represents the range of values from white representing zero catches to dark representing the highest catch values of 44 rockfish/1000 m³ for the west side and 32 rockfish/1000 m³ for the east).

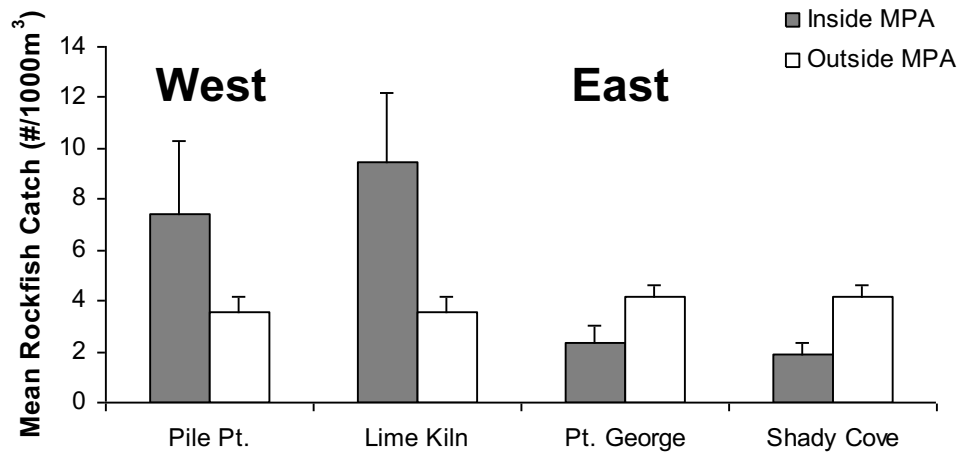


Figure 9. Plot of MPA effects divided by island side. The interaction between island side and MPA effect was significantly different from zero ($p < 0.05$).

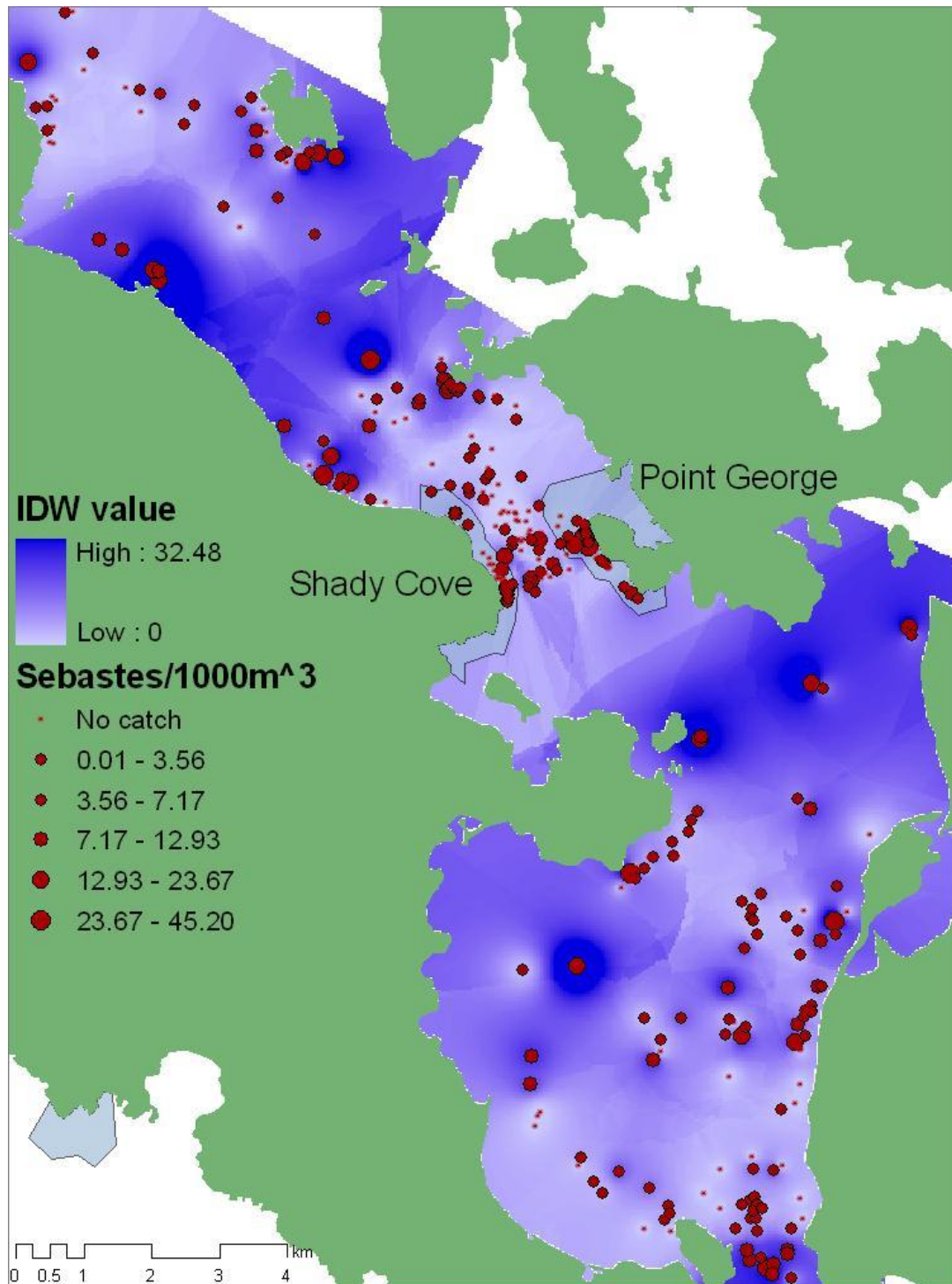


Figure 10. Inverse Distance Weighted rockfish densities for the east side of San Juan Island. The legend for catch size (points) was matched to west side values.

