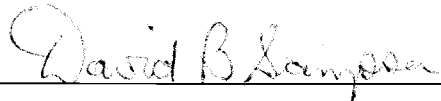


AN ABSTRACT OF THE THESIS OF

Yong Woo Lee for the degree of Doctor of Philosophy in Fisheries Science presented on July 29, 2002. Title: Oceanographic Effects on the Dynamics of Food Habits and Growth Condition of Some Groundfish Species of the Pacific Northwest.

Abstract approved: _____



David B. Sampson

Marine fish are subject to direct and indirect oceanographic variations operating at short and long time scales. In this study feeding habits and long-term growth condition of several groundfish species of the Pacific Northwest are examined to understand the relationship between variations in the fish's biological and life history components and the ocean environment. Stomach samples of three rockfish species, yellowtail rockfish (*Sebastes flavidus*), widow rockfish (*S. entomelas*), and canary rockfish (*S. pinniger*), which were collected seasonally off the Pacific Northwest in 1998 and 1999, provided quantitative information on the food habits of the species during and directly after the 1997-98 El Niño event. The diets of these co-occurring species were markedly different from each other. Unusual southern zooplankton species were found in the diets of all three species possibly due to the influence of the El Niño event. The diet of *S. flavidus* in 1998 summer (El Niño) was contrasted with results from a previous study based on 1980 summer samples (non-El Niño), and found to be different. An assessment of long-term changes in fish growth condition was conducted using data from Oregon market

samples, in which the fish weights are generally measured for aggregations of fish rather than individuals. Non-linear regression can be applied to this type of data to estimate the length-weight parameters and to detect long-term changes in growth condition. The reliability of the estimation method was tested using Monte Carlo simulation. The results demonstrate that the estimation method provides reasonably accurate estimates and is sufficiently powerful to detect small changes in the length-weight relationship. Using Oregon market sample data collected over several decades and the non-linear regression method, growth condition indices were developed and examined for five fish species: Dover sole (*Microstomus pacificus*), petrale sole (*Eopsetta jordani*), canary rockfish, yellowtail rockfish, and widow rockfish. No particular trend or close association with environmental variables was evident in the long-term growth condition indices for any of the species, but interannual and seasonal variations in condition were clearly evident. Possible reasons for the lack of long-term trends in condition and the lack of any close association with the environmental variables are discussed.

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July 29, 2002

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Oceanographic Effects on the Dynamics of Food Habits and Growth Condition of
Some Groundfish Species of the Pacific Northwest.

by

Yong Woo Lee

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APPROVED:

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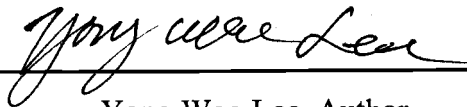
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OCEANOGRAPHIC EFFECTS ON THE DYNAMICS OF FOOD HABITS AND GROWTH CONDITION OF SOME GROUND FISH SPECIES OF THE PACIFIC NORTHWEST

CHAPTER 1: GENERAL INTRODUCTION

Traditional numerical population analysis techniques have been used to assess the harvestable size of the fish stocks and to model the patterns of marine organisms for improving our understanding and our management schemes. However, because of the complex nature of the ecosystem and its inherent variability, oftentimes this approach fails to correctly predict the trajectory of the populations (Gulland 1988). Recently the idea that environmental variability, either natural or anthropogenically induced, will have a strong influence on the biological responses of marine organisms has become more prominent amongst fisheries and oceanographic scientists as a possible mechanism to account for variability in aquatic plankton or fish populations that could not be adequately described by traditional population dynamics approaches (Rothschild 1995).

Although it is generally believed that over-exploitation of many fish stocks caused their drastic decline, even approaching extinction, there are some hypotheses and evidence that natural sources of variability (e.g., short-term or long-term climatic fluctuations, or combinations of physical, chemical, and biological processes, not

understood at present) are the major causes of fluctuations in fish populations and community structure. Drastic anomalous events in the ocean environment such as caused by El Niño events, when coupled with high exploitation rates, could alter the aquatic population structure in an irreversible manner.

All biological systems are comprised of mosaics of environmental conditions arising from physical, chemical, and biological processes operating on a diversity of temporal and spatial scales. The temporal scales could range from daily, seasonal, annual, and decadal, to longer time scales, and the spatial scales could range from local, to continental, to global. The variations could be the results of regular and predictable processes (e.g., local upwelling, seasonal changes in temperature, local current pattern, etc.) or irregular and unpredictable ones (e.g., El Niño and La Niña events, floods, droughts, etc.). By recognizing the patterns of biological responses to changing environmental conditions, we may be able to predict the scale and timing of future events and their level of influence. In this study I explore the potential oceanographic influences on certain biological processes that are associated with some commercial fish species off Oregon.

The Oregon coast has a relatively smooth and broad continental shelf with significant fresh water input from the Columbia River to the north, and a relatively rough and narrow continental shelf with little fresh water input to the south. North of Oregon the large scale Subarctic Current (West Wind Drift) bifurcates into two different current systems: the northward flowing Alaska Current and the southward

flowing California Current. The current off Oregon is a part of California Current system (Brodeur et al. 1996).

The main components of the California Current system consist of the California Current, the Davidson Current, and the California Under Current. Oceanographic conditions on the Oregon shelf exhibit strong seasonal patterns. Data from surface drift bottles indicate that surface movement over the Oregon shelf is southward during May through August (summer), northward during October through February (winter), and variable in March, April, and September (Purdy 1990). Upwelling induced by wind-driven Ekman transport brings cold nutrient-rich water from the deep-water mass (under the thermocline) into the euphotic zone along the coast and forms highly productive environments in the region. Coastal upwelling is seasonally observed off Oregon and it has important relationships with biological productivity there (Huyer 1983).

Since 1950 there have been 7 strong El Niño occurrences: during 1957-58, 65-66, 72-73, 82-83, 86-87, 91-92, and 97-98 (Philander 1990). The most recent event (1997-98) is considered one of the strongest El Niños in the 20th century, comparable to the record 1983 El Niño. A tropical El Niño is characterized by anomalous environmental conditions caused by a relaxation of the trade winds in the central and western Pacific. The event deepens the thermocline in the eastern Pacific and elevates the thermocline in the west and the heated surface water spreads out from the west to the east of the Pacific Ocean. It is often detectable along the West Coast of North America by increases in surface and near-surface water temperature,

a rise in coastal sea level, an increase in the depth of the thermocline, and anomalous coastal currents. During the 1983 El Niño event the sea surface temperature (SST) was elevated up to 4°C and salinity was 0.1~0.2 ppt above normal off California, and SST was 2°C above normal off Oregon (McLain 1984). Extremely strong northward currents were also observed along the California and Oregon coast during the summer of 1983 (Huyer and Smith 1985). El Niño events can have drastic ecological and economic consequences for biotic systems and fisheries. Examples of El Niño effects on the ecosystems are numerous, including disastrous effects on the reproductive physiology of various organisms, anomalous variations in recruitment of some fish stocks and changes in zooplankton abundance, and so on (Miller et al. 1985). Thus, it can be characterized as a major perturbation to the ecosystem.

In 1976 there was an abrupt change in the Pacific climate, called a regime shift (Ebbesmeyer et al. 1991), that resulted in a general warming, and some biological responses were observed. After the shift El Niño events were more frequent and longer lasting and there is some evidence that this warming resulted in a decline in zooplankton abundance. For example, Roemmich and McGowan (1995) reported an 80% decline of the macrozooplankton off southern California based on 43 years of observations, and they suggested that the observed decline was linked to the warming. As the sea surface is heated, the temperature difference across the thermocline increases. For a given along-shore wind stress, the upwelling displacement of the thermocline is inversely proportional to the stratification. Increased stratification could depress the upwelling strength, resulting in blockage to

The ocean environment could have direct effects on the organisms inhabiting the system. In turn, a perturbed group of organisms can have a secondary effect on trophically related groups if the connections between the groups are strong enough (e.g., a top-down effect or bottom-up effect). The goal of this dissertation is to examine the effects of ocean variations including El Niño events and other available environmental variables on certain marine fish species. There are three separate, but inter-related research topics that are covered in this dissertation. First, the food habits of three rockfish species off Oregon during the 1998 El Niño and 1999 La Niña were examined based on seasonal collections of stomach samples. The yellowtail rockfish food habits also were contrasted with previously published data that were collected during 1980, a non-El Niño year. This allowed me to investigate the possible effects of a major anomalous oceanographic event on the rockfish food habits. Secondly, a statistical simulation study was conducted on the use of a non-linear regression method to estimate length-weight relationships from market sample data, which are routinely collected for fishery stock assessment purposes on the U.S. west coast. One of the characteristics of these market sample data is that the measurements of fish weight are made from groups of fish, as “basket sample weight”, but individual length measurements are available for each basket sample. The applicability of the nonlinear regression method for assessing changes in growth condition was also tested and evaluated. Lastly, long-term variations in growth condition were examined for two flatfish and three rockfish species off Oregon based upon available market sample data and the non-linear regression method. Time series indices of

growth condition for these fish species were developed to examine temporal variations and possible relationships with environmental factors. The environmental variables of the ocean and climate of the Pacific Northwest exhibit strong seasonal and annual variations. The coastal waters off the Pacific Northwest are also subject to large environmental perturbations including El Niño, La Niña, and decadal-scale climate changes. Thus, one would expect that variations in the environment would be reflected in the growth condition of the study organisms.

CHAPTER 2: FOOD HABITS OF THREE CO-OCCURRING ROCKFISH SPECIES OFF THE PACIFIC NORTHWEST DURING ANOMALOUS OCEANOGRAPHIC EVENTS IN 1998 AND 1999

INTRODUCTION

Numerous rockfish species inhabit the waters off California, Oregon, and Washington. At least 69 species occur in the northeast Pacific (Chen 1975). Many of these species are important members of the region's commercially exploited groundfish resources. Despite the economic importance of these species, we have limited knowledge about their behavior and ecology, including how the individual species interact within the coastal ecosystem. During the unusual oceanographic events of the 1997-98 El Niño and the subsequent cooling phase called La Niña in 1999, the food habits of three commercially important rockfish species, yellowtail (*Sebastes flavidus*), widow (*S. entomelas*), and canary rockfish (*S. pinniger*), were studied. Their diets were described, the relationship between dietary variation and external factors examined, and comparison made to dietary data for yellowtail rockfish from 1980. The rockfish species are bottom oriented but feed on pelagic macrozooplankton species. It has not been established whether they are influenced by changes in the prey species community structure, but one would expect that these rockfish would be influenced by changes in zooplankton populations or community structure because these fish species feed heavily upon pelagic macrozooplankton species that are sensitive to environmental changes.

Brodeur and Pearcy (1984) studied the food habits of five rockfish species (*S. flavidus*, *S. pinniger*, *S. diploproa*, *S. alutus*, and *S. crameri*) from seasonal collections in 1980 and the NMFS 1980 summer survey in the northeast Pacific, in an attempt to understand the potential competition among these species in their use of prey resources and habitats. For the examination of seasonal and geographical variations in the food habits, their study focused on two species, *S. flavidus* and *S. pinniger*. Prior to this study, most studies on rockfish food habits focused on shallow-water species or were limited in geographic locations and sample collection times. Adams (1987) described the diets of widow rockfish (*S. entomelas*) from samples of commercial and partyboat landings at California's ports. Both of these studies showed that the diets of those rockfish species exhibited seasonal variations in prey composition.

Several studies report seasonal and interannual variations in the abundance and species composition of zooplankton in the northeast Pacific (Brodeur et al. 1996; Colebrook 1977; Mackas 1992, 1995; Pearcy 1976; Peterson and Miller 1975, 1977; Tanasichuk 1998a, 1998b). Changes in physical conditions such as upwelling strength or in climate conditions could be one of the causes (Francis et al. 1998; Mackas et al. 2001). Coastal upwelling is seasonally observed off Oregon and it has important relationships with biological productivity there (Huyer 1983).

The waters off California, Oregon, and Washington are subject to broad disturbance by El Niño events. The recent event (1997-98) is considered the first or second strongest El Niño in this century, comparable to the record 1983 El Niño. It is often detectable along the West Coast of North America by increased surface and near-surface water temperature, a rise in coastal sea level, an increase in the depth of the thermocline, and anomalous coastal currents (Huyer and Smith 1985). It reduces the intensity and magnitude of the upwelling along the coast, consequently leading to the reduction of nutrient concentrations, and reduced abundance of phytoplankton and zooplankton.

El Niño events can have drastic ecological and economic consequences for biotic systems and fisheries. Evidence of El Niño effects on the ecosystems are numerous. It can have disastrous effects on the reproductive physiology of various organisms, recruitment of some fish stocks, zooplankton abundance, and so on (Bailey et al. 1995; Chaves et al. 1999; Lenarz et al. 1995; Miller et al. 1985). Brodeur and Pearcy (1992) observed marked changes in the taxonomic composition of the diet of many pelagic species (e.g., salmon, anchovy, and squid) during the warm and low productivity El Niño event of 1983. They also noticed the effect of upwelling strength on the food habits, diet overlap, and food web complexity of pelagic fish species.

Peterson (1999) reported changes in species composition and biomass of the copepod community during the 1997-98 El Niño event off central Oregon. Dominance of warm-water copepod species during this period was detected.

Alternations in zooplankton community and the unusual southern zooplankton species were also noted in the northern coastal water off British Columbia during the same period (Mackas and Galbraith 2000).

This study aims to examine the possible changes in the diets of rockfish species due to the changes in lower trophic level organisms (zooplankton). More precise knowledge of the food habits of fish species would improve the trophic and ecosystem models as well as population assessment models (Livingston 1985; Livingston 1986).

The objectives of this study include 1) the description of food habits of three commercially important rockfish species (*S. flavidus*, *S. entomelas*, and *S. pinniger*) over the study period (1998-99), during which the ocean environment went under considerable changes, 2) examination on the relationship between the dietary variation and some external factors, and 3) the comparison on the diets of yellowtail rockfish collected during the 1998 El Niño with the diets reported during the 1980 non-El Niño year to examine the possible changes between the periods. The food habits of widow rockfish (*S. entomelas*) have never been closely examined in study area, off Oregon and Washington.

MATERIALS and METHODS

Sample Collection

Stomach samples of three rockfish species, yellowtail rockfish (*S. flavidus*), widow rockfish (*S. entomelas*), and canary rockfish (*S. pinniger*), were collected off the Oregon coast during 7 fishing trips aboard Oregon trawlers over six consecutive fishing seasons from spring of 1998 to fall of 1999. Each trip lasted two to four days of fishing. The samples of *S. flavidus* were also collected during the triennial bottom trawl survey conducted by the National Marine Fisheries Service (NMFS) in the summer of 1998, over the latitudes of Oregon and Washington. These were compared to samples collected during the NMFS 1980 survey in the same geographic area. A total of 545 seasonal stomach samples of the three rockfish species were collected from 49 different stations over the six seasons, and 360 additional *S. flavidus* stomach samples were collected from 56 stations during NMFS 1998 summer survey (Table 2.1).

The NMFS samples were collected at stations allocated according to a systematic-random design. The survey area was divided into three depth strata: continental shelf (55-183 m), shelf break (184-366 m), and uppermost continental slope (366-500 m). Stations were randomly assigned along tracklines that were laid across the depth strata. A minimum of one station was assigned in each depth stratum along each trackline segment. Each trawling was conducted for 30 minutes at a given station (Shaw et al. 2000). In contrast, the fishers selected the trawling

stations based upon sonar detection of large schools of rockfishes on the bottom.

These different sampling schemes resulted in different coverage of the study area.

Table 2.1. Number of stomachs samples collected from commercial fishing trawlers, and NMFS 1980 and 1998 summer survey cruises. The number of non-empty stomach samples are in parentheses.

Sampling dates	Fishing Vessels	No. of Stations	<i>S. flavidus</i>	<i>S. entomelas</i>	<i>S. pinniger</i>
5-8 Apr. 1998	<i>Pacific</i>	12	31 (29)	60 (37)	17 (15)
6-9 Aug. 1998	<i>Kelly Girl</i>	6	31 (29)	56 (48)	29 (24)
8-9 Nov. 1998	<i>Pacific</i>	7	24 (16)	37 (24)	13 (11)
13-14 Feb. 1999	<i>Pacific</i>	6	9 (7)	26 (7)	10 (9)
6-7 Apr. 1999	<i>Pacific</i>	11	54 (45)	48 (46)	27 (6)
16-18 Apr. 1999					
13-16 Sep. 1999	<i>Pacific</i>	7	18 (13)	47 (32)	8 (0)
27 Jun. 1998 ~ 7 Aug. 1998 (NMFS survey)	<i>Dominator</i> <i>Vesterallen</i>	56	360 (312)	-	-
12 Jul. 1980 ~ 28 Sep. 1980 (NMFS survey)	<i>Mary Lou</i> <i>Pat San Marie</i>	21	185 (147)	-	-

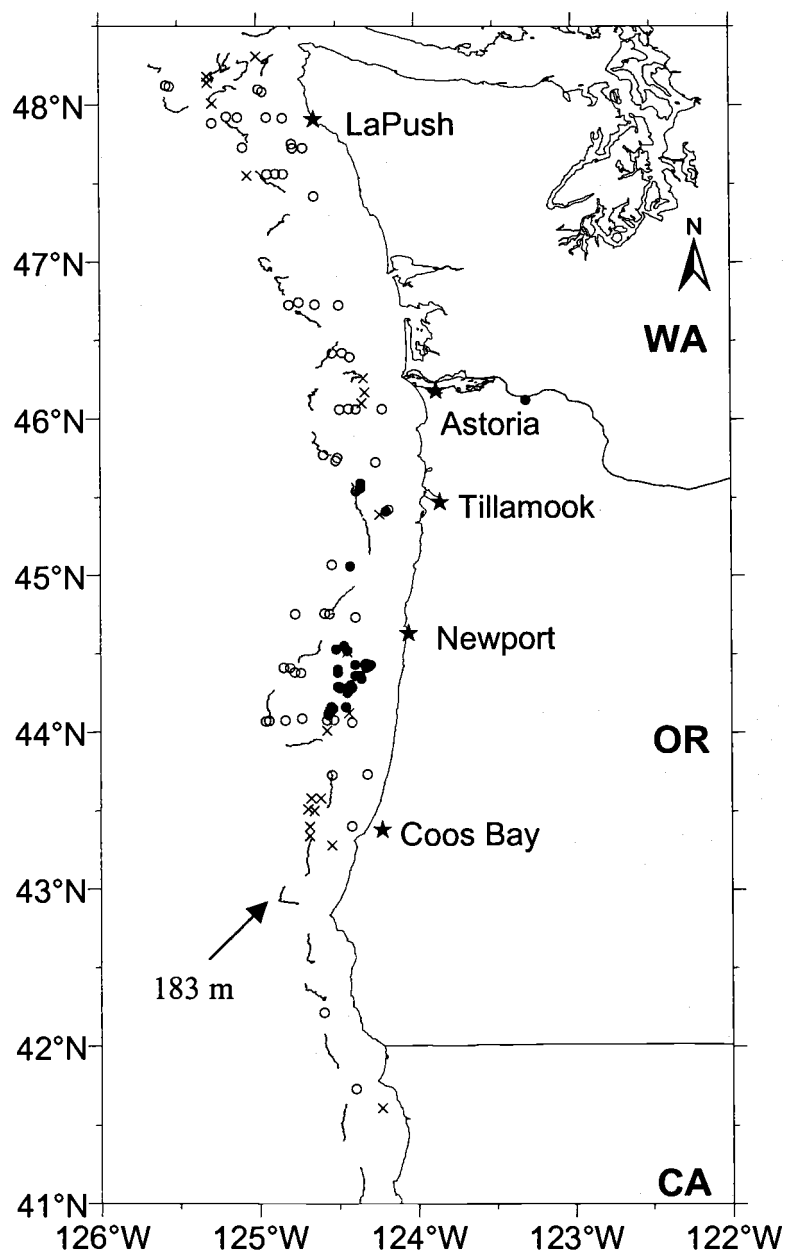
The seasonal samplings covered a confined area off the Oregon coast, while the NMFS survey covered a wider range of coastal waters (Figure 2.1).

Individuals of the targeted fish species were selected randomly from the catch and their stomachs were removed at sea. Before the stomach was removed, the buccal cavities were examined for evidence of stomach eversion, regurgitation, or net feeding. Fish were discarded if they showed signs of any of these problems. Each valid stomach was wrapped in a cloth bag with a specimen tag indicating the species type, sex, fork length (cm), date of sampling, and sampling location, and then preserved in a 10% buffered formalin solution. In the laboratory, the stomach samples were rinsed with water, and transferred and stored in 70% ethanol until the laboratory examination. For prey identification and associated measurements, each stomach was cut open and the contents were blotted dry with absorbent paper. The prey items were examined under a dissecting microscope and identified to the lowest possible taxonomic level. The wet weight of each individual category of prey item was measured to the nearest one-hundredth (0.01) of a gram and recorded.

Analysis of the Diets

For the description of the diets, frequency of occurrence (%) and percent by weight (%) of each prey item were calculated for each fish species over each season in a given year. Frequency of occurrence was calculated by dividing the number of stomachs containing a particular prey item by number of non-empty stomachs in a given season. Percent by weight was calculated by dividing the total weight of a

Figure 2.1. Map of the sampling locations. Each symbol represents different sampling collections: ● for seasonal collections, ○ for 1998 NMFS survey collections, × for 1980 NMFS survey collections.



particular prey item by the total weight of the stomach contents in a given season. Samples were grouped into four different seasons: winter (December-February), spring (March-May), Summer (June-August), Fall (September-November). These seasonal designations are based on sampling dates and knowledge of oceanographic conditions on the Oregon shelf (Huyer 1977; Huyer et. al. 1975; Purdy 1990).

Many factors potentially influence the diet patterns of the fish. These include biological factors (fish species, sex, length etc.), spatial factors (latitude and depth), and temporal factors (diurnal, seasonal, and annual). Many types of analysis methods, ranging from univariate to multivariate statistical techniques, have been proposed to examine the variation of diets in relation to extrinsic variables (Cortés 1997; Crow 1979; Crow 1982; Hyslop 1980; Somerton 1991). However, no method has been accepted as being the best to represent the variability of fish food habits. Food habits studies often aggregate the individual diet information to a population level or across certain external factors to statistically compare the diets. Many studies make no attempt to evaluate the variability. They are only concerned with the mean values. Such data reduction techniques attempt to overcome the multivariate nature of diet data as well as the highly variable and unequal weight of contents of individual stomach samples. However, data aggregation across a particular factor (e.g., combining samples by latitude class) results in the loss of important diet information at the individual level. It also may result in misleading conclusions about the significance of a factor to the diet variability because we cannot simultaneously account for other factors or assess the possible interactions with other factors.

For this study, I employed a multivariate method, Principle Component Analysis (PCA), to examine the patterns of individual diet compositions in relation with some extrinsic factors. PCA extracts the measures of diet composition in a low-dimensional ordination space based on the diet information from individual stomachs. We can then relate external factors to the ordination scores of stomach samples extracted from PCA to test whether or not the factors are related to the diet variability. We can also gauge the relative importance of the factors by variance partitioning in a linear model.

For the analysis of diet variation, two data matrices of species composition data were formed based on the sampling schemes: a seasonal sample data matrix for the three rockfish species collected from commercial fishing trips and a survey sample data matrix for the *S. flavidus* stomachs collected during the 1980 and 1998 NMFS surveys. Some unique external factors as well as shared factors are associated with each data matrix. The unique external factors associated with the seasonal data matrix were predator type and season. The differences among the fish species and their seasonal diet patterns were examined, however a latitudinal effect could not be explored due to the limited geographic coverage of the samples. The unique external factors associated with the survey data matrix were year (1980 and 1998) and latitude. The extensive and consistent geographic extent of the NMFS survey sampling of *S. flavidus* stomachs allowed an examination of the latitudinal variation in the diets and comparison of the diets between a strong El Niño year (1998) and a non-El Niño year (1980). Other external factors tested for with both data matrices

were depth, time of day, fish sex, and fish size. All the factors were treated as categorical variables. Summaries of the factors, their levels, and the number of corresponding stomach samples for each matrix are reported in Table 2.

For the analysis the prey species were grouped into seven major prey groups: *Euphausiids*, *Fish*, *Jellyfishes* (species other than salps and heteropods in the gelatinous zooplankton group), *Salps*, *Heteropod*, *Decapod*, and *Miscellaneous* prey items. For the PCA the weights of prey groups were standardized to proportions based on the total stomach contents weight for each individual fish stomach to remove the problem of unequal weights across the samples. In the data matrices, each row represents an individual fish stomach and each column represents a prey group. The value of each cell in a data matrix is the weight proportion of a particular prey group in each stomach. Prior to running PCA, the proportions (P) were transformed using the angular transformation, $(2/\pi) \arcsin(P^{1/2})$, which is considered to be an appropriate transformation for proportion data to improve the assumptions of normality and homogeneous variance (Sokal and Rohlf 1975). After running the PCA, a series of General Linear Models (GLM) were fitted to the sample scores extracted from the primary PCA axes to relate the external factors to the diet composition. For selecting variables, first the model was fitted with main effects only, then the most insignificant terms were eliminated one at a time until the none of the remaining variables was insignificant ($p\text{-value} > 0.05$). Next, a full model was fitted that had the selected main effects and all their possible two-way interactions. This full model was simplified by removing the most insignificant interaction terms

Table 2.2. External factors and their levels that were examined for the analyses of diet variability. Given in parentheses are the numbers of non-empty stomach samples for each level in a given factor across all other factors.

