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Habitat Associations and Distribution of Widow Rockfish, *Sebastes entomelas*, with Implications for Marine Reserve Design

by

Julie Ann Reynolds

B.A. (Pomona College) 1990
M.S. (University of California, Davis) 1994

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy
in
Integrative Biology

in the
Graduate Division
of the
University of California, Berkeley

Committee in charge:

Dr. Thomas M. Powell, Chair
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Fall 2001

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Habitat Associations and Distribution of Widow Rockfish, *Sebastes entomelas*, with Implications for Marine Reserve Design

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by

Julie Ann Reynolds

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Abstract

Habitat Associations and Distribution of Widow Rockfish, *Sebastes entomelas*, with Implications for Marine Reserve Design

by

Julie Ann Reynolds

Doctor of Philosophy in Integrative Biology
University of California, Berkeley

Dr. Thomas M. Powell, Chair

In this dissertation, I address fundamental ecological issues concerning widow rockfish (*Sebastes entomelas*) habitat use and distribution, which can be used as the foundation for appropriate marine reserve design. Although widow rockfish is one of the most commercially important rockfish species on the US West Coast, no previous work has specifically addressed the habitat requirements of this species. In **Chapter One**, I identify significant habitat associations between widow rockfish and three habitat variables; bottom depth, vertical depth of fish in the water column, and temperature. My results indicate that the average significant habitat association for widow rockfish includes bottom depths between 136-298 m, vertical depths between 101-197 m, and temperatures between 7.1-8.1°C. These results provide useful insights towards the definition of essential fish habitat (EFH) for this species.

In **Chapter Two**, I address fluctuations in habitat use through time. I detected no significant interannual, seasonal, or intraannual variation in the range of bottom depths preferred by widow rockfish, but I did detect a significant correlation between bottom depth and vertical depth. Fish are further off the bottom at deeper bottom depths, and this

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relationship varies significantly by season. Understanding the ecological phenomenon affecting this behavior could provide us with additional insight into the ecology and habitat requirements of this species. Finally, in **Chapter Three**, I investigated widow rockfish distribution, and changes through time. I detected three significant annual shifts in the spatial distribution within an 11-year time series (1988-1998), corresponding to the two major El Niño events that occurred within this time frame.

My results have the following implications for marine reserves design. First, the habitat encompassed in any marine reserve(s) designed for widow rockfish conservation must include the range of bottom depths and temperatures significantly associated with its distribution. Second, the marine reserve(s) should encompass both the inshore and offshore components of widow rockfish habitat. Finally, a single reserve may not afford equal protection to this species, particularly with regard to El Niño versus non-El Niño years. Therefore, in addition to seasonal habitat use, one must consider interannual shifts in distribution.

Thomas M. Powell 31 July 2001

Chair Date

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Dedicated to S.A.

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Special thanks are due to my graduate committee, Zack Powell, Steve Ralston, Wayne Getz, and Cherie Briggs, for providing guidance and advice in the preparation of this dissertation. I'd also like to thank Donald Pearson at the National Marine Fisheries Service, and Will Daspit and Christian Bantzer at the Pacific States Marine Fisheries Commission for their invaluable assistance with data collection. Thanks also to Dave Higdon at Duke University, and to Laura Gascue and Katerina Kechris at the University of California, Berkeley for statistical advice. Finally, I would like to thank my husband Barney Caton, my son Caleb, my sister Cheri Gaither, and my parents Jim and Marcy Reynolds for their love, encouragement, sacrifice, and support.

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Diploma, North Carolina School of Science and Mathematics , Durham, NC. 1984-1986.

RESEARCH EXPERIENCE

Graduate Research Associate, University of California, Berkeley. 1996 to present. Incorporated environmental factors into fisheries stock assessment models.

Intern, National Marine Fisheries Service, Tiburon, CA. January to August 1997. Co-authored Chilipepper rockfish (*Sebastes goodei*) stock assessment using "Stock Synthesis" stock assessment model.

Graduate Research Associate, University of California, Davis. 1991 to 1995. Analyzed the California sea urchin fishery and its market to Japan using an economic model and optimization techniques.

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California Sea Grant Fellow, Channel Islands National Marine Sanctuary, Santa Barbara, California. 1990 to 1991. Investigated the economic benefits that the Sanctuary derives from commercial and recreational businesses.

Intern, South Coast Air Quality Management District, Transportation Department, El Monte, California. February to June 1989. Assisted with policy implementation and standardization of departmental procedures.

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- *English conversation*, Lycée d'Octave Feuillet, Paris, France. Fall 1988. Taught English conversation to French high school students.

ADDITIONAL EXPERIENCE

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Davis Rural Land Trust office manager, Davis, California. 1992-1993. Administrator of a non-profit organization, including publishing a bimonthly newsletter, organizing fund-raising activities, managing finances and taxes, and facilitating monthly board meetings.

PUBLICATIONS

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- California Sea Grant Fellowship, 1990-1991.
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- Ecological Society of America (ESA)
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- Resource Modeling Association (RMA)

ACADEMIC AND COMMUNITY SERVICE

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- Treasurer, Ecology Graduate Student Association, UC Davis. 1993-1996.
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- Career Advisor, Sacramento chapter of Pomona College Alumni Association, 1992-1996.

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Introduction

Fisheries are in decline throughout the world's oceans. Although total global fishery production has increased over the past 45 years, approximately 60% of the major marine fisheries are over-exploited (FAO, 1994). Even fish stocks that that have been targeted with intensive management have experienced severe declines or collapses (Collie and Tsou 1996). In response to this crisis, marine reserves—areas where all fishing is banned—are gaining renewed attention (NRC 1999, Parker et al. 2000). Given the high degree of uncertainty in fisheries management (Ballantine 1997, Guenette et al. 1998), marine reserves are optimistically viewed by some as the most plausible mechanism to achieve sustainable fisheries (Carr 1993, Man et al. 1995, Murray et al. 1999).

Although the concept of reserves was first proposed over 40 years ago (Beverton and Holt 1957), and undoubtedly offer great potential as a management tool, there are many obstacles to effective design. These obstacles range from an inability to predict oceanographic conditions, to a lack of understanding of basic fish ecology (including habitat use and distributions), to problems with articulating unambiguous management goals (e.g., Agardy 2000, Ballantine 1997, Carr and Raimondi 1998, Guenette et al. 1998, Murray et al. 1999, Sladek Nowlis and Yoklavich 1998). While these problems are daunting, they must be addressed in a timely manner if marine reserves are to be effective tools to help reverse the decline in the world's fisheries.

It is within this framework that I initiated the study presented in this dissertation. I address some basic ecological issues related to habitat use and distributions that are essential for appropriate design of marine reserves for one of the most commercially important rockfish species on the West Coast of the United States: *Sebastes entomelas*

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(common name: widow rockfish) (Williams et al. 2000). The American Fisheries Society has classified this species as "vulnerable" to extinction (Musick et al. 2000), which is in large part a function of its low productivity (Musick et al. 2000, Wyllie Echeverria 1987). Since the development of this fishery in the late 1970s, U.S. landings peaked at 28,016 mt in 1980 but have steadily fallen thereafter (PFMC 1998). Hence, this species is a prime candidate to benefit from the use of marine reserves. As is the case for many fish species, little is known about its habitat use and distribution.

Ecology of widow rockfish

The potential benefits of marine reserves are most apparent for long-lived, slow-growing species with limited movement since such species are highly susceptible to overexploitation (Parker et al. 2000, Rowley 1992). A prime example is West Coast rockfish (Musick et al. 2000, Parker et al. 2000, Yoklavich 1998). Rockfish have low population growth rates, low productivity, delayed maturity, and are long-lived (Boehlert et al. 1982, Love 1990, Wyllie Echeverria 1987). Furthermore, adult rockfish often exhibit site fidelity (Carlson and Haight 1972, Hartmann 1987, Mathews and Barker 1983, Pearcy 1992, Stanley et al. 1994) and have widely dispersed larvae (Larson et al. 1994, Love et al. 1991). These life history characteristics, combined with their commercial importance, has resulted in a downward trend in their abundance (Ralston 1998). Fourteen rockfish species are currently considered in immediate danger (Musick et al. 2000), but the actual number is likely to be considerably higher since there have not been formal assessments of the status of the majority of these species.

As mentioned above, widow rockfish is known to be vulnerable to the risk of extinction. This species ranges from northern Baja California to southern Alaska (Miller

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and Lea 1972) although the commercial fishery is centered off the coast of Oregon. No research has been conducted to determine if genetically distinct subpopulations occur (Williams et al. 2000), although Pearson and Hightower (1991) found differences in the growth rate between the northern and southern ends of its range. While these results suggest a subpopulation response to differing environmental conditions, what these differences might be remains unknown.

Widow rockfish are viviparious, spawning between November and April, with peak spawning in February (NOAA 1991). Parturition for this species usually occurs in January-February, and there is no evidence that widow rockfish move to nursery areas (Ralston and Lenarz 2000). Larvae remain in the upper mixed layer for approximately 1 month and are pelagic for approximately 5 months (Ralston and Howard 1995), but little is known about the abundance and distribution of larvae and juveniles (Ralston and Lenarz 2000).

No previous work has specifically addressed the habitat requirements of widow rockfish. Adults of this semipelagic species are found primarily over rocky substrate with moderate relief near the edge of the continental shelf (NOAA 1991). The majority of commercial catches occur at bottom depths between 150-250 meters, although young fish occur in more shallow water and adults have been caught over bottom depths of more than 400 meters (Lenarz and Gunderson 1987). It is not known whether this depth range reflects the true habitat preference of widow rockfish or if this range simply reflects the distribution of commercial fishing effort.

In addition, there is scant information about ontogenetic or seasonal habitat preferences of widow rockfish, although such patterns occur in other species of *Sebastes* (Carlson and Barr 1977, Stanley et al. 1994). In a tagging study by Hartmann (1987),

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widow rockfish were recaptured at the same location where they were originally captured, some up to 28 months later. These results, while limited (widow rockfish made up only 1.5% of all species tagged), suggest territoriality or at least a preference for a specific habitat or location. Indirect evidence suggests that widow rockfish may undertake seasonal on- and off-shore migrations, perhaps in response to seasonal habitat requirements (Hartmann 1987, Love 1981, Mathews and Barker 1983). Love (1990) found temporal shifts in catch-per-unit-effort (CPUE) at prime fishing locations, and hypothesized that this may mean that there are shifts in adult populations. While suggestive, none of these studies provide strong evidence about the essential habitat of widow rockfish.

The schooling behavior of this species also provokes questions about habitat preferences. Widow rockfish form dense feeding schools at night, which disperse at dawn (Adams, 1987). They feed primarily on euphausiids, salps, sergestids, myctophics, and other small fish. Dense midwater schools form at night, presumably related to feeding and oceanographic conditions, but the ecological factors that trigger this behavior are unknown (Wilkins 1987).

For the past decade, the widow rockfish fishery has been assessed using the model *Stock Synthesis* (Methot 1990). This population has been modeled as a single stock throughout its range (Hightower and Lenarz 1986, Ralston and Pearson 1997, Rogers and Lenarz 1993) although several stock assessment scientists have questioned whether this assumption is valid (PFMC 1998). Discrepancies in the catch-at-age data in the northern versus southern ends of this species' range indicate that there may be at least two distinct stocks. A preliminary, two-area version of the model was explored as part of the last management cycle (PFMC 1998).

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Structure of Dissertation

It is evident that even for a species as economically important as widow rockfish, fundamental questions about its habitat use and distribution remain unanswered. What habitat does this species use? What environmental factors correlate with the population's distribution? Does the population's distribution change seasonally or annually? Is there any evidence that there are spatially distinct subpopulations? These questions are the focus of my dissertation.

Widow rockfish are poorly sampled by research surveys (Wilkins 1986), but extensive commercial data exist. In addition to traditional sources (e.g., landings data and port samples), California, Oregon and Washington all require commercial logbook records to track widow rockfish catch. The Pacific Coast Fisheries Information Network (PacFIN), a regional fisheries data network operated by the Pacific States Marine Fisheries Commission, made 11 years of logbook data available to me (PacFIN 2000). I focused exclusively on Oregon logbook data since they are the most extensive and have the most extensive quality controls (PacFIN 2000). I suspected these data to be somewhat limited, but they offered the potential to fill some voids in our knowledge of widow rockfish distribution and habitat associations since they provide location and depth of catch.

In **Chapter One**, I identify significant habitat associations between widow rockfish and three habitat variables: bottom depth, net depth, and temperature. This work is motivated by the 1996 amendment to the Magnuson-Stevens Fishery Conservation and Management Act, one of the most significant conservation legislation for marine fisheries. This Act requires the protection of essential habitat, defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" (FCMA 1996).

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Although considerable research has been undertaken to address habitat use by various marine species (e.g., Collins et al. 2000, Levin 1994, Monaco et al. 1998, Perry and Smith 1994), for most a comprehensive understanding is lacking. The first step in developing a quantitative understanding of essential habitat in marine environments is to identify the ecological requirements of the species (e.g., Bertignac et al. 1998, Monaco et al. 1998, Bakun and Parrish 1991). In marine systems, a common approach has been the use of correlation analyses (Agrelli Andrade and Eiras Garcia 1999, Sunye and Servain 1998). While helpful, such analyses can be misleading for various reasons, including spurious relationships, seasonal environmental changes, and seasonal migrations (Walters and Collie 1988, Perry and Smith 1994). Furthermore, most data used in fisheries research violate assumptions of traditional parametric statistics, such as linearity, normality, and independence. To overcome these limitations, I explored various nonparameteric techniques (e.g., Perry and Smith 1994, Syrjala 1996), which make such assumptions unnecessary.

In **Chapter Two**, I assess whether those habitat associations identified in Chapter One are variable through time, on both an annual and seasonal time resolution. Possible reasons for temporal fluctuations include habitat degradation (Bruton 1995, Chesney et al. 2000, Watling and Norse 1998), expanding or contracting population sizes (MacCall 1990), large-scale phenomena such as climate change (Smith et al. 1999), and seasonal shifts in habitat requirements (Bakun and Parrish 1991, Collins et al. 2000, Friedland et al. 1999, Levin 1994, Perry and Smith 1994, Stalnaker et al. 1996). Understanding both the patterns and processes underlying seasonal habitat dynamics is essential if seasonal closures of sensitive marine areas are to be effective.

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In addition to habitat associations, there are two critical pieces of information that must be known in order to identify appropriate placement for marine reserves: 1) the spatial structure of the target population(s) being managed; and 2) the interconnectedness of that spatial structure. Research on the design of marine reserves has concentrated considerable effort on understanding the interconnectedness of spatial structure, primarily in terms of larval production by "source" populations and larval transport between populations (e.g., Botsford 1994, Doebeli and Ruxton 1998, Hermann et al. 1996, Man et al. 1995, Rogers-Bennett et al. 1995, Sladek Nowlis and Yoklavich 1998). Equally important is an accurate understanding of the spatial structure of adult populations and their stability through time (e.g., Death 1996, Hoines et al. 1998, Stalnaker et al. 1996, Thiebaut et al. 1997). Of course, identifying distributions and elucidating their temporal stability is problematic if the species are poorly sampled by research surveys or, as is the case for myriad marine species, when no data exists. In **Chapter Three**, I map the spatial structure of the adult widow rockfish population off the coast of Oregon and Washington, and identify shifts in the distribution through time.

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Chapter One

Significant habitat associations for widow rockfish (*Sebastes entomelas*)

Introduction

Considerable research has been undertaken to elucidate the habitat requirements of exploited marine fish species (e.g., Bertignac et al. 1998, Monaco et al. 1998, Bakun and Parrish 1991). A better understanding of the association between species and habitat variables (such as depth, temperature, salinity, etc.) is critical for effective fisheries management, particularly in the context of defining Essential Fish Habitat, designing marine reserve (e.g., Guenette et al. 1998, Garcia-Charton and Perez-Ruzafa 1999, Maury and Gascuel 1999), and predicting the impacts of global climate change on the distribution and abundance of exploited species (Smith et al. 1999). In this paper we identify significant habitat associations for widow rockfish (*Sebastes entomelas*), one of the most commercially important and heavily fished rockfish species off the west coast of the United States (Williams et al. 2000).

Widow rockfish range from northern Baja California to southern Alaska (Miller 1972) although the commercial fishery is centered off the coast of Oregon. No research has been conducted to determine if genetically distinct subpopulations occur within this geographical range (Williams et al. 2000), although Pearson and Hightower (1991) found differences in the growth rate between the northern and southern ends of its range. While these results suggest a subpopulation response to differing environmental conditions, no study has identified what these differences might be.

Little is known about the habitat requirements of widow rockfish. The majority of commercial catches of widow rockfish occur at bottom depths between 150-250

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meters, although young fish occur in more shallow water and adults have been caught over bottom depths of more than 400 meters (Lenarz and Gunderson 1987). However, it is not known whether this depth range reflects the true habitat preference of widow rockfish or if this range simply reflects the distribution of commercial fishing effort. The schooling behavior of this species also provokes questions about habitat preferences. Dense midwater schools form at night, presumably related to feeding and oceanographic conditions, but the ecological factors that trigger this behavior are unknown (Wilkins 1987). Parturition for this species usually occurs in January-February, and there is no evidence that widow rockfish move to nursery areas (Ralston and Lenarz 2000). Larvae are pelagic for approximately 5 months, but little is known about the abundance and distribution of widow rockfish larvae and juveniles (Ralston and Lenarz 2000). In addition, there is scant information about ontogenetic or seasonal habitat preferences of widow rockfish, although such patterns occur in other species within the *Sebastes* genus (Carlson and Barr 1977, Stanley et al. 1994). Hartmann (1987) conducted a tagging study in which the only widow rockfish recovered (1.5% of those tagged) were recaptured at the same location where they were originally captured, some up to 28 months later. These results, while limited in scope, suggest a preference for a specific habitat or location. Indirect evidence suggests that widow rockfish may undertake seasonal on- and off-shore migrations, perhaps in response to seasonal habitat requirements (Hartmann 1987, Love 1981, Mathews and Barker 1983).

In marine systems, a common approach to identifying habitat associations is through correlation analyses (Agrelli Andrade and Eiras Garcia 1999, Sunye and Servain 1998). While helpful, these analyses can be misleading due to spurious relationships,

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seasonal environmental changes, or seasonal migrations (Walters and Collie 1988, Perry and Smith 1994). Furthermore, most data used in fisheries research violate assumptions of traditional parametric statistics, such as linearity, normality, and independence. An alternative approach to identifying habitat associations is a modified Kolmogorov-Smirnov statistical test, used by Perry and Smith (1994) to test the null hypothesis that there is a random association between fish distribution and habitat conditions (i.e., the measurement of the habitat variable at a particular time and place). Perry and Smith developed their methods using data from research trawl surveys. However, many exploited species, such as widow rockfish, are poorly sampled by research surveys (Wilkins 1986), and for other species no survey data exists.