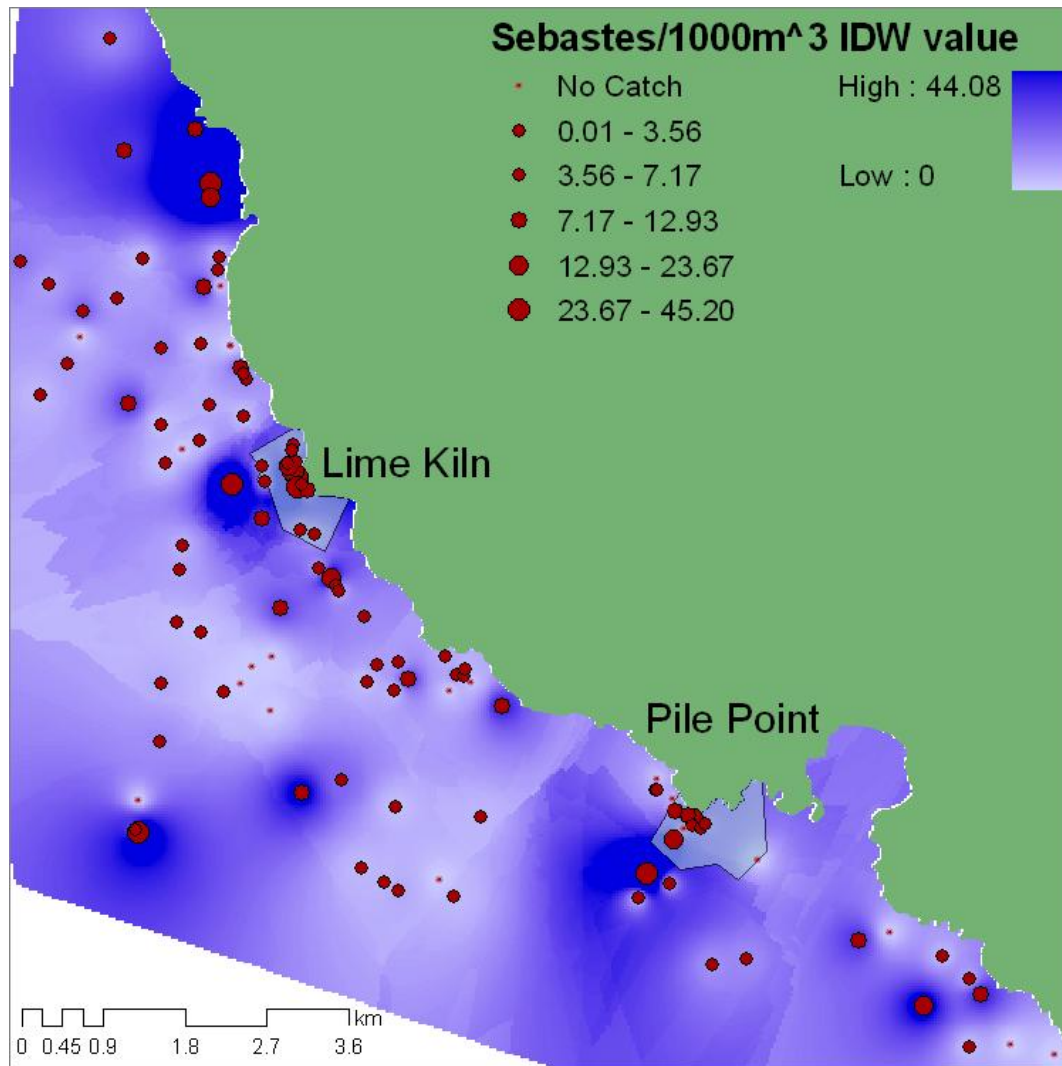


Figure 11. Inverse Distance Weighted rockfish densities for the west side of San Juan Island. High catch rates are dark while low catch are light.

Discussion

The target species for this study included lingcod, cabezon, and greenling species though few were caught. One explanation is that they exhibit surface-oriented behavior (Britt 2001). In contrast, rockfish larvae are not known to inhabit the neuston layer (Love et al. 2002). The sampling methods in this study did not target sampling the neuston layer. To sample the surface, the neuston net should have mounted near the bow to avoid the disturbing effect of the boat wake. Another factor affecting the paucity of cabezon larvae is a low density of adults in the area (Pacunski and Palsson personal communication December 20, 2003). These groups may also be more developed than rockfish at the time of sampling (Matarese et al. 1989) and thus better at gear avoidance. Greenlings were the second most abundant target group with 234 individuals caught. Nearly all of them were larger and better developed (primarily flexion or postflexion stages) than most of the rockfish larvae (nearly all preflexion). Kelp greenling adults are generally more abundant than either lingcod or cabezon in the area, as they are less sought after by fishers (Pacunski personal communication December 20, 2003).