Data matrix	Factors	No. of Levels	Levels
<u>Seasonal</u>	Predator	3	<i>S. flavidus</i> (139) <i>S. entomelas</i> (194) <i>S. pinniger</i> (65)
	Seasons	6	Six seasons (81, 101, 51, 23, 97, 45)
	Depth	2	< 146 meters (304), > 146 meters (94)
	Time of Day	3	Morning (before 10 AM) (90) Midday (10 AM ~ 5 PM) (230) Evening (after 5 PM) (78)
	Sex	2	Male (162), Female (236)
	Fish size	3	< 40 cm (136), 40~45 cm (203), > 45 cm (59)
<u>Survey</u>	Year	2	1998 (128), 1980 (312)
	Latitude	4	41°~43°5' (51), 43°5'~45° (153) 45°~47° (137), 47°~49° (99)
	Depth	3	< 110 meters (113) 110~165 meters (222) > 165 meters (105)
	Time of Day	3	Morning (before 10 AM) (58) Midday (10 AM ~ 5 PM) (260) Evening (after 5 PM) (122)
	Sex	2	Male (241), Female (199)
	Fish size	3	< 40 cm (125), 40~45 cm (208), > 45 cm (107)

at each step until none of the terms could be removed at significance level of 0.05. Higher order interactions (more than two-way interactions) were not considered in the analysis because of missing cells due to the limited number of samples (Table 2.2).

RESULTS

Description of the Diets in Seasonal Collections

Data from non-empty stomachs were used to analyze the food habits of the three rockfish species. The percentage of non-empty stomachs was highest during the summer of 1998 (88.6%) and lowest during the winter of 1998 (51.1%) (Table 2.1). The stomach contents data of these species were summarized in terms of frequency of occurrence and percent by weight over each season and year (Tables 2.3-2.6). A general description of diets for each species follows.

Yellowtail rockfish (*S. flavidus*)

Yellowtail rockfish preyed upon various groups of pelagic planktonic organisms (Table 2.3 for seasonal collection and Table 2.6 for survey collection). Although important prey species or groups varied from season to season, in general euphausiids (mainly *E. pacifica*) were the dominant prey group by both occurrence and weight across the seasons. Various fish species frequently occurred in the stomachs and comprised an important prey group, although the species types varied

Table 2.3. Summary of stomach contents of yellowtail rockfish, *S. flavidus*, from seasonal collections in 1998-99.

Year Season	98						99					
	April		August		November		February		April		September	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names												
Euphausiacea												
Euphausia pacifica	63.2	75.9	18.9	44.8	15.0	56.3	53.7	100.0	5.1	11.1	3.4	23.1
Thysanoessa spinifera	0.2	24.1	1.6	20.7	2.5	56.3	45.8	100.0	0.1	6.7	3.9	23.1
T. longipes	<0.1	3.4										
Nematoscelis difficilis	0.2	27.6										
Nyctiphanes simplex	0.6	65.5										
Euphausiid unidentified	4.4	48.3	6.0	55.2	3.1	37.5			0.2	6.7	0.8	7.7
Amphipoda												
Paraphronima	<0.1	3.4	<0.1	3.4	<0.1	6.3			<0.1	4.4	0.1	7.7
Parathemisto	<0.1	3.4	<0.1	24.1	0.1	31.3			<0.1	8.9	<0.1	15.4
Hyperoche	<0.1	10.3	<0.1	10.3	<0.1	18.8			<0.1	8.9	0.1	7.7
Streetsia	<0.1	3.4	<0.1	6.9	0.6	12.5			<0.1	2.2		
Vibilia					<0.1	6.3					0.1	7.7
Primno	<0.1	3.4	<0.1	13.8	<0.1	18.8			<0.1	2.2	0.2	15.4
Hyperiidea			<0.1	3.4	0.2	18.8						
Gammeridea	<0.1	3.4	<0.1	3.4	0.5	18.8			0.1	46.7		
Decapoda												
Sergestes similis	<0.1	13.8							0.4	13.3	9.8	30.8
Pandalus jordani					7.5	18.8			0.4	4.4		
Cancer sp. Megalopa	<0.1	6.9	<0.1	3.4			0.4	14.3			0.9	30.8
Decapod mysis larvae												
Cephalopoda												
Squid sp.	0.8	41.4	0.5	24.1	1.9	6.3						
Octopus sp.												

Table 2.3. *continued.*

Year Season	98						99					
	April		August		November		February		April		September	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names												
Gelatinous zooplankton												
Heteropoda												
Salpidae			<0.1	3.4					61.5	80.0		
Clionidae			<0.1	3.4								
Cymbuliidae	0.2	17.2			0.1	6.3			<0.1	2.2		
Siphonophora	0.5	10.3	0.5	3.4	0.4	6.3						
Ctenophora	15.5	20.7										
Unid. gelatinous zooplankton	11.5	44.8	6.8	41.3	0.4	6.3					71.1	46.2
Miscellaneous invertebrates												
Copepod	<0.1	24.1										
Isopoda			0.4	6.9								
Polychaeta	<0.1	3.4										
Tomopteridae	0.6	17.2							<0.1	4.4		
Sagitta elegans	0.1	13.8	<0.1	6.9					<0.1	2.2	2.7	7.7
Osteichthyes												
Ammodytidae			5.3	34.5								
Bathylagidae	<0.1	10.3	0.1	3.4								
Citharichthys sordidus	0.1	3.4							1.3	4.4		
Cotidae	<0.1	3.4										
Cyclopteridae												
Glyptocephalus zachirus					10.0	6.3			10.8	6.7		
Lyopsetta exilis					42.2	18.8			13.5	8.9		
Merluccius productus	0.1	17.2	37.4	62.1								
Microstomus pacificus	0.8	3.4										

Table 2.3. *continued.*

Year Season	98						99					
	April		August		November		February		April		September	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names												
Osteichthyes												
Myctophids							0.1	28.6			1.3	23.1
Paralepididae												
Sebastes sp.	<0.1	3.4										
Synodontidae			0.2	3.4								
Fish unidentified	0.2	34.5	21.0	48.3	14.2	31.3			6.7	11.1		
Unid. animal remains	0.7	3.4	1.0	6.9	1.5	18.8					5.9	15.4
No. of stomachs examined	31		31		24		9		54		18	
No. of stomachs with contents	29		29		16		7		45		13	

Table 2.4. Summary of stomach contents of widow rockfish, *S. entomelas*, from seasonal collections in 1998-99.

Year Season	98						99					
	April		August		November		February		April		September	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names												
Euphausiacea												
Euphausia pacifica	47.4	27.0	5.0	19.7	2.4	20.8	22.8	14.3			19.3	31.3
Thysanoessa spinifera	<0.1	5.4	0.0	1.5	6.7	37.5	5.1	14.3			2.2	9.4
T. longipes			0.0	1.5	0.9	4.2						
Nematoscelis difficilis	0.1	5.4			3.2	12.5						
Tessarabanchion oculatum					0.3	8.3						
Nyctiphanes simplex	<0.1	2.7										
Euphausiid unidentified	8.7	56.8	5.0	10.6	4.1	25.0			0.1	2.2	38.1	37.5
Amphipoda												
Paraphronima			<0.1	6.1	1.0	25.0			0.1	8.7		
Parathemisto			<0.1	1.5	0.1	8.3			<0.1	2.2	0.1	9.4
Hyperoche	<0.1	37.8	<0.1	33.3	0.1	16.7			<0.1	10.9	0.1	28.1
Streetsia	<0.1	8.1	<0.1	12.1	0.2	12.5			<0.1	8.7	0.1	15.6
Vibilia			<0.1	3.0	0.9	50.0			<0.1	2.2		
Primno	<0.1	5.4	<0.1	7.6					<0.1	6.5	0.1	6.3
Hyperiidea	<0.1	18.9	<0.1	13.6	0.2	12.5			<0.1	8.7	0.1	12.5
Gammeridea			0.2	15.2	0.4	12.5			0.1	50.0		
Decapoda												
Sergestes similis	2.4	13.5							0.4	6.5		
Pandalus jordani	0.8	5.4							0.2	4.3		
Cancer sp. Megalopa	<0.1	2.7	2.2	6.1							0.5	18.8
Decapod mysis larvae	<0.1	10.8	<0.1	1.5	0.2	4.2						

Table 2.4. *continued.*

Year Season	98						99					
	April		August		November		February		April		September	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names												
Cephalopoda												
Squid sp.	0.9	21.6	0.1	1.5	4.6	33.3	2.2	14.3	0.2	6.5		
Octopus sp.	<0.1	2.7										
Gelatinous zooplankton												
Heteropoda					45.3	45.8			0.4	2.2		
Salpidae	0.1	2.7	3.6	27.3	1.2	12.5	59.1	42.9	92.6	95.7	28.2	25.0
Clionidae			2.4	18.2					0.2	10.9		
Cymbuliidae	0.4	10.8	0.1	7.6	<0.1	4.2			0.1	4.3	<0.1	3.1
Siphonophora	4.9	10.8	11.7	15.2	4.0	8.3	4.4	14.3	4.8	17.4		
Ctenophora	26.7	27.0	3.9	3.0	2.9	4.2						
Unid. gelatinous zooplankton	3.3	48.6	62.2	74.2	12.2	25.0	5.0	57.1			8.7	21.9
Miscellaneous invertebrates												
copepod	<0.1	29.7	<0.1	4.5								
Isopoda	<0.1	2.7										
Polychaeta	0.4	16.2	0.1	3.0	2.9	8.3						
Tomopteridae	0.2	16.2	0.2	3.0					0.0	2.2	0.2	3.1
Sagitta elegans	0.2	13.5	0.2	4.5	0.2	4.2					2.2	21.9
Osteichthyes												
Bathylagidae	0.1	10.8										
Citharichthys sordidus	1.7	16.2										
Cyclopteridae			0.1	3.0								
Glyptocephalus zachirus			0.1	1.5								
Merluccius productus	0.1	5.4	0.7	3.0								
Microstomus Pacificus	0.5	2.7	<0.1	1.5	1.8	25.0						

Table 2.4. *continued.*

Year Season	98						99					
	April		August		November		February		April		September	
	WT	F.O	WT	F.O	WT	F.O	WT	F.O	WT	F.O	WT	F.O
Prey Names	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Osteichthyes												
Myctophids	0.2	2.7	0.1	3.0			1.4	14.3				
Paralepdidae	<0.1	2.7										
Sebastes sp.					0.3	4.2						
Unid. Fish	0.5	16.2	0.7	7.6	0.7	12.5			<0.1	2.2	0.2	3.1
Unid. animal remains	0.1	5.4	0.9	4.5	3.1	16.7			0.8	4.3		
No. of stomachs examined	60		81		37		26		48		47	
No. of stomachs with contents	37		66		24		7		46		32	

Table 2.5. Summary of stomach contents of canary rockfish, *S. pinniger*, from seasonal collections in 1998-99.

Year Season	98						99			
	April		August		November		February		April	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names										
Euphausiacea										
Euphausia pacifica	94.2	80.0	74.7	56.0	76.6	63.6	94.7	88.9	46.7	50.0
Thysanoessa spinifera	0.1	13.3	2.2	48.0	2.8	45.5	4.1	88.9		
Nyctiphanes simplex	0.8	66.7								
Euphausiid unidentified	3.8	13.3	22.8	48.0	16.7	81.8	0.8	11.1		
Amphipoda										
Paraphronima	<0.1	6.7					<0.1	11.1		
Parathemisto	<0.1	6.7					<0.1	11.1		
Hyperoche	<0.1	6.7					<0.1	11.1		
Vibilia							<0.1	11.1		
Primno	<0.1	6.7					<0.1	11.1		
Hyperiidea					0.1	9.1				
Gammaridea					0.1	9.1				
Decapoda										
Sergestes similis	0.2	20.0					0.3	22.2	1.2	16.7
Pandalus jordani					1.8	18.2				
Munida quadrisipina	0.3	13.3								
Gelatinous zooplankton										
Salpidae									2.5	16.7
Unid. gelatinous zooplankton	0.4	13.3	0.2	8.0						
Miscellaneous invertebrates										
Copepod	<0.1	6.7								
Isopoda	0.1	6.7								
Sagitta elegans	<0.1	6.7								

Table 2.5. *continued.*

Year Season	98						99			
	April		August		November		February		April	
	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)	WT (%)	F.O (%)
Prey Names										
Osteichthyes										
Bathylagidae	<0.1	6.7								
Glyptocephalus zachirus									30.3	16.7
Lyopsetta exilis									12.3	16.7
Merluccius productus	<0.1	6.7								
Fish unidentified			<0.1	4.0	2.0	18.2			6.9	16.7
No. of stomachs examined	17		33		13		10		27	
No. of stomachs with contents	15		25		11		9		6	

over the seasons. Pacific whiting (*M. productus*) was found in the samples of the 1998 spring and summer collections (seasonal and survey). It was not an important prey item during spring (0.1% by weight, 17.2% by occurrence), but it became the most important item by weight (37.4% in seasonal sampling, 32.5% in 1998 survey) in the summer of 1998 samples. Slender sole (*L. exilis*) was the top prey item as a single species by weight (42.2%) in the fall of 1998. Some prey types dominated the stomachs during certain seasons. Jellyfish species were important in spring and summer of 1998. However, because of the soft fragile body structure and high digestion rate in the stomach, it was challenging to make accurate species identification. Whitish mucus-like digested material was often encountered in the stomachs. It was categorized as *unidentified gelatinous zooplankton* because there were no other solid body elements or parts (such as skeleton or eyes) that could be associated with other plankton organisms and the material was also somewhat entangled, unlike other digested materials. The material was believed to be digested material of either *Siphonophora* or *Ctenophora*. This prey group constituted the most abundant prey item both by weight (71.1 %) and by occurrence (46.2%) in the stomachs of fall 1999. Shrimp species were moderately important by weight and occurrence in the fall of 1998 (*P. jordani*, 7.5%) and in the fall of 1999 (*S. similis*, 9.8%). Clions occurred frequently only in the summer 1998 samples of the seasonal and survey collections. This prey species was moderately important (10.7% by weight and 27.8% by occurrence) in the survey sample, but it was less frequent (3.4%) and did not make up more than 0.1% by weight in the seasonal samples.

Salps were the most important prey species by both weight (61.5%) and occurrence (80%) in the spring 1999 samples. The numerous planktonic amphipod species were frequently observed in all seasons except the winter of 1999, but it were of minor importance in terms of weight.

Widow rockfish (*S. entomelas*)

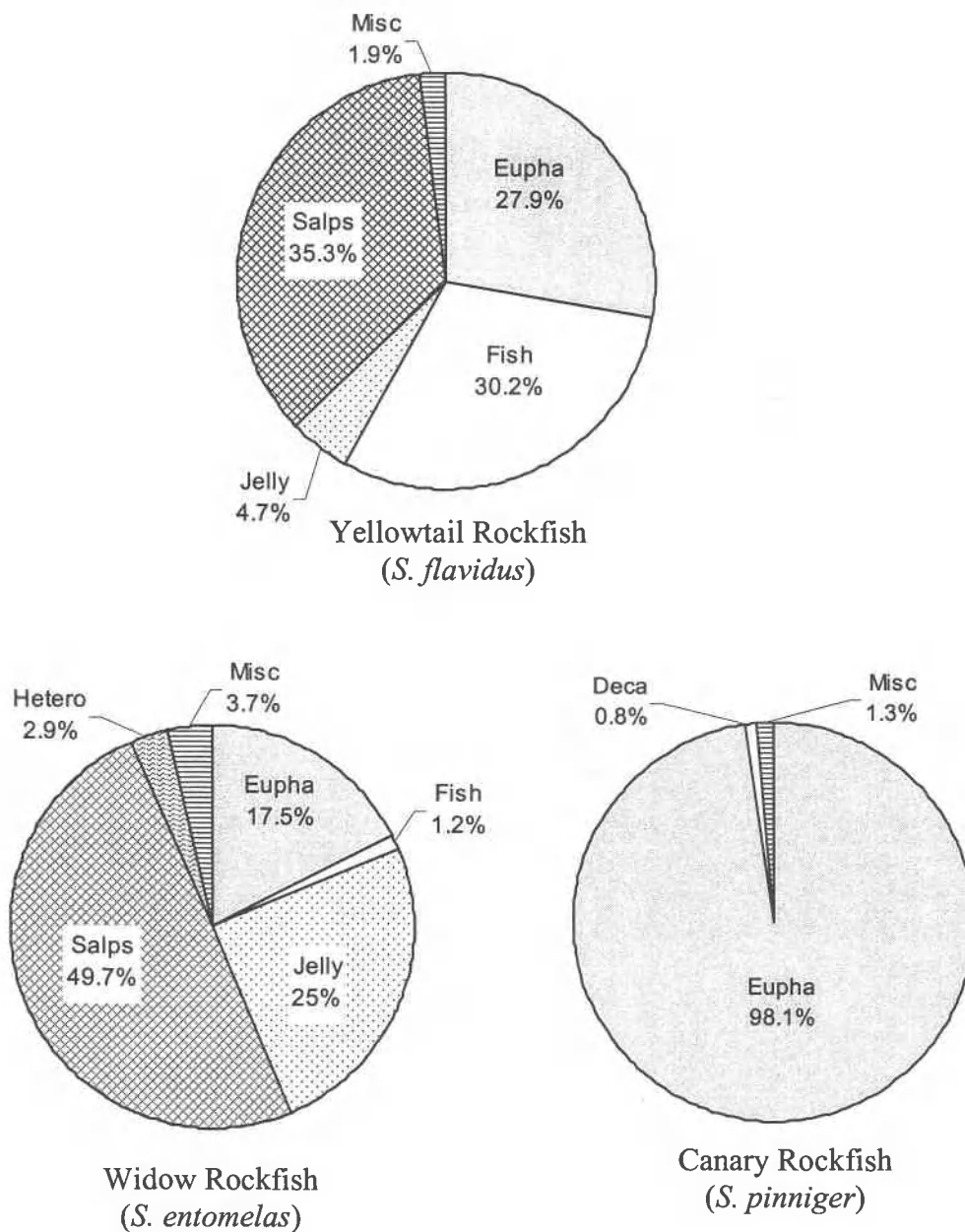
The prey groups eaten by widow rockfish were as varied as those eaten by *S. flavidus* (Table 2.4). However, the importance of the fish prey species in the overall diet was less than for *S. flavidus*. Pacific whiting occurred in the diets, as in the case of *S. flavidus*, during the spring and summer of 1998, but it was not an important prey in either season (< 0.7% in weight, < 5.4% in occurrence). Euphausiid species (mainly *E. pacifica* and *T. spinifera*) and jellyfish species were major prey items by both weight and occurrence in most of the seasons. Salps occurred in all seasons and became the most important prey in 1999. In particular, salps occurred in more than 95% of the stomach samples from the spring of 1999 and were an exceptional prey source in terms of weight (92.6%). This may be one reason for the absence of euphausiid species in the diets during that season. The Heteropoda was the highest prey group both in terms of weight (45.3%) and frequency of occurrence (45.8%) in the fall of 1998. Compared to *S. flavidus*, *S. entomelas* seems to have a greater preference for gelatinous prey organisms, such as jellyfishes and salps.

Canary rockfish (*S. pinniger*)

Non-empty stomachs for *S. pinniger* were unavailable for sampling in fall of 1999. The number of prey taxa found in the stomachs of *S. pinniger* were fewer than *S. flavidus* or *S. entomelas*, implying a narrower diet breadth (Table 2.5). Euphausiid species were the most dominant (>95%) prey group by weight in the diets over all seasons. In some seasons, decapods (shrimp) occurred frequently (around 20%) but with little contribution in weight. Salps did not appear in the stomachs even during the seasons when the salps were a major prey item for *S. flavidus* and *S. entomelas*. The dominance of euphausiid species in the stomachs and the narrow diet breadth during the study period conformed to the results of Brodeur and Percy (1984).

The prey species were grouped into seven major prey groups for a general comparison among the species and to examine the seasonal patterns of the stomach contents. If a prey group did not contribute more than 1% to the total, then it was included in the Miscellaneous species group for the graphical presentations. The weight proportions (average ratio) of the prey groups, calculated across the six seasons, demonstrate overall differences in the diets among the three rockfish species during the study period (Figure 2.2). Euphausiids were important for all three species, but especially for *S. pinniger* (98.1%). Salps were the most important item for both *S. flavidus* (35.3%) and *S. entomelas* (49.7%). *S. entomelas* had a tendency to prey more on jellyfishes (25 %), while fish species were a major item for *S. flavidus* (30.2 %). There were substantial seasonal variations of the prey groups by

Figure 2.2. Weight percentage of major prey groups in the stomach samples of three rockfish species from the seasonal collections.



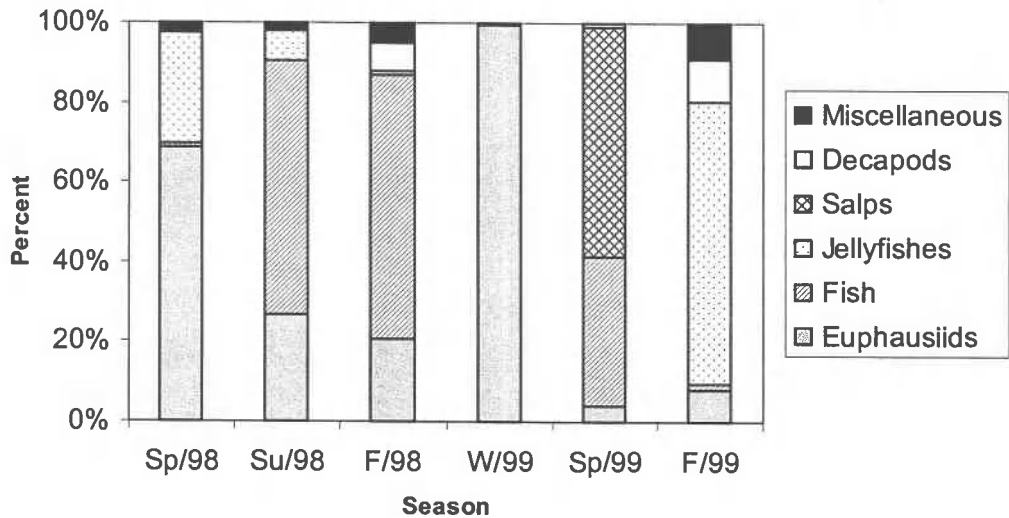
weight in the stomach contents of *S. flavidus* and *S. entomelas* (Figure 2.3). The dominance and the degree of contribution of the prey groups dynamically changed from season to season for these two fish species. While these two species actively changed their diets over the seasons, *S. pinniger* maintained its diet almost completely on euphausiids over the all seasons studied (> 96.1%).

Yellowtail rockfish (*S. flavidus*) from survey in 1980 and 1998

The major difference between the stomach contents of *S. flavidus* in 1980 versus 1998 is the occurrence of unusual southern prey species and the dominance of gelatinous zooplanktons in the 1998 samples (Table 2.6). The southern prey species, *N. simplex* (euphausiids) and juvenile *M. productus* (pacific whiting), were not found at all in the stomach samples of 1980. This is thought to be a major signature of El Niño in the diets of *S. flavidus*. Another major difference is the importance of gelatinous zooplankton species in 1998. Various gelatinous zooplankton species frequently occurred in the stomach samples, composing the second most important prey group by weight (Figure 2.4). The types of gelatinous zooplankton found in the 1980 stomach samples were *Sagitta elegas* and *Limacina helicina*, and they made a minimal contribution. It seems that *S. flavidus* depended more on euphausiids in 1980 than 1998. Even though fish was the second most important prey group in 1980 by weight (32.8%), the major fish species was herring (18.4%) which was not encountered in the 1998 stomach samples.

Figure 2.3. Seasonal variations in the food habits of the three rockfish species. Prey categories contributing more than 1% to the total prey weight in a given season were defined as separate prey categories. Trivial prey types contributing less than 1% were grouped into the miscellaneous category.

(A) Yellowtail Rockfish



(B) Widow Rockfish

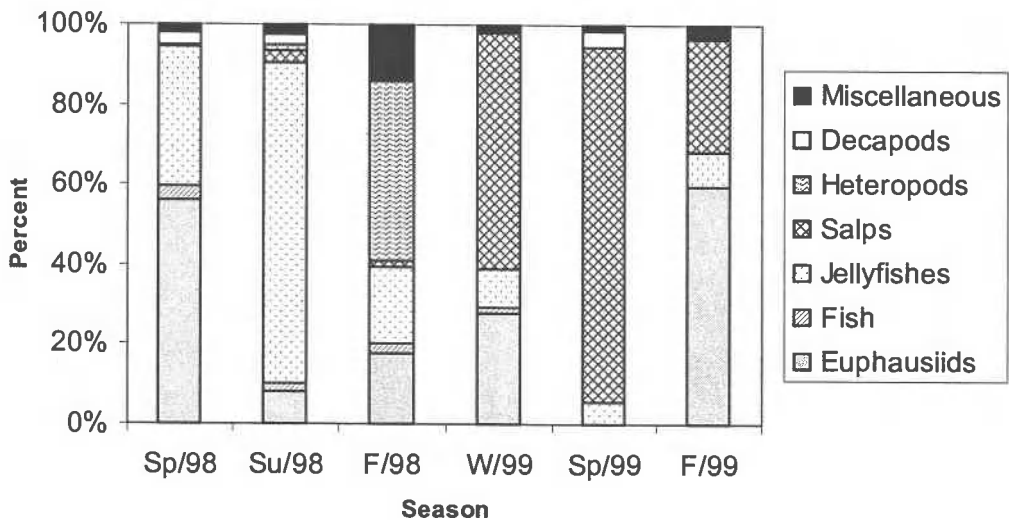


Figure 2.3. *continued.*

(C) Canary Rockfish

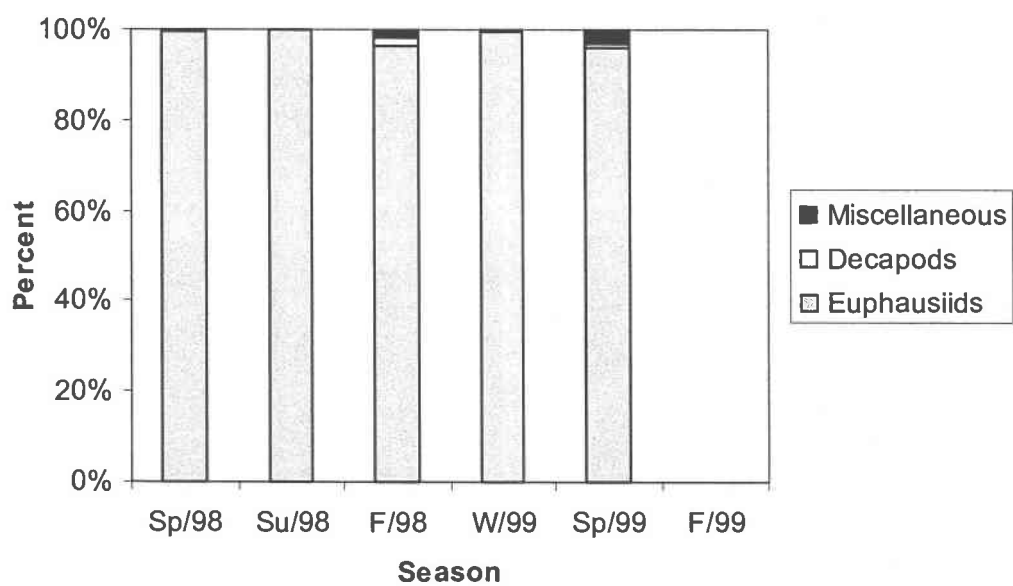


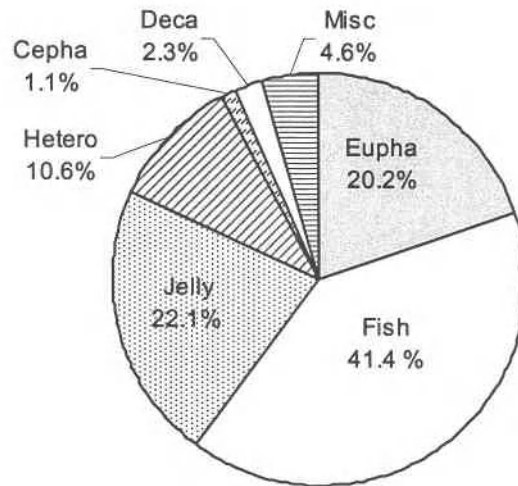
Table 2.6. Summary of stomach contents of yellowtail rockfish, *S. flavidus*, from the 1980 and 1998 NMFS summer surveys.