In this paper we generalize Perry and Smith's methods to utilize commercial logbook data, which have been shown to yield distribution patterns similar to research surveys (Fox and Starr 1996). Commercial logbooks provide extensive sampling of the spatial distribution of exploited species but the areas sampled are highly correlated with abundance. Our methods explicitly account for unequal spatial sampling and provide a new use for these data beyond their traditional uses in fisheries stock assessments. Our null hypothesis is that there is a random association between widow rockfish distribution and each habitat variable within the range of conditions sampled. Data limitations restrict this analysis to three habitat variables: bottom depth, vertical depth of fish in the water column, and temperature. For each variable, we define 'significant habitat association' as the range of habitat conditions for which 80% of widow rockfish catch is associated within a given sample period.

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Methods

Description of data

Although California, Oregon and Washington all require commercial logbook records to track widow rockfish catch, Oregon logbooks are the most extensive and have the most extensive quality controls (PacFIN 2000). Hence, for the analyses presented here, we utilized Oregon commercial logbook data from the Pacific Coast Fisheries Information Network (PacFIN), a regional fisheries data network operated by the Pacific States Marine Fisheries Commission (PacFIN 2000). Data for each tow consisted of: tow date, bottom depth, net depth, duration of tow, latitude, longitude, total pounds of fish caught (all species), total pounds of widow rockfish caught, and pounds of widow rockfish adjusted against fish ticket records (Table 1.1). We extracted all records for 1988-1998 for which there were no missing data, including records for which there was no widow rockfish catch. Approximately 10% of the records were complete, resulting in an annual sample size ranging from 342 records in 1998 to 3014 records in 1994. Incomplete logbook records most commonly omitted bottom depth and net depth data. However, we found that the spatial distribution of widow rockfish catch was not significantly different between the full data set and the subset of complete records (using the GEODISTN software program in Syrjala 1996). Thus, we assumed that the subset of data were representative of the overall widow rockfish distribution.

Logbook records do not include data on the physical properties of the water. Physical variables such as temperature, salinity, and dissolved oxygen are collected by research vessels and archived by the National Oceanographic Data Center (NODC), one of several national repositories for global environmental data operated by the National

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Oceanic and Atmospheric Administration (NOAA) of the U.S. Department of Commerce. Temperature data from the NODC Oceanographic Profile Database (NODC 1999) were selected for each year, corresponding to the range of the Oregon logbook data (Table 1.2). The spatial scale was defined as 0.5 degrees latitude (approximately 56 km) by 0.5 degrees longitude (approximately 40 km) by 10 meters depth. The temporal scale used was three-month periods (winter = January - March, spring = April - June, summer = July - September, fall = October - December). If more than one NODC record was available within the defined spatial and temporal scale, they were averaged. If a datum point was more than three standard deviations away from the mean value, it was considered to be an outlier and excluded from the analysis. This was done to omit data that appeared to be incorrectly entered into the NODC database (e.g., data entered as degrees Fahrenheit instead of degrees Celsius), and excluded on average only 2% of temperature data per year. Overall our approach yielded three habitat variables--bottom depth, vertical depth of fish in the water column (for which net depth is a proxy), and temperature--that we used in the following analyses.

Linking data

NODC temperature data were linked to logbook data by selecting records from both data sources collected within the same temporal and spatial bins (specified above). For every logbook record for which there was a match, temperature at net depth was added. The spatial and temporal scales selected were the smallest scales that generated an acceptable number of matches with logbook data to proceed with the statistical analyses. Although this binning is course, it was necessary due to limited temperature

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data. By averaging temperature data within bins, small-scale features are obviously lost, and the range of temperatures sampled is biased low due to the fact that data were averaged over large spatial and temporal scales. However, we assumed that water temperature varies little within this spatial and temporal scale, particularly at the depths explored.

Identifying associations between habitat variables and catch

For each sample period j (year or season), we split the sample area into equal-sized divisions h (all symbols defined in Table 1.3), where each division is a 0.1 degree latitude by 0.1 degree longitude bin. The total number of divisions in the sample area is L. For each habitat variable, x_{hi}, where i is the tow, we developed a cumulative distribution function (cdf) for fishing effort over all habitat conditions. The probability associated with each observation within a cdf is $1/n$, where n is the total number of tows (Zar 1999). To account for unequal sampling effort between divisions, the probability associated with each observation within a division is $1/n_h$ (Chambers and Dunstan 1986), where n_h is the number of tows in division h. An unbiased estimate of the cdf for the habitat sampled, given by Perry and Smith (1994), is:

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi}, t) \qquad \textbf{(Equation 1.1)}$$

where $I(x_{hi}, t)$ is an indicator function with the values

$$I(x_{hi}, t) = \begin{cases} 1, \text{if } x_{hi} \le t \\ 0, \text{otherwise} \end{cases} \qquad \textbf{(Equation 1.2)}$$

t is a habitat condition index, ranging from the lowest to the highest value of the habitat variable at the chosen step size, and W_h is the proportion of the sample area that is located

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within division h. For sample areas with equal sized divisions like those presented here, $W_h = 1/L$. Equation 1.1 is calculated for all values of t.

The unbiased estimate of the cdf for the habitat sampled weighted by catch (i.e., the habitat association) is:

$$g(t) = \sum_h \sum_i \frac{W_h}{n_h} \frac{y_{hi}}{\bar{y}_{st}} I(x_{hi}, t) \qquad \textbf{(Equation 1.3)}$$

where y_{hi} is an index of fish abundance and $\bar{y}_{st}$ is the estimated stratified mean abundance. Since y_{hi} is scaled by $\bar{y}_{st}$, $g(t)$ sums to 1 over all values of t. If large values of $y_{hi}/\bar{y}_{st}$ are consistently associated with particular habitat conditions, this suggests a strong habitat association (Perry and Smith 1994).

To determine the strength of the association between catch and the habitat variable, we compared $g(t)$ to $f(t)$ using a technique similar to the Kolmogorov-Smirnov test for goodness of fit (Perry and Smith 1994). Let

$$D = \max_{\forall t} | g(t) - f(t) | = \max_{\forall t} \left| \sum_h \sum_i \left(\frac{W_h}{n_h} \right) \left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{hi}, t) \right| \qquad \textbf{(Equation 1.4)}$$

Since sampling was unequal among divisions, standard look-up tables for the Kolmogorov-Smirnov test could not be used. Instead, we modeled the distribution of the test statistic D using Monte Carlo sampling to test the null hypothesis. This was accomplished by 1000 random pairings of $\frac{W_h}{n_h}\left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}} \right)$ and x_{hi} over all divisions and recalculating Equation 1.4 to give a pseudo-population of the test statistic D, i.e., D'. If the observed value of D is significantly different from that expected by chance, then there

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is a strong association between catch and the habitat variable. Figure 1.1 illustrates the distribution of D' at various resampling levels.

To determine the average significant habitat association, we averaged $g(t)$ over all sample periods j at the 10th percentile to determine the average lower boundary of the habitat association, and at the 90th percentile to determine the average upper boundary. The means were weighted by the p-value corresponding to each sample period (Equation 1.5).

$$\overline{g(t)} = \sum_j g_j(t) \frac{(1-p_j)^3}{\sum_j (1-p_j)^3} \qquad \textbf{(Equation 1.5)}$$

Results

Annual patterns

Of the three habitat variables examined, widow rockfish were most strongly associated with bottom depth and vertical depth within the water column. Significant associations with bottom depth occurred in all years between 1988-1998 except 1992 and 1997 (Table 1.4a). Significant habitat association for bottom depth, i.e., the range of bottom depths above which 80% of widow rockfish were caught, ranged from 112-233 m in 1991 to 154-384 m in 1998. In 1990, for example, 80% of widow rockfish was caught above bottom depths ranging from 150-234 m, whereas only 28% of bottom depths sampled occurred in this range (Figure 1.2). The average significant habitat association was 136-298 m.

In all years except 1992 and 1998, statistically significant associations between widow rockfish and vertical depth were also detected (Table 1.4b). Significant habitat

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association for fish depth ranged from 75-174 m in 1991 to 113-225 m in 1995, with an average significant habitat association for vertical depth of 101-197 m. In 1990, for example, 80% of the catch was associated with vertical depths between 105-188 m, whereas only 40% of habitat sampled was within this range (Figure 1.3).

Statistically significant associations between widow rockfish and water temperature were detected in only two years: 1989 and 1990 (Table 1.4c). The significant habitat association in 1989 was 7.6-8.4 ^{0}C, and in 1990 was 7.4-8.2 ^{0}C (Figure 1.4), and the average significant habitat association was 7.1-8.1 ^{0}C.

Seasonal patterns

For the 11 year period (1988-1998), a statistically significant association with bottom depth was detected for both the winter (p=0.05) and fall (p=0.05) seasons (Figure 1.5). In the fall, fish were associated with more inshore water (significant habitat association was 144-178 m) than in the winter (150-336 m). We also detected significant associations with vertical depth in winter (p<0.01), summer (p<0.01), and fall (p<0.01) (Figure 1.6). The significant habitat association for vertical depth was 109-188 m in winter, 94-150 m in summer, and 113-140 m in fall. Finally, we found significant associations with temperature in winter (p<0.01) and summer (p=0.05) (Figure 1.7). The significant habitat association for temperature in winter was 7.6-8.4 ^{0}C, whereas in summer it was 6.9-8.2 ^{0}C.

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Discussion

Annual habitat associations

Although the range of bottom depths above which the majority of widow rockfish catches occur had been determined (Lenarz and Gunderson 1987), prior to this study it was not clear whether this depth range reflected the true habitat preference of widow rockfish or simply the distribution of commercial fishing effort. We have shown that the distribution of widow rockfish among bottom depths is significantly different than the distribution of fishing effort in most years. The two years for which significant bottom depth associations were not detected were 1992 (p=0.10) and 1997 (p=0.10). The interpretation of this is simply that the distribution of fishing effort more closely tracked the distribution of widow rockfish in these years. However, given that both 1992 and 1997 were El Niño year raises the question of whether widow rockfish were easier to catch these years, and if so, was it due to a significant change in their distribution. Further research is needed to test the hypothesis that the distribution of widow rockfish changed between El Niño years and non-El Niño years.

We have also shown that in nine of the eleven years examined, the vertical depth distribution of widow rockfish within the water column was significantly different than the vertical distribution of fishing effort, indicating a true habitat preference for vertical positioning within the water column. This preference may be in response to a physical factor such as a frontal system or to a biological factor such as the presence of prey at these depths. No significant vertical depth association was detected was 1992, again raising the question of why fishing effort was able to track the fish distribution more closely during this year. The other year in which no vertical depth association was

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detected was 1998. Significant trip limits were imposed upon the fishery in this year (Williams et al. 2000) and it is possible that fishers switched from midwater trawls to less efficient bottom trawls so as not to exceed their trip limits for widow rockfish. A switch in gear could result in a change in the distribution of fishing effort by depth and could explain why no significant association between vertical depth and catch was detected. Furthermore, far fewer divisions were sampled in 1998, which could also be the result of management restrictions. Nevertheless, although no vertical depth associations were found in 1992 and 1998, overall it is clear that there are true habitat preferences for vertical depth.

The association between widow rockfish and temperature is less clear. Although the range of temperatures that comprise the average significant habitat association is relatively narrow (7.1-8.1 °C), caution should be exercised before generalizing these results too broadly since significant associations were not detected in nine of the eleven years examined. Possible reasons for this include the fact that the temperature data linked to the logbook data were averaged over relatively large spatial and temporal scales, thus the range of temperatures sampled was biased low because the data were averaged. For most sample periods, either the range of temperatures sampled was not large enough to identify true habitat preferences or widow rockfish do not exhibit habitat preferences within the range of temperatures sampled. To determine which scenario is more likely, one might explore alternative sources of temperature data and link it to logbook data at different spatial and temporal scales. Clearly a closer linking of abiotic data to catch data is needed to fully explore this relationship. Nevertheless, initial analyses provide some evidence that temperature does influence distribution.

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Seasonal habitat associations

It is possible that seasonal habitat preferences could mask true associations when averaged over the year. In fact, the significant habitat association for temperature in winter appears to be slightly warmer than in summer (7.6-8.4 ^{0}C versus 6.9-8.2 ^{0}C). Furthermore, widow rockfish appear to be associated with shallower bottom depths in the fall than in the winter (144-178 m versus 150-336 m). It is likely that the summer association with slightly cooler water is due to a shift in distribution in response to coastal upwelling of nutrient-rich cooler water. The seasonal bottom depth preference is indicative of an offshore migration in the winter months. Although no significant association was detected between bottom depth and catch in the summer, one possible explanation for this is that adult widow rockfish move onshore (to more shallow waters) in the summer/fall months to take advantage of nutrient rich, cooler waters for optimal feeding. Then, they move offshore (i.e., to deeper water) in the winter months for spawning, perhaps to avoid advection of larvae offshore.

Limitations

Numerous limitations emerge when using data for a purpose other than that for which it was originally designed. One risk with using commercial logbook data to describe fish distributions is that the data will be biased since there is no incentive for fishers to "sample" marginal habitats of the targeted species. To account for this limitation, we used logbook records from fishers targeting all groundfish species, which is why we have fishing data in areas other than optimal widow rockfish habitat. By tracking the behavior of a wide range of groundfish fishers, we increased the sample size

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for these analyses, and included "sampling" for widow rockfish in marginal habitat. However, it was necessary to assume that incidental widow rockfish catch is not discarded.

Secondly, this analysis is conservative given the fact that no assumptions were made about missing data (particularly net depth and bottom depth) from the Oregon commercial logbook records. However, it may be possible to infer the missing data if necessary (i.e., if one had insufficient data to proceed with an analysis). One may be able to estimate bottom depth from topographical maps, using the spatial coordinates of catch. One could also estimate net depth for certain gear types, especially bottom trawls. Third, this study was limited in scope since only three habitat variables were examined. A more complete picture of habitat use would be possible if more abiotic factors were available.

In addition to data limitations, there are two major limitation to the methods we used. First, this study was restricted along a one-dimensional gradient, and the relationships between habitat variables in a multi-dimensional space is needed to fully understand Essential Fish Habitat for widow rockfish. Second, we do not know if the habitat associations identified here are temporally stable. We do not know if there are significant distributions shift through time or if the seasonal distributions are significantly different. Although there is some evidence that seasonal shifts in the depth distribution occurred, further research is needed to determine if these shifts are statistically significant.

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Conclusion

In conclusion, the significant habitat associations identified in this paper reflect the true habitat preferences of widow rockfish. Commercial logbook data have been shown to be a useful--and underused--data source for identifying habitat associations. Using nonparametric methods, the distribution of catch has been shown to be significantly different from the distribution of fishing effort, although the ecological factors that influence these distributions are currently unknown. These results can be used not only to expand our basic understanding fish distributions, but also to improve fisheries management by providing insight into essential fish habitat (EFH), knowledge that is essential to the design of marine reserves.

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Table 1.1: Oregon commercial logbook data obtained from the Pacific Coast Fisheries Information Network (PacFIN) regional fisheries database (PacFIN, 2000) and a descriptions of column names.

PacFIN database column name	description	units
tow_date	tow date	month, day, year
depth1	depth	fathoms
depth_type1	description of depth1	B= Bottom depth
depth2	depth	fathoms
depth_type2	description of depth2	N=Net depth
duration	duration of tow	hours
set_lat	latitude	degrees
set_long	longitude	degrees
total(hpounds)	total pounds landed (all species), recorded by the fisher	pounds
wdow_hpounds	pounds of widow rockfish landed, recorded by the fisher	pounds
wdow_apounds	pounds of widow rockfish, adjusted against fish tickets	pounds

Table 1.2: Search criteria for temperature data from the NODC Oceanographic Profile Database Online Search engine (http://www.nodc.noaa.gov/IOPI), and the number of stations sampled each year that met the search criteria. Latitude and longitude are given in degrees, minutes, and seconds. Data were considered to be outliers if they were more than three standard deviations away from the mean annual temperature.

Starting date	Ending date	Lower latitude	Upper latitude	Left longitude	Right longitude	# of stations sampled	% of data that were outliers
1/1/88	12/31/88	42 00 00 N	48 30 00 N	127 00 00 W	123 30 00 W	596	0.5%
1/1/89	12/31/89	42 30 00 N	48 30 00 N	127 00 00 W	123 00 00 W	628	1%
1/1/90	12/31/90	42 30 00 N	48 30 00 N	127 00 00 W	124 00 00 W	762	1%
1/1/91	12/31/91	41 30 00 N	48 30 00 N	126 00 00 W	124 00 00 W	195	3%
1/1/92	12/31/92	40 30 00 N	48 30 00 N	129 00 00 W	124 00 00 W	1038	2%
1/1/93	12/31/93	42 00 00 N	48 30 00 N	128 00 00 W	124 00 00 W	101	3%
1/1/94	12/31/94	41 00 00 N	48 30 00 N	128 00 00 W	123 30 00 W	153	4%
1/1/95	12/31/95	42 00 00 N	48 30 00 N	126 00 00 W	123 00 00 W	22	4%
1/1/96	12/31/96	40 00 00 N	48 30 00 N	127 00 00 W	124 00 00 W	79	1%
1/1/97	12/31/97	40 00 00 N	48 30 00 N	128 00 00 W	123 00 00 W	15	2%
1/1/98	12/31/98	42 00 00 N	48 00 00 N	127 00 00 W	124 00 00 W	106	0.5%

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Table 1.3: Definition of symbols used in text.