Lingcod lay large egg masses in December-April which are paternally guarded (LaRiviere et al. 1981); yolk sac larvae hatch, entering the water column, in January-May. Cabezon spawn between January and March in British Columbia (Hart 1980). Kelp (*H. decagrammus*) and whitespotted (*H. stelleri*) greenling comprise the majority of the *Hexagrammos* species as pelagic larvae during the winter and spring months (Matarese et al. 1989) and they are the most common adults in the area (Pacunski personal communication). Masked (*H. octagrammus*) and rock (*H. lagocephalus*)

greenling are unlikely to be represented in this study. Masked greenling are uncommon in the San Juan Islands (Miller and Borton 1980); their range extends from British Columbia to Alaska (Matarese et al. 1989). Rock greenling spawn in June-August (Simenstad 1971). Because both kelp and whitespotted greenling could have had larvae in the water column during this study, the scarcity of catch supports the hypothesis that the gear failed to catch them due to their location or swimming speed.

Catch composition from the Kvichak trawl was very different from that of the Tucker or bongo nets. Visual acuity and swimming abilities of fish larvae improve significantly over short time periods with growth (Sugisaki et al. 2001). The low occurrence of larger larvae in the bongo and Tucker samples may be explained by their improved gear avoidance abilities. The Kvichak trawl captured larger individuals but in far lower numbers and the species composition was also different. Most notably the Kvichak caught 7,116 gadid larvae and only 38 rockfish larvae. The Kvichak trawl is more cumbersome, requiring a larger vessel, and cannot be used as near to shore or as close to the bottom as the Tucker trawl which might in part explain the differences. A habitat shift may also have occurred. Late larvae and juvenile fishes often switch from open water to more protected habitats (Love et al. 2002). Young copper rockfish settle out around macroalgae or eelgrass or close to the bottom when plant cover is absent (Love et al. 2002). Bull kelp (*Nereocystis luetkeana*) beds or high relief areas may serve as shelter in the San Juan Islands; these habitats are logistically difficult to survey and were not effectively sampled in this study. The Kvichak was also used later in the season, May-July rather than March-July. By mid-May Tucker catches of rockfish larvae

had declined (Figure 5) though Kvichak catches did not decline until early June (see Appendix 1). Differences in the timing of spawning for the assemblage of target and non-target species varies widely and may be another contributing factor. This temporal shift in sampling and the differences in gear and mesh size are likely responsible for most of the differences in catch composition between the Kvichak and Tucker trawls.

The temporal distribution of rockfish larvae (present from 28 March to 12 July, peaking in mid-April) is consistent between the pilot study in 2000 and 2002 and with the literature for parturition of the resident rockfish species (Table 1). In addition, proportions of other target species were similar as well for 2000 and 2002. Since at least eight species of rockfish release their larvae from March-August, and the larvae are not morphologically distinct, it was not possible to identify them in this study. It is worth noting that only three of the references (Table 1) include data from Washington (Hart 1980; Moulton 1975; Cooper 2003), and spawning periods in the study area could consequently differ from published results. However, a study of spawning copper rockfish found that few females were bearing young after the observed peak in larval rockfish (Cooper 2003). Puget Sound rockfish are common in the San Juan Islands but release their larvae in August-September (Moulton 1975) and thus they are unlikely to be present in this data set.

Table 1. Observed spawning times for rockfishes in the northeast Pacific.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Source
Copper				■									Hart 1973, Cooper 2003
Quillback				■	■	■							Love et al. 2002
Black	■	■	■	■									Westrheim 1975, Love et al. 2002
Yellowtail				■							■		Phillips 1964, Westrheim 1975
Tiger				■	■								Garrison and Miller 1982
Brown			■	■	■	■							Washington et al. 1978
China	■	■	■	■	■	■							Love et al. 2002
Splitnose				■	■	■	■	■	■				Hitz 1962, Hart 1973, Westrheim 1975
Yelloweye				■	■	■			■				Garrison and Miller 1982
Puget Sound				■				■	■				Moulton 1975

Since more than 98% of the rockfish were 4.0-6.0 mm SL, they probably were newly extruded larvae. Many northeast Pacific species, including the nine candidates in this study, are extruded at 3.6-6.7 mm SL (4.0-6.0 mm preserved) (Kendall personal communication). The small length range for the four-month duration of this study has three major implications. Since the larvae are virtually all newly extruded, they were collected near parturition in space and time. This is important because it reveals where and when females are releasing larvae. Second, the protracted period of collection of rockfish larvae (Figure 5) is evidence of multiple species releasing larvae from March-July. It is improbable that only one or two species is releasing larvae over a six-month period in the same area. Last, dispersal patterns cannot be inferred from these data. A wider range of sizes is required to detect direction and extent of larval transport.

The low catch rates of late-larval rockfish may also be due to increased mortality. Rockfish larvae are extruded with yolk sacs that are already utilized or become absorbed within a few days (Matarese et al. 1989). After the transition to an exogenous feeding state, they are highly vulnerable to starvation and predation. The mean mortality rate for marine fish larvae is estimated at 21.3% day⁻¹ (M=0.24) (Houde and Zastrow 1993) with some species as high as 50% day⁻¹ (Fuiman and Werner 2002). Their survival requirements are rapidly changing and continuously urgent; their ability to withstand starvation is very limited (Fuiman and Werner 2002). The abundance of large larvae is thus expected to be highly reduced.