Year	98		Year	80	
Season	Summer		Season	Summer	
Prey Names	WT (%)	F.O (%)	Prey Names	WT (%)	F.O (%)
Euphausiacea			Euphausiacea		
Euphausia pacifica	13.4	38.8	Euphausia pacifica (adults)	26.4	40.5
Thysanoessa spinifera	1.5	18.8	Thysanoessa spinifera (juv.)	0.9	6.0
T. longipes			Thysanoessa spinifera (adults)	6.4	23.2
Nematoscelis difficilis	<0.1	0.4	T. longipes	0.0	0.5
Nyctiphanes simplex	<0.1	2.2	Euphausiid unidentified	14.9	61.1
Euphausiid unidentified	4.7	55.8			
Amphipoda			Amphipoda		
Paraphronima	<0.1	2.6	Phronima sedentaria	<0.1	3.2
Parathemisto	<0.1	12.3	Paraphronima gracilis	<0.1	1.1
Hyperoche	<0.1	3.6	Hyperia medusarum	<0.1	2.7
Streetsia	<0.1	2.0	Hyperoche medusarum	1.5	2.7
Vibilia	<0.1	1.7	Streetsia challengerii	<0.1	4.9
Primno	<0.1	4.0	Vibilia propinqua	<0.1	0.5
Hyperiidea	<0.1	4.7	Primno macropa	<0.1	0.5
Gammaridea	<0.1	3.2	Hyperidea unidentified	<0.1	0.5
Decapoda			Decapoda		
Sergestes similis	0.1	1.6	Sergestes similis	0.7	2.7
Pandalus jordani	0.3	1.2	Pandalus jordani	1.9	1.1
Cancer sp. Megalopa	1.5	22.6	Munida quadrispina (juv.)	0.1	2.7
Decapod mysis larvae	0.4	5.0	Pinnotheridae megalopae	<0.1	0.5
Cephalopoda			Cancer sp. Megalopae	<0.1	4.3
Squid sp.	0.3	5.1	Decapod mysis larvae	<0.1	1.6
Octopus sp.	0.9	9.0	Copepoda		
Gelatinous zooplankton			Calanus pacificus	<0.1	0.5
Heteropoda	<0.1	0.4	C. marshallae	<0.1	1.6
Salpidae	0.7	4.1	Neocalanus sp.	<0.1	2.7
Clionidae	10.7	27.8	Euchirella sp.	<0.1	0.5
Cymbuliidae	0.2	0.7	Copepod unidentified	<0.1	2.2
Siphonophora	0.1	1.0	Cephalopoda		
Ctenophora			Gonatus sp.	<0.1	1.1
Unid. Gelatin. Zooplankton	21.6	42.9	Loligo opalescens	1.7	2.2
Miscellaneous invertebrates			Japattella heathi	0.3	1.6
Copepod	<0.1	7.1	Octopus sp. (juv.)	2.1	6.5
Isopoda			Cephalopod unidentified	1.7	2.2
Polychaeta	<0.1	0.9	Miscellaneous invertebrates		
Tomopteridae	<0.1	0.4	Sagitta elegans	<0.1	0.5
Sagitta elegans	0.1	3.1	Limacina helicina	<0.1	5.4

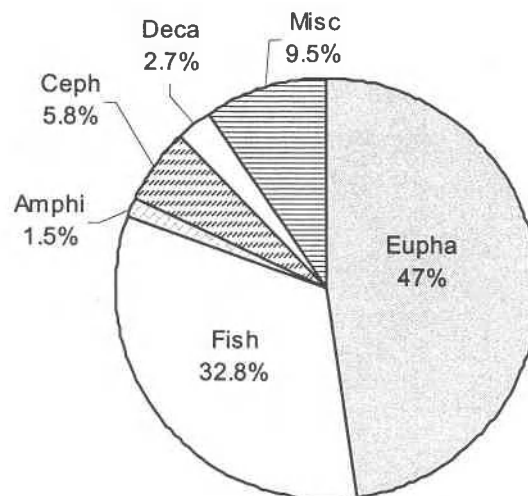
Table 2.6. *Continued.*

Year	98		Year	80	
Season	Summer		Season	Summer	
Prey Names	WT (%)	F.O (%)	Prey Names	WT (%)	F.O (%)
Osteichthyes			Osteichthyes		
Ammodytidae	1.0	12.0	Clupea harengus pallasii	18.4	3.8
Bathylagidae	<0.1	1.5	Sprinchus starksi	<0.1	0.5
Citharichthys sordidus	<0.1	2.2	Stenobranchius leucopsarus	0.2	0.5
Cotidae			Diaphus theta	1.8	0.5
Cyclopteridae	0.6	9.2	Myctophidae	0.1	0.5
Glyptocephalus zachirus	0.2	2.7	Nectoliparis pelagicus	0.1	1.6
Lyopsetta exilis	<0.1	2.5	Stichaeidae	0.1	1.1
Merluccius productus	32.5	36.8	Sebastes sp.	0.4	1.1
Microstomus pacificus	<0.0	2.3	Lyopsetta exilis	0.1	1.1
Myctophidae	0.5	2.5	Psettichthys melanostictus	<0.1	0.5
Paralepididae	<0.1	1.1	Fish unidentified	<0.1	1.1
Fish unidentified	6.9	9.3	Fish remains	11.6	8.1
Unid. animal remains	1.0	5.0	Unid. animal remains	8.4	38.4
No. of stomachs examined	312		No. of stomachs examined	185	
No. of stomachs with contents	360		No. of stomachs with contents	147	

Figure 2.4. Weight percentage of major prey groups in the stomach samples from the 1998 and 1999 survey collections of *S. flavidus*.



1998, El Nino



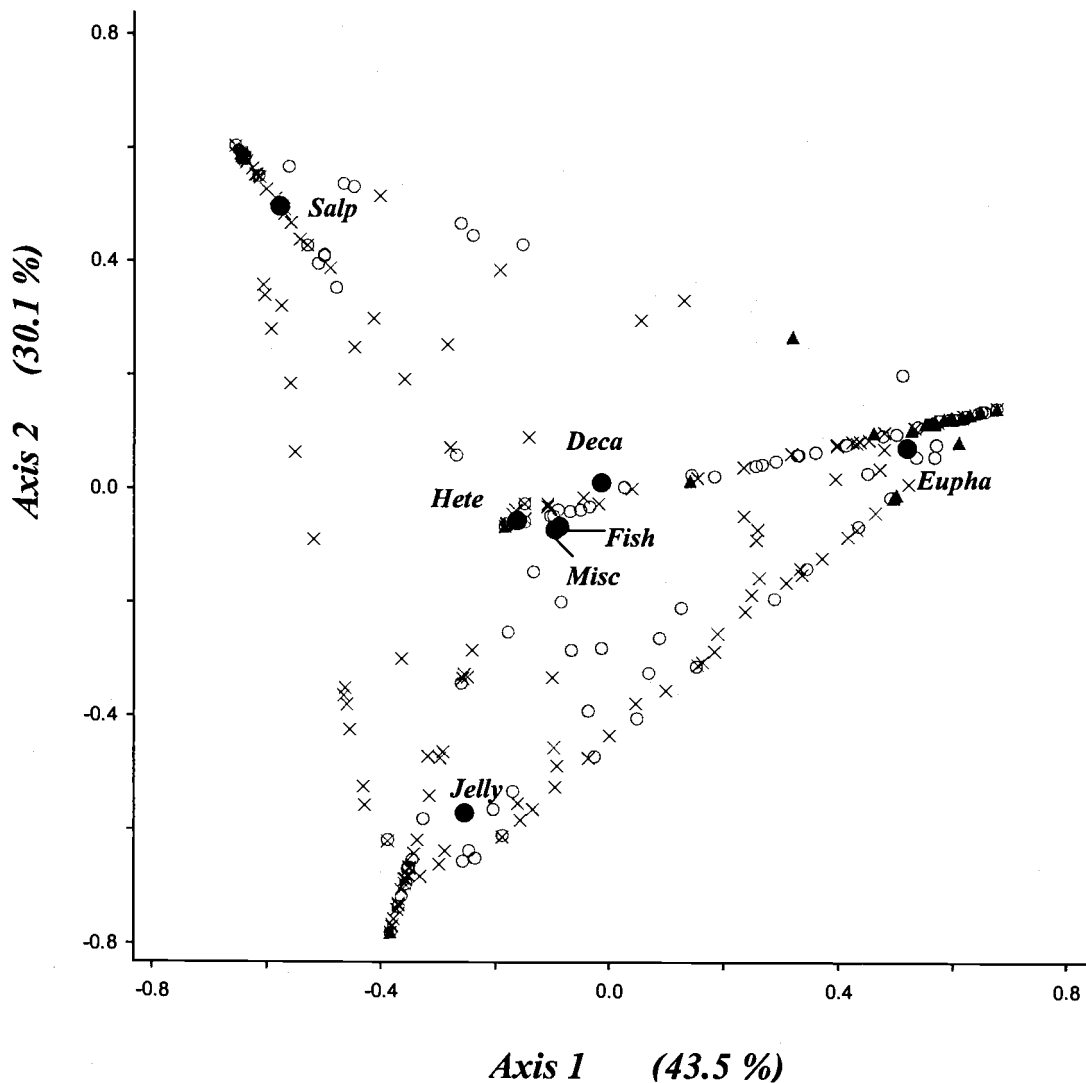
1980, Non-El Nino

Diet Variability in relation to External Factors

Principle Component Analysis was applied separately to the two data matrices, the seasonal collections for the three rockfish species and the survey collections in 1980 and 1998 for *S. flavidus*. The PCA for the data from the seasonal collections was successful in that the first two primary PCA axes accounted for 73.6% of the total variability in the prey composition data: 43.5% by Axis 1 and 30.1% by Axis 2. Similarly, the percentage of the total variability in the survey data that was explained by the first two PCA axes was 66.2%; 41.4% by Axis 1 and 24.8% by Axis 2. The amounts of variability explained by those PCA axes were sufficient to assure that the PCA components would represent the food habits of the fish species based on the individual stomach contents information.

The positions of the individual stomach samples along with the positions of prey species can be represented in the ordination space defined by PCA Axis 1 and Axis 2 (Figure 2.5). The *S. pinniger* points were tightly clustered near the largest PCA 1 score and a PCA 2 score of zero, corresponding to samples dominated by euphausiids. The triangular shape of PCA scatter plot is caused by the characteristics of the diet composition data. Oftentimes only a few prey items occur with dominance in a stomach. For example, there are points lined up along the left side of triangular shaped plot that correspond to *S. entomelas* stomach samples. The items found in the samples were mainly salps and jellyfishes. This clustering on the PCA plot means that stomach samples of the other fish species did not have the combination of salps and jellyfishes, as *S. entomelas* had. The shape of plot and the location of the prey

Figure 2.5. The PCA plot for diet compositions of the seasonal collections. The percentages of the total variance in the data explained by each axis are in parentheses. Each point represents an individual stomach sample. The sample points are identified by fish species; ○ for *S. flavidus*, ×, for *S. entomelas*, and ▲ for *S. pinniger*. The prey species groups (●) are overlayed in the same ordination space based on a weighted average of the individual PCA scores.



groups in the plot suggest that euphausiids, salps, and jellyfishes were the main diet items.

At first glance, the ordination patterns were not very clear because of the scattering and stacking of the data points in the plot. Thus a general linear model (GLM) was constructed to objectively model the food habits in relation to factors to examine which factors might account for the variability. The GLM models were constructed separately for PCA Axis 1 and Axis 2. The models for the PCA scores from the seasonal collections were highly significant ($F_{16, 381} = 43.96$, $P < 0.0001$, $R^2=0.649$ for Axis 1; $F_{16, 381} = 30.43$, $P < 0.0001$, $R^2=0.561$ for Axis 2), and indicated that the Axis 1 and Axis 2 scores were significantly related with “predator type”, “season”, and their interaction (Table 2.7). This implies that food habits were different between the species and changed over the seasons to different degrees. The Mean Square (MS) values can be used to gauge the relative predictive power of the variables. The variability of PCA Axis 1 was most explained by “predator” type (ms = 10.152, df = 2), and the variability of Axis 2 was most explained by “quarter” (ms = 1.643, df = 2). In other words, PCA Axis 1 mostly was associated with differences between the fish species and PCA Axis 2 mostly was associated with seasonal changes in the food habits. The other variables examined in the forward model building (depth, time of day, sex, and length class) were not significant factors (p-value > 0.05) in the models for the food habits of the three rockfish species from the seasonal collections. The PCA scores predicted by the GLMs for each axis summarize the diet variation of the species by seasons (Figure 2.6). It is shown in the

Table 2.7. Results of GLM analyses of the PCA Axis 1 and Axis 2 scores that were extracted from the data matrix of the seasonal collections of 1998 and 1999.

Axis 1 ($R^2=0.649$)

Source	df	SS	MS	F Value	Pr > F
Model	16	61.638	3.852	43.96	<.0001
Error	381	33.389	0.088		
Corrected Total	397	95.027			

Source	df	Type III SS	MS	F Value	Pr > F
Predator	2	20.304	10.152	115.84	<.0001
Quarter	5	9.049	1.810	20.65	<.0001
Predator*Quarter	9	6.503	0.723	8.25	<.0001

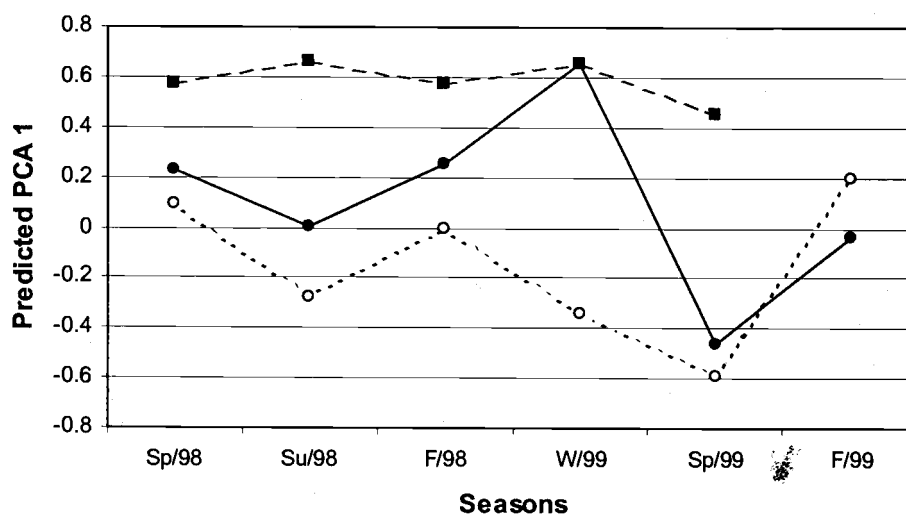
Axis 2 ($R^2=0.561$)

Source	df	SS	MS	F Value	Pr > F
Model	16	36.933	2.308	30.43	<.0001
Error	381	28.901	0.076		
Corrected Total	397	65.834			

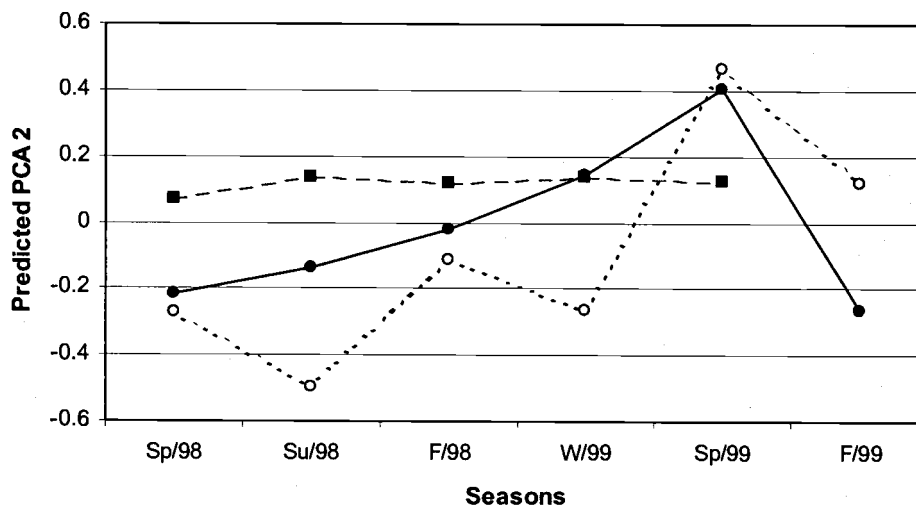
Source	df	Type III SS	MS	F Value	Pr > F
Predator	2	1.513	0.757	9.97	<.0001
Quarter	5	8.215	1.643	21.66	<.0001
Predator*Quarter	9	6.994	0.777	10.24	<.0001

Figure 2.6. Predicted values by fish species for each season from the GLMs fit to the (A) PCA Axis 1 scores and (B) PCA Axis 2 scores from the stomach composition data of the seasonal collections. Solid lines with solid circles indicate the values for *S. flavidus*, dotted lines with open circles are for *S. entomelas*, and broken lines with solid squares are for *S. pinniger*.

(A)



(B)



predicted PCA scores of both axes that *S. pinniger* was consistent over the seasons, while *S. flavidus* and *S. entomelas* varied with different levels and directions.

The diet data for 19 stomach samples of *S. flavidus* from the 1980 survey were not included in the data matrix for the PCA of 1980 and 1998 summer survey because those stomach samples were nearly empty (less than 0.1 gram of total stomach contents). The groupings of the 1980 and 1998 survey samples were fairly evident in the PCA ordination space (Figure 2.7), which had a similar triangular appearance as the PCA plot from the seasonal collections. The triangular shape suggests that euphausiids, fish, and jellyfishes were primary items determining the PCA plot. However, there were no 1980 survey samples in the upper portion of the scatter plot, which corresponds to samples where jellyfishes and heteropods were the major prey species. This agrees with the dominance of these prey groups in the stomachs of *S. flavidus* in the 1998 samples and minor role in the 1980 samples, based on the weight proportions calculated from the aggregated samples.

According to the general linear model for the PCA scores the diet composition of the *S. flavidus* from the survey collections were related with external factors in a more complicated fashion (Table 2.8) than was apparent in the seasonal samples. Year, latitude, and depth were significant main effects for the first PCA component scores, but the most influential variable was the interaction between year and latitude ($ms = 3.714$, $df=2$). Before adding the interaction terms to the model, however, year was the most significant factor. The model for the Axis 2 scores included a term for time of day along with those factors significant for Axis 1.

Figure 2.7. The PCA plot of the 1980 and 1998 summer survey collections. The percentage of total variance in the data explained by each axis is in parenthesis. Each point represents an individual stomach sample. The sample points are grouped by the collection years; ○ for the 1998 samples and ▲ for the 1980 samples. The prey species groups (●) are overlaid in the same ordination space based on a weighted average of the individual PCA scores.

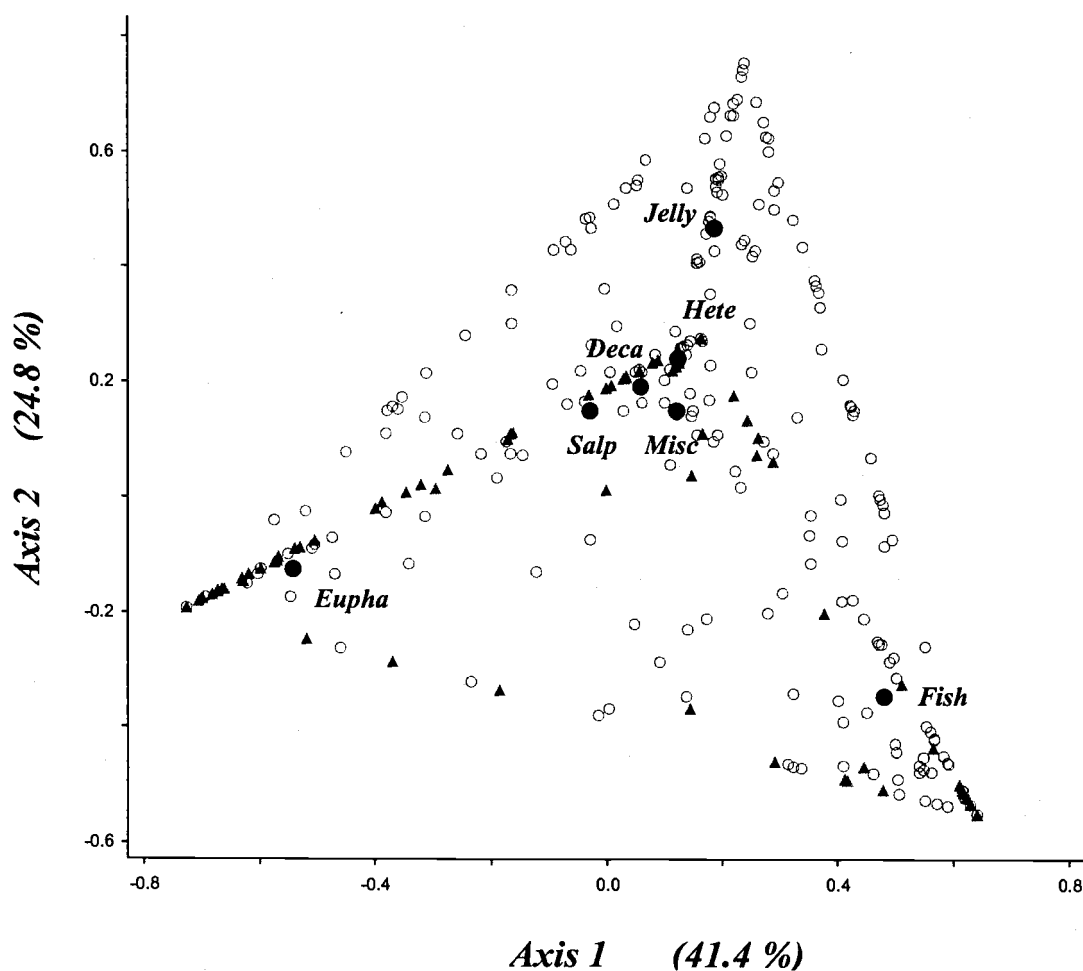


Table 2.8. Results of GLM analyses of the PCA Axis 1 and Axis 2 scores that were extracted from the data matrix of the NMFS summer survey collections of 1980 and 1998.