Symbol	Description, units
c_{hi}	biomass (kg) of fish caught in division h, tow i
d_{hi}	hours towed in division h, tow i
h	division
i	tow
$I(x_{hi}, t)$	indicator function = 1, if $x_{hi} \leq t$ = 0, otherwise
j	sample period (year or season)
L	number of division in sample area
n_h	number of tows in division h
n	$= \sum_{h=1}^{L} n_h$ = total number of tows
t	habitat condition index, ranging from lowest to highest value of habitat variable at the specified step size
W_h	$= 1/L$ = proportion of sample area in division h
x_{hi}	measurement of habitat variable in division h, tow i
y_{hi}	$= c_{hi}/d_{hi}$ = catch per unit effort in division h, tow i (kg/hour)
$\overline{y_h}$	$= \sum_{i=1}^{nh} \frac{y_{hi}}{n_h}$ = estimated mean abundance of fish in division h (kg/hour)
$\overline{y_{st}}$	$= \sum_{h=1}^{L} W_h \overline{y_h}$ = estimated stratified mean abundance of fish (kg/hour)

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Table 1.4: Range of habitat conditions sampled ($f(t)$), and range of habitat conditions in which widow rockfish were caught ($g(t)$). *P*-values are the probability that the value D was significantly different from the test statistic D'. h is the number of divisions sampled, n is the number of tows used in each analysis. Statistically significant years (i.e., $p \leq 0.05$) are indicated by an asterisk. a. habitat variable=bottom depth, b. habitat variable=vertical depth, c. habitat variable=temperature.

a. Habitat variable = bottom depth (m)

year	range of habitats sampled (i.e., f(t))			range of habitat sampled weighted by catch (i.e., g(t))			p	h	n
	10th percentile	50th percentile	90th percentile	10th percentile	50th percentile	90th percentile			
1988	82	189	459	140	169	262	0.05*	155	583
1989	116	215	546	128	161	287	0.01*	165	686
1990	116	210	574	150	178	234	<0.01*	141	708
1991	107	253	742	112	150	233	<0.01*	248	1823
1992	114	178	555	140	150	225	0.10	198	2304
1993	125	234	843	138	204	322	<0.01*	220	1920
1994	135	319	937	135	154	294	<0.01*	339	3014
1995	135	300	1014	131	188	300	<0.01*	342	2644
1996	122	281	760	131	188	300	<0.01*	245	2268
1997	118	188	560	140	168	460	0.10	174	891
1998	131	253	488	154	165	384	0.05*	90	342
weighted average	119	241	690	136	171	298			

b. Habitat variable = vertical depth (m)

year	range of habitats sampled (i.e., f(t))			range of habitat sampled weighted by catch (i.e., g(t))			p	h	n
	10th percentile	50th percentile	90th percentile	10th percentile	50th percentile	90th percentile			
1988	80	190	540	90	120	170	<0.01*	155	583
1989	112	188	557	95	113	174	<0.01*	165	686
1990	103	169	574	105	131	188	<0.01*	141	708
1991	80	227	647	75	116	174	<0.01*	248	1823
1992	84	146	444	113	135	191	0.10	198	2304
1993	105	188	769	112	150	219	<0.01*	220	1920
1994	116	266	950	108	141	210	<0.01*	339	3014
1995	112	225	1007	113	150	225	<0.01*	342	2644
1996	93	188	645	91	131	238	0.05*	245	2268
1997	80	150	450	105	121	155	<0.01*	174	891
1998	103	197	281	118	281	281	0.30	90	342
weighted average	97	195	650	101	136	197			

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c. Habitat variable = temperature (degrees C)

year	range of habitats sampled (i.e., f(t))			range of habitat sampled weighted by catch (i.e., g(t))			p	h	n
	10th percentile	50th percentile	90th percentile	10th percentile	50th percentile	90th percentile			
1988	5.2	6.8	7.8	6.7	6.8	8.2	0.20	40	82
1989	5.9	7.7	8.6	7.6	8.2	8.4	0.05*	44	226
1990	5.3	7.5	8.2	7.4	7.8	8.2	0.05*	23	54
1991	5.1	6.9	7.9	6.7	7.9	8.0	0.50	51	130
1992	6.9	7.7	10.2	6.9	7.6	8.2	0.95	69	506
1993	6.6	7.7	8.3	7.5	7.8	7.7	0.95	21	100
1994	5.9	6.9	7.5	6.5	7.2	7.6	0.40	48	318
1995	4.5	6.7	8	6.3	6.3	8.4	0.85	13	61
1996	4.5	5.9	6.7	5.8	6.4	6.7	0.40	5	12
1997	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0
1998	6.6	7.4	8.2	7.0	7.6	8.2	0.80	51	197
weighted average	5.4	7.2	8.1	7.1	7.6	8.1			

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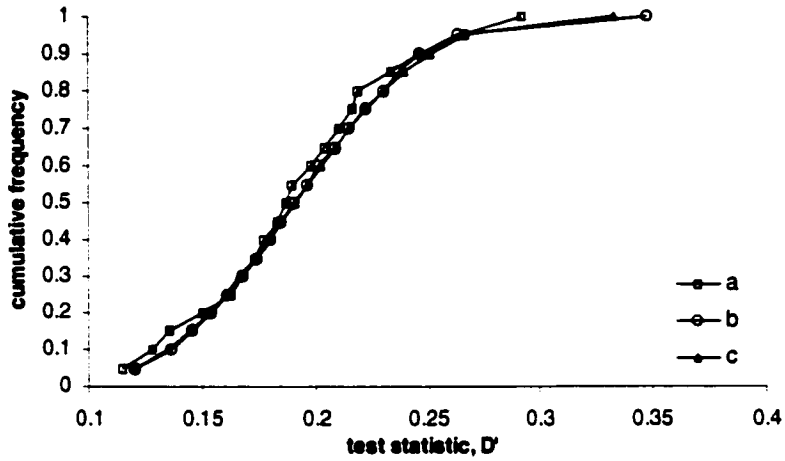

Figure 1.1: Cumulative frequency distribution for test statistic *D'* under various resampling regimes. a. 100 randomizations, b. 1000 randomizations, c. 10,000 randomizations. This example is for the analysis of bottom depth in 1990 with *D*=0.408. The probability (*p*) of a statistic greater than or equal to this value occurring by chance is <0.01.

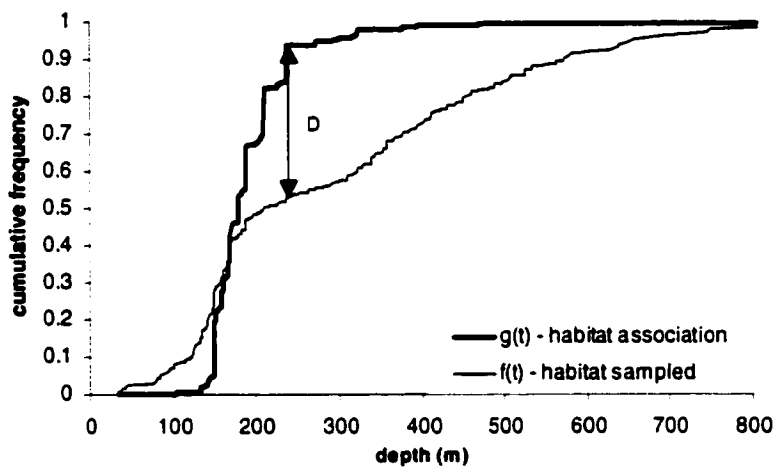

Figure 1.2: Cumulative distribution functions for observed bottom depth, *f*(*t*), and bottom depth weighted by the biomass of widow rockfish caught, *g*(*t*), in 1990. These distributions are significantly different (*p*<0.01), indicating a strong association between the distribution of widow rockfish and bottom depth. Eighty percent of the catch was associated with bottom depths between 150 - 234 meters, whereas only 28% of habitat sampled was within this range.

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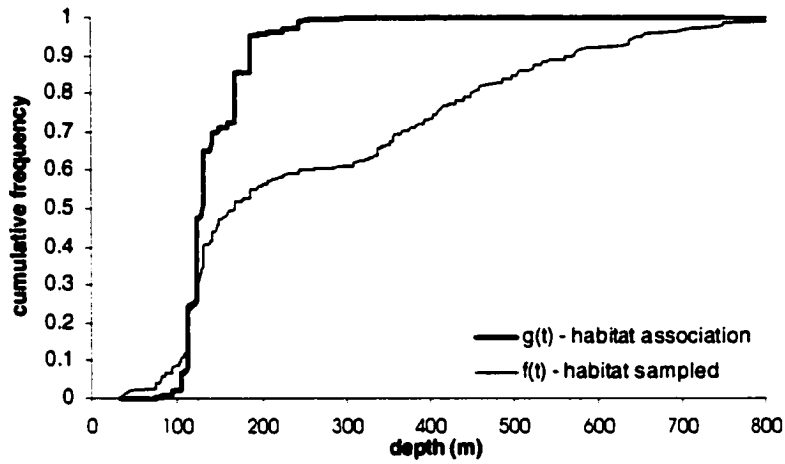

Figure 1.3: Cumulative distribution functions for observed vertical depth, $f(t)$, and vertical depth weighted by the biomass of widow rockfish caught, $g(t)$, in 1990. These distributions are significantly different ($p<0.01$), indicating a strong association between the distribution of widow rockfish and vertical depth. Eighty percent of the catch was associated with vertical depths between 105 - 188 meters, whereas only 40% of habitat sampled was within this range.

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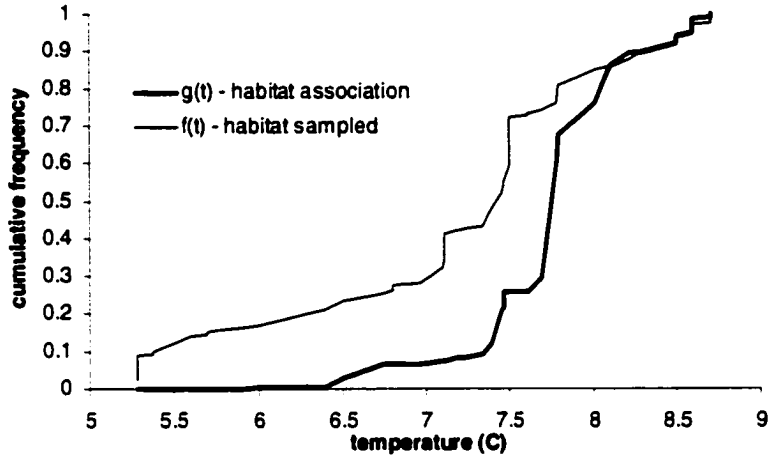

Figure 1.4: Cumulative distribution functions for observed temperature, $f(t)$, and temperature weighted by the biomass of widow rockfish caught, $g(t)$, in 1990. These distributions are significantly different ($p<0.01$), indicating a strong association between the distribution of widow rockfish and temperature. Eighty percent of the catch was associated with temperatures between 7.4 - 8.2 degrees Celsius, whereas only 43% of habitat sampled was within this range.

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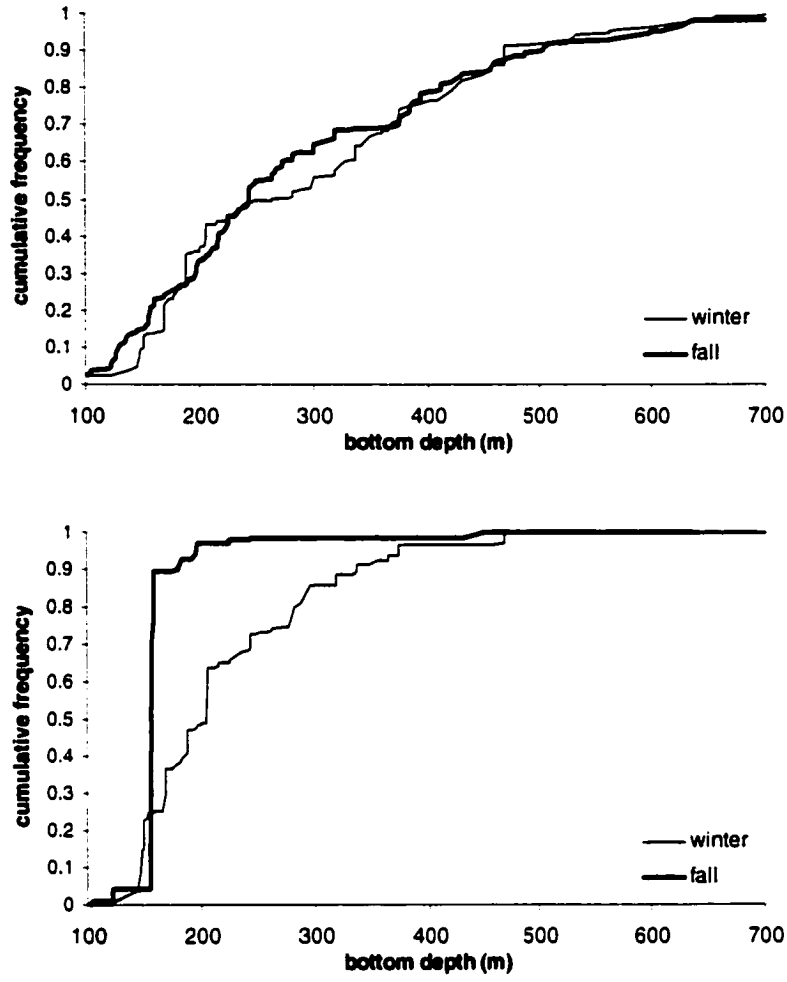

Figure 1.5: Cumulative distribution functions for $f(t)$, the distribution of bottom depths sampled (top panel), and $g(t)$, the distribution of bottom depths sampled weighted by widow rockfish catch (bottom panel), by season. $g(t)$ was only significantly different from $f(t)$ in winter (p=0.05) and fall (p=0.05). The significant habitat association was 144-178 m in winter and 150-336 m in fall.

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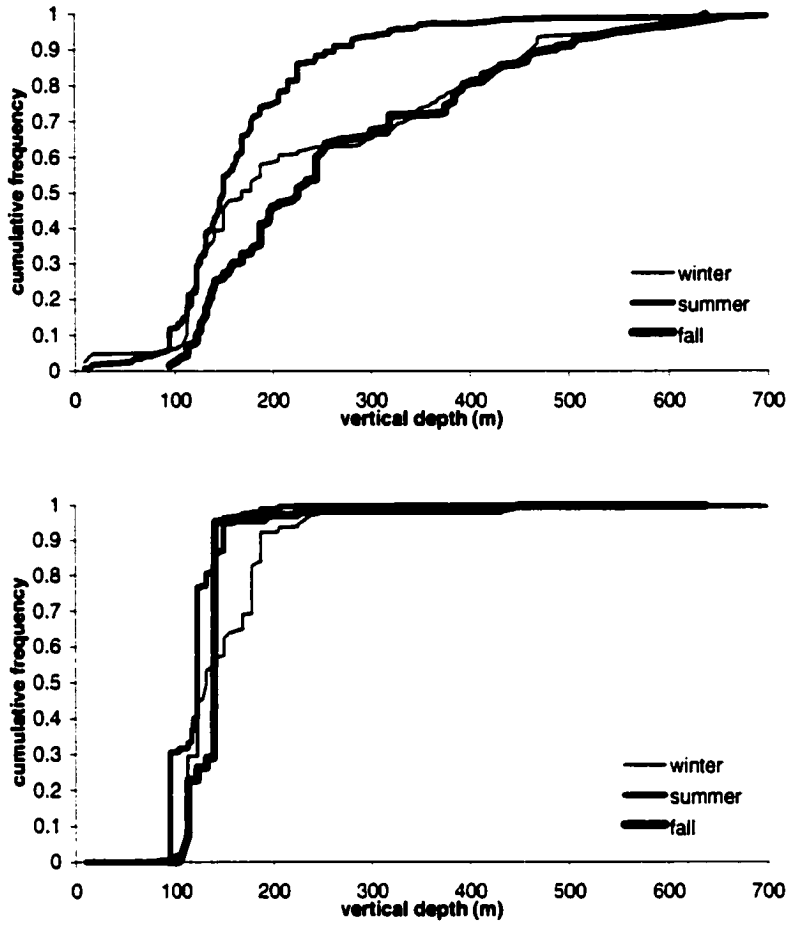

Figure 1.6: Cumulative distribution functions for $f(t)$, the distribution of vertical depths sampled (top panel), and $g(t)$, the distribution of vertical depths sampled weighted by widow rockfish catch (bottom panel), by season. $g(t)$ was only significantly different from $f(t)$ in winter ($p<0.01$), summer ($p<0.01$), and fall ($p<0.01$). The significant habitat association was 109-188 m in winter, 94-150m in summer, and 113-140m in fall.

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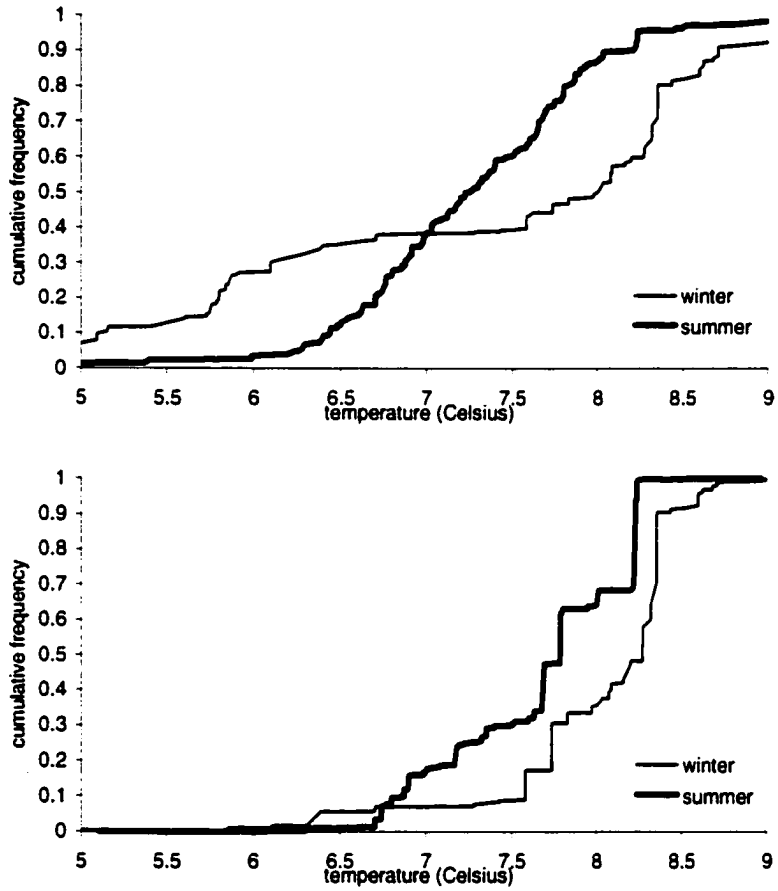

Figure 1.7: Cumulative distribution functions for $f(t)$, the distribution of temperatures sampled (top panel), and $g(t)$, the distribution of temperatures sampled weighted by widow rockfish catch (bottom panel), by season. $g(t)$ was only significantly different from $f(t)$ in winter ($p<0.01$) and summer ($p=0.05$). The significant habitat association was 7.6-8.4 °C in winter and 6.9-8.2 °C in summer.

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Chapter Two

Temporal stability of the association between widow rockfish (*Sebastes entomelas*) and bottom depth

Introduction

A fundamental principle of conservation biology is that habitat must be protected in order for species to survive (Meffe and Carroll 1997). A 1996 amendment to the Magnuson-Stevens Fishery Conservation and Management Act, one of the most significant conservation legislation for marine fisheries, requires the protection of essential habitat, defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" (FCMA 1996). Although considerable research has been undertaken to address habitat use by various marine species (e.g.,Collins et al. 2000, Levin 1994, Monaco et al. 1998, Perry and Smith 1994), a comprehensive understanding of essential habitat is lacking for most species.

Fluctuations in habitat use through time are a major obstacle in quantifying essential habitat. Reasons for fluctuations include habitat degradation (Bruton 1995, Chesney et al. 2000, Watling and Norse 1998), expanding or contracting population sizes (MacCall 1990), large-scale phenomena such as global climate change (Smith et al. 1999), and seasonal habitat requirements (Bakun and Parrish 1991, Collins et al. 2000, Friedland et al. 1999, Levin 1994, Perry and Smith 1994, Stalnaker et al. 1996). Understanding seasonal habitat use, for example, is essential if seasonal closures of sensitive areas are to be effective. Similarly, setting fixed boundaries for marine protected areas may be ineffective if habitat use by the targeted species changes by

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season or through time. Hence, in addition to identifying essential habitat, fisheries biologists must also elucidate the temporal stability of habitat associations.