The observed uniform vertical distribution of rockfish larvae could be evidence of their limited swimming abilities and a well-mixed water column. Previous research suggests they do not exhibit vertical migration (Love et al. 2002) but instead may be transported by hydrographic forces. This apparent lack of active transport may be due to the relatively undeveloped state of small rockfish larvae, but swimming ability tests have not been done. Though they have functional eyes, jaws and pectoral fins at extrusion, yolk sacs are still present (Matarese et al. 1989) and they tend to be fragile. The other target species are all demersal spawners. Demersally spawned larvae generally enter the plankton in more advanced stages than larvae spawned in the water column and could vertically migrate (Carr and Reed 1993). Lingcod and greenling larvae are larger and more developed at the same age. Lingcod hatch at 7-10 mm SL; the greenling species all hatch at 7-9 mm SL (Matarese et al. 1989). As mentioned previously, lingcod and greenling have been observed to vertically migrate (Britt 2001).

The significant interaction effect between island side (east/west) and location inside or out of MPAs from the ANOVA suggests that the dynamics of larval distribution vary across the island. When examined spatially, MPAs on the west side had significantly higher densities of larvae than non-reserve areas while east side MPAs had significantly lower densities than non-reserve areas. The differences in catch rates would be predicted if MPAs have larger individuals or more individuals producing larvae on the west side than on the east side. Higher mortality due to limited food supply could contribute to the lower larval catches on the east side. This is unlikely because the larvae were generally too small for starvation to be a factor. While the data suggest Lime Kiln

and Pile Point could be dispersing as well as accumulating larvae (Figure 11), long distance dispersal seems to be the primary mechanism operating near Shady Cove and Point George (Figure 10) assuming larval production is greater inside these MPAs. Since all MPAs in the San Juan Islands are adjacent to shore, it is not possible to examine these effects independently.

Many factors contribute to the spatial distribution of fish larvae. Some fish are believed to spawn at specific times and places to utilize distinct circulation patterns (the larval retention or member/vagrant hypothesis) though direct evidence is often lacking (Fuiman and Werner 2002). Larval behavior may be a contributing factor to spatial distribution patterns. It is possible that larvae use boundary layers or vertical migration to position themselves in the water column (Roberts and Polunin 1991). Larval fish of several species seem to have the ability to exhibit active transport, placing themselves near natal reefs or other features (Marliave 1986; Brogan 1994; Jones et al. 1999; Swearer et al. 1999; Taylor and Hellberg 2003) though this has not been observed for rockfish and is not apparent from their vertical distribution (Figure 8). Areas of larval accumulation may also mean that local scale oceanographic processes entrain larvae in those areas coincidentally.

The oceanographic forces in the San Juan Islands are highly influential in local patterns. Located at the confluence of Puget Sound, the Strait of Juan de Fuca and the Strait of Georgia (the Northwest Straits), the region is subject to highly variable conditions. Tidally driven currents, freshwater input from the Fraser River and Puget Sound, and complex bottom topography all contribute to the dynamic oceanography. On

both sides of the island, prevailing currents flow north during flood tide and south during ebb tides. The large variation in the magnitude of tides makes current dynamics difficult to predict (Zamon 2001; Zamon 2002). Eddies often occur when strong currents flow past the headlands of the island creating upwelling systems for both nutrients and passive particles (Zamon 2001; Zamon 2002).

Hydrographic features such as eddies and convergence fronts are often persistent on scales relevant to larval duration (Ebbesmeyer et al. 1991), influencing biological characteristics of marine systems (Zamon 2002). Mixing of reef waters can be a major cause of particle retention (Black et al. 1991). Currents were shown to have a major impact in an extensive drift card study in the Northwest Straits region 1999; 70% of recoveries occurred on only 15% of the shorelines (Klinger and Ebbesmeyer 2001). There are several prominent tidal eddies in the eastern Strait of Juan de Fuca, and one is located directly off the west side of San Juan Island (Ebbesmeyer et al. 1991). Eddy formation and dissipation may alternately aggregate and distribute propagules on a regular basis. Local physical oceanography is likely to influence meroplanktonic organisms and populations in this area greatly.

San Juan Island currents, MPAs, and rockfish larval dynamics resulted in a wide distribution throughout the study area. A single spatial pattern was not observed, instead areas of high abundance were interspersed with areas having consistently low catch rates. This provides insight into the level of potential dispersal pathways between release and settlement areas. The potential for reserves to enhance fished stocks depends heavily on pathways of larval dispersal (Roberts and Polunin 1991). Understanding more about

larval transport patterns will facilitate the identification of larval linkages between sites. Nearshore accumulation of larval fishes has been observed in several studies (Marliave 1986; Brogan 1994; Jones et al. 1999) and could result in a “closed” system with little dispersal (Cowen et al. 2000). However, the broad distribution of rockfish larvae suggests dispersal and a potentially high degree of connectivity between sites in the San Juan Islands. With both accumulation and dispersal occurring, networks of MPAs are expected to provide greater benefits than individual, isolated reserves (Roberts 1995; Pacunski and Palsson 2001). The existing MPAs are capable of supplying larvae to and receiving larvae from other sites in the Northwest Straits region (Klinger and Ebbesmeyer 2001). Because rockfish are territorial, well-connected MPAs could serve as an extremely useful management strategy given the strong currents of the SJIs.