Axis 1 ($R^2=0.376$)

Source	df	SS	MS	F Value	Pr > F
Model	14	36.399	2.600	18.28	<.0001
Error	425	60.438	0.142		
Corrected Total	439	96.837			

Source	df	Type III SS	MS	F Value	Pr > F
Year	1	0.409	0.409	2.88	0.0907
Latitude	3	2.883	0.961	6.76	0.0002
Depth	2	2.967	1.484	10.43	<.0001
Year*Latitude	2	7.428	3.714	26.12	<.0001
Latitude*Depth	5	5.128	1.026	7.21	<.0001

Axis 2 ($R^2=0.395$)

Source	df	SS	MS	F Value	Pr > F
Model	21	22.950	1.093	12.99	<.0001
Error	418	35.179	0.084		
Corrected Total	439	58.129			

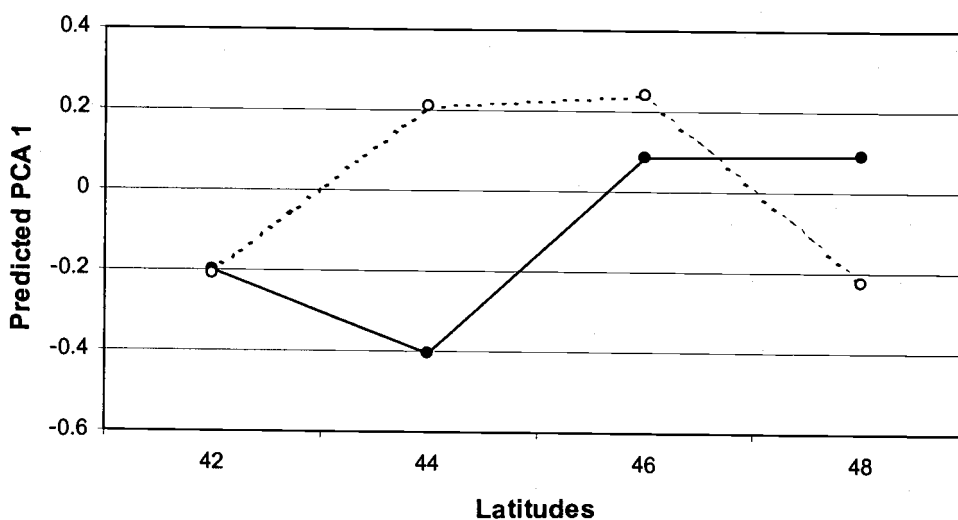
Source	df	Type III SS	MS	F Value	Pr > F
Year	1	0.196	0.196	2.33	0.1276
Latitude	3	4.824	1.608	19.11	<.0001
Depth	2	0.116	0.058	0.69	0.5025
Time of Day	2	1.987	0.993	11.8	<.0001
Year*Depth	2	1.794	0.897	10.66	<.0001
Latitude*Depth	5	1.808	0.362	4.3	0.0008
Latitude*Time of Day	5	8.231	1.646	19.56	<.0001

The interaction between latitude and time of day was the most influential term in the model ($ms = 8.231$, $df = 5$). Latitude was most influential variable before the interactions were introduced in the model. Considering only the main effects, PCA Axis 1 is mainly associated with the difference between the years in the food habits and PCA Axis 2 with latitudinal effects. The values of the PCA 1 scores predicted by the GLM for each year and latitude zone illustrate that the diets of *S. flavidus* were different in 1998 and 1980, and the year effects varied over the latitudes differently (Figure 2.8). Similarly, the predicted PCA 2 scores for time of day by latitude show that the diet pattern differs by time of feeding and the geographic location of feeding. The eigenvectors of the first three PCA axes for the seasonal data matrix of the three rockfish species and survey data matrix of *S. flavidus* are reported in Table 2.9. The GLM coefficients of the factors for the PCA axes are given in Appendix A.

The complication of the models and the significant interactions between temporal and geographical factors indicates that the food habits are not determined by single factors alone. It also suggests an opportunistic feature of *S. flavidus*' feeding habits. Interestingly, as in the case of the seasonal collection, biological factors (sex and size class) were not significant explanatory variables for the food habits of *S. flavidus* from the survey collection.

Figure 2.8. (A) Predicted values by year for each latitude zone from the GLM fit to the PCA Axis 1 scores from diet composition data of the survey collections. The solid line with solid circles is for the 1998 samples and the dotted line with open circles is for the 1980 samples. (B) Predicted values by time of day for each latitude zone from the GLM fit to the PCA Axis 2 scores from diet composition data of the survey collections. The solid line with solid circles is for the morning samples, the dotted line with open circles is for the midday samples, and the broken line with squares is for the evening samples.

(A)



(B)

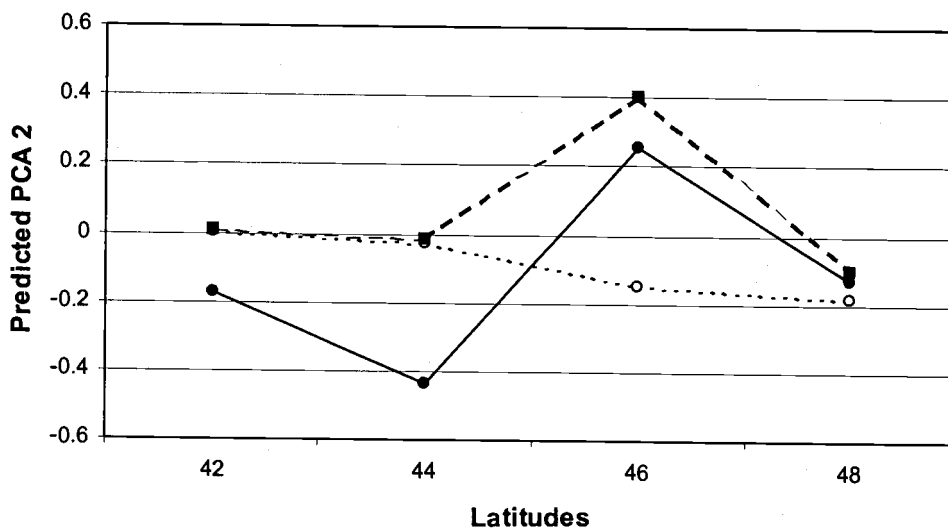


Table 2.9. The eigenvectors of the first three PCA axes for the seasonal data matrix of the three rockfish species (A) and the survey data matrix of *S. flavidus* (B).

(A) Seasonal data matrix

Preys	Axis1	Axis2	Axis3
Euphausiids	0.827	0.171	-0.271
Fish	-0.036	-0.039	0.809
Jellyfishes	-0.236	-0.754	-0.383
Salps	-0.508	0.633	-0.328
Heteropod	-0.017	-0.008	0.033
Decapod	-0.002	0.002	0.043
Miscellaneous	-0.031	-0.032	0.124

(B) Survey data matrix

Preys	Axis1	Axis2	Axis3
Euphausiids	-0.813	-0.309	-0.163
Fish	0.554	-0.666	-0.213
Jellyfishes	0.153	0.638	-0.512
Salps	-0.002	0.013	0.003
Heteropod	0.043	0.143	-0.013
Decapod	0.016	0.087	0.064
Miscellaneous	0.078	0.161	0.813

DISCUSSION

The three rockfish species examined in this study, which covered a period of unusual oceanographic events, an El Niño and a La Niña, mostly preyed upon mesopelagic macrozooplankton. This result generally concurred with the findings of other studies on the diets of rockfish species during normal ocean conditions (Brodeur and Pearcy 1984; Lorz et al. 1983; Pereyra et al. 1969). However, the dominant prey species were different from previous studies.

S. flavidus and *S. entomelas* exhibit substantial seasonal variations in the diet. Seasonal variations in the diets of these species were also reported in other studies (Brodeur and Pearcy 1984; Adams 1987). Interestingly, while these two species changed their diets from season to season, possibly responding to the changes in the prey field, *S. pinniger* exclusively preyed on euphausiids over all seasons. The exclusive dominance of euphausiids in the diets of *S. pinniger* over the seasons is consistent with the previous study based on samples taken in 1980 (Brodeur and Pearcy 1984).

The results from PCA on dietary variability of fish species suggest that patterns in the diets are associated with geographical components (latitude, depth), temporal components (annual, seasonal, diurnal), and their interactions. The complicated interactions between the geographical and temporal variables in the model for *S. flavidus* from survey collections suggest that its predation pattern was temporally localized and opportunistic. A study on the diets of the pelagic stages of

five juvenile rockfish species (*S. flavidus*, *S. entomelas*, *S. goodei*, *S. jordani*, and *S. paucispinis*) off central California found strong annual variation as well as spatial variation (latitude, depth, and interaction) in the diets, but no significant variation with size class (Reilly et al. 1992). Even though the life stage of the samples was different from this study (juveniles vs adults), there was a strong similarity in terms of the significant external factors related to dietary variability. Both studies demonstrate that some rockfish species are opportunistic feeders.

One interesting finding to note is that the early juvenile stage of Pacific whiting (3-5 cm) often occurred in the stomachs of *S. flavidus* and *S. entomelas* in the spring and summer of 1998. Juvenile whiting first started showing up in the stomachs in the spring of 1998 and were quite prevalent in the samples from summer 1998 for *S. flavidus* and *S. entomelas*. It occupied 32.6% of the total diet weight of *S. flavidus* and was the dominant prey species during the summer of 1998, but then disappeared from both in the later sampling seasons. Previous studies have not reported that whiting was preyed upon by *S. flavidus* in the northeast Pacific. Pacific whiting are generally known to spawn off southern California during winter (Bailey et al. 1982). The appearance of whiting in the diets of *S. flavidus* may be due to the anomalous effects of the 1997/98 El Niño event.

Another unusual southern species in the diets was the euphausiid species *Nyciphanes simplex*. This prey species commonly occurred in the stomach samples of all three rockfish species in the spring of 1998. Frequency of occurrence was fairly high in the stomachs of *S. flavidus* (65.5%) and *S. pinniger* (66.7%) during that

season. Brodeur (1986) found this southern euphausiid species in the diets of some fish species off Pacific northwest during the 1983 El Niño. Brodeur and Percy's study (1984) during the non-El Niño year of 1980 did not report *N. simplex* in the diet of either *S. flavidus* or *S. pinniger*. The study of zooplankton off Vancouver Island, further north than the sampling locations of Brodeur and Percy (1984) and this study, confirms the appearance of some southern species during the 1997/98 El Niño years (Mackas and Galbraith 2000).

Another noteworthy finding is that jellyfish species became the dominant prey for *S. flavidus* and *S. entomelas* in some seasons. The amount and the occurrence of jellyfish species in the diets of *S. flavidus* from the 1998 survey collection was much higher than reported in Brodeur and Percy (1984). The importance of euphausiids as prey for many planktivorous fish populations including rockfish species in the northeast Pacific Ocean has been recognized from previous studies. However, jellyfish species (gelatinous zooplanktons) were ordinarily regarded as minor food sources, specially for rockfish species. The population biology of jellyfish species is poorly understood and has never been closely monitored over time in the study area. Interactions between fish fauna and jellyfishes is complicated in that it operates both negatively and positively (Purcell and Arai 2001). Jellyfishes prey on fish eggs and larvae while being preyed upon by juvenile and adult fish and serving as shelter for some fish species. Increase in the biomass and the frequency of jellyfish blooms have been reported (Brodeur et al. 1999; Mills 2001). The suggested reasons for this phenomenon are climate changes,

eutrophication, pollution, overfishing, and invasion of introduced species into coastal ecosystems.

Jellyfishes have been recognized as potentially important food sources for fish fauna. Kashkina's (1986) review of the literature reported that more than 47 fish species feed on salps around the oceans. Twenty different fish species out of 69 fish species examined off the Argentine continental shelf contained ctenophores and gelatinous items in their stomach contents (Mianzan et al. 1996). Recently, filter-feeding species like anchovies were reported to prey on gelatinous plankton, even though many believed this behavior would be avoided because of the potential problem of clogging the filtering device. This feeding behavior, observed during periods of low biomass of the usual prey species, was thought to be a survival feeding behavior (Mianzan et al. 2001). Although jellyfishes were identified as major prey species in some seasons for rockfish species in this study, their quantitative measures still might be underestimated because of fast digestion rate and difficulties in identification due to the damage during digestion.

Gelatinous zooplankton populations have not been closely monitored off Oregon, either before or during this study period. Thus the composition and distribution of the populations in the area during the period are unknown. Observations off Monterey Bay in California detected changes in the species composition and the abundance of the jellyfish species during the El Niño events of 1991-92 and 1997-98 (Raskoff 2001). It was found that common jellyfish species became scarce and a rare species abundant. Considering the opportunistic features of

their rapid growth rate and turnover times, it may have been possible to become a dominant component of the system disturbed by El Niño and the transition to La Niña during the study period.

An interesting feature of diet variation over the seasons is that the stomach contents of *S. pinniger* were very constant on euphausiids, while the other two rockfish actively shifted their diets to different prey items. It is intriguing because these rockfish are co-occurring species in the fishery and are considered to occupy the same habitat. The difference between the species is not just an artifact of sampling. There were 15 trawling hauls where all three species concurrently occurred, out of 49 hauls of the seasonal collections in 1998 and 1999. The proportions by weight of the major prey groups using only the data from those 15 hauls were very similar to the results based on all 49 stations (Table 2.10). This verifies that the fish species had different diets even when they occurred at the same tow locations and thus had access to the same prey field.

The diet analyses in this study suggest that these rockfish species occupy similar geographical extents but have evolved to become parts of different feeding guilds and to acquire different trophic adaptability (Dill 1983). *S. flavidus* and *S. entomelas* seem to be more opportunistic in their feeding habits with greater feeding plasticity to changing prey environments, and *S. pinniger* is a specialist with very limited feeding plasticity. It is not possible to make an inference about which feeding habits are more advantageous without having supporting data on zooplankton abundance during the time period and caloric values of the major prey

Table 2.10. Percentages by weight of major prey groups for the fish species that occurred in the same trawling hauls during the seasonal collections. There were 15 hauls where all three fish species concurrently occurred out of total of 49 hauls.

Prey Groups	<i>S. flavidus</i>	<i>S. entomelas</i>	<i>S. pinniger</i>
Euphausiids	25.8	7.8	95.6
Fish	32.1	0.4	3.8
Jellyfishes	1.4	24.8	0.2
Salps	39.5	63.6	0.2
Heteropods	< 0.1	1.7	-
Decapods	0.6	0.5	0.2
Miscellaneous	0.6	1.2	< 0.1
No. of non-empty stomachs	87	104	42

species. But, in an environment where food resources are scarce, the fish species with specialized feeding habits would have a harder time coping with the situation. It is not known whether euphausiids species have become a limited food source for these rockfish species as well as other fish species. It has been noted that euphausiid populations (*E. pacifica* and *T. spinifera*) have decreased 5-fold in abundance since the early 1990s near Barkley Sound, a southwest Vancouver Island coastal embayment (Tanasichuk 1998a, 1998b). If there was a similar decreasing pattern for the euphausiids populations off Oregon, this might be an explanation for *S. flavidus* and *S. entomelas* shifting to other available prey resources, and *S. pinniger* might have suffered from the decreased availability of euphausiids. These inferences, however, would be speculative due to the lack of information for the macrozooplankton in the area.

Seasonal and interannual changes in zooplankton biomass and community composition have been observed off southern Vancouver Island (Mackas 2001). The observed changes were reasoned to be the responses of the zooplankton community to ocean climate fluctuations and changing current patterns. It is clear that lower trophic level organisms in the coastal ecosystem are strongly influenced by long-term and short-term environmental perturbations. However, the observations in the diets of the three rockfish species in this study indicate that not all rockfish species respond in the same way to the changes. It may depend largely upon the evolutionary traits of individual species and how well they can adapt to changing food environments. It is not known whether strong seasonal variations and the frequent

dominance of gelatinous zooplankton in the diets of *S. flavidus* and *S. entomelas* were just a short-term response to the changes in the zooplankton community caused by anomalous oceanic events, El Niño and La Niña, or more of a chronic phenomenon caused by long-term and large-scale climate change. Further monitoring of these rockfish species, as well as other fish species, coupled with parallel investigations of the macrozooplankton community is recommended for better understanding of the relationship between the different trophic levels and the potential consequences of diet changes to the physiology and population biology of these fish species.

CHAPTER 3: MONTE CARLO SIMULATION STUDY OF THE PROPERTIES OF NONLINEAR REGRESSION ESTIMATORS FOR AGGREGATED LENGTH-WEIGHT DATA

INTRODUCTION

In fishery science, it is a common practice to measure the relationship between the length and weight of individual fish and summarize the relationship using the power function $W = a \cdot L^b$. If a fish does not change shape or density as it grows (isometric growth), then parameter b will have the value 3 and parameter a is the density. This mathematical relationship is used to convert the length measurements to the expected weight measurements, or vice versa. The relationship can also be utilized to assess the condition of the individuals, groups, or populations of the fish species (Murphy and Willis 1996).

The two parameters, a and b , in the function are estimated by applying a regression method, either ordinary linear least-square regression on log-transformed variables or nonlinear regression on non-transformed variables. In general, linear regression on log-transformed variables is preferred by fishery scientists over the non-linear regression approach because of its conceptual and computational simplicity (Pienaar and Thomson 1969).

The two methods are fundamentally different in the assumptions of the underlying error structure. The application of linear regression after taking log transformations of the weight and length measurements makes the assumption that

the error term is log-normally distributed and in a multiplicative form of the allometric growth function (Eq.1). Consequently, the parameters become linear with a normally distributed additive error term after the log transformation (Eq. 2).

$$W = a \cdot L^b \cdot \varepsilon_1 \quad (\text{Eq. 1})$$

where ε_1 follows the lognormal $(0, \sigma_{\varepsilon_1}^2)$ distribution.

$$\log(W) = \log(a) + b \cdot \log(L) + \log(\varepsilon_1) \quad (\text{Eq. 2})$$

where $\log(\varepsilon_1)$ follows the normal $(0, \sigma_{\varepsilon_2}^2)$ distribution.

One of the major assumptions of the non-linear regression approach is that the error term is additive, as in

$$W = a \cdot L^b + \varepsilon_2 \quad (\text{Eq. 3})$$

where ε_2 follows normal $(0, \sigma_{\varepsilon_2}^2)$ distribution.

For many West Coast groundfish species individual length and weight measurements are not routinely collected. However, data in the form of individual fish lengths and aggregated weights are widely available from the market sampling programs in Oregon and California. The primary purpose of market sampling programs is to provide information on species and age compositions of the landings, along with biological characteristics such as sex ratios, maturity stages, and length

distributions for stock assessments (Sampson and Crone 1997). Several market categories have been established by the Oregon Department of Fish and Wildlife for fishery monitoring purposes. A market category may refer to either single fish species or a mixture of species depending on the monitoring unit (e.g., yellowtail rockfish, widow rockfish, and canary rockfish are single species market categories; large rockfish and small rockfish are mixed-species market categories).

In Oregon target sampling rates for each rockfish market category are set each year to obtain a certain number of boat trip samples per 100 tons of the category landed in each port during each quarter of the year. Within each market category, two to six baskets with fixed weights of fish (25-lb or 50-lb) are subsampled. Prior to 1989, the sampling was conducted on the basis of a fixed-number of fish per sample (e.g., 50 or 100 fish) rather than a fixed weight of fish. For each basket subsample, the total weight of the fish and the lengths of each individual fish are measured for each sex. Individual weights of fish are not measured but only their total weight, because measuring individual fish weights is time-consuming and is not a primary task of market sampling. This type of sampling protocol results in data consisting of the aggregate weight (total fish weight) and the associated individual length measurements.

Non-linear regression can be applied to this type of aggregated data to estimate the parameters of the length-weight relationship (Cammen 1980). For an aggregated sample of fish (i.e., a basket of fish), the total weight of the fish in the

sample is just the sum of the individual weights, which can be estimated from the individual fish lengths.

$$WT = \sum_{i=1}^n W_i = \sum_{i=1}^n (a \cdot L_i^b \cdot \varepsilon_i) \quad (\text{Eq. 4})$$

This equation assumes multiplicative errors but additive errors could be assumed instead. Then, with a given number ($N \geq 3$) of aggregate samples (i.e., data from multiple baskets of fish), we can apply non-linear least squares to find the values of a and b .

$$WT_j = \sum_{i=1}^{n_j} W_{i,j} = \sum_{i=1}^{n_j} (a \cdot L_{i,j}^b \cdot \varepsilon_{i,j}) \quad (\text{Eq. 5})$$

where $j = 1, 2, \dots, N$.

The method of non-linear least squares estimates the parameter values by minimizing the sum across all samples of the squared differences between the observed dependent variable and the predicted dependent variable. If we use the total weight (WT) as the dependent variable then the least-squares estimates for (a, b) satisfy

$$\text{Min}_{a,b} \sum_{j=1}^N \left\{ \left(\sum_{i=1}^{n_j} W_{i,j} \right) - \sum_{i=1}^{n_j} (a \cdot L_{i,j}^b) \right\}^2 \quad (\text{Eq. 6})$$

If the number of fish in each aggregate sample is variable, then the average fish weight from each sample rather than the total weight can be used as the dependent variable and thus eliminate the extra variability associated with larger samples.

Applying the logarithmic transformation to eq.(5) does not result in any simplification, hence, non-linear regression is applicable to this estimation problem but linear regression is not.

Application of the non-linear method to data consisting of aggregated weight and individual lengths was proposed and illustrated with simulated data by Cammen (1980). However, the simulation was quite limited in the number of replicates and sample sizes. Also, the data also were simulated in a simple hypothetical format without regard to the characteristics of actual data. Hence, the reliability of this non-linear regression technique and the properties of the estimates have not been fully explored. In this study, a series of Monte Carlo simulation experiments were conducted after close examination on a real market sample data collected over decades by the Oregon Department of Fish and Wildlife (ODFW).

The main objectives of this study are: (1) to determine whether the non-linear regression method can produce reasonably accurate estimates of the parameters of the length-weight relationship under different sampling scenarios and identify the factors that influence the accuracy of the estimates; (2) to evaluate the properties of the parameter estimates in relation to sample size (number of baskets), and (3) to test

whether the residuals from the non-linear regression could be analyzed to detect temporal changes in the length-weight relationship.

The motivation for the third objective is to explore the applicability of the non-linear regression method as a tool for assessing changes in fish condition. The market sample data in Oregon have been collected on a regular basis for several decades. If the underlying relationship between fish weight and length changed during this period, those changes should be evident in the residuals when a single non-linear regression model is fitted to the long-term data series.

MATERIALS and METHODS

Examination of the Characteristics of the Oregon Market Sample Data.

Prior to developing the data simulation for the Monte Carlo experiments I examined some actual data sets and measured their general characteristics. Grouped measurements of weights with associated individual lengths were available for some fish species over the period 1972-2000 from the market sample data collected by the ODFW. Some measurements of individual fish weights and lengths were also available from the databases because the data were collected sporadically to determine length-weight relationships. Length was measured in centimeters and weight in grams.

Data for two groundfish species, yellowtail rockfish and Dover sole, were examined. Individual data for these species were analyzed to specify the parameter

values a , b , and σ_w^2 (variance of the error term) for the data simulation. The parameters for these fish species, separately by sex, were estimated by linear regression after taking log-transformation of both the weight and length variable (Table 3.1). Although the two species are considerably different in their morphology, the parameter estimates of their weight and length relationships were similar with the b estimates being around 3 and the a estimates around 0.01. The variance of the error term (σ_w^2) was estimated by the Mean Square Error (MSE) and its maximum value did not exceed 0.0128. Thus the Monte Carlo simulations of this study used values of 0.01, 3, and 0.014 for a , b , and σ_w^2 , respectively, to generate the simulated length and weight data.

The grouped measurement data for these two groundfish species, in which only total weights were available for the samples, were examined to understand the characteristics of the samples and identify potentially influential factors. Histograms of the number of fish per basket showed similar patterns over the species by sex (Figure 3.1). It ranged from 2 fish to more than 80. The distribution has a long tail on the right side due to the different sampling scheme prior to 1991, when the samples were collected with fixed numbers of fish per basket (100 fish). The frequency distribution looks close to normal if we consider the range only up to around 50 fish/basket. The length distributions were also similar across the species and sexes (Figure 3.2). The distributions were fairly close to normal, although they were skewed either slightly left or right. The average and standard deviation of length changed over time for both species (Figure 3.3). There is a decreasing trend in

Table 3.1. Estimated values of the parameters from the log-linear regression models for individual length and weight measurements of yellowtail rockfish and Dover sole.

Species	Sex	<i>a</i>	<i>b</i>	MSE	df
Yellowtail RF	Male	0.0158	2.9988	0.0096	2651
	Female	0.0173	2.9743	0.0126	2253
Dover Sole	Male	0.0077	3.0406	0.0128	3784
	Female	0.0062	3.1058	0.0126	6181

Figure 3.1. Histogram of the number of fish per basket for male yellowtail rockfish. The histograms for the female yellowtail rockfish and the male and female Dover sole had the same general shape.

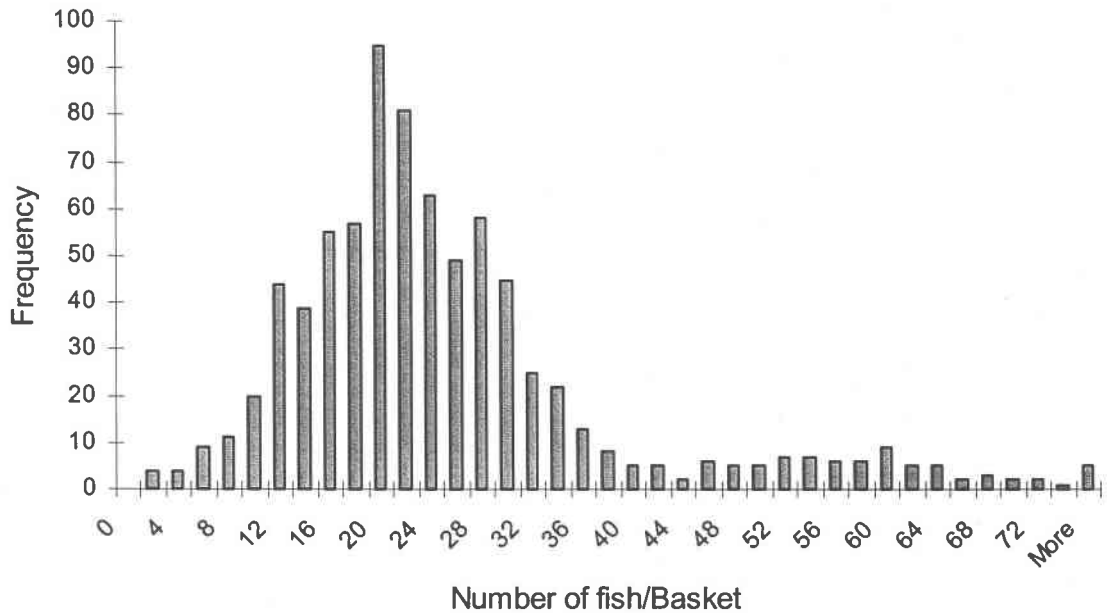


Figure 3.2. Length distribution of male yellowtail rockfish. The length distribution of the female yellowtail rockfish and the male and female Dover sole had the same general shape.