In this paper, we assess the temporal stability of the association between widow rockfish (*Sebastes entomelas*), which forms the basis of an important West-coast groundfish fishery, and bottom depth. In an earlier study, we found rockfish populations to be strongly associated with bottom depths between 136-298 m (Reynolds et al. 2001). Indirect evidence suggests that widow rockfish may undertake seasonal offshore migrations (Hartmann 1987, Love 1981, Mathews and Barker 1983, Wilkins 1986), which corresponds with deeper bottom depths. Very little is known about ontogenetic or seasonal habitat use, however, and no study has explicitly questioned whether widow rockfish's habitat use changes through time, although a tagging study by Hartmann (1987) suggests that they may exhibit homing or territorial behavior

We define 'habitat association' as the range of habitat conditions--in this case bottom depths--for which 80% of widow rockfish catch is associated within a given sample period (Reynolds et al 2001). An understanding of this association is necessary when defining the "substrate necessary for spawning, breeding, feeding or growth" and is a first step in quantifying essential habitat. Furthermore, bottom depth is a fixed aspect of the habitat (i.e., the spatial coordinates of habitat conditions do not change through time) and data for bottom depth are readily available in commercial logbook records. Consequently, bottom depth is a prime candidate for use as a proxy for essential habitat by fisheries managers.

The widow rockfish fishery is centered off the coast of Oregon, although the species ranges from southern Alaska to Baja California (Miller and Lea 1972). Widow

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rockfish are poorly sampled by research surveys (Wilkins 1986), so we use Oregon commercial logbook records, which have been shown to yield distribution patterns similar to research surveys (Fox and Starr 1996). Covering an 11 year period from 1988-1998, we employ a two-step procedure: first, we identify significant habitat associations within sample periods and, second, the distributions of habitat associations between sample periods are compared. The stability of the association is examined at three temporal scales: interannual, seasonal, and intraannual.

Methods

Description of data

We utilized Oregon commercial logbook data from the Pacific Coast Fisheries Information Network (PacFIN), a regional fisheries data network operated by the Pacific States Marine Fisheries Commission (PacFIN 2000). Although California, Oregon, and Washington all require commercial logbook records to track widow rockfish catch, Oregon logbooks are the most exhaustive and have the most extensive quality controls (PacFIN 2000). Data for each tow consisted of: tow date, bottom depth, net depth, duration of tow, latitude, longitude, total pounds of fish caught (all species), total pounds of widow rockfish caught, and pounds of widow rockfish adjusted against fish ticket records (Table 2.1). We extracted all records for 1988-1998 for which there were no missing fields of data in a record, including records for which there was no widow rockfish catch. Approximately 10% of the records were complete, resulting in an annual sample size ranging from 342 records in 1998 to 3014 records in 1994. Incomplete logbook records most commonly omitted bottom depth and net depth data. However, we

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found that the spatial distribution of widow rockfish catch was not significantly different between the full data set and the abridged data set (Table 2.2) and thus assumed that the abridged data set was representative of the overall widow rockfish distribution.

Two-step methodology

The methodology employed involved two-steps. In Step 1 we identified significant habitat associations within sample periods. The periods of interest are three temporal scales: interannual, intraanual, and seasonal, the latter defined as three-month periods: winter (January - March), spring (April - June), summer (July - September) and fall (October - December). Since the distribution of commercial catch may simply be a function of the distribution of fishing effort, we used a modified Kolmogorov-Smirnov test to identify significant differences between these distributions (Reynolds et al. 2001). Our null hypothesis, H_o, is that there is no difference between the distribution of the habitat association and the distribution of habitat sampled within each sampling period. We proceeded to Step 2 only for those sample periods in which H_o was rejected.

In Step 2 we compared the distributions of habitat associations between sampling periods. Our goal was to determine whether there were temporal shifts in the distribution of habitat associations and, if so, were such shifts independent of changes in the distribution of habitat sampled. This was explicitly addressed by testing two null hypotheses. The first, H_1, states that the distribution of habitat sampled does not change through time. The second, H_2, is that the distribution of the habitat association does not change through time. If both H_1 and H_2 are rejected, this is indicative of a temporal shift in widow rockfish distribution. However, since the range of habitats sampled has

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changed through time, it is impossible to determine if shifts in habitat association reflects a true shift in habitat use or simply a shift in the distribution of effort. If we only reject H_2 then this is indicative of a shift in widow rockfish distribution since the temporal shift in the distribution of habitat associations occurred without detecting a change in the distribution of fishing effort. A rejection of H_1 only is indicative of the temporal stability of the habitat association since we do not detect a change in the distribution of the habitat association even though the distribution of the habitat sampled does change. Finally, a failure to reject both null hypotheses may indicate temporal stability of the habitat association, but interpretation of this scenario must be weighted by the probability of a Type II statistical error.

Step 1: Comparing distributions within sample periods

For each sample period j (year or season), we split the sample area into equal-sized divisions h, where each division is a 0.1 degree latitude by 0.1 degree longitude bin (all symbols defined in Table 2.3). The total number of divisions in the sample area is L_j. For each habitat variable, x_{hij}, where i is the tow observation, we developed a cumulative distribution function (cdf) for fishing effort over all habitat conditions. The probability associated with each observation within a cdf is $1/n_j$, where n_j is the total number of tows during sample period j (Zar 1999). To account for unequal sampling effort between divisions, the probability associated with each tow observation within a division is $1/n_{hj}$ (Chambers and Dunstan 1986). An unbiased estimate of the cdf for the habitat sampled which accounts for different sized divisions, given by Perry and Smith (1994), in sample period j is:

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$$f_j(t) = \sum_h \sum_i \frac{W_{hj}}{n_{hj}} I(x_{hij}, t) \qquad \textbf{(Equation 2.1)}$$

where $I(x_{hij}, t)$ is an indicator function with the values

$$I(x_{hij}, t) = \begin{cases} 1, \text{ if } x_{hij} \le t \\ 0, \text{ otherwise} \end{cases} \qquad \textbf{(Equation 2.2)}$$

t is an index, ranging from the lowest to the highest value of the habitat variable at the chosen increment size, and W_{hj} is the proportion of the sample area that is located within division h in sample period j. In Step 1, t is continuous. For data with equal sized divisions, such as those presented here, $W_{hj} = 1/L_j$. Equation 2.1 is calculated for all values of t.

The unbiased estimate of the cdf for the habitat sampled weighted by catch (i.e., the habitat association) in sample period j is:

$$g_j(t) = \sum_h \sum_i \frac{W_{hj}}{n_{hj}} \frac{y_{hij}}{\overline{y_{stj}}} I(x_{hij}, t) \qquad \textbf{(Equation 2.3)}$$

where y_{hij} is an index of fish abundance (catch per unit effort of tow i, in division h, during sample period j) and $\overline{y_{stj}}$ is the estimated stratified mean abundance in sample period j. Since y_{hij} is scaled by $\overline{y_{stj}}$, $g_j(t)$ sums to 1 over all values of t. If large values of $y_{hij}/\overline{y_{stj}}$ are consistently associated with particular habitat conditions, this suggests a strong habitat association (Perry and Smith 1994).

To determine the strength of the association between the habitatassociation and habitat sampled, we compared $f_j(t)$ to $g_j(t)$ using a technique similar to the Kolmogorov-Smirnov test for goodness of fit (Perry and Smith 1994). Let

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$$D_j = \max_{\forall t} | g_j(t) - f_j(t) | = \max_{\forall t} \left| \sum_h \sum_i \left(\frac{W_{hj}}{n_{hj}} \right) \left(\frac{y_{hij} - \overline{y_{stj}}}{y_{stj}} \right) I(x_{hij}, t) \right| \qquad \textbf{(Equation 2.4)}$$

Since sampling was unequal among divisions, standard look-up tables for the Kolmogorov-Smirnov statistic could not be used. Instead, we modeled the distribution of the test statistic D_j using Monte Carlo sampling to test the null hypothesis. This was accomplished by 1000 random pairings of $\frac{W_{hj}}{n_{hj}} \left(\frac{y_{hij} - \overline{y_{stj}}}{y_{stj}} \right)$ and x_{hij} over all divisions and recalculating Equation 2.4 to give a pseudo-population of the test statistic D_j, i.e., D_j^*. If the observed value of D_j is significantly different from that expected by chance, then there is a strong association between catch and the habitat variable. The distribution of D_j^* at various resampling levels is given in Reynolds et al. (2001).

To determine the average significant habitat association, we averaged $g(t)$ over all sample periods j at the 10th percentile to determine the average lower boundary of the habitat association, and at the 90th percentile to determine the average upper boundary. The means were weighted by the p-value corresponding to each sample period as follows:

$$\overline{g(t)} = \sum_j g_j(t) \frac{(1 - p_j)^3}{\sum_j (1 - p_j)^3} \qquad \textbf{(Equation 2.5)}$$

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Step 2: Comparing distributions between sampling periods

To compare the distributions of habitat associations between sample periods, we used a generalized Birnbaum-Hall test, which requires equal sample sizes for all distributions being compared (Conover 1980). Therefore, the following modifications to the data were made. Since sampling does not occur at deeper depths in some years, we truncated the range of depths over which comparisons were made. The lower boundary used in the comparison (t_{min}) was the lowest t-value (i.e., the habitat condition) at the 10th percentile of any cdf in the time series; similarly, the upper boundary (t_{max}) was the largest t-value at the 90th percentile in the time series. Thus, the hypothesis test focuses on changes in the distribution within the significant habitat range. Since data outside the significant range were discarded, data between t_{max} and t_{min} must be normalized within each sample period which enables a comparison of distributions between sample periods independent of interannual differences in abundance (Syrjala 1996). We normalized observations by dividing each observation by the sum of all observations for that sample period:

$$\left(\frac{W_{hj}}{n_{hj}}\right) = \frac{\frac{W_{hj}}{n_{hj}}}{\sum_{h}\sum_{t}\frac{W_{hj}}{n_{hj}}} \qquad \textbf{(Equation 2.6)}$$

Next, we increased the increment size for t since not all depths were sampled each sample period. Increasing t aggregates the data into habitat bins. Since the Kolmogorov-Smirnov class of test statistics are most accurate using continuous variables (Zar 1999), when discrete variables are used--as in this case to correct for unequal sample size between sample periods--then the smallest increment size ensures the largest sample size (Conover 1980). Therefore, we chose the smallest increment size that ensured at least

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one observation per bin per sample period. The increment size for depth went from t = continuous in Step 1 to t= discrete (10m habitat bins) in Step 2. The normalized, unbiased, weighted cdf for the habitat sampled in sample period j is:

$$F_j(t) = \sum_h \sum_i \left(\frac{W_{hj}}{n_{hj}} \right) I(x_{hij}) \qquad \textbf{(Equation 2.7)}$$

where t is the habitat condition index for the indicator function I ranging from t_{min} to t_{max} at increment size 10m.

The distribution of the habitat association was normalized in a manner similar to Equation 2.6:

$$\left(\frac{W_{hj}}{n_{hj}} \frac{y_{hij}}{y_{stj}} \right) = \frac{\frac{W_{hj}}{n_{hj}} \frac{y_{hij}}{y_{stj}}}{\sum_h \sum_i \frac{W_{hj}}{n_{hj}} \frac{y_{hij}}{y_{stj}}} \qquad \textbf{(Equation 2.8)}$$

and the normalized, unbiased, weighted cdf for the habitat association in sample period j is:

$$G_j(t) = \sum_h \sum_i \left(\frac{W_{hj}}{n_{hj}} \frac{y_{hij}}{y_{stj}} \right) I(x_{hij}) \qquad \textbf{(Equation 2.9)}$$

To determine if these distributions were significantly different, we generalized the Birnbaum-Hall test, which compares three independent random samples simultaneously (Conover 1980), to compare multiple samples. Let $H_j(t)$ represent an empirically-derived cdf (i.e., either $G_j(t)$ or $F_j(t)$). The test statistic S' considers the maximum vertical distance between every possible pair of cdf's. Therefore, for J sample periods, the number of pairs to compare is:

$$P_J = \frac{1}{2} \left(\frac{J!}{(J-2)!} \right) \qquad \textbf{(Equation 2.10)}$$

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For each pair (sample periods a and b) we calculated

$$S_{ab} = \max_{\forall t} |H_a(t) - H_b(t)| \qquad \textbf{(Equation 2.11)}$$

The test statistic S' is the maximum of all S_{ab}, i.e.,

$$S' = \max_{\forall j} |S_{ab}| \qquad \textbf{(Equation 2.12)}$$

Monte Carlo simulations similar to those used in Step 1 were used to determine the statistical significance of S'.

Results

Step 1 results: Significant habitat associations within sample periods

Overall, the distribution of the habitat association is significantly different from the distribution of habitat sampled, indicating that widow rockfish have a strong association with a specific range of bottom depths (Table 2.4, Tables A1-A2). Looking at each year as a whole, we see that over the 11 year period this difference is significant in all years except 1992 (p=0.10) and 1997 (p=0.10). For example, in the 1988 comparison between $f_j(t)$ and $g_j(t)$ (Figure 2.1), 80% of widow rockfish catch occurred between 140-262m, whereas only 45% of the depths sampled occurred within this range. Since $g_j(t)$ is significantly different from $f_j(t)$ (p=0.05), we can reject H_o.

The trend within the four seasons is less clear. For example, we detected a strong habitat association in 8 of 11 spring seasons, but only 5 out of 11 summer seasons (Table 2.4, Table A2). Looking within years, we see that in 1994, for example, the habitat association is strong in all seasons, whereas in 1988, we only detected a strong habitat association in spring. The average of these habitat associations (weighted as indicated in Equation 2.5) indicates little change between seasons at the lower boundary of the

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associations (i.e., the 10th percentile of the cdf), but a possible difference in the upper boundary (i.e., the 90th percentile, Figure 2.2). The significance of these results was tested in Step 2.

Step 2 results: A comparison of distributions between sample periods

We detected no temporal shifts in the association between widow rockfish and bottom depth among the 9 years examined. The greatest difference in distributions of habitat associations between any two years, $S^{'}$, occurred for a=1994 and b=1998 (Figure 2.3, Table A3), but the p-value is not significant (p=0.90) so we failed to reject H_2. Differences in the distributions of habitat sampled were also not significant among the 9 years examined (Figure 2.4), $S^{'}$ occurred for a=1988 and b=1991 (p=0.95). Thus we also failed to reject H_1.

Similarly, we failed to reject both H_1 and H_2 for the winter, spring, and summer comparisons (Table 2.5, Table A4-A6). Although we rejected H_1 for the fall comparison (S' occurred between fall 1991 and fall 1992 with p=0.05, Table A7), we failed to reject H_2. This is indicative of temporal stability of the habitat association in fall. Finally, we failed to reject both H_1 and H_2 for all intraannual comparisons (Table 2.6, Table A8).

Discussion

Within the majority of sample periods (Step 1), the habitat association was significant, i.e., widow rockfish exhibited a preference for a specific range of bottom depths, and the association was independent of the distribution of fishing effort. In the comparison of significant habitat associations between sample periods (Step 2), we

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detected no significant interannual, seasonal, or intraannual variation in the range of bottom depths preferred by widow rockfish. At all temporal scales, we failed to reject the null hypothesis H_2 (i.e., there is no significant difference in the range comprising habitat associations through time), and in all but one case we failed to reject H_1 (i.e., there is no significant difference in the range of habitats sampled through time). When H_1 is rejected, i.e., the interannual fall comparison, this is indicative of the temporal stability of the habitat association. Although we detected a significant shift in the distribution of habitat sampled in the fall, we did not detect a corresponding shift in the distribution of the habitat association. This is the most convincing result we found. In every other case we failed to detect any change in the distribution of the habitat sampled or in the distributions of the habitat association at the scales examined.

We suggest that there is temporal stability in the habitat association at the scales examined, although there are limitations to the methods we employed. The Birnbaum-Hall test requires equal sample sizes, which necessitated truncating the data series and aggregating data into habitat bins. Not only does this reduce the sample size, but the test also becomes more conservative when the independent variable is not continuous (Conover 1980). In other words, the test it is more likely to yield a Type II error when data are aggregated. We examined the statistical power of these analyses by examining the correlation between S' (the maximum vertical distance between the distributions being compared) and the corresponding p-value (Figure 2.5, Roberts et al. 1998). The probability that the two distributions are identical when S' is small is negligible (i.e., p approaches 1.0). Conversely, as S' increases, the probability of rejecting the null hypothesis increases (i.e., p decreases). We conclude that one would not expect to find

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statistically significant differences (i.e., $p = 0.05$) unless S' was greater than 0.85 in the case of $F_j(t)$ or 1.15 in the case of $G_j(t)$ (these values were obtained by solving the regression equations in Figure 2.5 for S' when $p = 0.05$). S' values of these magnitudes would represent major differences in the distributions, and therefore we must conclude that the statistical power of our analysis is relatively low.

Further support for the notion that the habitat associations are temporally stable, however, lies in a comparison of coefficients of variation (CV)(Perry and Smith 1994). Since the CV for the 50th percentile of $G_j(t)$ is less than the CV for $F_j(t)$ in most cases (Table 2.5, 2.6), we conclude that the range of depths comprising the habitat association is less variable than the range of depths sampled through time. A notable exception is the CV for the interannual fall comparison. In this case, we did detect a significant difference among $F_j(t)$, but conversely the CV for $F_j(t)$ was less than the CV for $G_j(t)$. The interpretation of this is simply that the variability of the median values was slightly less for the habitat sampled than for the habitat association. However, the overall distribution of the habitat sampled changed significantly among fall seasons, whereas the overall distribution of the habitat association did not, illustrating that the combined methods provide a more complete picture than either alone.

Other limitations are worth noting. First, there may be seasonal changes in the habitat association that occur at spatial and temporal scales other than those examined here. It is possible, for example, that significant onshore-offshore movement occurs (Hartmann 1987, Love 1981, Mathews and Barker 1983, Wilkins 1986), but on a finer scale than examined here. It is unlikely that a subtle shift in distribution within the range of bottom depths that comprise the significant habitat association would be picked up

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using our approach. Second, the habitat associations identified here pertain only to adult widow rockfish susceptible to the commercial fishery. Ontogenetic changes in the habitat association have been suggested for rockfish species (Carlson and Barr 1977, Stanley et al. 1994), and further research is merited to explore this issue.