Understanding direct and indirect effects of protecting particular species within a reserve is fundamental to reserve design (Carr and Reed 1993). Reserve placement must be carefully planned because habitat requirements vary according to species and life history stage. Ideally, MPAs protect a range of habitats suitable for multiple species and developmental stages (Crowder et al. 2000). On the east side of San Juan Island, fewer larvae were found in and around MPAs which may also be an indirect result of protecting more large fish, which could also increase the predation pressure (Paddack and Estes 2000; Planes et al. 2000). More likely, comparatively low numbers of larvae may be the result of transport by swift currents due to differences in geology and resulting oceanography rather than a negative consequence of protected designation. The east side is a channel approximately 20 km long, 1.2-6.0 km wide with complex topography

reaching approximately 185 m in depth. The west side is a comparatively open water region with the nearest mainland about 10 km away and depths reaching more than 300 m. Flow is far more restricted and turbulent in the channel thus larval fishes are generally subject to greater physical forces on the east side. It is possible that high current velocities might simply limit the effectiveness of the gear. Rockfish larvae may be less abundant or simply may be dispersed more quickly.

Location is another key component to MPA success because habitat suitability can vary dramatically. The San Juan Islands are characterized by high relief rocky reefs and intermittent kelp beds interspersed with shallow soft-bottom stretches with eelgrass (*Zostera marina* and *Z. japonica*) (WADNR shorezone inventory). The target species in this study are all associated with complex, rocky substrate as adults (Pacunski and Palsson 2001). Point George and Shady Cove MPAs were created for university research purposes while the San Juan County MPAs were selected because they were formerly good fishing spots for rockfish and lingcod. Adult and sub-adult copper rockfish were patchily distributed along San Juan Island shores in surveys conducted by the WDFW in 1994 and 2000 (Palsson personal communication December 16, 2003.). In both years, they were present at three of the four MPAs, absent only at Shady Cove.

Mark-recapture, trace element analysis, and genetic mapping can be used to address the questions of larval dispersal directly. Embryonic larvae could be chemically marked, locations of spawning females could be identified, and subsequent sampling could provide definitive information on dispersal. This has successfully been done with a damselfish species (Jones et al. 1999) but they lay demersal eggs and are not live-

bearers. Handling pregnant rockfish frequently causes them to spawn prematurely, making this method difficult (Matarese et al. 1989). Trace element analysis of larval otoliths may reveal geographic signatures identifying their origins. This would be more appropriate for fish that utilize estuaries, since rivers can have distinct trace element concentrations (Thorrold et al. 1998; Forrester and Swearer 2002). Modeling has shown genetic analyses can also provide direct measures of larval dispersal (Palumbi 2003). By creating genetic maps of larvae and adults, the data could measure correlation and distribution over time. Some research has been done on adult copper rockfish finding significant genetic divergence among North American coastal populations which indicates limits to migration and/or dispersal (Buonaccorsi et al. 2002). Examining genetic relatedness of larvae and adults within the same populations is the next step and would contribute greatly to knowledge of larval dispersal. Measuring dispersal requires high resolution knowledge of the currents and additional techniques to track planktonic dispersal.

Conclusions

The objectives of this study were twofold: to determine whether larval rockfish production was greater in and around MPAs and whether dispersal patterns could be detected. My methodology also describes an adequate sampling protocol for monitoring larval abundance with results presented. A stratified random sampling design with high frequency sampling and a large spatial extent provides a representation of larval distribution. This study suggests larval production was greater near Pile Point and Lime Kiln MPAs on the west side of San Juan Island but not for the MPAs on the east side.

Dispersal patterns could not be described in this study. To measure dispersal, the hydrography of the SJIs must be quantified because currents guide direction and extent of larval dispersal. This study provides a valuable map of larval rockfish distribution patterns both spatially and temporally but techniques to trace larvae from parturition to settlement are required to fully examine dispersal.

References

- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8(1):S79-S92.
- Black, K. P., P. J. Moran, and L. S. Hammond. 1991. Numerical models show coral reefs can be self-seeding. *Marine Ecology Progress Series* 74:1-11.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4(2):144-150.
- Britt, L. L. 2001. Aspects of the vision and feeding ecology of larval lingcod (*Ophiodon elongatus*) and kelp greenling (*Hexagrammos decagrammus*). Master's Thesis. University of Washington, Seattle, Washington.
- Brogan, M. W. 1994. Distribution and retention of larval fishes near reefs in the Gulf of California. *Marine Ecology Progress Series* 115:1-13.
- Buonaccorsi, V. P., C. A. Kimbrell, E. A. Lynn, and R. D. Vetter. 2002. Population structure of copper rockfish (*Sebastes caurinus*) reflects a postglacial colonization and contemporary patterns of larval dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* 59(8):1374-1384.
- Carr, M. H. and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2019-2028.
- Cooper, D. 2003. Possible differences in copper rockfish (*Sebastes caurinus*) fecundity and parturition with maternal size and age. Master's Thesis. University of Washington, Seattle, Washington.
- Cowen, R. K., K. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olsen. 2000. Connectivity of marine populations: open or closed? *Science* 287:857-859.
- Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66(3):799-820.
- DeLacy, A. C., B. S. Miller, and S. F. Borton. 1972. Checklist of Puget Sound fishes. Division of marine resources, University of Washington, Seattle, Washington.
- Dygert, P. H. and D. R. Gunderson. 1991. Energy utilization by embryos during gestation in viviparous copper rockfish, *Sebastes caurinus*. *Environmental Biology of Fishes* 30:165-171.