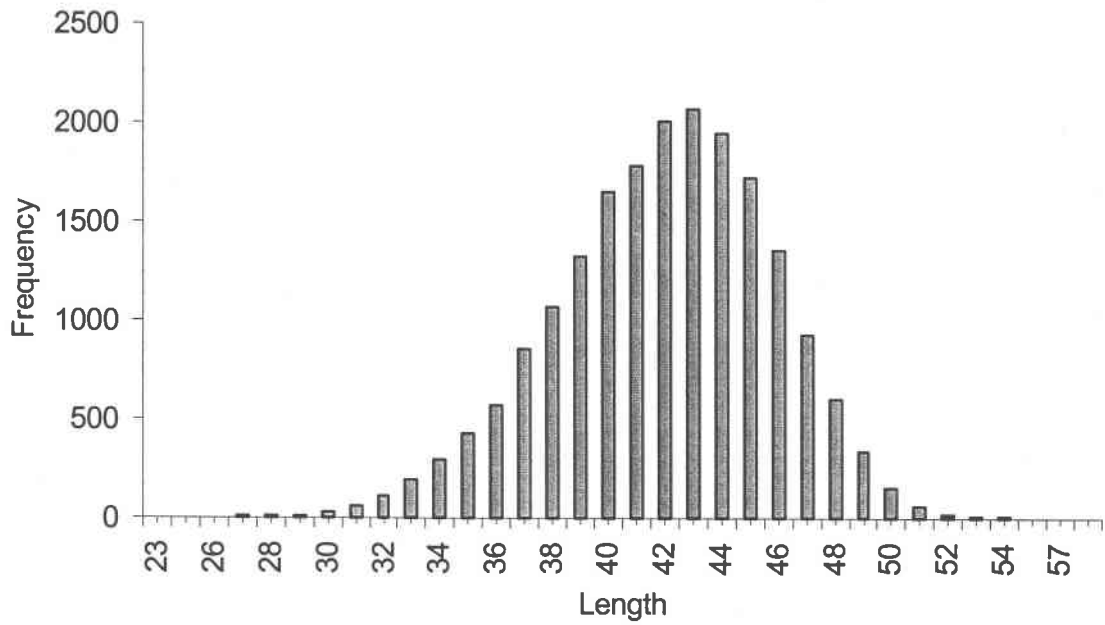
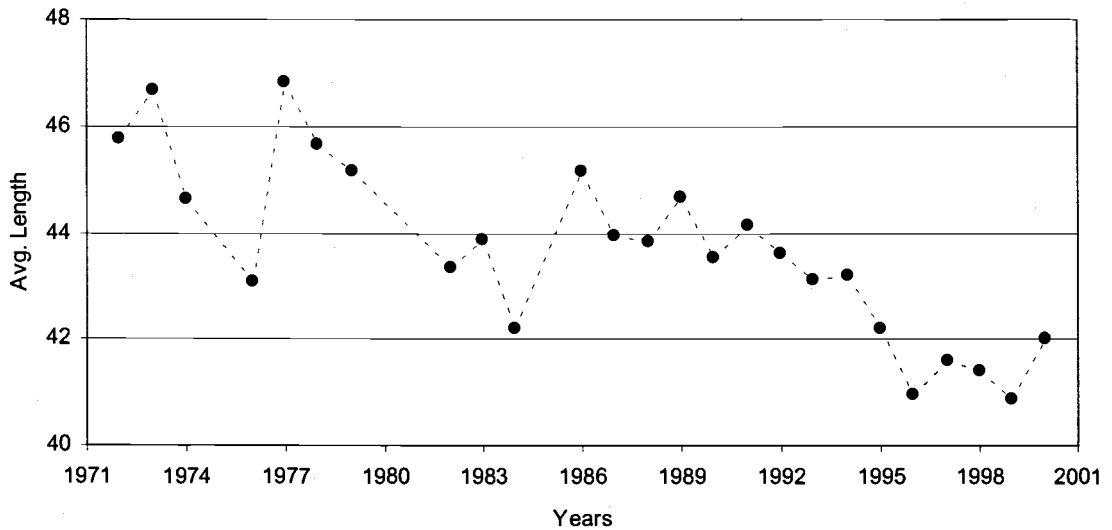
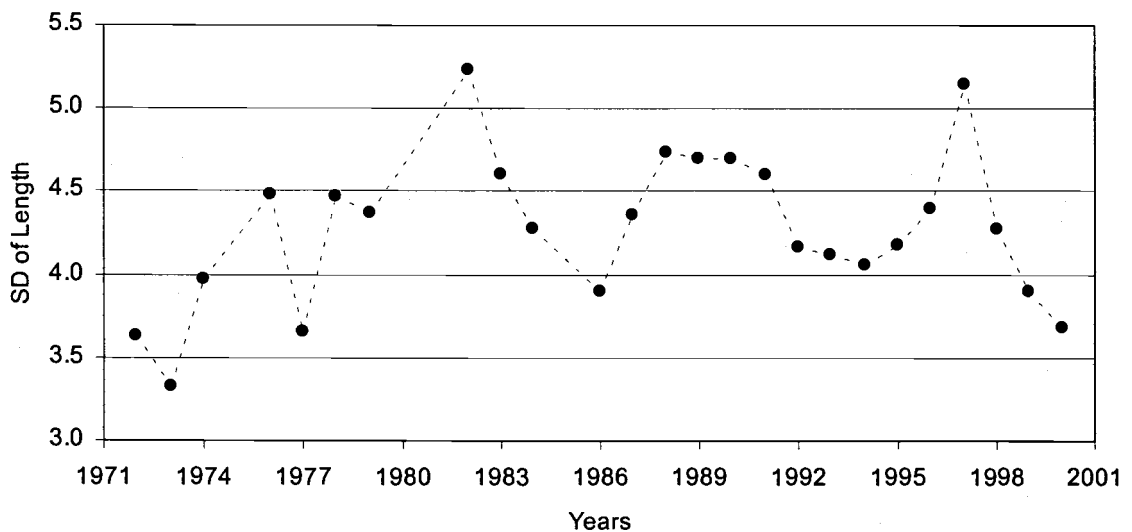


Figure 3.3. Average and standard deviation of lengths for yellowtail rockfish (combined sexes) over the years 1972-2000. The Dover sole lengths and weights had similar declining patterns.

(A) Average lengths over the years. The standard errors values are small, ranging from 0.08 to 0.32.



(B) Standard deviation of lengths over the years



average length over the years, and no particular trend in the standard deviation of length although it changed from year to year.

Generating the Random Data Sets

The truncated normal distribution was used to simulate the length distribution,

$$\begin{cases} f(L) = \frac{\varphi(L; \mu, \sigma)}{1 - 2\Phi(\tau; \mu, \sigma)} & , \text{ for } \mu - \tau\sigma < L < \mu + \tau\sigma \\ 0 & , \text{ otherwise} \end{cases} \quad (\text{Eq. 7})$$

where,

$$\begin{aligned} \varphi(L; \mu, \sigma) &= [\sigma(2\pi)^{1/2}]^{-1} \exp\{-0.5[(L - \mu)/\sigma]^2\} \\ \Phi(L; \mu, \sigma) &= \int_{-\infty}^{\mu - \tau\sigma} \frac{1}{\sigma(2\pi)^{1/2}} \exp\{-0.5[(L - \mu)/\sigma]^2\} dL \end{aligned}$$

The truncation was made at $\tau = 3$ to control the ending points of the length distribution so that comparisons of the influence of the average length and range of length would be more distinguishable, and also the generation of negative lengths is prevented. The range of $\mu \pm 3\sigma$ covers 99.74% of the total area of the normal distribution. For each treatment in the experimental designs, the data were generated and the parameters were estimated using the following algorithm.

Step (1): A random length value was generated from the truncated normal distribution with specified Avg (L) and σ_L .

Step (2): Using the length L from (1) a random weight value was generated from $W = a \cdot L^b \cdot \exp(\varepsilon)$, where $a = 0.01$, $b = 3$, and $\varepsilon \sim N(0, \sigma_w^2 = 0.014)$.

Step (3): Steps (1) and (2) were repeated as necessary to generate the number of lengths and weights in a basket for each treatment. For each basket the distribution of fish lengths and the corresponding total fish weight were tabulated.

Step (4): Steps (1)-(3) were repeated as necessary to generate the number of baskets for each treatment.

Step (5). Steps (1)-(4) were repeated to generate 500 replicate data sets for each treatment.

Step (6). SAS procedure NLIN (SAS 1994) with the Gaussian-Newton iteration method was applied to the total fish weight and length frequency data in each random data set to estimate the parameters. A set of 500 parameter values of a and b were estimated for each treatment.

Experiment 1: Analysis of Influential Factors

After examining the data, four variables were considered as potentially influential factors in the estimation of the length-weight parameters: the number of basket samples, the number of fish per basket sample, the variance of the lengths, and the average of the lengths. There are several reasons why these factors were considered as potentially influential. In a statistical estimation process various factors may influence the accuracy of the estimates, sample size being one of the major ones. There are two different types of sample size in the grouped measurement data: the number of basket samples and the number of fish in a given basket. Thus, it seemed necessary to examine the influence of both types of sample size. In standard linear regression, the spread of the independent variable (e.g., the variance of X) directly affects the precision of the estimated slope parameter. The wider the spread of the independent variable, the smaller the standard error of the slope estimate. The average of the independent variable would be another influential factor in a case where error in the dependent variable is proportional to the independent variable (as with multiplicative error). In length-weight relationships for fish, it is often observed that the variability in weight is proportional to the length; the error tends to expand at bigger lengths. Thus, the estimation accuracy may be affected by whether samples are from small or large length classes. From the examination of actual market sample data, we found that the numbers of fish per basket, and the variance and average length varied from sample to sample. Therefore, it seemed important to incorporate

these factors in the simulation experiment to understand their relative influence on the accuracy of the estimators.

A full factorial experimental design was constructed with these four factors and two levels within each factor, resulting in a total of 16 ($= 2^4$) treatments (Table 3.2). The levels of each factor were chosen to amplify the potential influence of the factors. For the number of basket samples 10 and 90 were chosen on an arbitrary basis. For the levels of fish per basket fixed values of 10 and 50 were chosen because the number of fish in a given basket would not generally exceed 50 with the current fixed-weight market sampling design. The levels for the average and the standard deviation of length were based on an examination of actual market sample data: 42 cm and 46 cm for the average, and 4 and 5 for the standard deviation.

One sample t-tests were used to assess the bias of the set of parameter estimates from each treatment. To identify and gauge the importance of the factors on the accuracy of the estimates among the treatments, the squared deviation of each estimate from the underlying true value of the parameter was calculated,

$$Deviation^2 = (Estimated - True)^2,$$

and analyzed after suitable transformation as a response variable using a general linear model (GLM) approach. I constructed models (GLMs) by starting with main

Table 3.2. (A) The factors and their levels used in the simulations. (B) The experimental design.

(A)

Level	Factor			
	N_Basket	Avg(L)	σ_L	N_Fish/Basket
1	10	42	4	10
2	90	46	5	50

(B)

Treatment	N_Basket	Avg(L)	σ_L	N_Fish/Basket
1	10	42	4	10
2	10	42	4	50
3	10	42	5	10
4	10	42	5	50
5	10	46	4	10
6	10	46	4	50
7	10	46	5	10
8	10	46	5	50
9	90	42	4	10
10	90	42	4	50
11	90	42	5	10
12	90	42	5	50
13	90	46	4	10
14	90	46	4	50
15	90	46	5	10
16	90	46	5	50

effects and all possible interactions of the main effects, then sequentially removed insignificant terms until only significant ones remained ($p\text{-value} < 0.05$).

Experiment 2: Sample Size Effects

Among the potentially influential factors that were identified from actual market samples, samplers do not have any control over selecting the sizes of the fish (i.e. length distribution of fish) or the number of fish per fixed-weight basket sample for a given sex because the samplings are conducted in a random manner. However, an increase in the number of basket samples should improve the accuracy of the estimates. To examine the large-sample properties of the estimates, random data sets were simulated that had a sequence of six different basket sample sizes (30, 60, 120, 240, 480, and 960), generated by doubling the base line sample size of 30 baskets. Except for the basket sample size, the other influential factors were fixed. The number of fish per basket was 25/basket, the average fish length was 44 cm, and the lengths ranged from 32 cm to 56 cm with $\sigma_L = 4$. The other parameter values ($a = 0.01$, $b = 3$, and $\sigma_w^2 = 0.014$), estimation method, and simulation procedures were the same as in the first experiment. Bias of the mean of the estimates for a and b was tested with one-sample t-tests. The Root Mean Square Error (RMSE) was used to measure the accuracy of the estimates for each set.

$$RMSE(P) = \sqrt{(Average(Estimate - True))^2} = \sqrt{Var + Bias^2}$$

Experiment 3: Detecting Parameters Changes from the Residuals

Changes in the parameter values of the length-weight relationship over time, which correspond to changes in the condition of the fish, should be reflected in the residuals when one single estimation model is applied to the complete data series. The question is how sensitive are the residuals to changes in the parameters. To evaluate this, data were simulated in the same manner as in second experiment in terms of the number of fish per basket sample (25), average length (44), and the standard deviation of length ($\sigma_L = 4$), but the basket sample size was fixed at 30 for each time step. The parameter values a and b were allowed to change systematically with each of five time step. In one data set parameter b was fixed at 3 and parameter a was changed with an increment of 0.0001 at each time step, starting from 0.01, which is about a 1% change with each time step. In a second data set, the parameter a was fixed at 0.01 and b was incremented by 0.003 at each time step from 3.0, which is equivalent to about 0.1% change with the each step.

With each data set the five steps of data were compiled and analyzed together as if the data were collected from a single population, then the data were fitted with a single non-linear regression. The studentized residuals from the model were then analyzed with ANOVA to evaluate whether there were significant differences among the time steps. To test which means were different, all pairwise combinations of the means from the steps were compared by the Student-Newman-Keuls (SNK) multiple range test to control the Type I experimentwise error rate at $\alpha = 0.05$.

RESULTS

Experiment 1: Analysis of Influential Factors

The parameter values, a and b , were estimated by nonlinear regression (SAS Proc NLIN) for each treatment. One sample t-tests of b estimates from each treatment compared to the pre-specified value of $b = 3$ provided no statistical evidence that the estimator was biased. However, the variability of the estimates differed among the treatment (Table 3.3, Figure 3.4(A)). The most noticeable difference among the treatments is that the estimates from the treatments with the basket sample size of 90 (treatments 9-16) have higher precision estimates (smaller CV). The box plots of the b estimates displayed no apparent skewness.

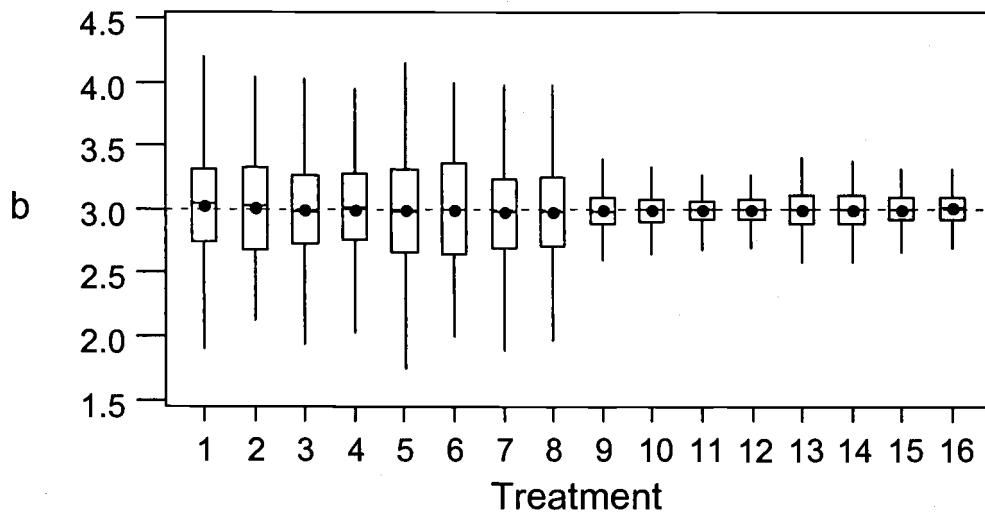
Unlike the estimates of b , the estimates of a for all treatments were highly skewed toward higher values and were biased (one sample t-test that $a = 0.01$; $p\text{-value} < 0.0001$ for all treatments). As in the case of the parameter b estimates, the estimates of a with the basket sample size of 90 (treatments 9-16) showed distinctively a higher precision compared to those with the basket sample size of 10 (treatments 1-8), as well as reduced skewness (Table 3.3, Figure 3.4(B)). Interestingly, there is a highly correlated linear relationship ($\rho = -0.9999$) between the b estimates and the log of the a estimates (e.g., Figure 3.5). This high correlation indicates that the estimates are almost perfectly predictable, one from the other. One sample t-tests of the log-transformed a estimates revealed that they were not

Table 3.3. The mean of the parameter estimates from each treatment over the 500 simulated data sets. The underlying true values of the parameters are 3 for b and 0.01 for a . The p-value from a t-test of parameter $b = 3$ is reported for each treatment. The p-values for t-tests of parameter $a = 0.01$ were <0.0001 for all treatments.

Treatment	b	$CV(b)$	$Pr > t $	a	$CV(a)$
1	3.0325	16.2%	0.140	0.05640	377.1%
2	3.0237	13.8%	0.204	0.02610	150.6%
3	2.9970	14.3%	0.874	0.04224	431.9%
4	3.0058	13.5%	0.751	0.03038	212.4%
5	2.9967	16.8%	0.882	0.05359	241.7%
6	2.9964	14.1%	0.851	0.03146	166.4%
7	2.9771	14.9%	0.249	0.04829	337.6%
8	2.9866	12.8%	0.435	0.02955	186.5%
9	2.9943	5.0%	0.400	0.01202	60.6%
10	2.9968	4.6%	0.605	0.01171	59.1%
11	2.9947	4.0%	0.333	0.01141	48.8%
12	2.9958	3.9%	0.419	0.01127	45.8%
13	2.9997	5.2%	0.964	0.01209	66.2%
14	3.0018	5.3%	0.796	0.01208	69.3%
15	3.0003	4.2%	0.952	0.01132	51.9%
16	3.0100	4.3%	0.084	0.01095	52.2%

Figure 3.4. (A) Box-whisker plots of the estimates of parameter b for the treatments. The dotted line at 3 represents the true underlying value of b . The circle in each box indicates the mean of the estimates and the bar indicates the median. The mean and the median in each treatment closely overlap, implying that estimates are not skewed. (B) Box-whisker plots of the estimates of parameter a for the treatments. The dotted line at 0.01 represents the true underlying value of a . The mean and the median are considerably different in the treatments with the basket sample size equal to 10, implying that the estimates are positively skewed.

(A)



(B)

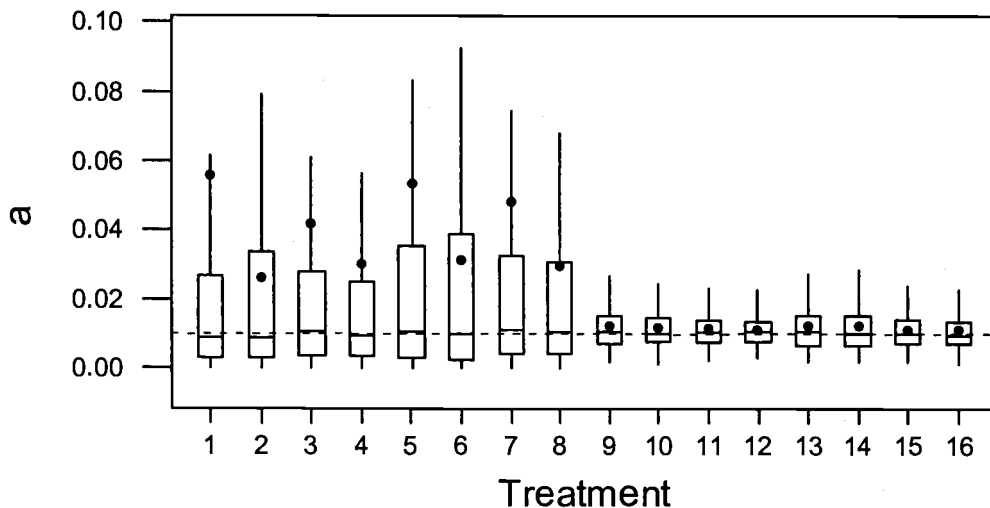
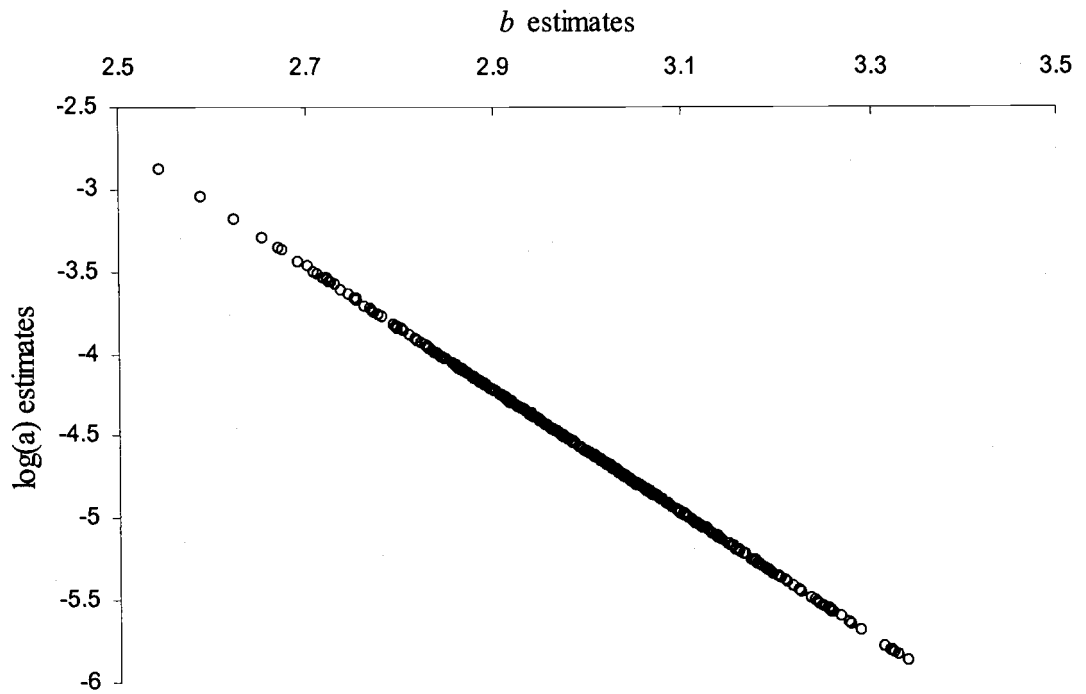


Figure 3.5. Scatter plot of estimates of $\log(a)$ and b from treatment 4. The correlation coefficient is -0.9999 .



statistically different from the log of the prespecified value of 0.01, which suggests that the estimates of parameter a are lognormally distributed.

The GLM analyses of the squared deviation of each estimate demonstrated that “N_Basket” (basket sample size) was the most influential factor by far for the accuracy of both the a and b estimates (Table 3.4, Table 3.5). The GLM was applied after taking proper transformation of the response variable (the squared deviations) to improve the normality and homogeneous variance assumptions. The square root transformation was used for the deviations of the b estimates and the log transformation was used for the deviations of the a estimates. No interaction terms were significant in the GLM of the b deviations and the “Avg(L)” factor also was not significant among the main effects (F-test, p -value = 0.1056). This suggests that the average length of the fish is not a key factor in the accuracy of the b estimates. Although the factor “ σ_L ” (standard deviation of fish length) and “N_Fish” (number of fish per basket) were statistically significant in the model, their degree of influence was almost negligible compared with the ‘basket sample size’ effect. In terms of the mean partial sums-of-squares, the MS for “N_Basket” was about 48 times larger than the MS of the second most influential factor in the model, “ σ_L ” (Table 3.4).

As in the case of the b estimates, “N_Basket” was the dominant factor in determining the accuracy of the a estimates. The influence level of the “N_Basket” factor was almost 69 times larger than the second most significant factor, “ σ_L ”, in terms of MS amount (Table 3.5). All the main factors and the interaction between

Table 3.4. Results from the GLM analysis of the squared deviations of the estimates of b . The response variable was transformed with the logarithm function prior to the analysis.

Source	DF	SS	MSE	F Value	Pr > F
Model	3	116.894	38.965	1110.3	<.0001
Error	7996	280.611	0.035		
Corrected Total	7999	397.505			
R-Square = 0.294					

Source	DF	Type III SS	MSE	F Value	Pr > F
N_Basket	1	114.289	114.289	3256.67	<.0001
σ_L	1	2.381	2.381	67.85	<.0001
N_Fish	1	0.224	0.224	6.39	0.0115

Table 3.5. Results from the GLM analysis of the squared deviations of the estimates of a . The response variable was transformed with the logarithm function prior to the analysis.

Source	DF	SS	MSE	F Value	Pr > F
Model	5	15.626	3.125	290.17	<.0001
Error	7994	86.094	0.011		
Corrected Total	7999	101.719			
R-Square = 0.154					

Source	DF	Type III SS	MSE	F Value	Pr > F
N_Basket	1	15.119	15.119	1403.88	<.0001
σ_L	1	0.220	0.220	20.44	<.0001
N_Fish	1	0.136	0.136	12.58	0.0004
Avg(L)	1	0.073	0.073	6.74	0.0095
N_Basket * N_Fish	1	0.078	0.078	7.23	0.0072

“N_Basket” and “N_Fish” were significant factors in the model. However, except for the “N_Basket” effect, the influence of other factors in the model was very trivial. Although the GLM models for the transformed a and b deviations were highly significant, the R-square of the models were low (29.4% for the b deviations; 15.4% for the a deviations), indicating that there were still large amounts of variation unexplained by the models.