Third, we examined only one habitat variable due in part to the data limitations of commercial logbook record. In order to gain a more complete picture, additional habitat variables must be examined. Although we had considerable data on net depth, which can be used as a proxy for the vertical location of fish within the water column (Reynolds et al., 2001), preliminary analyses of these data indicated that there was no change in the association with vertical depth through time. Nevertheless, we detected an interesting correlation between bottom depth and the location of fish relative to the bottom (Appendix B, Tables B1-B3). We found that the fish were further off the bottom at deeper bottom depths, and that this relationship varied significantly by season. This is noteworthy for three reasons. First, although the association with bottom depth is time invariant at the scales examined, the fish are obviously exhibiting some seasonal vertical movement. Second, we suggest that it may be the correlation between bottom depth and vertical depth that varies rather than the habitat association with vertical location *per se*. Third, although the mechanisms are unknown, this behavior may be in response to environmental cues such as seasonal upwelling. Understanding the ecological phenomenon affecting this behavior could provide us with additional insight into the ecology and habitat requirements of this species.

The implication of our findings to fisheries management is that it establishes that there is a significant habitat association between widow rockfish and bottom depth, and

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there is some indication that the habitat association of adult widow rockfish is stable through time and between seasons. Sedentary species, i.e., species for which there is little migration of individuals once they reach a fishable size (Mathews and Barker 1983), such as widow rockfish may require more restrictive management since there is less of a spatial refuge from commercial fishing. Furthermore, the fact that widow rockfish is a long-lived, slow-growing species, which makes this species even more susceptible to overexploitation (Roberts 1997), also indicates that this species may require more restrictive management. Combined, these facts suggest that widow rockfish may be a prime candidate for management using marine reserves.

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Table 2.1: Oregon commercial logbook data obtained from the Pacific Coast Fisheries Information Network (PacFIN) regional fisheries database (PacFIN, 2000) and a descriptions of column names.

PacFIN database column name	description	units
tow_date	tow date	month, day, year
depth1	depth	fathoms
depth_type1	description of depth1	B= Bottom depth
depth2	depth	fathoms
depth_type2	description of depth2	N=Net depth
duration	duration of tow	hours
set_lat	latitude	degrees
set_long	longitude	degrees
total(hpounds)	total pounds landed (all species), recorded by the fisher	pounds
wdow_hpounds	pounds of widow rockfish landed, recorded by the fisher	pounds
wdow_apounds	pounds of widow rockfish, adjusted against fish tickets	pounds

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Table 2.2: A comparison of the spatial distribution of all logbook records versus the subset of logbook records for which there were no missing fields of data (ie, the abridged data set). Distributions were compared using the GEODISTN software program in Syrjala (1996). *P*-values are the probability that the two distributions are identical.

year	n for full data set	n for abridged data set	p-value
1988	15,885	583	0.70
1989	20,920	686	0.55
1990	18,120	708	0.65
1991	25,223	1823	0.40
1992	21,920	2304	0.60
1993	26,178	1920	0.80
1994	19,469	3014	0.75
1995	16,370	2644	0.55
1996	16,583	2268	0.45
1997	16,523	891	0.90
1998	14,934	342	0.80

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Table 2.3: Definition of symbols used in text.

Symbol	Description, units
c_{hij}	biomass (kg) of fish caught in division h, tow i, sample period j
d_{hij}	hours towed in division h, tow i, sample period j
h	division (0.1 °N latitude by 0.1 °W longitude)
i	tow observation
$I(x_{hij})$	indicator function = 1, if $x_{hij} \leq t$ = 0, otherwise
j	sample period (year or season) (a, b, ... J)
L_j	total number of division in sample area during sample period j
n_{hj}	number of tows in division h, sample period j
n_j	$= \sum_h n_{hj}$ = total number of tows during sample period j
t	habitat condition index, ranging from lowest to highest value of habitat variable at the specified increment size
t_{min}	for Step 2 analyses, the lowest value for the habitat condition at the 10th percentile of any cdf in the time series
t_{max}	for Step 2 analyses, the highest value for the habitat condition at the 90th percentile of any cdf in the time series
W_{hj}	$= 1/L_j$ = proportion of sample area in division h, sample period j
x_{hij}	measurement of habitat variable in division h, tow i, sample period j
y_{hij}	$= c_{hij}/d_{hij}$ = catch per unit effort in division h, tow i, sample period j (kg/hour)
$\overline{y_{hj}}$	$= \sum_{i=1}^{n_{hj}} \frac{y_{hij}}{n_{hj}}$ = estimated mean abundance of fish in division h (kg/hour)
$\overline{y_{stj}}$	$= \sum_h W_{hj}\,\overline{y_{hj}}$ = estimated stratified mean abundance of fish (kg/hour)

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Table 2.4: Step 1 results: Within-sample period test results for statistical differences between $f_j(t)$ and $g_j(t)$. Significant p-values are indicated with *.

year	whole year		winter only		spring only		summer only		fall only	
1988	0.05	*	0.15		0.05	*	0.95		0.15	
1989	0.01	*	<0.01	*	0.95		0.05	*	<0.01	*
1990	<0.01	*	<0.01	*	0.25		0.15		<0.01	*
1991	<0.01	*	<0.01	*	<0.01	*	0.15		0.05	*
1992	0.10		0.60		<0.01	*	0.55		0.05	*
1993	<0.01	*	<0.01	*	0.25		<0.01	*	0.15	
1994	<0.01	*	0.05	*	<0.01	*	0.05	*	<0.01	*
1995	<0.01	*	<0.01	*	0.05	*	0.10		<0.01	*
1996	<0.01	*	0.05	*	0.05	*	0.05	*	0.55	
1997	0.10		0.10		<0.01	*	0.05	*	0.50	
1998	0.05	*	n/a		0.05	*	0.70		n/a	

Table 2.5: S' values for interannual comparisons between $F_j(t)$ and $G_j(t)$, and corresponding p-values. Significant p-values are indicated with *. The average value, standard deviation and coefficient of variation of the median (50^{th} percentile) of bottom depth are calculated for both $F_j(t)$ and $G_j(t)$ from 1988-1998.

Interannual comparison	S'	p-value	average value of 50^{th} percentile	standard deviation	coefficient of variation
whole year					
$F_j(t)$	0.224	0.95	238	47	20%
$G_j(t)$	0.461	0.90	170	17	10% †
Winter only					
$F_j(t)$	0.357	0.95	328	114	35%
$G_j(t)$	0.554	0.35	179	26	15% †
Spring only					
$F_j(t)$	0.401	0.95	237	62	26%
$G_j(t)$	0.485	0.65	170	23	13% †
Summer only					
$F_j(t)$	0.194	0.99	199	37	19%
$G_j(t)$	0.610	0.70	170	40	24%
Fall only					
$F_j(t)$	0.387	0.05 *	283	68	24%
$G_j(t)$	0.533	0.70	197	50	26%

† indicates the habitat association, $G_j(t)$, for which the coefficient of variation was less than the corresponding coefficient of variation for the habitat sampled, $F_j(t)$.

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Table 2.6: S' values for interannual comparisons between $F_j(t)$ and $G_j(t)$, and corresponding p-values. The average value, standard deviation and coefficient of variation of the median (50th percentile) of bottom depth are calculated for both $F_j(t)$ and $G_j(t)$ from 1988-1998.

Intra-annual, seasonal comparison	S'	p-value	average value of 50th percentile	standard deviation	coefficient of variation
1988					
$F_j(t)$	n/a	n/a	223	84	38%
$G_j(t)$			188	40	21% †
1989					
$F_j(t)$	0.302	0.95	226	64	28%
$G_j(t)$	0.684	0.60	165	21	13% †
1990					
$F_j(t)$	0.154	0.95	226	83	37%
$G_j(t)$	0.280	0.99	174	10	6% †
1991					
$F_j(t)$	0.277	0.60	298	130	44%
$G_j(t)$	0.596	0.70	167	27	16% †
1992					
$F_j(t)$	0.159	0.95	189	24	13%
$G_j(t)$	0.307	0.95	155	10	6% †
1993					
$F_j(t)$	0.203	0.95	284	70	24%
$G_j(t)$	0.291	0.95	239	59	25%
1994					
$F_j(t)$	0.224	0.90	329	57	17%
$G_j(t)$	0.449	0.60	170	20	12% †
1995					
$F_j(t)$	0.278	0.90	335	130	39%
$G_j(t)$	0.329	0.90	175	24	14% †
1996					
$F_j(t)$	0.317	0.95	281	93	33%
$G_j(t)$	0.299	0.90	172	14	8% †
1997					
$F_j(t)$	0.245	0.95	202	27	13%
$G_j(t)$	0.271	0.95	158	20	12% †
1998					
$F_j(t)$	n/a	n/a	262	27	10%
$G_j(t)$			223	82	37%

† indicates the habitat association, $G_j(t)$, for which the coefficient of variation was less than the corresponding coefficient of variation for the habitat sampled, $F_j(t)$.

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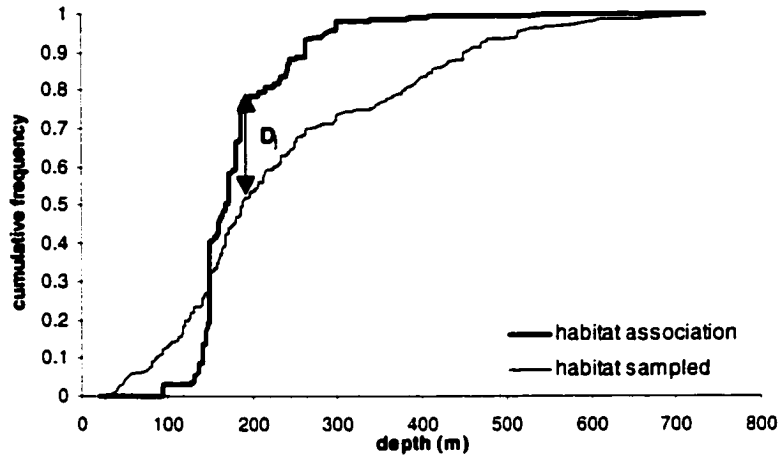

Figure 2.1: Cumulative distribution functions for bottom depth sampled, $f_j(t)$, and bottom depth weighted by the biomass of widow rockfish caught, the habitat association $g_j(t)$, in 1988. These distributions are significantly different (p=0.05), indicating a strong association between the distribution of widow rockfish and bottom depth. Eighty percent of the catch was associated with bottom depths between 140-262 meters, whereas only 45% of habitat sampled was within this range.

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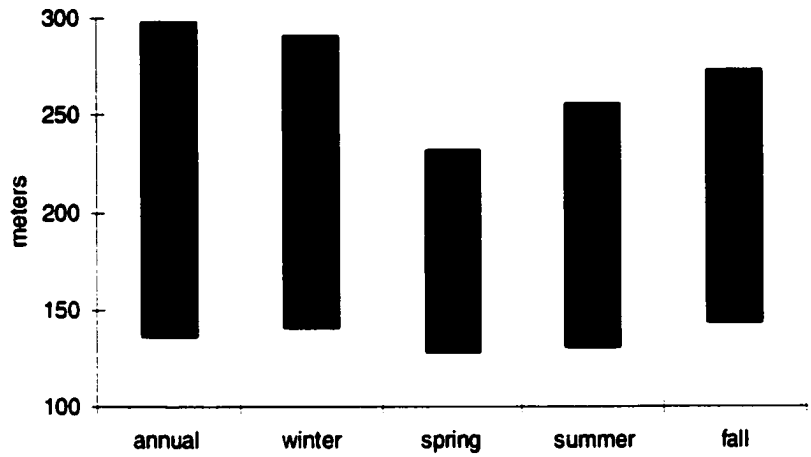

Figure 2.2: Average habitat associations for widow rockfish, as calculated by Equation 5. For the annual time step, the average association for widow rockfish and bottom depth is 136-298 m, whereas in winter it is 141-291m, in spring it is 128-232m, in summer it is 131-256m, and in fall it is 143-273m. The upper boundary of the average association is the weighted average of the 90th percentile of cdfs for all sample periods, and the lower boundary is the weighted average of the 10th percentile of all cdfs.

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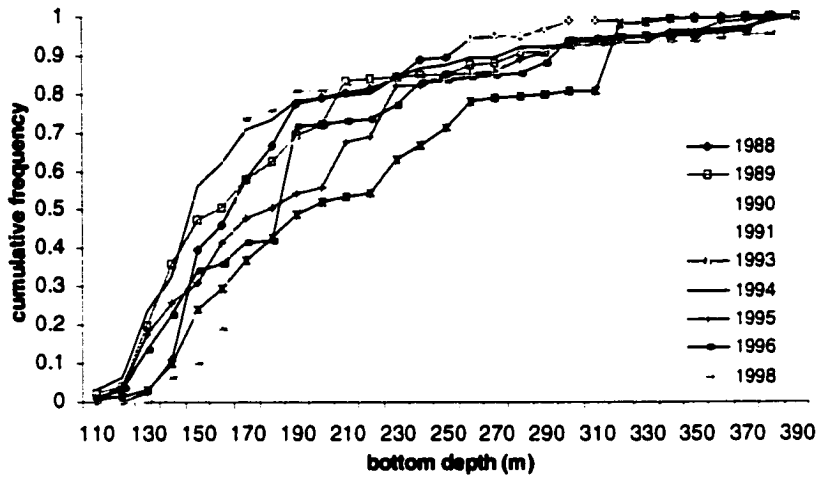

Figure 2.3: Significant annual habitat associations, $G_j(t)$. The maximum vertical distance between any two distributions, S', occured between 1994 and 1998 with a p-value of 0.90, indicating no significant difference in the annual depth distribution of widow rockfish through time. t_{min}=110m, t_{max}= 390m.

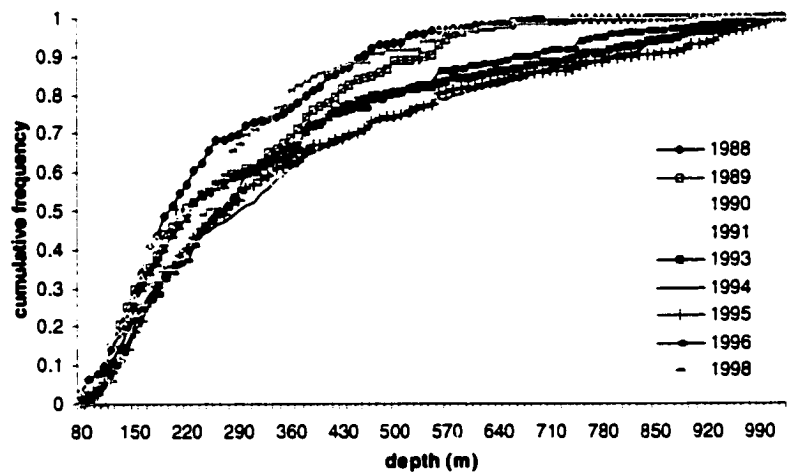

Figure 2.4: Annual distribution of habitats sampled, $F_j(t)$. The maximum vertical distance between any two distributions, S', occured between 1988 and 1991 with a p-value of 0.95, indicating no significant difference in the depth distribution of commercial fishing effort. t_{min}=80m, t_{max}=1020m.

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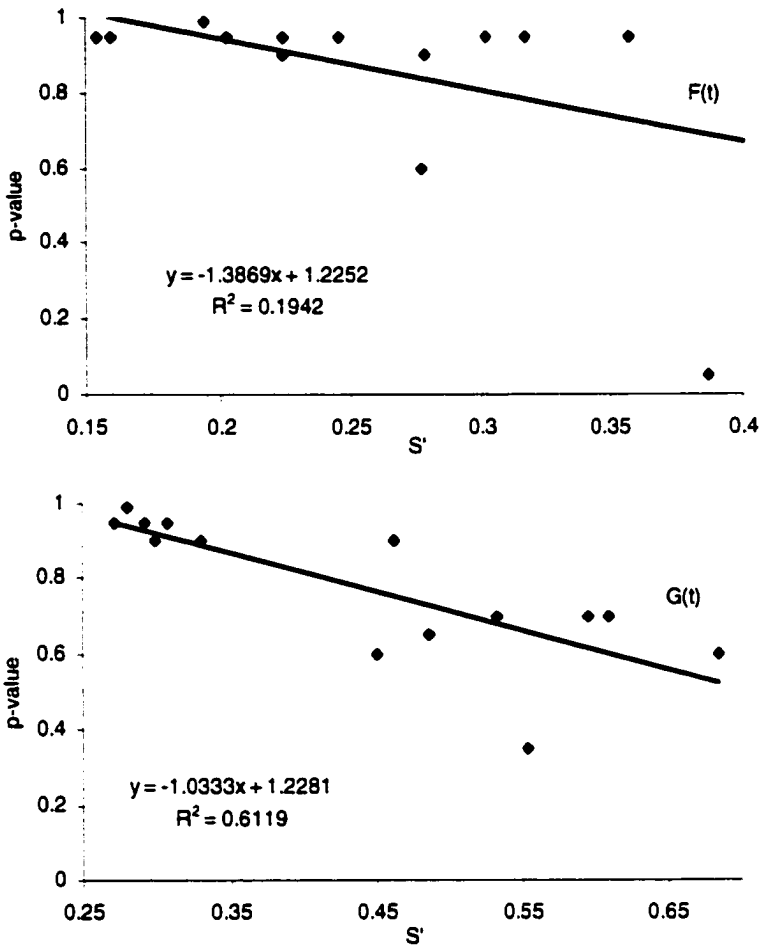

Figure 2.5: Statistical power analysis of modified Birnbaum-Hall test. Plotted are S' values (the maximum distance between cdfs) and their corresponding p-value (the probability that the cdfs are identical) for $F_j(t)$ (top panel) and $G_j(t)$ (bottom panel). Solving the regression equations for p=0.05, we find that the magnitude of the difference between cdfs necessary to yield statistically significant results are $S' > 1.15$ for $F_j(t)$ and $S' > 0.85$ for $G_j(t)$. Since these magnitudes represent very large differences in the distributions, we conclude that the statistical power of this test is low.