- Ebbesmeyer, C. C., C. A. Coomes, J. M. Cox, and B. L. Salem. 1991. Eddy induced beaching of floatable materials in the Eastern Strait of Juan de Fuca. *Puget Sound Research '91 Proceedings* 1:86-98.
- Edgar, G. J. and N. S. Barrett. 1997. Short term monitoring of biotic changes in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology* 213:261-279.
- Eisenhardt, E. 2002. Effect of the San Juan Islands marine preserves on demographic patterns of nearshore rocky reef fish. Master's Thesis. University of Washington, Seattle, Washington.
- Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8(1):37-52.
- Forrester, G. E. and S. E. Swearer. 2002. Trace elements in otoliths indicate the use of open-coast versus bay nursery habitats by juvenile California halibut. *Marine Ecology Progress Series* 241:201-213.
- Fuiman, L. A. and R. G. Werner, editors. 2002. *Fishery science: the unique contributions of early life stages*. Blackwell Science Limited, Oxford.
- Garrison, K. J. and B. S. Miller. 1982. Review of the early life history of Puget Sound fishes. Report of the University of Washington Fisheries Research Institute to the National Marine Fisheries Service, Seattle, Washington.
- Gunderson, D. R. 1993. *Surveys of fisheries resources*. John Wiley and Sons, Inc., New York.
- Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries* 8:251-272.
- Haldorson, L. and M. Love. 1991. Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. *Marine Fisheries Review* 53(2):25-31.
- Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13(1):S117-S137.
- Halpern, B. S. and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. *Ecology Letters* 5:361-366.
- Hart, J. L. 1980. *Pacific fishes of Canada*. Minister of supply and services Canada, Ottawa.
- Hastings, A. and L.W. Botsford. 1999. Equivalence in yield from marine reserves and

- traditional fisheries management. *Science* 298:1537-1538.
- Hitz, C. R. 1962. Seasons of birth of rockfish (*Sebastes* spp.) in Oregon coastal waters. *Transactions of the American Fisheries Society* 91:231-233.
- Houde, E. D. and C. E. Zastrow. 1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science* 53:290-335.
- Johnston, K., J. M. Ver Hoef, K. Krivoruchko, and N. Lucas. 2001. Using ArcGIS geostatistical analyst. ESRI, USA.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402:802-804.
- Kendall, A. W. and S. J. Picquelle. 2003. Marine protected areas and the early life history of fishes. NOAA Alaska Fisheries Science Center, Report 2003-10, Seattle, Washington.
- Klinger, T. 2000. Potential larval linkages within the Juan de Fuca region of Washington State. Report prepared for the Environmental Defense Fund, New York.
- Klinger, T. and C. Ebbesmeyer. 2001. Using oceanographic linkages to guide marine protected area design. Puget Sound Research. Puget Sound Action Team, Olympia, Washington.
- LaRiviere, M. G., D. D. Jessup, and S. B. Mathews. 1981. Lingcod, *Ophiodon elongatus*, spawning and nesting in San Juan Channel, Washington. *California Department of Fish and Game* 67:231-239, San Francisco.
- Lauk, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8(1):S72-S78.
- Leaman, B. M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environmental Biology of Fishes* 30:253-271.
- Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the northeast Pacific. University of California Press, Berkeley.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* 13(1):S3-S7.

- Marliave, J. B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions of the American Fisheries Society* 115:149-154.
- Martell, S., C. J. Walters, and S.S. Wallace. 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *Bulletin of Marine Science* 66(3):729-743.
- Matarese, A. C., A. W. Kendall, D. M. Blood, and B. M. Vinter. 1989. Laboratory guide to early life history stages of Northeast Pacific fishes. National Marine Fisheries Service, NOAA Technical Report 80, Seattle, Washington.
- Matthews, K. R. 1990. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. *Fishery Bulletin* 88(2):223-239.
- McClanahan, T. R. and B. Kaunda-Arara. 1996. Fishery recovery in a coral reef marine park and its effect on the adjacent fishery. *Conservation Biology* 10(4):1187-1199.
- Miller, B. S. and S. F. Borton. 1980. Geographical distribution of Puget Sound fishes: maps and data source sheets, Volume 2. Washington Sea Grant Program and Washington State Department of Ecology, 219 pp.
- Morgan, L. E. and L. W. Botsford. 1998. The influence of larval transport and retention on recruitment patterns and the design of harvest refugia for rockfish. National Marine Fisheries Service, NOAA Technical Report NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Mosquera, I., I. M. Côté, S. Jennings, and J. D. Reynolds. 2000. Conservation benefits of marine reserves for fish populations. *Animal Conservation* 3:321-332.
- Moulton, L. L. 1975. Life history observations on the Puget Sound rockfish, *Sebastes emphaeus*. *Journal of the Fisheries Resources Board of Canada* 32:1439-1442.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A. McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* 24(11):11-25.
- Musik, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, E. L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, S. J. Parker, S. G. Poss, P. Sala, T. W. Schmidt, G. R. Sedberry, H. Weeks, and S. G. Wright. 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25(11):6-30.