Experiment 2: Large-Sample Properties of Estimates

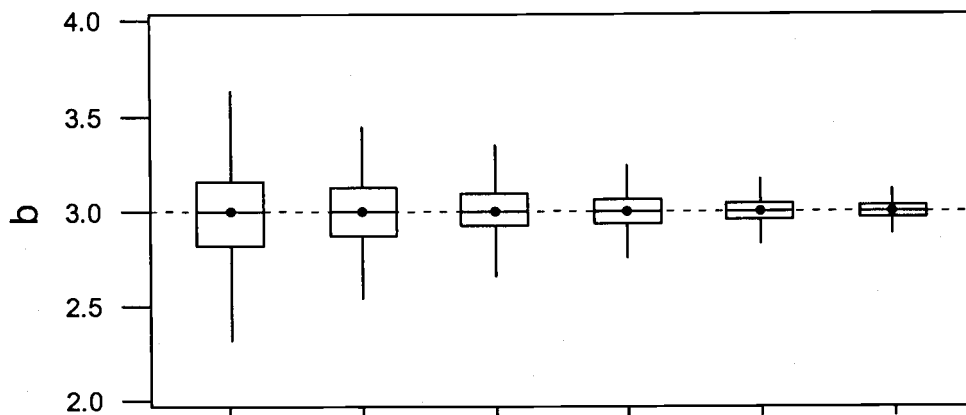
The estimates of parameters a and b were tested for unbiasedness by one-sample t-tests for each basket sample size treatment. The means of the b estimates for all sample size classes were not statistically different from the pre-specified parameter value of $b = 3$, suggesting that the estimator for b is unbiased even with the smallest sample size used in the experiment 30 (Table 3.6). The precision of the b estimates consistently improved as the sample size increased (Figure 3.6(A)). However, the estimates of a were skewed toward higher values and the one sample t-tests of the parameter a estimates confirmed that they were biased across all sample sizes (Table 3.6, Figure 3.6(B)). However, as the sample size increased, the degree of skewness decreased considerably and the precision of estimates improved. The actual means of the a estimates became fairly close to the underlying true value of $a = 0.01$ for the sample sizes more than 240, but the estimates for a were still right skewed and significantly different from the true value based on one-sample t-tests.

Table 3.6. The mean of the estimates for parameters from each sample size over the 500 simulations. The underlying true values of the parameters are 3 for b and 0.01 for a .

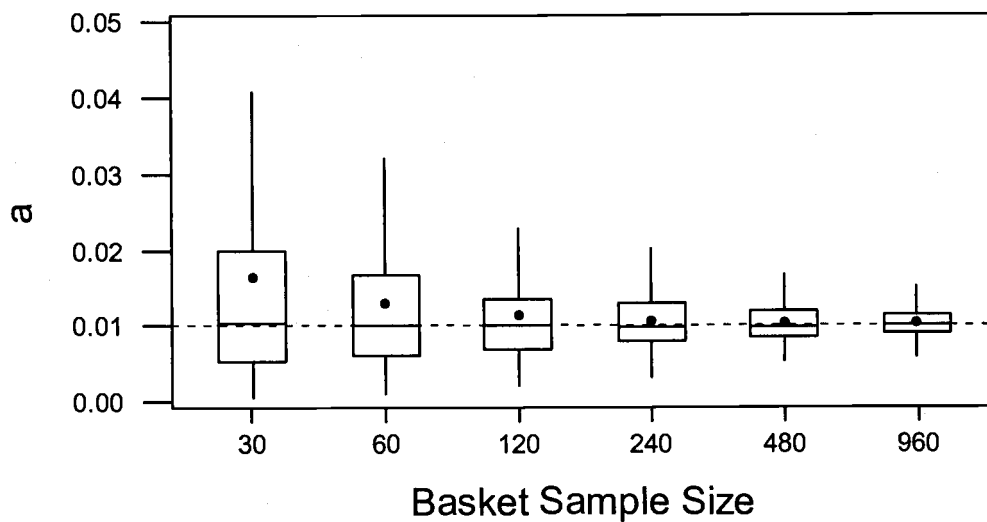
Sample size	b	$CV(b)$	$Pr > t $	a	$CV(a)$	$Skew(a)$	$Pr > t $
30	2.9970	8.7%	0.7945	0.01648	124.2%	4.296	<0.0001
60	2.9987	6.2%	0.8742	0.01302	78.7%	2.318	<0.0001
120	3.0008	4.4%	0.8964	0.01142	55.4%	1.790	<0.0001
240	2.9997	3.0%	0.9338	0.01070	35.0%	0.892	<0.0001
480	2.9996	2.1%	0.8945	0.01039	24.7%	0.765	0.0008
960	2.9990	1.5%	0.6428	0.01027	17.7%	0.518	0.0012

Figure 3.6. (A) Box-whisker plot of b estimates from the different sample sizes. The dotted line at 3 represents the true underlying value of b . (B) Box-whisker plot of a estimates from the different sample sizes. The dotted line at 0.01 represents the true underlying value of a . The circle in each box indicates the mean and the bar indicates the median of the estimates.

(A)



(B)



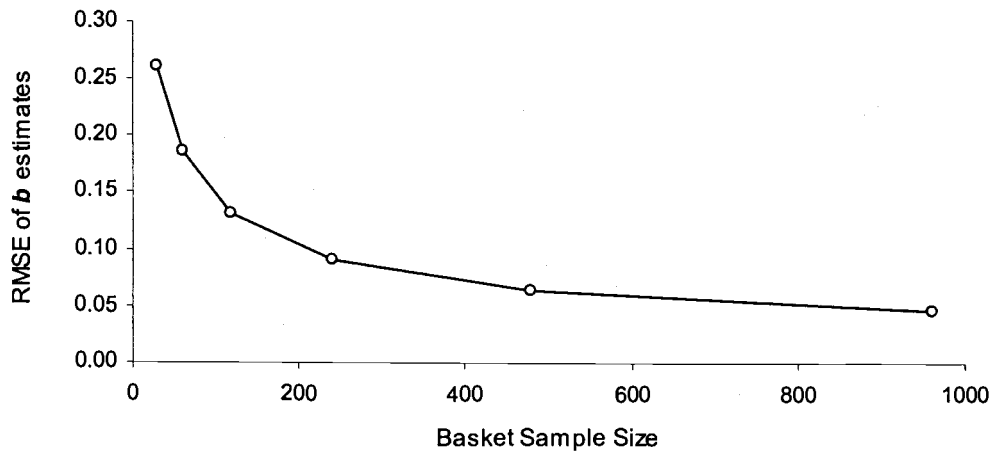
The accuracy of the estimates of a and b , measured by the RMSE, improved rapidly as the sample size increased (Figure 3.7) to about 240, then declined very gradually.

Experiment 3: Detectability of Parameter Changes from Residuals

The box plots of the studentized residuals from the models clearly show differences among the residuals at each time step, in keeping with the underlying changes in parameter b (Figure 3.8(A)) and the underlying changes in parameter a (Figure 3.8(B)). The ANOVA test of the studentized residuals associated with the steps confirms that there was at least one significant difference among the means (F-test, $p\text{-value} < 0.001$). Pairwise comparisons for the means of the studentized residuals were made to gauge the significance of changes in residuals between pairs of time steps. For parameter b , the averages of the residuals from adjacent steps were not different from each other except between steps 3 and 4, but the residuals from non-adjacent steps were significantly different from each other for all combinations (Figure 3.9). The results were similar for parameter a ; the neighboring steps only differed for steps 2 and 3, but all non-adjacent steps were significantly different from each other. The results imply that the residuals from a single non-linear regression model fitted to the data series could be used to identify changes as small as 0.2% in parameter b and 2% in parameter a , given basket sample sizes of at least 30 for each of two time intervals.

Figure 3.7. Plot of the RMSE of the estimates for each sample size.

(A) RMSE of the b estimates



(B) RMSE of the a estimates

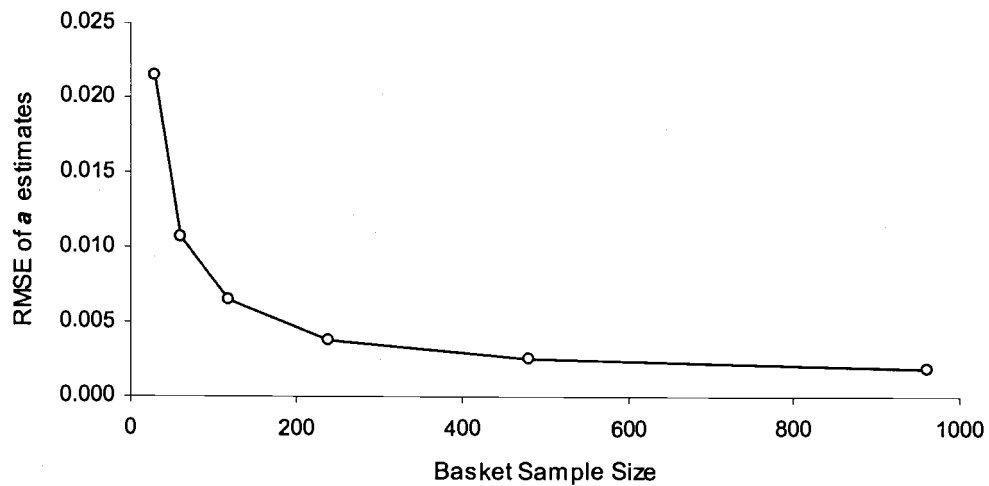
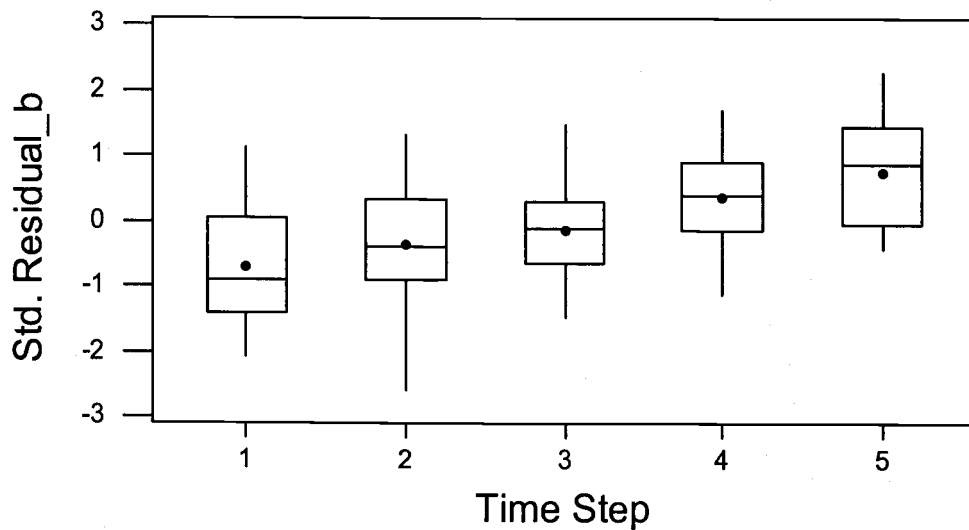


Figure 3.8. Box-whisker plots of the studentized residuals from the experiment to evaluate the power of the nonlinear regression method to detect changes in the length-weight relationship. The circle in each box represents the mean value of the residuals in each time step. (A) The increment of change in b was 0.003 (0.1%) for each time step. (B) The increment of change in a was 0.0001 (1%) for each time step.

(A)



(B)

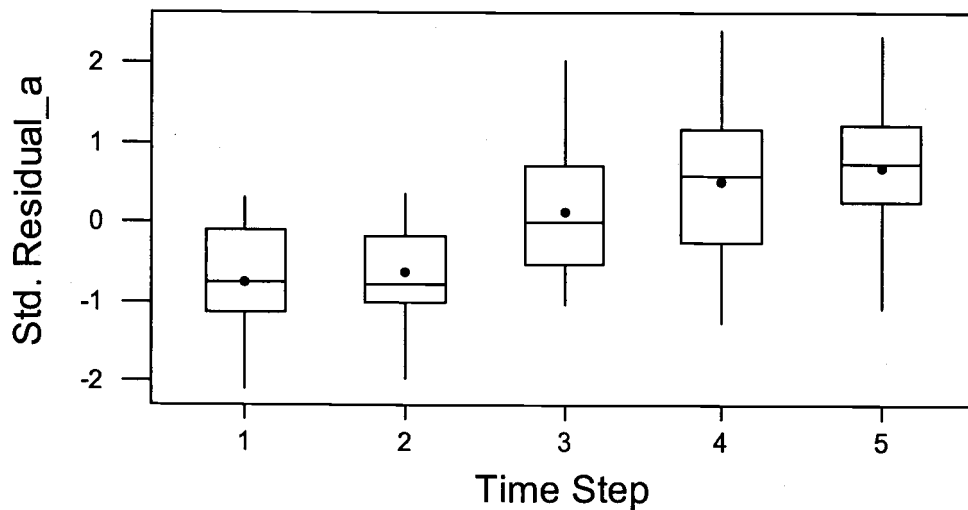


Figure 3.9. Results from pairwise comparisons between the time steps using the Student-Newman-Keuls (SNK) multiple range test. Each cell represents a pair of the time steps. The cells in upper right of the diagonal axis are the ones where parameter b changed over the steps. The cells in the lower left of the diagonal axis are the ones where parameter a changed over the steps. The cells for pairs that were statistically different ($p\text{-value} < 0.05$) are indicated by star marks (*).

		< Changes in b >				
		Steps				
		1	2	3	4	5
< Changes in a >	1			*	*	*
	2				*	*
	3	*	*		*	*
	4	*	*			
	5	*	*	*		

DISCUSSION

The experiments in this study demonstrated that parameter b can be estimated with no apparent bias by the nonlinear regression method applied to group measurement data, even in the worst case scenario (10 baskets each with 10 fish). However, estimates for parameter a were still statistically biased even with large samples, although the precision improved steadily as sample size increased. The bias and skewness of the a estimates at large sample sizes suggest that there is a problem with an inherent nonlinearity in the estimation method.

The characteristics of the a estimates may be caused by violation of the fundamental assumption in nonlinear regression of additive errors, because the data were generated with multiplicative error. The multiplicative error structure was assumed for the data generation in this study because heteroskedasticity (increase in weight variability with increase in length) is a common feature of length-weight relationships of fish species in general.

The estimate of parameter a is also not free from bias even in the log-transformed linear model for individual measurements. Transformation bias is introduced when the estimate of $\log(a)$ is back-transformed by exponentiation to get a , because $\log(a)$ is normally distributed but a is lognormally distributed (Hayes et al 1995). A few methods have been proposed to correct for this transformation bias (Neyman and Scott 1960; Ricker 1973; Miller 1984), however, these are not applicable to the nonlinear regression model for grouped measurements. Another

possible explanation for the bias of the estimates would be the inherent properties of nonlinearity of parameters in nonlinear models. Often reparameterization or weighted regression could help to improve the performance of a basic nonlinear regression model (Ratkowsky 1989). The analysts must decide on an estimation method either based on additive error or multiplicative error, regardless of the true underlying error structure in the length-weight relationship. The lack of bias in the b parameter estimates in this study indicates the robustness of the method to a violation of the error structure assumption. This is a good feature of the method because the true underlying error structure is always unknown.

A striking feature of the Oregon market sample data was the decline in the average length of the fish. It is not clear whether the changes in average length were driven by biological changes, market changes, or a combination of both. It is possible that strong fishing pressure removed large size classes of fish species and consequently forced the market to allow landings of smaller size classes. The changes in the range of lengths from year to year are possibly a random sampling artifact. There is some evidence in some species that the length of the fish has become shorter at a given age, possibly because of long-term environmental changes. Those biological changes, whether they are induced by the environment or sampling plans, could be potentially influential factors in the parameter estimation for length and weight relationship.

A previous study by Hayes et al. (1995) on efficient sampling designs for accurately estimating length-weight parameters indicated that sampling designs

emphasizing both ends of the length distribution or ones with uniform sampling over the range of the length distribution would improve the accuracy of the estimates. However, such sampling designs are implausible in this kind of group measurement data because the primary purpose of the data collection is not to obtain the length-weight relationship. The sampler cannot deliberately select fish based on their lengths because the samples are supposed to reflect the underlying length distribution. However, this form of limitation on the sample selection should not limit the applicability of a non-linear regression estimation for grouped measurements. Even though the factors related to the length distribution, average length and range of length, were statistically significant factors influencing the accuracy of the estimates, the levels of influence from those factors were very minimal. It is important, however, that analysts should understand the characteristics of their data and pay more attention to these factors for the diagnosis and the analysis of data. It is recommended that analysts use basket sample sizes of at least 100 for more precise estimates.

A simulation experiment in this study illustrated that residuals from the model are fairly sensitive to changes in the underlying length-weight relationship. Thus, the method can be used for assessing variations in growth condition between different populations or over a certain time period.

This study investigated the properties and reliability of estimates from nonlinear regression applied to group measurements of length and weight. The results indicate that, in general, the method should be an excellent alternative when

individual length and weight measurement data are not available. Further studies are needed on methods for correcting the bias in the estimates of parameter a in conjunction with alternative assumptions about the underlying error structure.

CHAPTER 4: LONG-TERM VARIATIONS IN GROWTH CONDITION OF FIVE GROUND FISH SPECIES OF THE PACIFIC NORTHWEST

INTRODUCTION

In the previous chapter, I demonstrated that a non-linear regression technique can be successfully applied to group measurement data consisting of individual fish lengths and the group weights to assess changes in the long-term length-weight relationship of the fish. The main objective of this chapter is to apply the non-linear regression technique to available Oregon market sample data for several different fish species and assess the long-term variability in their growth condition. These data were collected over a period of several decades by the Oregon Department of Fish and Wildlife from landings of commercial catches off Oregon. The fish species examined in this study were Dover sole (*Microstomus pacificus*), petrale sole (*Eopsetta jordani*), canary rockfish (*Sebastes pinniger*), yellowtail rockfish (*S. flavidus*), and widow rockfish (*S. entomelas*).

It is widely accepted that for most fish species, environmental factors exert an important influence on life history traits, such as growth rates, mortality, age at maturation, fecundity, maximum body size, and maximum age (Stearns 1976). The growth condition of fish, measured by length-specific weight based on a length-weight relationship, assumes that heavier fish at a given length are in better condition (Murphy and Willis 1996). This type of condition measurement is an indicator of the

general physical fitness of the fish in a population. The notion of growth can refer to increases in the length or weight of an individual as it ages, as well as to the changes in the body form associated with metamorphosis for some species. Growth condition is affected by physical factors (temperature, salinity, dissolved oxygen levels, etc.), food availability, and interactions between them (Paloheimo and Dickie 1965, 1966). Because fish are cold-blooded, growth is sensitive to ambient water temperature. Increases in temperature leads to higher rates of metabolism and ingestion. However, temperatures above the thermal range of a particular species often inhibit the growth. Within the thermal range, higher temperature generally results in more growth when food is not limiting.

In the natural environment, however, the factors which potentially influence the growth are rarely constant. The factors shape a wide range of environmental regimes and feeding opportunities in the habitat (Weatherly 1976). Thus, the growth of fish would not be governed by single factors alone, but by the complicated interactions of these factors and by the species' specific adaptations. The physical factors directly influence both the physiology of fish growth and the communities of prey organisms. Many studies have reported that the composition and abundance of lower trophic levels of potential prey organisms are subject to change due to the variation of the environmental factors. Therefore, it is believed that the physical factors are both direct and indirect determinants of fish growth.

The coastal waters off the Pacific Northwest have experienced occasional strong El Niño events, and years of extended periods of warm ocean temperature

alternating with years of cool ocean temperatures, and great variability in the intensity of upwelling. Also, there have been highly significant interannual and interdecadal fluctuations in the biomass of zooplankton in the northwest Pacific subarctic gyre and the California Current (Brodeur et al. 1996; Brodeur and Ware 1992; Mackas 1992, 1995; Mackas et al. 2001). Investigations of zooplankton off southern California (California Current domain) reported zooplankton biomass declines of 80% in that region based on 43 years of observations, whereas studies in the Alaska Gyre (Alaska Current domain) reported a two-fold increase over roughly the same period (Brodeur and Ware 1992; Roemmich and McGowan 1995). Thus there appears to be an inverse relationship between these two subarctic domains in the alternations of zooplankton biomass (Brodeur et al. 1996). It is suggested that the observed decline of zooplankton in southern California is linked to a general warming of the California Current. The phenomenon in the Alaska Current domain possibly reflects shifts in decadal climatic conditions favorable to zooplankton populations in the region during the period.

However, long-term changes in the zooplankton community in Oregon's coastal waters have not been established, although seasonal and interannual variations have been reported (Pearcy 1976; Peterson and Miller 1975, 1977). Changes in the prey fields due to the variable environment were reflected in the food habits of some pelagic fish species (Brodeur and Pearcy 1992). In Chapter 2 of this dissertation, two rockfish species were found to have marked temporal changes in

their diets, possibly due to changes in the prey fields that were altered by large scale events such as El Niño and La Niña.

Numerous studies have reported changes in the growth of fish species in Northeast Pacific. The growth of Pacific salmon species, Chinook salmon (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye (*O. nerka*), is reportedly affected by ocean conditions and the mean length-at-age of some species has decreased (Lawson 1994; Bigler et al. 1996). Pacific hake (*Merluccius productus*) in the region have also undergone significant negative changes in growth (Barry et al. 1990; Dorn 1992), as have Pacific herring (*Clupea pallasii*) (Tanasichuck 1977) and Pacific halibut (*Hippoglossus stenolepis*) (Hagen and Quinn 1991; Clark et al. 1999). These studies examined growth variation based on length-at-age or based on the information of increments recorded on the hard structures of the body, such as otoliths or scales, but not based on length-specific weights (growth condition).

The purpose of this study is to develop a time series of condition indices for five fish species inhabiting the marine waters off Oregon by utilizing available market sample data. Variations in the growth condition were examined for possible trends and were correlated with a suite of environmental factors. The growth conditions for the fish populations of the NE Pacific have not been closely examined on a long-term basis. If environmental factors are important determinants of fish growth, one would expect that long-term variations in the growth condition of the fish would be related to variations in the underlying environmental conditions.

MATERIALS and METHODS

Biological Data

Monthly market sample data, consisting of group weight measurements by sex and individual measurement of fish lengths for five different fish species, two flatfish and three rockfish species, were obtained from the Oregon Department of Fish and Wildlife. The group weights of the fish were measured in tenths of a pound and the individual fish lengths were measured in centimeters. The completeness and the time span of the monthly data differ between the species, even though data were available through year 2000 for all the species (Appendix). The time series for flatfish species was longer than the record for rockfish species. The time series data were available for Dover sole (*DOV*) from 1972, for petrale sole (*PET*) from 1971, for canary rockfish (*CAN*) from 1977, for yellowtail rockfish (*YEL*) from 1977, and for widow rockfish (*WID*) from 1984. However, data were missing for some years and months for all the species. The acronyms for the names of the fish species shown in parentheses are used in the tables, figures, and the remainder of the document.

Oceanographic Data

Monthly data for several oceanographic variables for the period 1971 to 2000 were obtained from the web sites of research institutes and individual researchers. These include the large-scale variables (e.g., the Southern Oscillation Index) and

local variables (e.g., sea surface temperature). The oceanographic data were related to the growth condition index of the fish species to examine the associations. The descriptions of oceanographic variables that were used in this study are as follows.

Multivariate ENSO Index (MEI)

The MEI is calculated as the first principal component of six main variables observed over the tropical Pacific. These six variables are: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and the total cloudiness fraction of the sky. The index has been developed in an attempt to better monitor the development of El Niño/Southern Oscillation events (ENSO) (Wolter and Timlin 1998). The data were obtained from NOAA-CIRES Climate Diagnostics Center (<http://www.cdc.noaa.gov>).

Pacific Decadal Oscillation Index (PDO)

The PDO index is defined as the first principal component of the North Pacific monthly sea surface temperature variability, poleward of 20°N. It is often described as a long-lived El Niño-like pattern of Pacific climate variability. PDO regimes, cool or warm, persist for a long-time period, 20-to-30 years (Mantua and Hare 2002). The cool phase of the PDO prevailed from 1947 to 1976 and the warm phase from 1977 through the mid 1990s. The PDO phases have been correlated with major changes in northeast Pacific marine ecosystems (Mantua et al. 1997). The coastal ocean productivity was noted to be enhanced in Alaska and inhibited off the

U.S. west coast during the warm PDO phase, and the pattern is reversed during the cold PDO phase. Data were obtained from Joint Institute for the Study of the Atmosphere and Oceans (<http://tao.atmos.washington.edu/pdo>).

North Pacific Index (NPI)

The NPI is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W (Trenberth and Hurrell 1994). The index measures the intensity of Aleutian Low during winter months. A deeper and eastwardly shifted Aleutian Low pressure system during winter advects warmer and moister air along the west coast of the U.S. and into Alaska, and colder air over the north Pacific. This results in increased upper ocean temperatures over the area but conversely in a decrease over the central north Pacific. The changes in the physical environment due to the Aleutian Low pressure system appear to be associated with biological systems; a stronger Aleutian Low is inversely correlated with productivity in the NE Pacific. Low values of the NPI indicate the stronger Aleutian Low. The data were obtained from Dr. James Hurrell with National Center for Atmospheric Research (<http://www.cgd.ucar.edu/~jhurrell>).

Southern Oscillation Index (SOI)

The SOI is the anomaly in the sea level pressure difference between Tahiti (18°S-150°W) and Darwin (10°S-130°E). The SOI is a good indicator of tropical

variations related to El Niño events. The data were obtained from NOAA-CIRES Climate Diagnostics Center (<http://www.cdc.noaa.gov>).

Northern Oscillation Index (NOI)

The NOI is the anomaly in the sea level pressure difference between the North Pacific High (35°N-135°W) and Darwin (10°S-130°E). While the SOI would be a good measure for the tropical system, the NOI may better represent the environmental variability in Northeast Pacific, because it is partially based on the Northeast Pacific. The NOI is a reliable indicator for monitoring and predicting climate fluctuations, and their physical and biological consequences in the Northeast Pacific (Schwing et al. 2002). The data were obtained from the Pacific Fisheries Environmental Laboratory (<http://www.pfel.noaa.gov>).

Upwelling Index at 45°N (UPI)

Upwelling is a seasonal phenomenon off the Oregon coast. Offshore Ekman transport of surface waters induced by wind stress results in the displacement of subsurface waters during the summer. Upwelling indices are calculated based upon Ekman's theory of mass transport due to wind stress (Huyer 1983). Upwelling is closely related with biological productivity in coastal waters. The data were obtained from Pacific Fisheries Environmental Laboratory (<http://www.pfel.noaa.gov>).