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Appendix A:

Additional Data Tables

Table A1: Annual range of depths sampled (meters), and range of depths above which widow rockfish were caught. P-values are the probability that the two distributions are identical, h is the number of divisions sampled, n is the number of tows used in the analysis.

year	range of depths sampled (i.e., $f_i(t)$)			range of depths sampled weighted by catch (i.e., $g_i(t)$)			p	h	n
	10th percentile	50th percentile	90th percentile	10th percentile	50th percentile	90th percentile			
1988	82	189	459	140	169	262	0.05	155	583
1989	116	215	546	128	161	287	0.01	165	686
1990	116	210	574	150	178	234	< 0.01	141	708
1991	107	253	742	112	150	233	< 0.01	248	1823
1992	114	178	555	140	150	225	0.10	198	2304
1993	125	234	843	138	204	322	< 0.01	220	1920
1994	135	319	937	135	154	294	< 0.01	339	3014
1995	135	300	1014	131	188	300	< 0.01	342	2644
1996	122	281	760	131	188	300	< 0.01	245	2268
1997	118	188	560	140	168	460	0.10	174	891
1998	131	253	488	154	165	384	0.05	90	342
average	118	238	680	136	170	298			
standard deviation	15	47	190	11	17	70			
coefficient of variation	13%	20%	28%	8%	10%	23%			

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Table A2: Range of depths sampled (meters), and range of depths above which widow rockfish were caught by season. *P*-values are the probability that the two distributions are identical, *h* is the number of divisions sampled, and *n* is the number of tows used in the analysis.

year	season	range of habitats sampled (i.e., $f_i(t)$)			range of habitat sampled weighted by catch (i.e., $g_i(t)$)			p	h	n
		10th percentile	50th percentile	90th percentile	10th percentile	50th percentile	90th percentile			
1988	winter	150	197	467	143	188	272	0.15	47	168
	spring	56	174	431	56	171	197	0.05	76	236
	summer	105	173	240	146	150	213	0.95	45	122
	fall	116	347	469	169	244	244	0.15	34	54
1989	winter	133	281	563	148	191	318	<0.01	83	254
	spring	112	173	247	144	169	206	0.95	14	50
	summer	111	169	429	111	140	184	0.05	83	256
	fall	150	281	497	150	159	197	<0.01	53	132
1990	winter	146	336	563	150	188	281	<0.01	79	279
	spring	138	169	346	167	168	247	0.25	23	59
	summer	84	155	304	138	169	231	0.15	67	208
	fall	150	244	652	150	169	221	<0.01	58	158
1991	winter	154	431	721	140	188	290	<0.01	70	315
	spring	114	201	656	114	160	178	<0.01	104	363
	summer	99	174	618	99	131	193	0.15	141	544
	fall	144	388	806	122	188	285	0.05	144	598
1992	winter	129	188	797	141	169	212	0.60	56	366
	spring	133	212	313	135	150	230	<0.01	57	535
	summer	105	156	412	118	150	180	0.55	130	1042
	fall	146	201	493	135	150	246	0.05	86	357
1993	winter	140	351	750	139	232	262	<0.01	60	228
	spring	136	223	712	150	225	253	0.25	91	460
	summer	116	225	825	146	178	251	<0.01	164	865
	fall	144	337	675	150	320	322	0.15	98	364
1994	winter	150	369	863	144	169	281	0.05	130	487
	spring	153	363	1013	140	159	225	<0.01	146	848
	summer	128	245	796	133	154	337	0.05	216	1284
	fall	165	337	843	140	198	337	<0.01	133	395
1995	winter	148	523	1050	131	144	300	<0.01	132	266
	spring	146	300	975	140	199	341	0.05	214	1279
	summer	114	225	937	140	187	356	0.10	199	943
	fall	135	292	937	140	169	303	<0.01	77	157
1996	winter	153	412	843	144	178	288	0.05	64	163
	spring	120	275	618	120	154	300	0.05	139	688
	summer	112	245	712	131	169	300	0.05	148	1351
	fall	133	195	656	133	187	309	0.55	34	67
1997	winter	140	187	965	131	140	337	0.10	23	48
	spring	148	236	562	140	150	193	<0.01	63	270
	summer	108	176	468	144	157	191	0.05	135	545
	fall	144	211	562	150	186	562	0.50	15	29
1998	winter	--	--	--	--	--	--	na	0	0
	spring	165	281	468	155	165	193	0.05	38	97
	summer	129	243	436	150	281	403	0.70	63	227
	fall	--	--	--	--	--	--	na	0	0

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Table A3: Step 2 results: Pair-wise comparisons of (whole year) interannual distributions. Table entries are S_{ab} values for the habitat associations, $G_j(t)$, with S_{ab} values for the habitat sampled, $F_j(t)$, in parentheses. S' (p=0.90) occurred for a=1994 and b=1998, t_{min}=110m, t_{max}= 390m . For habitat sampled, S' (p=0.95) occurred for a=1988 and b=1991, t_{min}=80m, t_{max}=1020m.

	1988	1989	1990	1991	1993	1994	1995	1996
1989	0.251 (0.117)							
1990	0.166 (0.152)	0.319 (0.073)						
1991	0.386 (**0.224**)	0.306 (0.172)	0.416 (0.128)					
1993	0.287 (0.147)	0.301 (0.127)	0.316 (0.084)	0.379 (0.098)				
1994	0.216 (0.220)	0.131 (0.162)	0.331 (0.137)	0.284 (0.088)	0.338 (0.113)			
1995	0.230 (0.197)	0.164 (0.153)	0.217 (0.143)	0.320 (0.087)	0.189 (0.093)	0.249 (0.047)		
1996	0.247 (0.193)	0.204 (0.134)	0.186 (0.144)	0.311 (0.104)	0.228 (0.110)	0.312 (0.084)	0.172 (0.077)	
1998	0.297 (0.190)	0.375 (0.132)	0.268 (0.139)	0.438 (0.221)	0.363 (0.155)	**0.461** (0.205)	0.265 (0.197)	0.336 (0.170)

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Table A4: Pair-wise comparisons of winter distributions. Table entries are S_{ab} values for the habitat association, with S_{ab} values for the habitat sampled in parentheses. S' for the habitat association occurred for a=winter 1990 and b=winter 1995 (p=0.35). S' for the habitat sampled occurred for a=winter 1989 and b=winter 1995 (p=0.95).

	1989	1990	1991	1993	1994	1995
1990	0.112 (0.097)					
1991	0.176 (0.249)	0.262 (0.244)				
1993	0.295 (0.173)	0.358 (0.141)	0.211 (0.147)			
1994	0.229 (0.242)	0.158 (0.182)	0.403 (0.135)	0.261 (0.072)		
1995	0.551 **(0.357)**	**0.554** (0.303)	0.495 (0.204)	0.454 (0.191)	0.540 (0.164)	
1996	0.393 (0.250)	0.397 (0.205)	0.339 (0.103)	0.297 (0.125)	0.383 (0.083)	0.335 (0.164)

Table A5: Pair-wise comparisons of spring distributions. Table entries are S_{ab} values for the habitat association, with S_{ab} values for the habitat sampled in parentheses. S' for the habitat association occurred for a=spring 1997 and b=spring 1998 (p=0.65). S' for the habitat sampled occurred for a=spring 1992 and b=spring 1994 (p=0.95).

	1988	1991	1992	1994	1995	1996	1997
1991	0.387 (0.234)						
1992	0.449 (0.184)	0.436 (0.285)					
1994	0.395 (0.303)	0.207 (0.162)	0.229 **(0.401)**				
1995	0.306 (0.282)	0.330 (0.190)	0.359 (0.346)	0.361 (0.129)			
1996	0.323 (0.280)	0.310 (0.217)	0.253 (0.336)	0.171 (0.183)	0.236 (0.077)		
1997	0.458 (0.184)	0.445 (0.157)	0.073 (0.248)	0.238 (0.229)	0.371 (0.148)	0.236 (0.166)	
1998	0.225 (0.208)	0.352 (0.226)	0.466 (0.174)	0.353 (0.312)	0.288 (0.197)	0.362 (0.200)	**0.485** (0.122)

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Table A6: Pair-wise comparisons of summer distributions. Table entries are S_{ab} values for the habitat association, with S_{ab} values for the habitat sampled in parentheses. S' for the habitat association occurred for a=summer 1989 and b=summer 1993 (p=0.70). S' for the habitat sampled occurred for a=summer 1989 and b=summer 1994 (p=0.99).

	1989	1993	1994	1996
1993	**0.610** (0.177)			
1994	0.262 (**0.194**)	0.348 (0.064)		
1996	0.526 (0.185)	0.202 (0.063)	0.404 (0.059)	
1997	0.480 (0.072)	0.424 (0.157)	0.273 (0.193)	0.339 (0.188)

Table A7: Pair-wise comparisons of fall distributions. Table entries are S_{ab} values for the habitat association, with S_{ab} values for the habitat sampled in parentheses. S' for the habitat association occurred for a=fall 1989 and b=fall 1991 (p=0.70). S' for the habitat sampled occurred for a=fall 1991 and b=fall 1992 (p=0.05).

	1989	1990	1991	1992	1994
1990	0.097 (0.124)				
1991	**0.533** (0.273)	0.467 (0.228)			
1992	0.493 (0.249)	0.481 (0.186)	0.396 (**0.387**)		
1994	0.405 (0.196)	0.355 (0.212)	0.227 (0.164)	0.334 (0.365)	
1995	0.351 (0.101)	0.339 (0.096)	0.320 (0.217)	0.254 (0.198)	0.305 (0.231)

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Table A8: Intraannual pair-wise comparison of the distribution of habitat associations and of habitats sampled by season. Table entries are S_{ab} values for the habitat association, with S' for each intra-annual comparison indicated in bold typeface. P-values for S' are in parentheses. a. Habitat association. b. Habitat sampled.

a. Habitat association, $G_j(t)$

year	winter-spring	winter-summer	winter-fall	spring-summer	spring-fall	summer-fall
1988	n/a	n/a	n/a	n/a	n/a	n/a
1989	n/a	0.645	0.402	n/a	n/a	**0.684** (0.60)
1990	n/a	n/a	**0.280** (0.99)	n/a	n/a	n/a
1991	**0.596** (0.70)	n/a	0.215	n/a	0.568	n/a
1992	n/a	n/a	n/a	n/a	**0.307** (0.95)	n/a
1993	n/a	**0.291** (0.95)	n/a	n/a	n/a	n/a
1994	0.245	0.242	0.330	0.277	**0.449** (0.60)	0.402
1995	**0.329** (0.90)	n/a	0.296	n/a	0.328	n/a
1996	0.218	0.219	n/a	**0.299** (0.90)	n/a	n/a
1997	n/a	n/a	n/a	**0.271** (0.95)	n/a	n/a
1998	n/a	n/a	n/a	n/a	n/a	n/a

b. Habitat sampled, $F_j(t)$

year	winter-spring	winter-summer	winter-fall	spring-summer	spring-fall	summer-fall
1988	n/a	n/a	n/a	n/a	n/a	n/a
1989	n/a	0.274	0.091	n/a	n/a	**0.302** (0.95)
1990	n/a	n/a	**0.154** (0.95)	n/a	n/a	n/a
1991	**0.277** (0.60)	n/a	0.098	n/a	0.251	n/a
1992	n/a	n/a	n/a	n/a	**0.159** (0.95)	n/a
1993	n/a	**0.203** (0.95)	n/a	n/a	n/a	n/a
1994	0.091	0.192	0.195	0.199	0.135	**0.224** (0.90)
1995	0.248	n/a	**0.278** (0.90)	n/a		n/a
1996	0.278	**0.317** (0.95)	n/a	0.166	n/a	n/a
1997	n/a	n/a	n/a	**0.245** (0.95)	n/a	n/a
1998	n/a	n/a	n/a	n/a	n/a	n/a

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Appendix B:
Correlation analysis between bottom depth and the location of widow rockfish relative to bottom depth

While examining the habitat association between widow rockfish and bottom depth, we detected a linear relationship between bottom depth and the location of widow rockfish relative to the ocean floor. Of the tows with positive widow rockfish catch (i.e., CPUE>0), 72% occurred at least 5 meters above the ocean floor. Using these data, we found a significant correlation between the dependent variable (i.e., the location of fish above the bottom) and the independent variable (i.e., bottom depth, Table B1). Similarly, we found significant correlations within each season.

To determine if the relationship between the location of the fish and bottom depth changes by season, we conducted an analysis of covariance (Zar 1999). From our four seasonal regressions (k=4), we can calculate a "pooled" residual sum of squares, SS_p, by summing the values of the four regression residual sum of squares (Table B2). Similarly, the "pooled" residual degrees of freedom, DF_p, is the sum of the four regression residual degrees of freedom. The values of $\sum x^2$, $\sum xy$, and $\sum y^2$ for each of the four regressions can be summed, and from these sums a residual sum of squares may be calculated to yield the "common" residual sum of squares, SS_c.

To test for a difference among slopes, our null hypothesis is that the four regression lines have the same slopes. We calculated the F statistic as follows:

$$F = \frac{\left(\frac{SS_c - SS_p}{k-1}\right)}{\left(\frac{SS_p}{DF_p}\right)} \qquad \textbf{(Equation B1)}$$

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where the degrees of freedom for the numerator are (k-1) and for the denominator are DF_p. Our calculated F statistic was 13.35, and since $F_{0.01(1),3,5977} \approx 5.91$, we rejected our null hypothesis.

Since we concluded that the four regression line slopes are not all equal, we then exployed Tukey's multiple comparison test to determine which slopes are different from which others. To compare slopes between line A and B, we used the following test statistic:

$$q = \frac{b_B - b_A}{SE} \qquad \textbf{(Equation B2)}$$

where

$$SE = \sqrt{\frac{SS_p}{2DF_p}\left[\frac{1}{(\sum x^2)_A} + \frac{1}{(\sum x^2)_B}\right]} \qquad \textbf{(Equation B3)}$$

Our results indicated that the slope of the spring regression was significantly different than all other seasons (TableB3) and that the slopes of summer and fall are significantly different. The implication of these results is that widow rockfish do exhibit seasonal vertical movement. Within the range of bottom depths comprising their significant habitat association, widow rockfish are found closest to the bottom in the spring, and furthest from the bottom in winter.

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Table B1: Simple linear regressions between bottom depth (x) and location of fish (y) in meters above bottom depth. Data are limited to tows with positive widow rockfish catch that occurred at least 5 meters above the bottom.

data	regression	n	R^2
all data	y = 0.7442x - 98.57	5983	0.80
winter	y = 0.6987x - 79.90	602	0.71
spring	y = 0.7869x - 118.79	1897	0.85
summer	y = 0.7364x - 92.24	3044	0.80
fall	y = 0.6688x - 85.71	440	0.67

Table B2: Testing for significant differences among slopes and elevations of 4 simple linear regression lines

regression	$\sum x^2$	$\sum xy$	$\sum y^2$	Residual SS	Residual DF
winter	2886765	2017103	1981495	572061.09	600
spring	29817724	23459340	21709530	3252701.08	1897
summer	55329736	40747338	37607638	7599442.14	3042
fall	3751063	2508805	2509649	831696.51	438
"pooled" regression				SS_p = 12255900.8	DF_p = 5977
"common" regression	91785288	68732586	63808311	SS_c = 12338533.5	DF_c =5980

Table B3: Data for Tukey's multiple comparison test to determine which slopes are different from which others.

line A	line B	slope of A	slope of B	SE	Tukey's q	DF	cutoff value	decision
spring	winter	0.787	0.699	0.020	4.46	5977	3.633	reject null
summer	winter	0.736	0.699	0.019	1.95	5977	3.633	fail to reject null
fall	winter	0.669	0.699	0.025	1.19	5977	3.633	fail to reject null
summer	spring	0.736	0.787	0.007	6.92	5977	3.633	reject null
fall	spring	0.669	0.787	0.018	6.72	5977	3.633	reject null
fall	summer	0.669	0.736	0.017	3.96	5977	3.633	reject null

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Chapter Three

Changes in the spatial distribution of widow rockfish (*Sebastes entomelas*) off the Oregon coast with implications for marine reserve design

Introduction

Marine reserves, areas where fishing is banned, are a hotly debated topic in marine fisheries management. Although the concept of marine reserves was first proposed over 40 years ago (Beverton and Holt 1957), traditionally they have been rejected in favor of less conservative management techniques, such as fleet and gear control (Guenette et al. 1998). Currently, less the one half of one percent of the world's oceans are set aside as marine protected areas (MPAs), and only a fraction of these ban fishing (Roberts and Hawkins 2000). However, marine reserves are gaining renewed attention in part due to the growing global fisheries crisis (NRC 1999, Parker et al. 2000), the high degree of uncertainty in fisheries management (Ballantine 1997, Guenette et al. 1998), and renewed optimism that marine reserves will be the answer to sustainable fisheries (Carr 1993, Man et al. 1995, Murray et al. 1999).

The potential benefits of marine reserves are perhaps most striking for long-lived, slow growing species with limited movement since such species are highly susceptible to overexploitation (Parker et al. 2000, Rowley 1992). West Coast rockfish are prime candidates for management by marine reserves due to their life history traits and overexploited status (Musick et al. 2000, Parker et al. 2000, Yoklavich 1998). Rockfish have low population growth rates, low productivity, delayed maturity, and are long-lived (Boehlert et al. 1982, Love 1990, Wyllie Echeverria 1987). Furthermore, adult rockfish often exhibit site fidelity (Carlson and Haight 1972, Hartmann 1987, Mathews and

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Barker 1983, Pearcy 1992, Stanley et al. 1994) and have widely dispersing larvae (Larson et al. 1994, Love et al. 1991). Perhaps because of these life history characteristics and their commercial importance, the majority of rockfish species that have been assessed exhibit a downward trend in abundance (Ralston 1998). Fourteen rockfish species are of immediate concern to conservationists (Musick et al. 2000), but the actual number is likely to be considerably higher since there have not been formal assessments of the status of the majority of rockfish species. Widow rockfish, *Sebastes entomelas*, is one of the most commercially important rockfish species on the US West Coast (Williams et al. 2000), but due to overfishing, the American Fisheries Society has classified widow rockfish as vulnerable to the risk of extinction (Musick et al. 2000). This species' vulnerability is primarily due to its life history limitations, particularly the fact that widow rockfish productivity is very low (Musick et al. 2000, Wyllie Echeverria 1987).

Although widow rockfish and other rockfish species would likely benefit from management by marine reserves, gaps in our understanding of marine systems hinder our ability to design effective reserves. Various authors offer suggestions as to what the most critical gaps in our knowledge are, including our inability to predict oceanographic conditions, our lack of basic understanding of fish ecology, and unclear management goals (e.g., Agardy 2000, Ballantine 1997, Carr and Raimondi 1998, Guenette et al. 1998, Murray et al. 1999, Sladek Nowlis and Yoklavich 1998). From a scientific perspective, however, there are two critical pieces of information that must be known in order to identify appropriate placement for marine reserves: 1) the spatial structure of the population(s) being managed, and 2) the interconnectedness of the spatial structure. Considerable effort by those interested in marine reserve design has been on

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understanding the interconnectedness of spatial structure, primarily in terms of larval production by "source" populations and larval transport between populations (e.g., Botsford 1994, Doebeli and Ruxton 1998, Hermann et al. 1996, Man et al. 1995, Rogers-Bennett et al. 1995, Sladek Nowlis and Yoklavich 1998). Equally important, however, is an accurate understanding of the spatial structure of adult populations and their stability through time (e.g., Death 1996, Hoines et al. 1998, Stalnaker et al. 1996, Thiebaut et al. 1997). However, identifying distributions and understanding their temporal stability is problematic when species are poorly sampled by research surveys, or for myriad species for which no research data exists.