- Myers, R. A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280-283.
- North, E. W. and E. D. Houde. 2000. Time, space, food and physics: the temporal and spatial distribution of anadromous fish larvae in an estuarine turbidity maximum. *ICES Journal of Marine Science* 23:1-17.
- Pacific Fishery Management Council (PFMC). 2003. Groundfish stock assessments. Available: <http://www.pcouncil.org/groundfish/gfstocks.html>.
- Pacunski, R. E. and W. A. Palsson. 2001. Macro- and micro-habitat relationships of adult and sub-adult rockfish, lingcod, and kelp greenling in Puget Sound. Puget Sound Research. Puget Sound Action Team, Olympia, Washington.
- Paddack, M. J. and J. A. Estes. 2000. Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications* 10(3):855-870.
- Palumbi, S. R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(1):S146-S158.
- Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). 2002. The Science of Marine Reserves. Available: <http://www.piscoweb.org>. 22 pp.
- Pauly, D., V. Christensen, S. Gu nette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson and D. Zeller. 2002. Toward sustainability in world fisheries. *Nature* 418: 689-695.
- Pew Oceans Commission. 2003. A report to the nation: recommendations for a new ocean policy, Report to the U.S. Congress and citizens, Arlington, Virginia.
- Phillips, J. B. 1964. Life history studies of ten species of rockfish (genus *Sebastes*). California Department of Fish and Game 126:70 pages.
- Planes, S., R. Galzin, A. G. Rubies, R. Go ni, J. Harmelin, L. L. Dir ach, P. Lenfant, and A. Quetglas. 2000. Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. *Environmental Conservation* 27(2):126-143.
- Puget Sound Action Team. 2002. Puget Sound Update. Available: http://www.psat.wa.gov/Publications/update_02/ps_update_2002-sec.pdf
- Richardson, S. L. and W. G. Pearcy. 1977. Coastal and oceanic upwelling off Yaquina Bay, Oregon. *Fishery Bulletin* 75:125-145.

- Roberts, C. M. 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. *Conservation Biology* 9(4):815-826.
- Roberts, C. M., J.A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294(5548):1920-1923.
- Roberts, C. M. and J. P. Hawkins. 1999. Extinction risk at sea. *Trends in Ecology and Evolution* 14(6):241-246.
- Roberts, C. M. and N. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* 1:65-91.
- Russ, G. R. and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Marine Ecology Progress Series* 132(1-3):1-9.
- Shenker, J. M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. *Fishery Bulletin* 86:299-317.
- Shima, M. and K. M. Bailey. 1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye pollock (*Theragra chalcogramma*). *Fisheries Oceanography* 3(1):50-59.
- Simenstad, C. A. 1971. The feeding ecology of the rock greenling, *Hexagrammos lagocephalus* in the inshore waters of Amchitka Island, Alaska. Master's Thesis. University of Washington, Seattle, Washington.
- Soh, S., D. R. Gunderson, and D. H. Ito. 2001. The potential role of marine reserves in the management of shortraker rockfish (*Sebastes borealis*) and rougheye rockfish (*S. aleutianus*) in the Gulf of Alaska. *Fishery Bulletin* 99:168-179.
- Starr, R. M., M. H. Carr, J. Caselle, J. A. Estes, C. Syms, D. A. VenTresca, and M. M. Yoklavich. 2002. A review of the ecological effectiveness of subtidal marine reserves in central California, Part II. Report to the Monterey Bay National Marine Sanctuary, Monterey Bay, California.
- Stoner, A. W and M. Ray. 1996. Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. *Fishery Bulletin* 94:551-565.
- Sugisaki, H., Bailey K., and R. Brodeur. 2001. Development of the escape response in larval walleye pollock (*Theragra chalcogramma*). *Marine Biology* 139(1):19-24.
- Swearer, S. E., J. E. Caselle, D. W. Lea, R. R. and Warner. 1999. Larval retention and recruitment in an island population of a coral reef fish. *Nature* 402:799-802.

- Taylor, M. S. and M. E. Hellberg. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* 299:107-109.
- Thomson, R. E. 1981. Oceanography of the British Columbia Coast. Department of Fisheries and Oceans, Report 56, Ottawa.
- Thorrold, S. R., C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 1998. Trace element signatures in otoliths record natal river of juvenile American shad (*Alosa sapidissima*). *Limnology and Oceanography* 43:1826-1835.
- Valles, H., S. Sponaugle, and H. A. Oxenford. 2001. Larval supply to a marine reserve and adjacent fished area in the Soufrière Marine Management Area, St. Lucia, West Indies. *Journal of Fish Biology* 59(Supplement A):152-177.
- Washington State Department of Natural Resources (WADNR). 2002. Washington State shorezone inventory. Available:http://www2.wadnr.gov/nearshore/research/projectpages.asp?pagename=shorezone_page1&id=9
- Washington, P. M., R. Gowan, and D. H. Ito. 1978. A biological report on eight species of rockfish (*Sebastes* spp.) from Puget Sound, Washington. National Marine Fisheries Service, NOAA Proceedings Report of the Northwest Alaska Fisheries Center, Seattle, Washington.
- Westrheim, S. J. 1975. Reproduction, maturation and identification of larvae of some *Sebastes* (Scorpaenidae) species in the Northeast Pacific Ocean. *Journal of the Fisheries Resources Board of Canada* 32:2399-2411.
- Yoklavich, M. M. and V. J. Loeb. 1996. Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event, 1991-1993. *Fishery Bulletin* 94:766-782.
- Zamon, J. E. 2001. Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography* 10:353-366.
- Zamon, J. E. 2002. Tidal changes in copepod abundance and maintenance of a summer *Coscinodiscus* bloom in the southern San Juan Channel, San Juan Islands, USA. *Marine Ecology Progress Series* 226:193-210.