Sea Level (SL)

Monthly data for SL at Crescent City, CA (41°44.7'N, 124°11.0'W) were obtained from University of Hawaii Sea Level Center (<http://uhslc.soest.hawaii.edu>). The SL is an index of the volume transport of the California Current system. In general, high SL indicates the anomalous northward flow and low SL indicates normal equatorward flow (Chelton and Davis 1982; Chelton et al. 1982).

Sea Surface Temperature (SST)

Monthly SST data measured at the mouth of South Slough (43°N), OR were obtained from Peter Lawson (National Marine Fisheries Service, Newport, OR).

Data Analysis

Prior to calculating the relative growth condition market sample data with fewer than five fish in the basket sample were removed from the data file, because such small samples would likely yield highly imprecise estimates of the length-weight relationship. Non-linear regression (SAS procedure NLIN) was applied to the remaining market sample data for each species by sex. The sample data associated with large studentized residual values (absolute value ≥ 4) were examined as being possible outliers and were compared with the original ODFW data sheets to check if there had been data input errors or other error sources. If an error was identified, then it was corrected in the electronic data file. If there was no discrepancy between the

hard copy and electronic file but it seemed that errors had occurred during sampling, then those data were removed from the file.

The corrected data sets for each species were fitted with a non-linear regression model of the form,

$$\frac{WT_j}{n_j} = \left\{ \sum_{i=1}^{n_j} (a \cdot L_{i,j}^b) \right\} / n_j$$

Because the number of individual fish samples could be different from basket to basket, instead of using the total weight of the fish in a sample as the independent variable, the average weight of the fish was used to compensate for the problem of unequal sample size across aggregate samples (basket samples).

The studentized residuals (the residuals divided by the square root of the average squared residual) from the model were then used as relative growth condition indices. Associated with each residual for a given species are the external factors year, month, latitude, and sex.

The residuals for each fish species were then analyzed with General Linear Models (SAS procedure GLM) to explore how the growth condition index was related to the external factors. The GLM approach allows one to examine the relative influence of external factors and their possible interactions on the growth condition index. The factors considered in the analysis were year, month, latitude and sex. All factors were treated as categorical variables in the model. Latitude had three

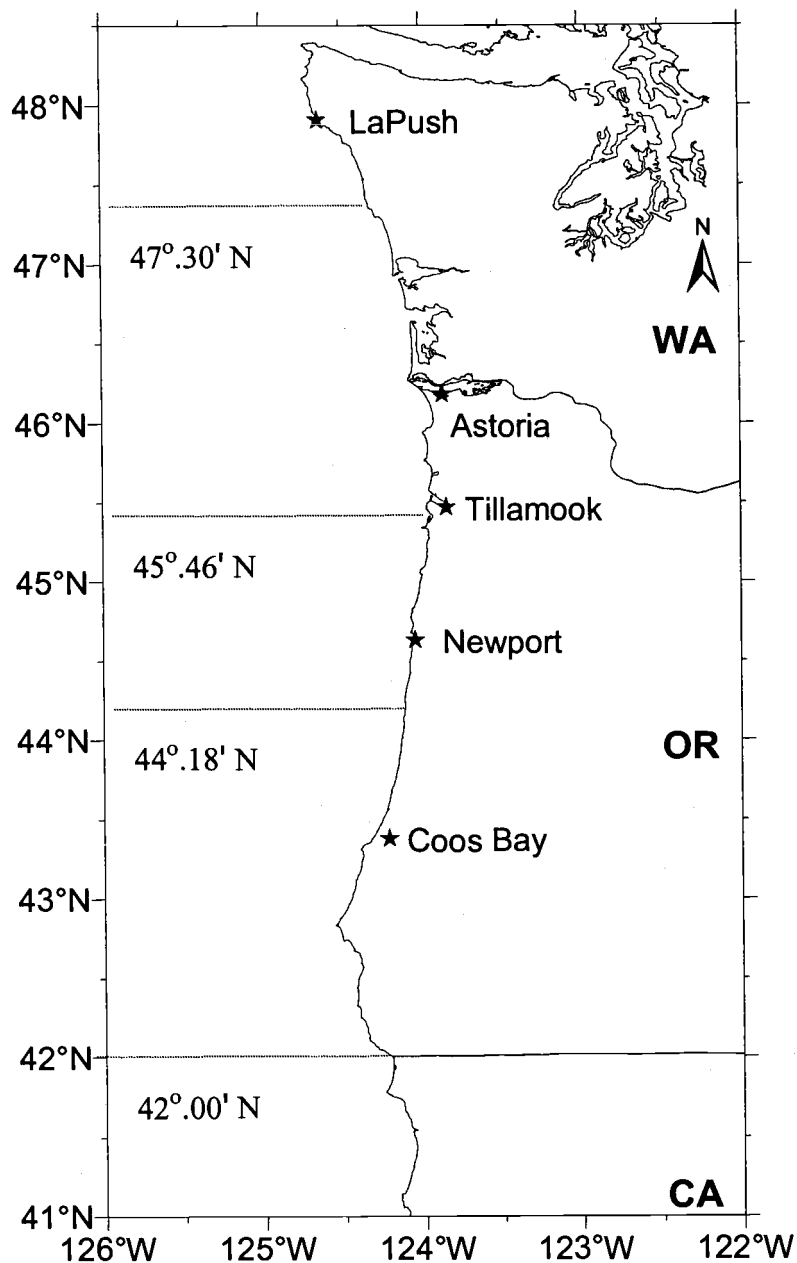
categories based on the location of the catches: southern ($42^{\circ}00'N - 44^{\circ}18'N$), central ($44^{\circ}18'N - 45^{\circ}46'N$), and northern ($45^{\circ}46'N - 47^{\circ}30'N$) (Figure 4.1).

A major reason for using the GLM on the residuals was to develop a time series of predicted values of the growth condition indices that could be compared with the oceanographic data series. The raw residual values would not be good to use as growth condition indices because the data are highly unbalanced. Data are missing in some months and the sample sizes (the number of basket samples) are also highly variable from month to month (Appendix B). To accommodate these problems, the GLMs were used to calculate predicted values that would best represent the growth condition factors for each species and sex over the time period.

The external variables and interactions were selected for the model using a backward elimination approach at the 0.05 significance level, starting from a full model with all the main effects and all possible two-way interactions. The most insignificant variables were eliminated one by one until all the variables in the model were significant. Once a set of variables was selected, then the higher order interactions of the selected variables (three-way interactions and greater) were examined for possible inclusion in the model.

The monthly time series data for the oceanographic variables and predicted growth condition indices for each species were plotted to examine for trends or obvious patterns, as well as to look for synchrony in the variations of growth condition among the species. Pearson correlation coefficients were used to quantify

Figure 4.1. Map of the study area.



the relationships between the growth condition indices and the environmental factors, based upon different time averages: by month, quarter, half-year, and year.

RESULTS

Monthly time series data of the environmental variables suggest that each index represents variations in the environment occurring at different frequencies (Figure 4.2). Some indices appear to measure long-term environmental fluctuations (decadal) and others measure rather short-term fluctuations (interannual and seasonal variations). For example, the MEI and PDO clearly illustrate patterns of long-term variation, while the NPI, UPI, SL, and SST indices exhibit different patterns of short-term variation. The signals of the strong El Niños of 1983 and 1997/98 are clearly shown in the indices, regardless of the index type.

Correlation matrices of all the environmental variables, based on time averages at four different scales (monthly, quarterly, half-yearly, and yearly) show that many of the variables are highly inter-correlated (Table 4.1). This suggests that the variables may be measuring a signal of common environmental variation. The strength of the correlations between the variables generally improved as the time-scale of averaging increased (from monthly to yearly). Some coefficients that were not significant at shorter time scales also become statistically significant at the longer scales. For example, the correlation between SL and SST was not significant for the

Figure 4.2. Time series of the environmental indices for the period 1971-2000 used in the analysis.

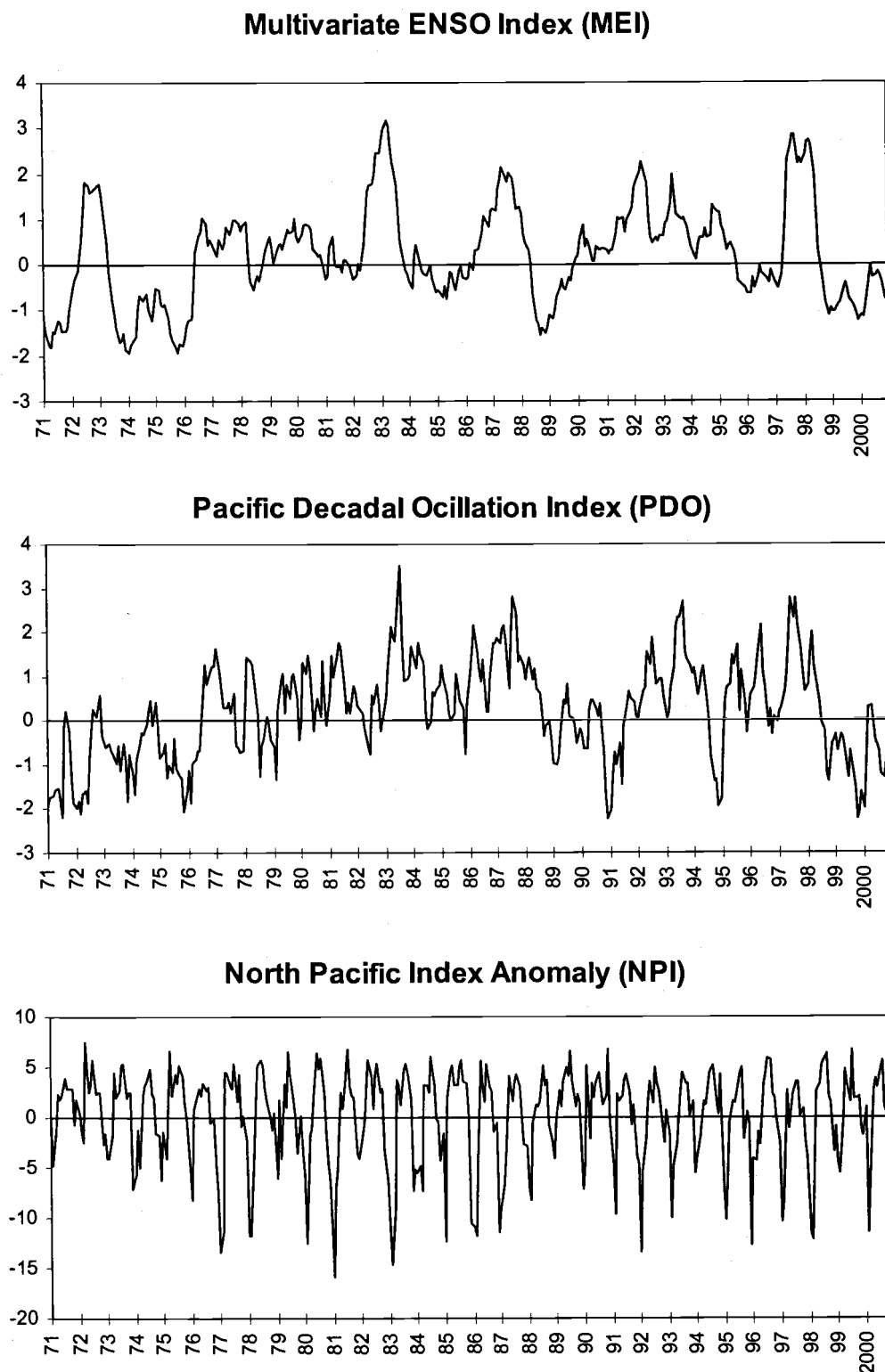


Figure 4.2. continued.

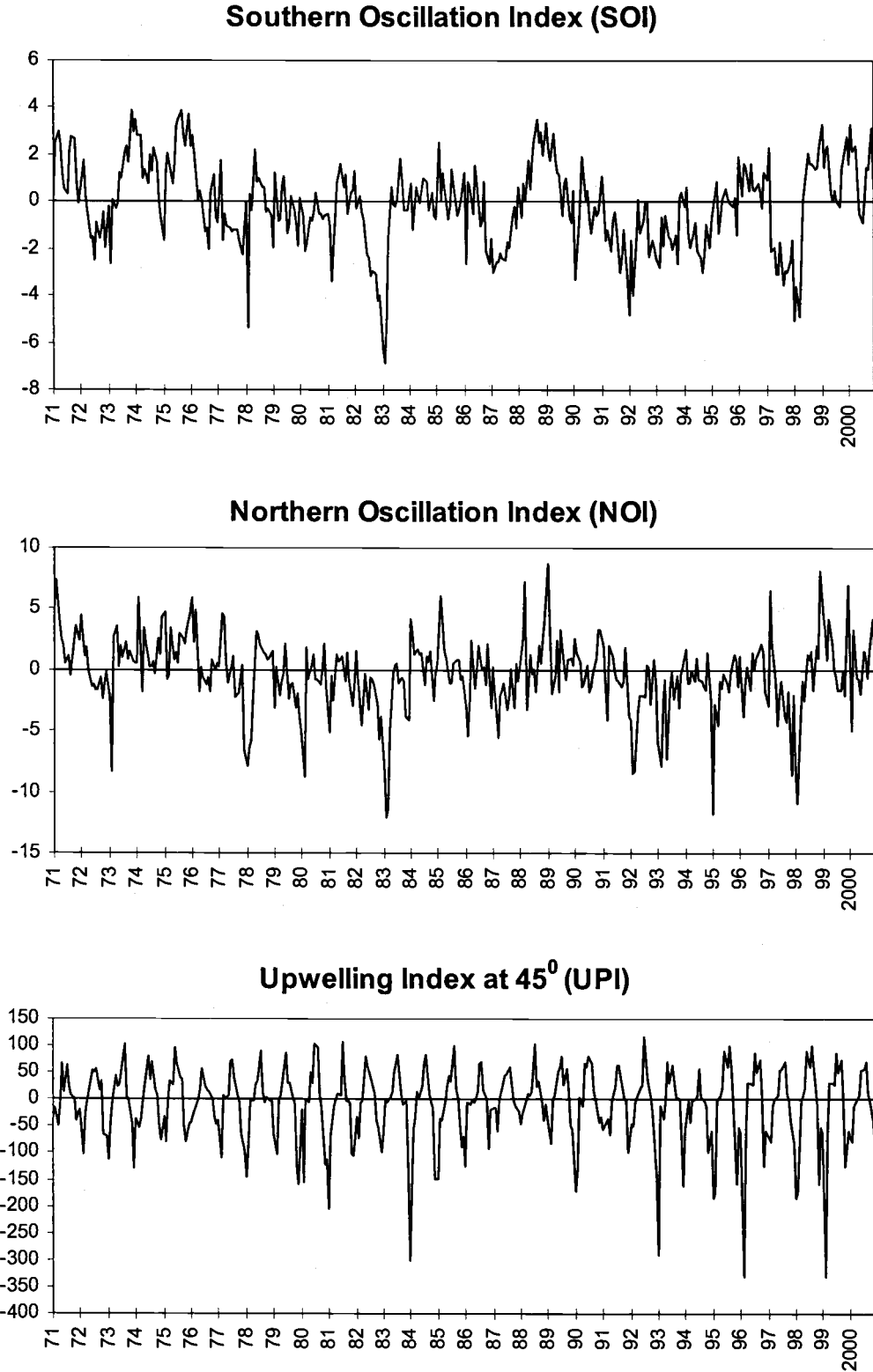


Figure 4.2. continued.

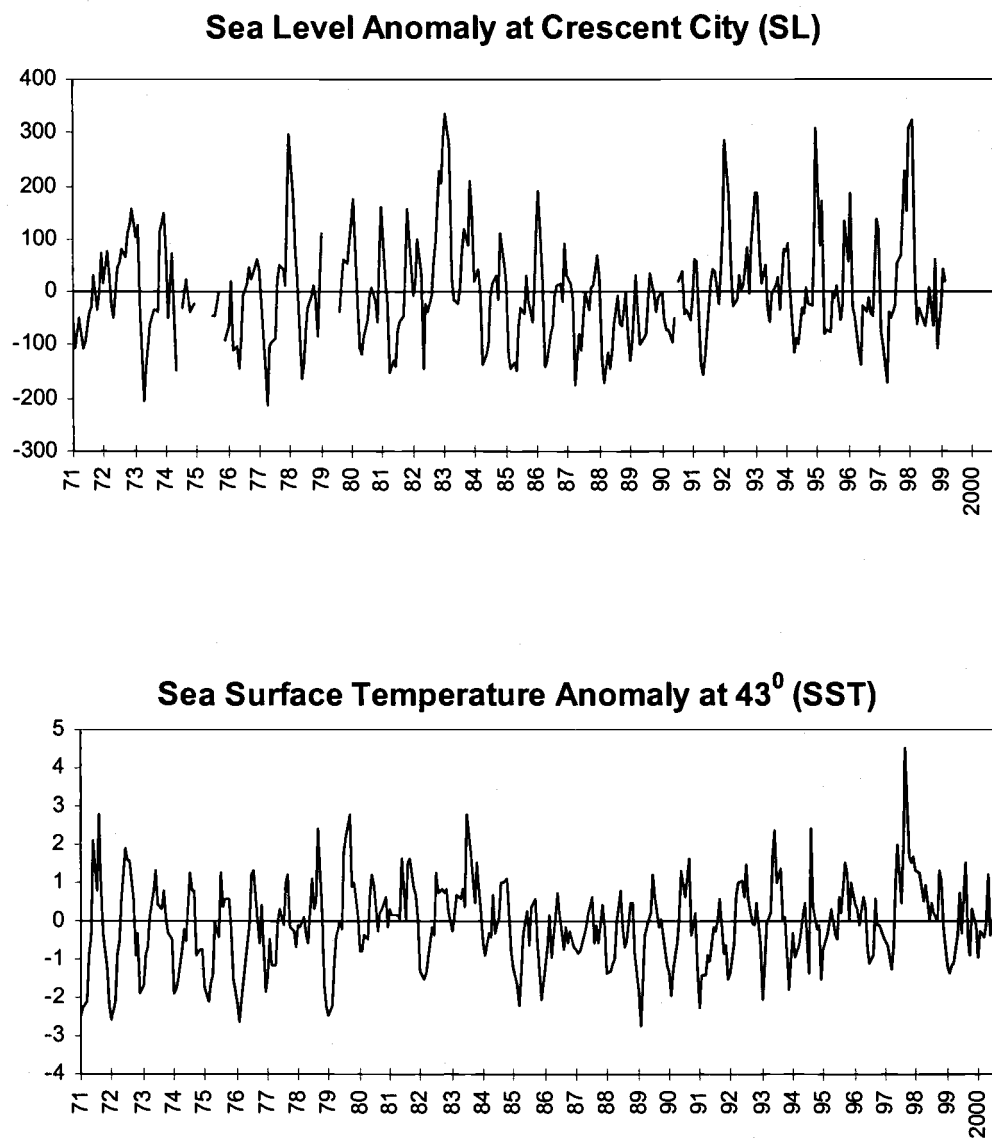


Table 4.1. Pearson correlation coefficients among the environmental variables for different time-scale averages. Insignificant correlations (p -value < 0.05) are omitted. P-values for the correlation coefficients are given in parentheses. (A) Correlations over monthly (upper diagonal section) and quarterly averages (lower diagonal). (B) Correlations over half-yearly period averages (upper diagonal section) and yearly averages (lower diagonal).

(A)

		Monthly							
(df)		MEI (360)	PDO (360)	NPI (360)	SOI (360)	NOI (360)	UPI (360)	SL (323)	SST (357)
Quarterly	MEI (120)		0.547 ($<.0001$)		-0.785 ($<.0001$)	-0.580 ($<.0001$)		0.336 ($<.0001$)	0.284 ($<.0001$)
	PDO (120)	0.587 ($<.0001$)		-0.109 (0.039)	-0.379 ($<.0001$)	-0.330 ($<.0001$)			0.341 ($<.0001$)
	NPI (120)				0.206 ($<.0001$)	0.318 ($<.0001$)	0.636 ($<.0001$)	-0.590 ($<.0001$)	0.250 ($<.0001$)
	SOI (120)	-0.867 ($<.0001$)	-0.453 ($<.0001$)	0.263 (0.003)		0.591 ($<.0001$)		-0.363 ($<.0001$)	-0.177 ($<.001$)
	NOI (120)	-0.694 ($<.0001$)	-0.436 ($<.0001$)	0.349 ($<.0001$)	0.722 ($<.0001$)		0.124 (0.018)	-0.698 ($<.0001$)	-0.249 ($<.0001$)
	UPI (120)			0.898 ($<.0001$)	0.191 (0.037)	0.292 ($<.0001$)		-0.439 ($<.0001$)	0.321 ($<.0001$)
	SL (120)	0.401 ($<.0001$)		-0.616 ($<.0001$)	-0.451 ($<.0001$)	-0.712 ($<.0001$)	-0.603 ($<.0001$)		
	SST (120)	0.326 ($<.001$)	0.384 ($<.0001$)	0.352 ($<.0001$)	-0.229 (0.012)	-0.332 ($<.001$)	0.322 ($<.001$)		

Table 4.1. *Continued.*

(B)

		Half-yearly							
		MEI (60)	PDO (60)	NPI (60)	SOI (60)	NOI (60)	UPI (60)	SL (57)	SST (60)
Yearly	(df)								
	MEI (30)		0.645 (<0.0001)	-0.275 (0.003)	-0.929 (<0.0001)	-0.825 (<0.0001)		0.456 (<0.001)	0.491 (0.0036)
	PDO (30)	0.665 (<0.0001)		-0.353 (0.006)	-0.551 (<0.0001)	-0.614 (<0.0001)			0.374 (0.003)
	NPI (30)	-0.406 (0.006)	-0.696 (<0.0001)		0.276 (0.033)	0.372 (0.003)	0.467 (<0.001)	-0.569 (<0.0001)	-0.452 (<0.001)
	SOI (30)	-0.955 (<0.0001)	-0.592 (<0.001)			0.751 (<0.0001)		-0.395 (0.0024)	-0.405 (0.0013)
	NOI (30)	-0.893 (<0.0001)	-0.715	0.564 (0.0012)	0.836			-0.623 (<0.0001)	-0.646 (<0.0001)
	UPI (30)	-0.370 (<0.0001)	-0.506 (0.004)	0.684 (<0.0001)		0.557 (0.014)		-0.472 (<0.001)	
	SL (29)	0.627 (<0.0001)		-0.368 (0.049)	-0.555 (0.018)	-0.788 (<0.0001)	-0.608 (<0.0001)		0.569 (<0.0001)
SST (30)	0.540 (0.002)	0.522 (<0.0001)	-0.490 (0.006)	-0.433 (0.017)	-0.673 (<0.0001)	-0.648 (<0.0001)	0.656 (<0.0001)		

monthly and quarterly averages but became significant for the half-yearly and yearly averages.

The results of the GLM analyses on the studentized residuals from the non-linear regression for each fish species suggest that there are significant and considerable interactions among temporal (year, month) and geographical (latitude), and biological (sex) factors associated with the variations in growth condition (Table 4.2). The interaction Year*Month was significant for all species, indicating that the pattern of monthly variation in the growth condition indices is not simply maintained from year to year. Similarly, the Month*Sex interaction was also significantly present in all species except petrale sole. This interaction implies that the pattern of monthly variation in growth condition differs by sex. The Year*Latitude interaction was significant for Dover sole, petrale sole, yellowtail, and widow rockfish, which suggests that the pattern of annual change in the growth condition varies geographically for these species. Models with three-way interactions were also tested for all species, but only widow rockfish had a significant three-way interaction (Year*Month*Latitude), which means that growth condition variations for this species are much more complicated than they are for the other fish species considered in this study.

The total variation of the growth condition explained by the models ranges from low ($R^2 = 0.334$ for yellowtail rockfish) to moderate ($R^2 = 0.578$ for petrale sole). Considering the complexity of the models, their relatively poor explanatory power suggests that the growth condition indices are highly variable. It is possible

Table 4.2. Results from GLM analyses of the studentized residuals from the non-linear regression of length-weight data for each fish species.

Dover sole

$R^2 = 0.357$, Total SS = 1983.37, df = 1981

Source	DF	Type III SS	MS	F Value	Pr > F
Year	28	77.617	2.772	3.52	<.0001
Month	11	32.190	2.926	3.72	<.0001
Latitude	2	4.590	2.295	2.92	0.0543
Sex	1	0.447	0.447	0.57	0.4511
Year*Month	240	291.022	1.213	1.54	<.0001
Year*Latitude	45	103.078	2.291	2.91	<.0001
Month*Latitude	22	27.591	1.254	1.59	0.0395
Month*Sex	11	54.352	4.941	6.28	<.0001

Petrale sole

$R^2 = 0.578$, Total SS=817.09, df=813

Source	DF	Type III SS	MS	F Value	Pr > F
Year	25	56.645	2.266	3.7	<.0001
Month	11	59.410	5.401	8.82	<.0001
Latitude	2	2.680	1.340	2.19	0.113
Sex	1	1.089	1.089	1.78	0.1828
Year*Month	164	264.437	1.612	2.63	<.0001
Year*Latitude	31	62.015	2.000	3.27	<.0001
Month*Sex	11	11.970	1.088	1.78	0.0547

Table 4.2. *Continued.***Canary rockfish** $R^2 = 0.371$, Total SS = 976.74, df = 975

Source	DF	Type III SS	MS	F Value	Pr > F
Year	23	62.909	2.735	3.35	<.0001
Month	11	24.716	2.247	2.75	0.0017
Latitude	2	8.481	4.240	5.19	0.0058
Sex	1	0.835	0.835	1.02	0.3124
Year*Month	175	193.274	1.104	1.35	0.0042
Month*Sex	11	21.895	1.990	2.44	0.0055

Yellowtail rockfish $R^2 = 0.334$, Total SS = 1498.34, df = 1497

Source	DF	Type III SS	MS	F Value	Pr > F
Year	19	93.470	4.919	6.19	<.0001
Month	11	44.676	4.061	5.11	<.0001
Latitude	2	10.662	5.331	6.71	0.0013
Sex	1	2.309	2.309	2.91	0.0884
Year*Month	166	214.459	1.292	1.63	<.0001
Year*Latitude	31	60.090	1.938	2.44	<.0001
Month*Sex	11	37.314	3.392	4.27	<.0001

Table 4.2. *Continued.***Widow rockfish** $R^2 = 0.408$, Total SS = 2690.91, df = 2689

Source	DF	Type III SS	MS	F Value	Pr > F
Year	16	174.397	10.900	14.88	<.0001
Month	11	156.011	14.183	19.37	<.0001
Latitude	2	23.244	11.622	15.87	<.0001
Sex	1	3.330	3.330	4.55	0.0331
Year*Month	166	243.371	1.466	2	<.0001
Year*Latitude	32	45.890	1.434	1.96	0.0011
Year*Sex	16	24.980	1.561	2.13	0.0055
Month*Sex	11	101.522	9.229	12.6	<.0001
Year*Month*Latitude	259	242.651	0.937	1.28	0.0029

that other explanatory variables, for which we had no data, would account for some of the unexplained variability. The GLM coefficients of the factors for each fish species are given in Appendix C.