In this paper, we examine the spatial (geographic) distribution of the widow rockfish populations off the Oregon coast. Since widow rockfish are poorly sampled by research surveys (Wilkins 1986), we use commercial logbook data, which are much more readily available than research survey data, to describe the distribution of widow rockfish through time. Although commercial logbook records have been shown to yield distribution patterns similar to research surveys (Fox and Starr 1996), we filter the data based on our knowledge of this fishery to generate a consistent index of abundance through time. We test the sensitivity of our results to the various assumptions we have made. Finally, we discuss the implications of these preliminary findings to marine reserve design.

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Methods

Description of study area

The study area consists of all locations between 42.5^0 - 46.5^0 north latitude and 124.4^0 - 125^0 west longitude. The geographic boundaries of our analysis were limited to encompass an area with sufficient commercial sampling over time. The study area was divided into eight regions, measuring 1^0 latitude by 0.3^0 longitude (Figure 3.1). Each region is divided into 30 division, each measuring 0.1^0 latitude by 0.1^0 longitude.

Description of data

We utilized Oregon commercial logbook data from the Pacific Coast Fisheries Information Network (PacFIN), a regional fisheries data network operated by the Pacific States Marine Fisheries Commission (PacFIN 2000). Data for each tow consisted of: tow date, duration of tow, latitude, longitude, total pounds of fish caught (all species), total pounds of widow rockfish caught, and pounds of widow rockfish adjusted against fish ticket records (Table 3.1). We extracted all records for 1988-1998 for which there were no missing data, including records for which there was no widow rockfish catch.

To look at changes in spatial distribution through time, a consistent index of abundance is needed. Catch-per-unit-effort (CPUE) derived from commercial logbook records may change through time due to fishers' behavior, in addition to changing in response to fluctuations in abundance (Quinn and Deriso 1999). Based on the work of Ralston and Pearson (1997) we filtered logbook data to remove known biases. We applied the following four data filters to the logbook records: 1) the tow location must have been within the study area, 2) the tow must have occurred in January, February or

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March, 3) the tow must have had an adjusted widow rockfish catch ≥ 100 lbs, and 4) the fishing gear used must have been either bottom trawl or roller gear (i.e., bottom trawl gear fitted with large rollers to assist it going over hard substrates). Only records meeting these criteria were included in our Baseline Index of abundance. Filter 2 excludes tows occurring in seasons other than winter since fisher targeting behavior may change later in the year in response to trip limit effects, biasing CPUE low. We also assume that tows < 100 lbs of widow rockfish (Filter 3) were not targeting this species, which could also bias CPUE low. Finally, we filtered the data based on gear type (Filter 4) since the catchability of bottom trawls is unlikely to be equal to that of midwater trawls, the other major gear type used to catch widow rockfish. Differences in catchability (the scalar that relates CPUE to abundance) between gear types are primarily due to the fact that search time, a considerable component of fishing effort associated with midwater trawls fishing for schools of widow rockfish, is unaccounted for in the commercial logbook records.

Commercial sampling never occurred in 37 of the 240 divisions within our study area, and the number of divisions sampled per sample period ranged from 26-144. Therefore, we assume that if sampling did not occur within a division during a particular sample period, then CPUE was zero in that division. Additionally, since we cannot distinguish between actual changes in distribution and changes in catchability through time, we assume that any changes in catchability occurred uniformily across the study area.

In addition to conducting analyses on the Baseline Index of abundance (Table 3.2), we examined the sensitive of results to the aforementioned assumptions. Within sample periods, we compared the spatial distribution of the Baseline Index to indices

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created by relaxing assumptions or filters. We also compared the pattern of temporal shifts in spatial distribution between the Baseline Index and other indices.

We generated four additional indices to compare to the Baseline Index (Table 3.3). The "All Tows" Index includes data from all tows regardless of how much widow rockfish was caught, thus eliminating Filter 3. This index not only increases sample size compared to the Baseline Index, but also increases the number of divisions sampled (Table 3.4). The "Midwater Trawl" Index includes data from midwater trawl gear, which accounts for 9-89% of total catch within sample periods (Figure 3.2, Table 3.5). There is no overlap in data between this and the Baseline Index. Next, we were interested in knowing if the scale of analysis affected our results. The "Large Divisions" Index increases the division size to 0.2^0 latitude by 0.2^0 longitude, and consequently the only change from the Baseline Index was the number of divisions sampled (Table 3.6). This was the only other spatial scale we examined since data are not available on a finer spatial scale, and further increases in scale resulted in an inadequate sample size. Finally, we relaxed the assumption that CPUE = 0 in divisions not sampled within a given sample period (Filter 4) to create the "Divisions Sampled" Index. For this index, if a division was not sampled in both sample periods being compared, that division was excluded from the analysis. There were no data differences between this index and the Baseline Index, only the statistical treatment differs.

Statistical test

Our null hypothesis is that within the study area, the distribution of widow rockfish does not change from one year to the next. The alternative hypothesis is that

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there is an unspecified, but significant, difference in the distributions. To test this hypothesis we used the statistical test developed by Syrjala (1996), which is based on a bivariate generalization of the Cramer-von Mises nonparametric test for a difference between two univariate probability distribution functions (see also Conover 1980). In Syrjala's test, the random variable is the observed population density at each sampling location, rather than the sampling location itself (as would be the case in a true bivariate generalization of the Cramer-von Mises test).

Population density $d_j(x_k, y_k)$ is estimated for each sampling period j in each division k, where (x_k, y_k) denotes the longitude and latitude coordinates of division k (all symbols are defined in Table 3.7). Population density was estimated as the average CPUE within a division, calculated as:

$$d_j(x_k, y_k) = \frac{\sum_i \frac{c_{ij}(x_k, y_k)}{f_{ij}(x_k, y_k)}}{n_j(x_k, y_k)} \qquad \textbf{(Equation 3.1)}$$

where $c_{ij}(x_k, y_k)$ is the pounds of widow rockfish caught in tow i, region k during sample period j, $f_{ij}(x_k, y_k)$ is the duration of the tow, and $n_j(x_k, y_k)$ is the number of tows in division k in ample period j.

Density observations are normalized so that the comparison of distributions between sample periods is independent of changes in abundance through time. The normalized density observations are:

$$\gamma_j(x_k, y_k) = \frac{d_j(x_k, y_k)}{D_j} \qquad \textbf{(Equation 3.2)}$$

where

$$D_j = \sum_k d_j(x_k, y_k) \qquad \textbf{(Equation 3.3)}$$

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The cumulative distribution function in division k during sample period j is:

$$\Gamma_j(x_k, y_k) = \sum_{\forall x \le x_k, \forall y \le y_k} \gamma(x, y) \qquad \textbf{(Equation 3.4)}$$

The test statistic, analogous to the Cramer-von Mises test statistic, is the squared difference between the two cumulative distribution functions, summed over all divisions:

$$\Psi = \sum_k \left(\Gamma_j(x_k, y_k) - \Gamma_{j+1}(x_k, y_k)\right)^2 \qquad \textbf{(Equation 3.5)}$$

To calculate the test statistic Ψ and its associated level of significance, we used the Microsoft *QuickBasic* program GeoDistn (Syrjala 1996).

Results

Temporal shifts in the spatial distribution detected by the Baseline Index

The annual winter spatial distributions of widow rockfish from 1989 through 1998 are shown in Figures 3.3a-k. We detected three significant shifts in the spatial distribution within the 11-year time series using our Baseline Index of abundance (Table 3.8). The first occurred between 1991-1992 (Figure 3.4a), indicating a shift from the northern end of the sample area (off the coast of Astoria and Tillamook Head) to the middle and southern end of the range (primarily increasing off Heceta Head and Coos Bay). In 1991, 45% of the population biomass was located in region 1b (see Figure 3.1), whereas in 1992 only 12% of population biomass was within this region (Table 3.9). Conversely, in 1991 only 15% of biomass was located within region 3a, but in 1992 this percentage rose to 37%.

The second shift occurred between 1996-1997 (Figure 3.4b), again shifting away from the northern end of the range to the south, but with the biggest increases seen further south, primarily off Cape Blanco. The biggest decrease in biomass occurred in

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region 1b (26% in 1996 versus 8% in 1997), and the largest increase in biomass occurred in region 4a (4% in 1996 versus 27% in 1997).

The third detectable shift in distribution occurred between 1997-1998 (Figure 3.4c). We detected a shift northward from Cape Blanco and Coos Bay, but the increase occurs in the middle of our study area, primarily off Newport. The biggest decrease in biomass occurred in region 4a (27% in 1997 versus 8% in 1998). The largest increases in biomass occurred in regions 2b (13% in 1997 versus 24% in 1998) and region 1b (8% in 1997 versus 16% in 1998).

Temporal shifts in the spatial distribution detected by other indices

The temporal shifts detected by the Baseline Index appear to be robust to the assumption that CPUE=0 in regions not sampled and to spatial scale (Table 3.8). Both the Large Division Index and the Divisions Sampled Index detected the 1991 and 1997 shifts. The All Tows Index also detected the 1997 shift but not the 1991 shift. Two additional distribution shifts were detected in indices other than the Baseline Index: between 1988-1989 detected by the All Tows Index, and between 1993-1994 detected by the Midwater Trawl Index. These discrepancies are addressed in the Discussion section.

Intraannual comparison between Baseline Index to All Tows Index

To determine how sensitive our results were to Filter 3 (tows $\geq$100 lbs widow), we compared the Baseline Index to the All Tows Index. In nine out of eleven years examined, there is no significant different between the two distributions (Table 3.10). The two exceptions are 1991 and 1998. In both years, the inclusion of tows with < 100

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lbs widow rockfish (including tows where CPUE=0) indicate relatively more biomass inshore (i.e., within "b" regions) than the Baseline Index would suggest (Table 3.11). In 1991, the Baseline Index predicts that 68% of biomass was located inshore versus 80% predicted by the All Tows Index. Similarly in 1998, the Baseline Index predicts 69% of biomass inshore versus 78% predicted by the All Tows Index.

Intraannual comparison between Baseline Index to Midwater Trawl Index

The distribution of catch by midwater trawl is significantly different than the distribution of catch by bottom gear in 7 out of 11 years (Table 3.10). The major difference appears to be that the distribution of catch by bottom trawl gear is primarily inshore whereas the distribution of fish caught by midwater gear are predominately offshore (i.e., within "a" regions, Table 3.12). This is most striking in 1991 and 1993, but this pattern also occurs in 1992 and 1994. In 1989 and 1996, however, the inshore-offshore proportions are essentially identical between the Baseline Index and Midwater Trawl Index. In 1989, the main difference is that bottom trawl CPUE is highest in the southern end of the study area (primarily regions 4a and 4b) whereas midwater trawl CPUE is highest in more northern regions (primarily regions 2a, 2b and 3a). 1998 results from Midwater Trawl Index are derived from only 5 tows, and are therefore ignored.

Regional changes in bottom trawl CPUE appear to be unaffected by changes in midwater trawl CPUE. For example, between 1991-1992 our Baseline Index detected large shifts in region 1b, a region not even sampled by the Midwater Trawl Index in those years, and in region 3a, a region in which the Midwater Trawl Index is essentially unchanged between 1991 and 1992 (Table 3.13).

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Discussion

The two shifts in widow rockfish distribution detected by the Baseline Index of abundance correspond to the two major El Niño events occurring between 1988-1998. The first was an extended El Niño that lasted from December 1991-June 1993 (Yoklavich et al. 1996). Although we detected a shift to the southern end of the study area between 1991-1992, we did not detect a corresponding shift back to the northern regions after the El Niño event was over. We assume that the shift back to the non-El Niño distribution was simply too gradual to detect. The second began in the spring of 1997 and was the strongest El Niño event ever recorded (Storlazzi et al. 2000). In this case we detected both a southern shift at the beginning of the El Niño event, and a northern shift towards the end of the event.

Shift in population distribution should be interpreted as changes in the relative fishing success between El Niño and non-El Niño years at a particular location. Most likely, fish are moving in response to the environmental changes associated with the El Niño events, such as changes in water temperature or decreased upwelling. Movement of individuals may be between the northern and southern ends of the study area, but based on previous research on movement in rockfish species, we think that long-distant movement of adults is unlikely (Carlson and Haight 1972, Hartmann 1987, Mathews and Barker 1983, Pearcy 1992, Stanley et al. 1994). Alternatively, movement may be between adjacent regions or occur along a longitudinal gradient, which agrees with other indirect evidence that widow rockfish exhibit inshore-offshore migrations (Hartmann 1987, Love 1981, Mathews and Barker 1983). Yet another possibility is that there may not be substantial movement between regions, but rather individuals may become

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relatively more or less accessible to fishing gear within certain regions under different environmental conditions. A clear understanding of the movement of individuals is beyond the scope of this paper, but merits additional investigation.

Given that we have insufficient fisheries-independent data for widow rockfish, we have no way to validate the assumption that the Baseline Index of abundance is consistent through time. Nevertheless, the sensitivity analyses presented here increases our confidence in these preliminary findings. Results are robust to the choice of spatial scale (i.e., division size), and perhaps more surprisingly, to the assumption that CPUE=0 in divisions not sampled. Given that the baseline results are robust to the latter assumption allows us to maintain more information about the spatial distributions of the population. In other words, if one division had a large CPUE during one sample period, but was not sampled the next sample period, then this information would have to be discarded unless we assumed that CPUE=0 in the sample period during which the division was not sampled.

Filtering data on a minimum widow rockfish catch addresses targeting behavior by fishers, and the possible increase of widow rockfish bycatch. If the Baseline Index correctly identifies population distribution shifts, then widow rockfish appear to be more prevalent offshore during El Niño years (1992 and 1997). Recall that the Baseline Index and the All Tows Index are significantly different in both 1991 and 1998, and the All Tows Index indicates a higher percent of widow rockfish inshore. Therefore, either CPUE from vessels targetting widow rockfish decrease inshore, or CPUE for vessels not targetting widow rockfish increase inshore, or a combination of both.

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Finally, although the All Tows Index predicts a more inshore distribution than the Baseline Index in 1991, the Midwater Trawl Index indicates that at least 37% of total catch occurred offshore in this sample period. These facts must be balanced when thinking about the "true" population distribution. Although the distribution predicted by the Midwater Trawl Index was significantly different that the Baseline Index (i.e., more offshore) during most sample periods, these offshore areas may be less accessible to bottom trawl gear. Clearly the Baseline Index, while it may be most consistent, does not account for a significant proportion of the population in some years (i.e., those accounted for in the Midwater Trawl Index), and that it therefore biases the distribution inshore. Average CPUE weighted by a catchability factor for gear types would allow a simultaneous analysis of the entire widow rockfish commercial catch, but currently no good estimates of catchability exist. Therefore, we think that this parallel analysis of gear types is most appropriate, and that the filters used on the Baseline Index are appropriate.

In conclusion, we feel that an accurate description of the true population distribution of widow rockfish may be difficult with fisheries data, given the sometimes contradictory results from different indices of abundance. Nevertheless, the patterns of shifts in abundance are consistent regardless of the filters used. Therefore, we believe that using commercial logbook records to detected changes in the spatial distribution of exploited populations is appropriate, particularly when using nonparametric techniques.

The implications of these results to marine reserve design are fairly straightforward. First, since the distribution of widow rockfish is variable, a single reserve may not afford equal protection to this species in El Niño versus non-El Niño years. Second, any system of marine reserves with the goal of widow rockfish protection

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should encompass both the inshore and offshore components of widow rockfish habitat. Although previous work has investigated significant habitat associations for widow rockfish (Reynolds et al. 2001a, Reynolds et al. 2001b), considerable work remains to be done to determine the mechanism behind habitat choices and shifts. Nevertheless, since reserve sites can include both high and low levels of human disturbance, even if these results do not reflect the true population distribution, and only reflect regions of high catch, this is useful information for identifying key locations for marine reserves.

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Table 3.1: Oregon commercial logbook data obtained from the Pacific Coast Fisheries Information Network (PacFIN) regional fisheries database (PacFIN, 2000) and a descriptions of column names.

PacFIN database column name	description	units
tow_date	tow date	month, day, year
duration	duration of tow	hours
set_lat	latitude	degrees
set_long	longitude	degrees
total(hpounds)	total pounds landed (all species), recorded by the fisher	pounds
wdow_hpounds	pounds of widow rockfish landed, recorded by the fisher	pounds
wdow_apounds	pounds of widow rockfish, adjusted against fish tickets	pounds

Table 3.2: Data used for Baseline Index of abundance, where n_j is the total number of tows used in the analysis and k_j is the number of divisions with widow rockfish catch ≥ 100 lbs. The percent of total catch reflects the proportion of the total catch that occurred in the winter months within the study area that were included in this index.

year	n_j	k_j	lbs widow	percent of total catch in sample period
1988	106	26	329,888	13%
1989	217	59	1,058,634	24%
1990	424	91	954,513	43%
1991	453	113	929,833	50%
1992	556	115	1,030,176	60%
1993	273	86	488,597	60%
1994	654	144	885,996	61%
1995	334	97	673,213	80%
1996	334	91	440,022	60%
1997	274	94	933,394	69%
1998	191	76	246,997	89%

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Table 3.3: Description of the Baseline Index of abundance and four indices created to test the sensitivity of baseline results to various assumptions. All indices are restricted to the study area bound by 42.5^0 - 46.5^0 north latitude and 124.4^0 -125^0 west longitude, and include only tows that occurred in the winter months.