Appendix 1: The Kvichak Trawl

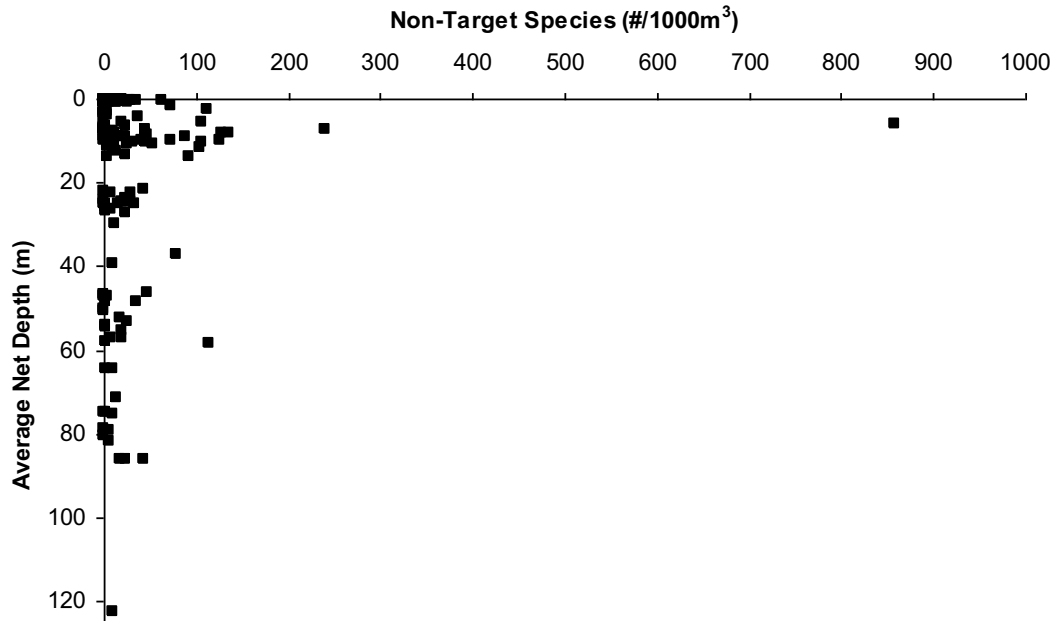
The Kvichak trawl is a specialized frame type, mid-water gear designed for sampling juvenile salmonids in Alaskan waters. It is towed by a single bridle attached to a spool of cable, strung through an elevated pulley from one vessel (Appendix 1a). Four cables run from the bridle to each corner of the mouth. The net is attached to two horizontal metal bars that frame the opening. Two steel balls are suspended from each end of the lower bar. The mouth area is rectangular and measures 2.0 m x 1.8 m. The mesh is largest near the mouth, decreasing gradually to the zippered cod end. The Kvichak trawl was deployed experimentally in this study to catch large rockfish larvae and juveniles. Sampling took place throughout the survey area, east and west of San Juan Island, from May 20 to July 26, 2002. Hauls were conducted for 10 minutes at depths of 10, 15, 25, 50, 75 and 100 m. Each depth was not sampled every time per station. Depths were randomly selected before each day of sampling.

The Kvichak did not effectively sample rockfish or any other target species. Only 38 rockfish and one cabezon larvae were caught in 119 hauls. It was successful at catching Gadidae species; 7,116 were caught. Though not identified to species, the most likely candidates are Pacific tomcod (*Microgadus proximus*), walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) as they are the only known gadids in the San Juan Islands. Other than gadids and target species, 7,538 other fish larvae were sampled with the Kvichak for a total of 14,694 fish larvae.

Appendix 2: Non-target Species Results (Tucker and Bongo)

Non-target species comprised 90% of the total catch, numbering 36,948 larvae. Three individuals were not identified as target or non-target due to their damaged state. They were excluded from analyses. The families and species most commonly represented in the samples were Gadidae (*Theragra chalcogramma*, *Microgadus proximus*, and *Gadus macrocephalus*), Cottidae, Pacific hake (*Merluccius productus*), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), Pleuronectidae and Paralichthyidae. Their abundance peaked in late-April (slightly later than the peak in rockfish) (Appendix 2a). Depth did not affect their vertical distribution (Appendix 2b). These results are based on a broad category including the full gamut of ecological characteristics, linked only by what the larvae are not. Without biological context, there may be little meaning to the results.

Invertebrates were a large component of most samples throughout the survey. Though not quantified, the most common groups represented were adult copepods (*Calanus marshallae* and *C. pacificus*), crab zoea (e.g. *Cancer magister* and *C. productus*), mysids, shrimp, chaetognaths and cnidarians (jellyfishes). Asteroidea, octopus, molluscs and polychaete worms were also present in fewer numbers.



Appendix 2b. Non-target catch rates are shown on the x-axis with the average net depth in meters on the y-axis. Most catch values were less than 125 larvae/1000m³. The outlier is haul 111.2 (858 larvae/1000m³) for which the water volume sampled was estimated due to an error in the flowmeter reading. It may be an overestimate.