Filters	Baseline Index	All Tows Index	Midwater Trawl Index	Large Division Index	Divisions Sampled Index
≥ 100 lbs widow rockfish per tow	√		√	√	√
bottom trawl only (gear code 390-391)	√	√		√	√
midwater trawl only (gear code 360)			√		
division size = 0.1^0 latitude by 0.1^0 longitude	√	√	√		√
division size = 0.2^0 latitude by 0.2^0 longitude				√	
assumed CPUE = 0 in divisions not sampled	√	√	√	√	

Table 3.4: Data used for All Tows Index, where n_j is the total number of tows used in the analysis and k_j is the number of divisions with widow rockfish catch > 0 lbs. The percent of total catch reflects the proportion of the total catch that occurred in the winter months within the study area that were included in this index.

year	n_j	k_j	lbs widow	percent of total catch in sample period
1988	118	65	332,644	13%
1989	258	80	1,060,190	24%
1990	518	131	959,107	44%
1991	653	130	937,927	50%
1992	748	137	1,047,042	61%
1993	430	115	498,749	60%
1994	942	147	904,689	62%
1995	462	137	680,759	81%
1996	488	125	444,000	61%
1997	376	125	935,251	69%
1998	324	119	250,841	91%

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Table 3.5: Data used for Midwater Trawl Index, where n_j is the total number of tows used in the analysis and k_j is the number of divisions with widow rockfish catch ≥ 100 lbs. The percent of total catch reflects the proportion of the total catch that occurred in the winter months within the study area that were included in this index.

year	n_j	k_j	lbs widow	percent of total catch in sample period
1988	140	29	2,204,794	86%
1989	225	28	3,395,718	76%
1990	103	23	1,177,280	54%
1991	83	13	834,313	45%
1992	45	12	610,356	36%
1993	19	6	266,980	32%
1994	52	18	505,648	35%
1995	23	13	147,168	17%
1996	27	14	284,590	39%
1997	34	18	396,457	29%
1998	5	3	25,274	9%

Table 3.6: Data used for Large Divisions Index, where n_j is the total number of tows used in the analysis and k_j is the number of divisions with widow rockfish catch ≥ 100 lbs. The percent of total catch reflects the proportion of the total catch that occurred in the winter months within the study area that were included in this index. Note that the only difference between this index and the Baseline Index is k_j.

year	n_j	k_j	lbs widow	percent of total catch in sample period
1988	106	22	329,888	13%
1989	217	33	1,058,634	24%
1990	424	51	954,513	43%
1991	453	61	929,833	50%
1992	556	57	1,030,176	60%
1993	273	51	488,597	60%
1994	654	77	885,996	61%
1995	334	50	673,213	80%
1996	334	54	440,022	60%
1997	274	60	933,394	69%
1998	191	46	246,997	89%

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Table 3.7: Definition of symbols used in text

Symbol	Description, units
$c_{ij}(x_k, y_k)$	adjusted total pounds caught by tow i in sample period j in division k
$d_j(x_k, y_k)$	population density in sample period j in division k
D_j	$= \sum_k d_j(x_k, y_k)$ = total population density in sample period j
$f_{ij}(x_k, y_k)$	duration of tow i in sample period j in division k (hours)
i	tow observation
j	sample period, a 3-month period each year from January to March
k	division, defined as a 0.1 °N latitude by 0.1 °W longitude area, whose longitude and latitude coordinates are (x_k, y_k)
$n_j(x_k, y_k)$	number of tows in sample period j in division k
$\gamma_j(x_k, y_k)$	normalized population density in sample period j in division k
$\Gamma_j(x_k, y_k)$	cumulative distribution function in sample period j in division k
Ψ	test statistic based on a bivariate generalization of the Cramer-von Mises nonparametric test

Table 3.8: Results of interannual comparisons of spatial distributions. Table entries are p-values. Significant difference in the spatial distribution between sample periods (i.e., $p \leq 0.05$) are indicated by an asterisk.

sample periods compared	Baseline Index	All Tows Index	Midwater Trawl Index	Large Division Index	Divisions Sampled Index
1988-1989	0.07	0.05 *	0.10	0.33	0.46
1989-1990	0.40	0.57	0.86	0.94	0.40
1990-1991	0.06	0.17	0.56	0.03 *	0.04 *
1991-1992	0.02 *	0.07	0.71	0.01 *	0.01 *
1992-1993	0.67	0.92	0.13	0.86	0.63
1993-1994	0.43	0.70	0.01 *	0.62	0.60
1994-1995	0.06	0.58	0.54	0.27	0.14
1995-1996	0.21	0.16	0.62	0.11	0.22
1996-1997	0.04 *	0.02 *	0.36	0.02 *	0.02 *
1997-1998	0.01 *	0.15	0.07	0.06	0.01 *

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Table 3.9: Baseline Index, percent of relative population biomass located within each region, and summed over all offshore regions ("a" regions) and inshore regions ("b" regions). Regions shown in Figure 3.1.

year	regions								$\sum_a$	$\sum_b$
	1a	1b	2a	2b	3a	3b	4a	4b		
1998	0	17	2	19	13	16	32	1	47	53
1989	0	9	11	5	9	4	33	28	53	47
1990	1	18	4	12	16	4	23	23	44	56
1991	1	45	6	8	15	9	10	7	32	68
1992	2	12	9	9	37	8	8	15	56	44
1993	0	16	8	13	28	9	6	20	42	58
1994	1	30	6	10	13	26	8	6	28	72
1995	0	11	7	17	36	13	10	6	53	47
1996	3	26	5	11	22	14	4	15	34	66
1997	3	8	2	13	27	8	27	16	59	41
1998	2	16	5	24	16	8	8	20	31	69
average	1	19	6	13	21	11	15	14	44	56
standard deviation	1	11	3	5	10	6	11	8	11	11

Table 3.10: Results of intraannual comparisons of spatial distributions. Table entries are p-values. Significant difference in the spatial distribution between indices (i.e., $p \leq 0.05$) are indicated by an asterisk.

year	Baseline Index vs All Tows Index	Baseline Index vs Midwater Trawl Index
1988	0.31	0.13
1989	0.17	<0.01 *
1990	0.17	0.06
1991	0.03 *	<0.01 *
1992	0.09	<0.01 *
1993	0.16	<0.01 *
1994	0.57	<0.01 *
1995	0.22	0.39
1996	0.38	0.04 *
1997	0.25	0.10
1998	<0.01 *	<0.01 *

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Table 3.11: Sensitivity analysis, comparison of Baseline index to All Tows Index. Table entries are relative percent of population biomass located within each region in a given sample period, and summed over all offshore regions ("a" regions) and inshore regions ("b" regions). Regions shown in Figure 3.1.

year	regions									
	1a	1b	2a	2b	3a	3b	4a	4b	$\sum_a$	$\sum_b$
baseline 1991	1	45	6	8	15	9	10	7	32	68
Index 1 - 1991	1	60	3	3	9	7	7	10	20	80
baseline 1998	2	16	5	24	16	8	8	20	31	69
Index 1 - 1998	1	21	3	25	16	14	2	18	22	78

Table 3.12: Sensitivity analysis, comparison of Baseline Index to Midwater Trawl Index. Table entries are relative percent of population biomass located within each region in a given sample period, and summed over all offshore regions ("a" regions) and inshore regions ("b" regions). Regions shown in Figure 3.1.

year	regions									
	1a	1b	2a	2b	3a	3b	4a	4b	$\sum_a$	$\sum_b$
baseline 1989	0	9	11	5	9	4	33	28	53	47
Index 2 - 1989	0	11	26	37	21	1	4	1	50	50
baseline 1991	1	45	6	8	15	9	10	7	32	68
Index 2 - 1991	12	0	40	18	30	0	0	0	82	18
baseline 1992	2	12	9	9	37	8	8	15	56	44
Index 2 - 1992	0	0	48	14	34	0	0	5	82	18
Baseline 1993	0	16	8	13	28	9	6	20	42	58
Index 2 - 1993	0	0	63	6	31	0	0	0	94	6
Baseline 1994	1	30	6	10	13	26	8	6	28	72
Index 2 - 1994	0	1	9	8	47	31	0	4	56	44
Baseline 1996	3	26	5	11	22	14	4	15	34	66
Index 2 -1996	0	16	16	46	22	0	0	0	38	62
Baseline 1998	2	16	5	24	16	8	8	20	31	69
Index 2 - 1998	0	100	0	0	0	0	0	0	0	100

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Table 3.13: Midwater Trawl Index, percent of relative population biomass located within each region, and summed over all offshore regions ("a" regions) and inshore regions ("b" regions). Regions shown in Figure 3.1.

year	regions								$\sum_a$	$\sum_b$
	1a	1b	2a	2b	3a	3b	4a	4b		
1998	0	21	24	30	15	1	8	1	47	53
1989	0	11	26	37	21	1	4	1	50	50
1990	0	23	24	11	29	13	0	0	53	47
1991	12	0	40	18	30	0	0	0	82	18
1992	0	0	48	14	34	0	0	5	82	18
1993	0	0	63	6	31	0	0	0	94	6
1994	0	1	9	8	47	31	0	4	56	44
1995	0	2	14	41	26	8	4	5	44	56
1996	0	16	16	46	22	0	0	0	38	62
1997	2	7	4	34	18	19	0	16	24	76
1998	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
average	1	8	27	25	27	7	2	3	57	43
standard deviation	4	9	18	15	9	11	3	5	22	22

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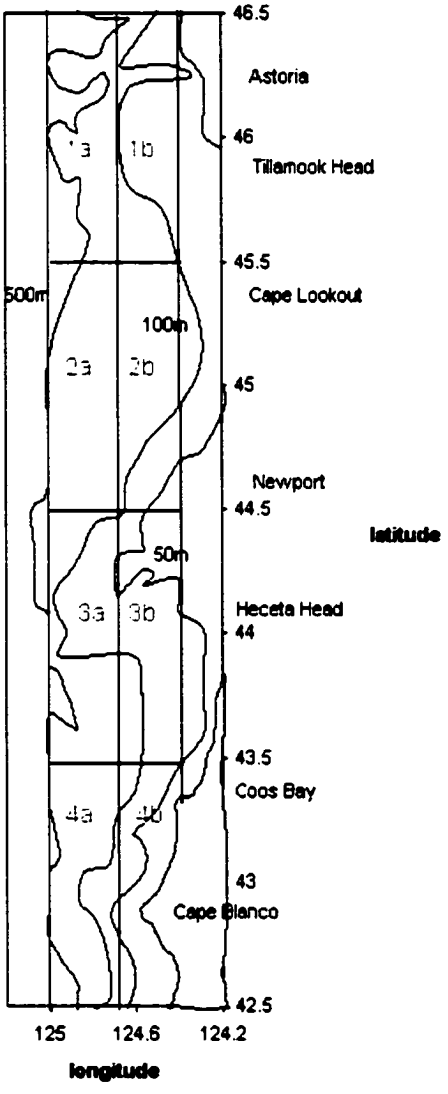

Figure 3.1: Regions within study area. The study area is bounded by 42.5^0-46.5^0 N latitude and 124.4^0-125^0 W longitude. In text, the "a" regions are referred to as the offshore regions, and the "b" regions are the inshore regions. Also illustrated are the 50m, 100m, and 500m depth contour lines.

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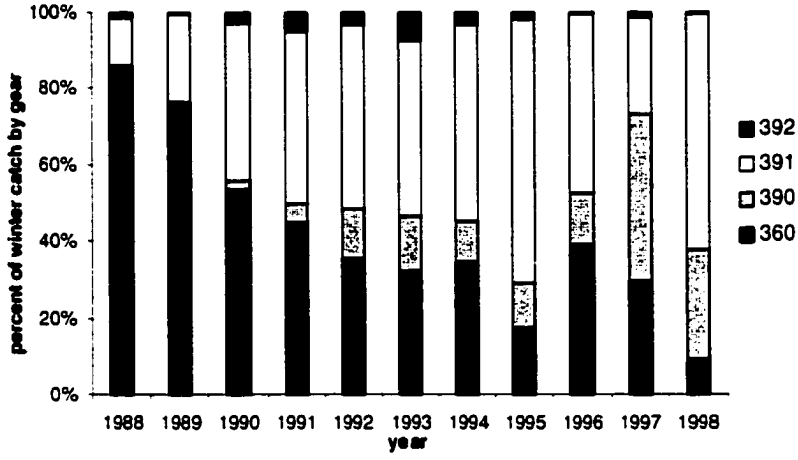

Figure 3.2: Proportion of widow rockfish caught by gear in the winter months (January - March) within the study area enclosed by the boundaries 42.5^0-46.5^0 N latitude, 124.4^0-125^0 W longitude. Gear code 360=midwater trawl, 390=bottom trawl, 391=roller gear, 392= sole net. Data are from Oregon commercial logbook records.

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Figure 3.3: Annual winter spatial distribution of widow rockfish from 1988 through 1998 estimated from the Baseline Index of abundance. Circle width represents the average abundance per division relative to other divisions during the sample period. Each sample period is normalized to control for changes in abundance through time.

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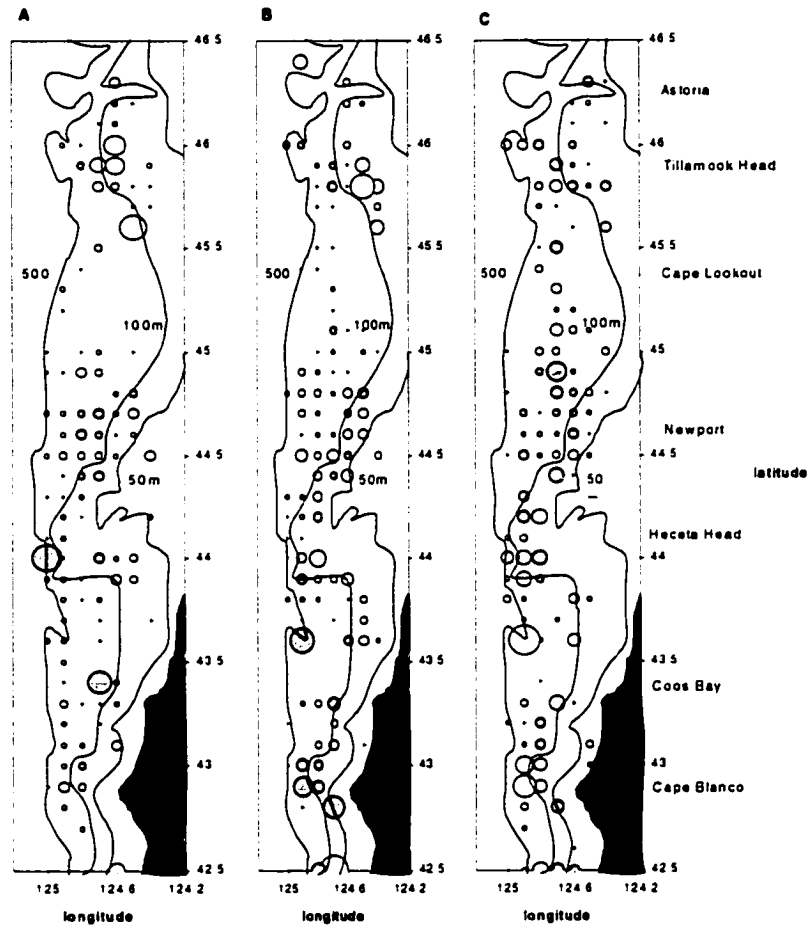

Figure 3.4: Temporal shifts in the spatial distribution of widow rockfish as detected by the Baseline Index of abundance. Open circles indicate a decrease in abundance from sample period *j* to *j*+1. Filled circles indicate an increase in abundance from sample period *j* to *j*+1. The width of the circle represents the relative magnitude of the change in abundance within the sample period among divisions sampled. A. sample periods 1991-1992. B. sample periods 1996-1997. C. sample periods 1997-1998.

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Summary

My goal for this dissertation was to address fundamental issues about widow rockfish habitat use and distribution, which could be used as the foundation for effective marine reserve design. Prior to this work, considerable gaps in our understanding of the widow rockfish fisheries existed. No previous work has specifically addressed the habitat requirements of widow rockfish. Although considerable information exists about the location of widow rockfish commercial catch (Lenarz and Gunderson 1987, NOAA 1991), my research was the first work to assess whether these locations reflect true habitat preferences, or whether they simply reflect the distribution of commercial fishing effort. In **Chapter One**, I identified significant habitat associations between widow rockfish and three habitat variables; bottom depth, vertical location of fish in the water column, and temperature. I defined 'habitat association' as the range of habitat conditions for which 80% of widow rockfish catch is associated within a given sample period, and concluded that these associations were significant if and only if the fish distribution pattern was independent of the pattern of fishing effort. Results indicate that the average significant habitat association for widow rockfish includes bottom depths between 136-298 m, vertical depth between 101-197 m, and temperatures between 7.1-8.1°C. These results provide the first insight into habitat preferences by widow rockfish, which should prove useful in defining essential fish habitat (EFH) for this species.

A major obstacle in developing a clear understanding of essential habitat is fluctuations in habitat use through time. In **Chapter Two**, I detected no significant interannual, seasonal, or intraannual variation in the range of bottom depths preferred by

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widow rockfish. However, given the low statistical power of the test, these results have limited value. Research for other rockfish species (Carlson and Barr 1977, Stanley et al. 1994) and indirect evidence on widow rockfish (Hartmann 1987, Love 1981, Love 1990, Mathews and Barker 1983) suggest that adult widow rockfish have limited home ranges, but they may undertake seasonal on- and off-shore migrations in response to seasonal habitat requirements. I did detect an interesting correlation between bottom depth and the vertical location of fish relative to the bottom. I found that the fish were further off the bottom at deeper bottom depths, and that this relationship varied significantly by season. This is interesting for three reasons. First, although the association with bottom depth is time invariant at the scales examined, the fish are obviously exhibiting some seasonal vertical movement. Second, I suggest that it is the correlation between bottom depth and vertical depth that varies rather than the habitat association with vertical location *per se*. Third, although the mechanisms are unknown, this behavior may be in response to environmental cues such as seasonal upwelling. Understanding the ecological phenomenon affecting this behavior could provide us with additional insight into the ecology and habitat requirements of this species.

Prior to this work, there was some indirect evidence that subpopulations of widow rockfish exist, or at least that populations in different locations are responding to differing environmental conditions (Pearson and Hightower 1991, Ralston and Pearson 1997). Based on these preliminary findings, I investigated the patterns of distribution for this species. In **Chapter Three**, I examined the spatial (geographic) distribution of the widow rockfish populations off the Oregon coast. I detected three significant annual shifts in the spatial distribution within the 11-year time series (1988-1998). The first was

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between 1991-1992, the second was between 1996-1997, and the third was between 1997-1998. These shifts correspond to the two major El Niño events occurring within this time frame. The first was an extended El Niño that lasted from December 1991-June 1993 (Yoklavich et al. 1996). Although I detected a shift to the southern end of the study area between 1991-1992, I did not detect a corresponding shift back to the northern regions after the El Niño event was over. I assume that the shift back to the non-El Niño distribution was simply too gradual to detect. The second began in the spring of 1997 and was the strongest El Niño event ever recorded (Storlazzi et al. 2000). In this case I detected both a southern shift at the beginning of the El Niño event, and a northern shift towards the end of the event.

Implications of results to marine reserve design

The implications of my results to marine reserve design are fairly straightforward. First, any system of marine reserves with the goal of widow rockfish protection should encompass Essential Fish Habitat (EFH) for this species. Although a complete description of EFH is beyond the scope of this dissertation, the significant habitat associations identified in Chapter One provide the basis for such a description. Specifically, the habitat encompassed in any marine reserve(s) for this species should include the range of bottom depths and temperatures significantly associated with widow rockfish distribution. Second, the marine reserve(s) should encompass both the inshore and offshore components of widow rockfish habitat. Although considerable work remains to be done to determine the mechanism behind the seasonal habitat shifts identified in Chapter Two, an awareness of these shifts is crucial for effective reserve

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design. Finally, a single reserve may not afford equal protection to this species in El Niño versus non-El Niño years. In Chapter Three, I found that the geographic distribution of widow rockfish is significantly different in El Niño years, although the mechanisms for these shifts still remain unclear. Therefore, in addition to seasonal habitat use, one must consider interannual shifts in distribution.

Marine reserves are once again at the cutting edge of fisheries management. Although I do not advocate a single-species approach to management, I do believe that habitat information for keystone species will be critical for the creation of effective marine reserves. Given that widow rockfish is one of the most commercially important rockfish species on the west coast, any system of marine reserves should consider the habitat requirements of this species. Furthermore, the methods identified here may prove useful for identifying the habitat associations and distributions of other west-coast fish species.

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