Predicted growth condition indices were calculated based on the GLM for each species. Correlations between the indices by species and sex were tested for each of the four time-scale averages (Table 4.3). There was no particularly strong correlation between different types of species at the monthly scale, but correlations between the sexes within the same species were fairly strong (e.g., $r = 0.901$ for canary rockfish, $r = 0.960$ for petrale sole). These correlations improved at the longer time scales and became perfectly correlated for petrale sole on the half-yearly basis and canary rockfish on the yearly basis.

Correlations in the condition indices between the rockfish species were stronger than the ones between the flatfish. Among the rockfish group, yellowtail and widow rockfish were the most highly correlated, yellowtail and canary rockfish were moderately correlated, and canary and widow rockfish were the least correlated. For the correlations between the rockfish and flatfish groups, petrale sole were more highly correlated with the rockfish than dover sole were. The generally low correlations in the condition indices between the species even within the same species group suggest that the variations in fish growth condition are not synchronous across the fish species as would occur if the different species were reacting in common to an environmental factor. Because of the close relationship

Table 4.3. Pearson correlation coefficients among the fish species for different time-scale averages. Insignificant correlations (p -value < 0.05) are omitted. P-values for the correlation coefficients are given in parentheses. Next to the species acronyms, "M" denotes the males and "F" denotes the females. (A) Correlations over monthly (upper diagonal section) and quarterly averages (lower diagonal). (B) Correlations over half-yearly (upper diagonal section) and yearly averages (lower diagonal).

(A)

		Monthly									
Quarterly	(df)	DOV.M (348)	DOV.F (348)	PET.M (312)	PET.F (312)	CAN.M (288)	CAN.F (288)	YEL.M (241)	YEL.F (241)	WID.M (204)	WID.F (204)
	DOV.M (116)		0.848 (<0.0001)	0.160 (0.0047)	0.196 (0.0005)						0.157 (0.0246)
	DOV.F (116)	0.872 (<0.0001)								-0.156 (0.0259)	
	PET.M (104)	0.374 (<0.0001)	0.205 (0.037)		0.960 (<0.0001)				0.142 (0.0371)		0.259 (0.0005)
	PET.F (104)	0.387 (<0.0001)	0.225 (0.0216)	0.994 (<0.0001)					0.180 (0.0077)		0.300 (<0.0001)
	CAN.M (96)						0.901 (<0.0001)				
	CAN.F (96)	0.225 (0.0272)		0.266 (0.0146)	0.265 (0.015)	0.946 (<0.0001)			0.205 (0.0014)		0.184 (0.0086)
	YEL.M (81)					0.284 (0.0102)	0.259 (0.0197)		0.886 (<0.0001)	0.385 (<0.0001)	0.255 (0.0004)
	YEL.F (81)			0.270 (0.021)	0.275 (0.0185)	0.286 (0.0097)	0.384 (0.0004)	0.897 (<0.0001)		0.165 (0.022)	0.379 (<0.0001)
	WID.M (68)							0.535 (<0.0001)	0.247 (0.049)		0.760 (<0.0001)
	WID.F (68)			0.378 (0.0029)	0.346 (0.0068)		0.316 (0.0087)	0.387 (0.0016)	0.506 (<0.0001)	0.709 (<0.0001)	

Table 4.3. *Continued.*

(B)

Half-yearly											
	DOV.M (58)	DOV.F (58)	PET.M (52)	PET.F (52)	CAN.M (48)	CAN.F (48)	YEL.M (41)	YEL.F (41)	WID.M (34)	WID.F (34)	
Yearly	DOV.M (29)	0.964 ($<.0001$)	0.318 (0.0214)	0.321 (0.0203)		0.289 (0.0467)					
	DOV.F (29)	0.964 ($<.0001$)									
	PET.M (26)	0.431 (0.0281)	0.431 (0.0281)	1.000 ($<.0001$)		0.392 (0.0103)		0.367 (0.0255)		0.485 (0.0066)	
	PET.F (26)	0.431 (0.0281)	0.431 (0.0281)	1.000 ($<.0001$)		0.397 (0.0093)		0.370 (0.0243)		0.490 (0.006)	
	CAN.M (24)					0.850 ($<.0001$)	0.349 (0.0253)				
	CAN.F (24)				1.000 ($<.0001$)		0.334 (0.0327)	0.478 (0.0016)		0.374 (0.0295)	
	YEL.M (21)				0.446 (0.0426)	0.446 (0.0426)		0.948 ($<.0001$)	0.595 (0.0003)	0.641 ($<.0001$)	
	YEL.F (21)				0.480 (0.0275)	0.480 (0.0275)	0.985 ($<.0001$)		0.424 (0.0156)	0.754 ($<.0001$)	
	WID.M (17)						0.650 (0.0064)	0.650 (0.0064)		0.727 ($<.0001$)	
	WID.F (17)						0.712 (0.002)	0.712 (0.002)	0.862 ($<.0001$)		

between the sexes within a species, the sexes were combined for the time series plots and for the correlation analyses with the environmental variables.

Time series plots of the monthly predicted growth condition indices did not show distinctive trends over time (increasing or decreasing) for any of the fish species, even though substantial variations are evident from year to year (Figure 4.3). Interestingly, no species appears to have responded to the strong El Niño of 1997/98, except possibly Dover sole. However, the condition index for this species during 1997/98 was not exceptionally low compared to other low condition index values in the series. Also, the index for Dover sole did not seem to respond to the 1983 El Niño. The index for canary rockfish seems to have responded to the 1983 El Niño but not to the 1997/98 event. The timing of low dips and high peaks are not consistent across the species. For example, the lowest condition index value for yellowtail rockfish was between 1988 and 1989, but no other species have particularly low values during this period. In contrast, Dover sole and widow rockfish both had positive condition index values during the time period. As suggested by the correlation analyses between the species, synchrony of variations in the condition indices across the species and their responsiveness to unusual oceanographic events are not particularly evident or consistent.

The predicted monthly growth condition indices by species and sex were averaged across the years and other factors to show the seasonal patterns of growth condition (Figure 4.4). These seasonal patterns may reflect the reproductive cycle of the species. Most species tend to have a positive condition index during summer

Figure 4.3. Monthly time series of the predicted growth condition indices of the fish species. The thick solid line represents the 5-month running average of the time series.

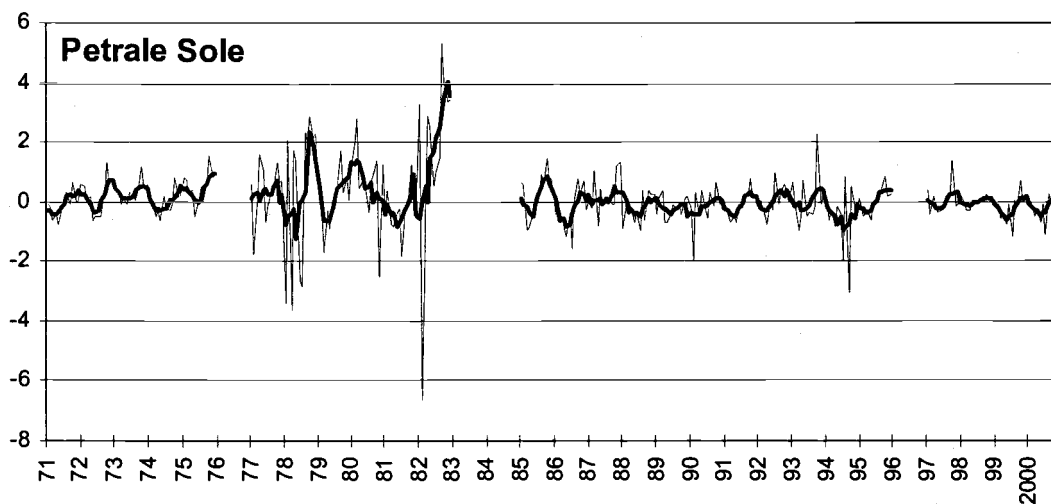
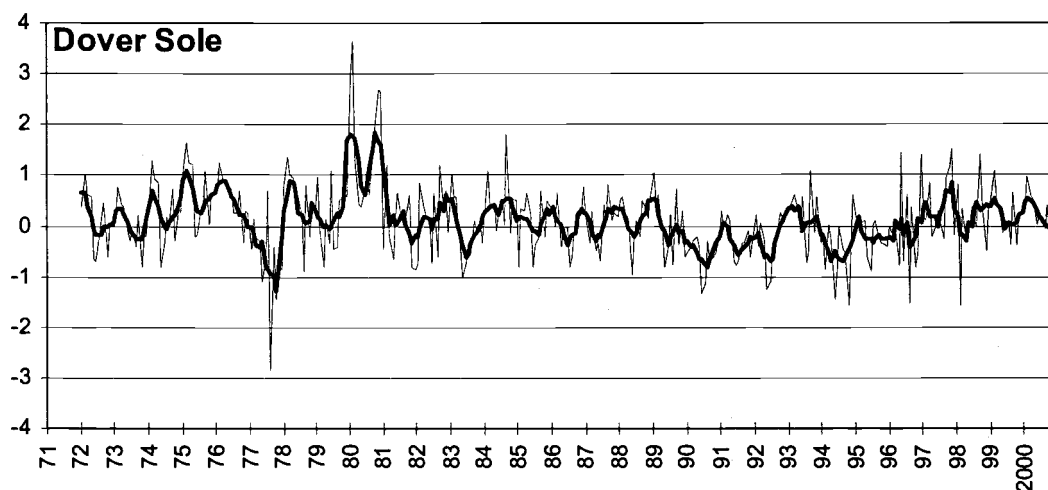


Figure 4.3. Continued.

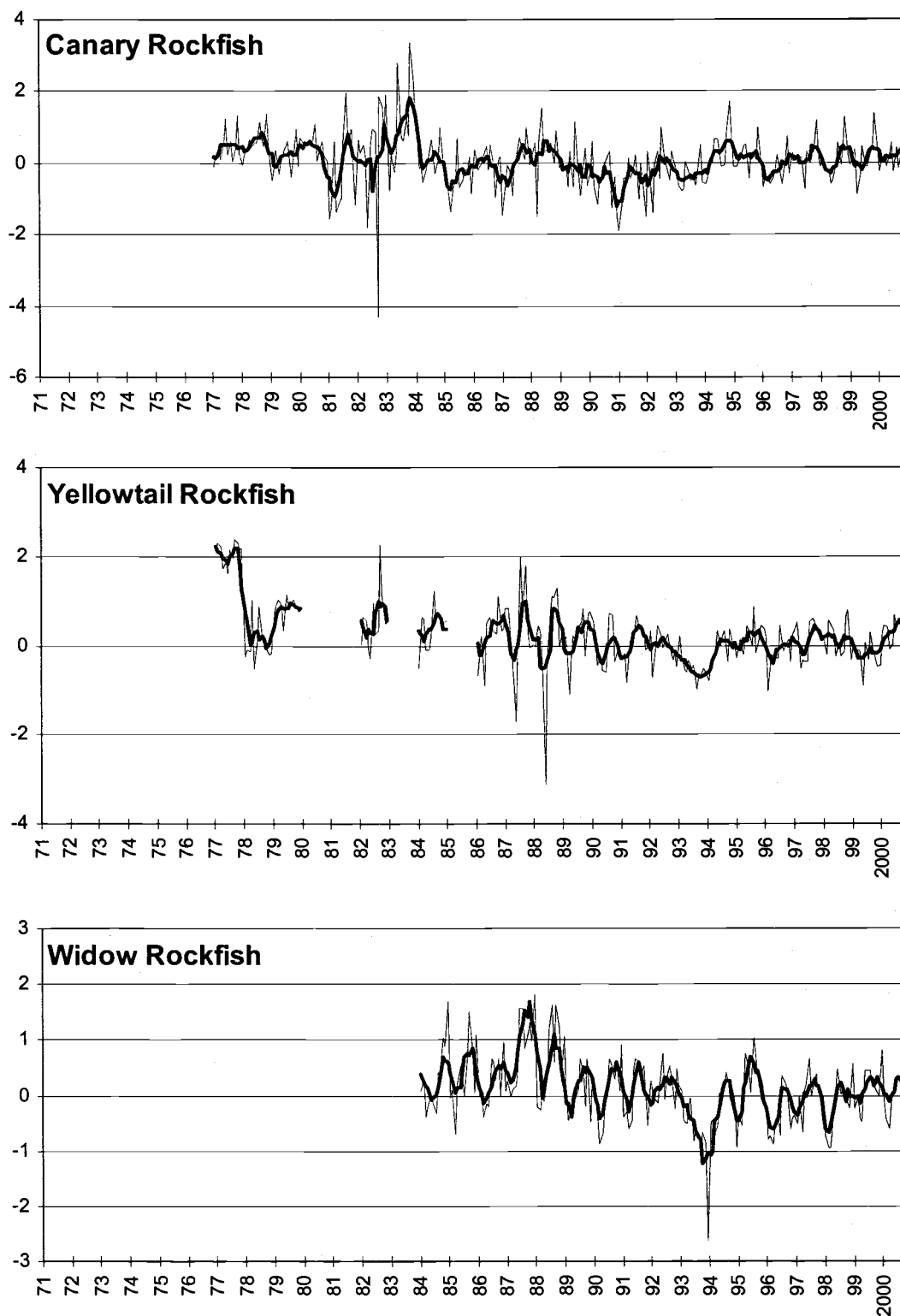


Figure 4.4. Average monthly condition factors for each fish species by sex. The solid lines represent the females and the broken lines the males.

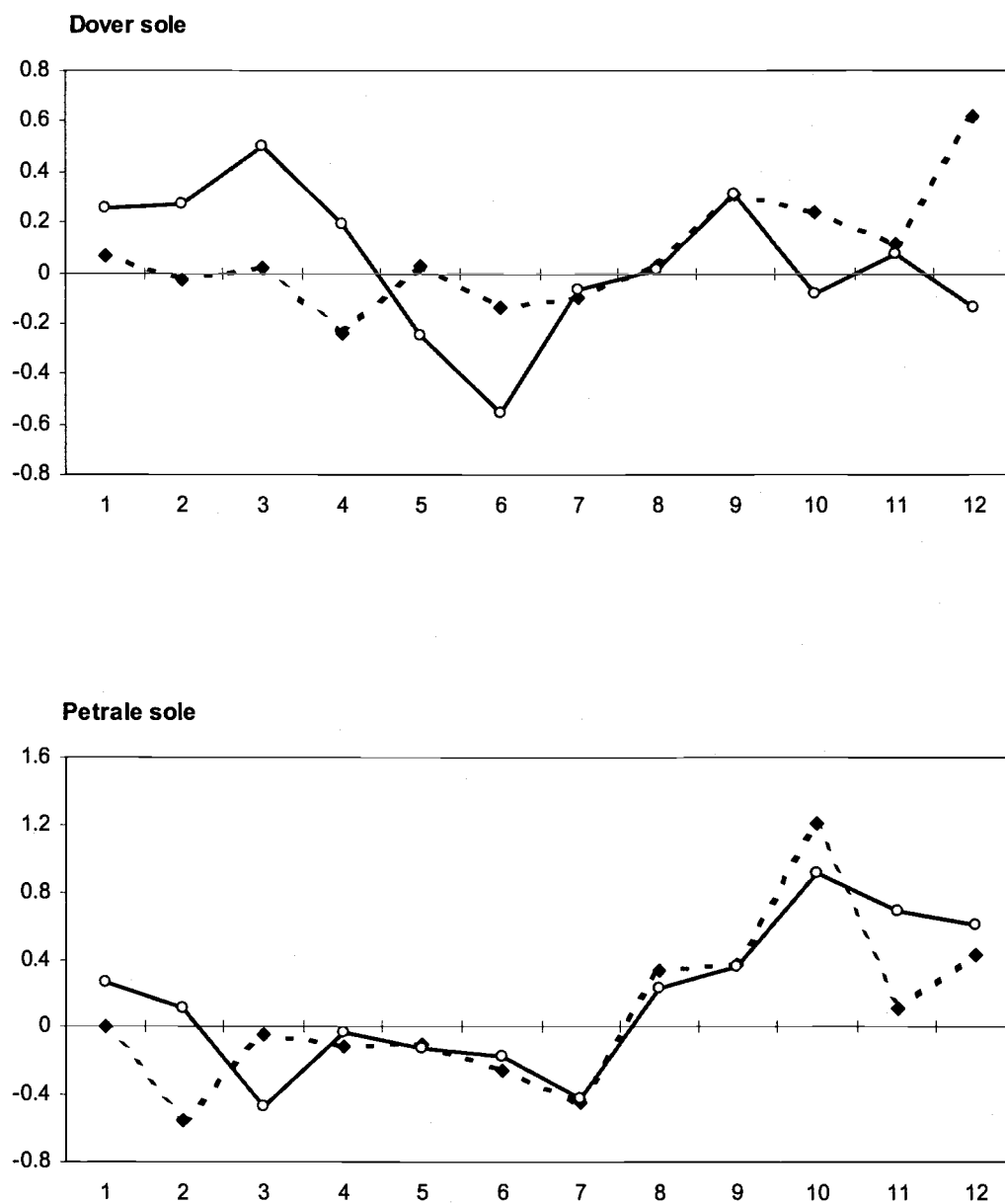
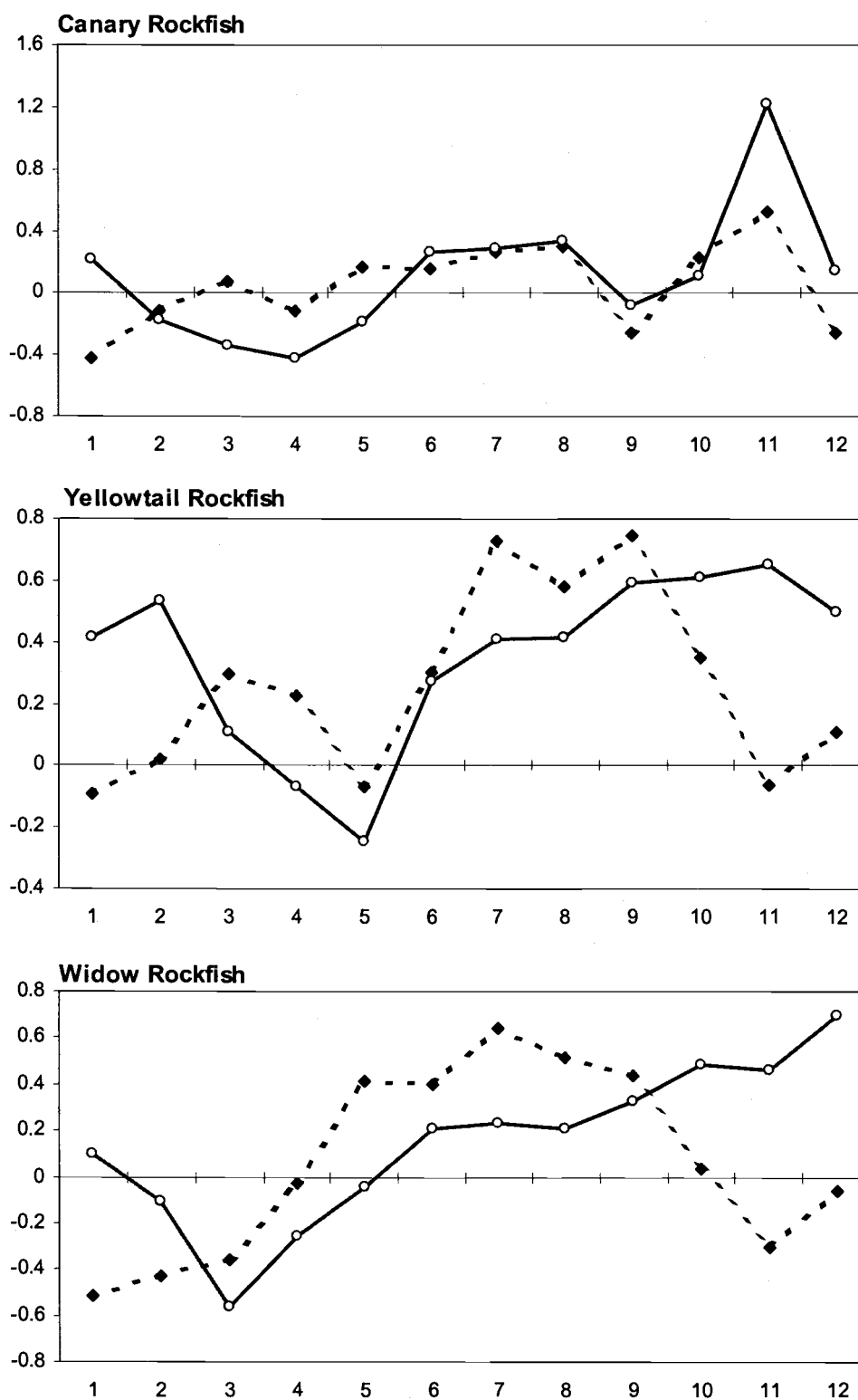


Figure 4.4. Continued.



through fall (even into the winter for some species) that then declines from winter through spring. Other studies have shown that all five species spawn during the winter. Peak spawning is during December through February for Dover sole off Northern California (Hagerman 1952) and is probably similar for the fish off Oregon. Petrale sole off Oregon spawn during December and January (Sampson and Lee 1999). The rockfish species examined in this study have a spawning season during winter (November-March) according to a coast-wide survey (Echeverria 1987).

Among the rockfish group, the indices for yellowtail and widow rockfish show an interesting pattern for the males versus the females. The indices for the females maintain positive index values for a few months after the start of the declines in the male condition index. This may reflect differences in the male versus female reproductive cycles and the viviparous feature of rockfish reproduction. During the spawning season in the fall males inseminate the females, consequently resulting in depletion of the males' gonads and reduction in their weight, but the females keep developing their fertilized ovaries for several months through the embryogenesis and gestation periods until extruding the larvae. In contrast to the pattern shown by yellowtail and widow rockfish, canary rockfish shows substantially less monthly variation in the condition index and a relatively short peak period in winter. Also, there is much less of a difference in the pattern between the males and females.

While the other species show only one annual cycle of increase and decrease in the growth condition indices, for Dover sole the indices seem to have two peaks, one in spring and the other in fall. The male and female petrale sole have concurrent monthly patterns of development in growth condition.

The growth condition indices of the five species were not strongly correlated with the environmental variables over the four different time-scales examined, although the degree of correlation improved at the longer time-scales (Table 4.4). On the monthly scale the index for Dover sole was correlated with more environmental variables (five out of eight variables) than the other species, but the correlations were very weak. Other species' correlations with the environmental variables were not particularly noteworthy. On the quarterly scale, the Dover sole index was negatively correlated with MEI and SST, and positively with SOI, suggesting that warming episodes may suppress the growth condition of this species. However, the strengths of the correlations were still too weak to draw a meaningful conclusion. The index for widow rockfish was positively correlated to a low degree with the NPI and UPW variables, which are closely related with local productivity. This may suggest that the growth condition of widow rockfish would be more responsive to the enhanced production in the area than the other species.

At the half-yearly scale, the indices for canary rockfish and petrale sole were significantly correlated with environmental variables that were not evident at the shorter time scales: NPI, UPW, and SL for petrale sole; and NPI, SL, and SST for canary rockfish. The Dover sole index was correlated with MEI and SOI, as in the

Table 4.4. Pearson correlation coefficients between the condition indices and environmental variables over the different time scale averages: monthly, quarterly, half-yearly period, and yearly. P-values for the correlation coefficients are given in the parentheses. The significant coefficients (p-value < 0.05) are underlined.

Monthly					
(df)	DOV (348)	PET (312)	CAN (288)	YEL (241)	WID (204)
MEI	<u>-0.170</u> (0.001)	0.094 (0.09)	0.007 (0.906)	0.074 (0.252)	-0.045 (0.527)
PDO	<u>-0.139</u> (0.009)	-0.003 (0.951)	-0.013 (0.825)	-0.047 (0.464)	0.018 (0.802)
NPI	<u>-0.111</u> (0.039)	-0.042 (0.45)	0.053 (0.372)	0.018 (0.781)	<u>0.204</u> (0.003)
SOI	<u>0.156</u> (0.004)	<u>-0.115</u> (0.039)	0.012 (0.842)	-0.100 (0.122)	0.039 (0.575)
NOI	0.084 (0.12)	-0.039 (0.48)	-0.037 (0.53)	0.016 (0.8)	0.119 (0.091)
UPI	-0.095 (0.076)	-0.046 (0.413)	0.005 (0.938)	0.103 (0.11)	<u>0.281</u> (<0.0001)
SL	0.085 (0.134)	<u>0.147</u> (0.013)	0.091 (0.145)	0.016 (0.816)	<u>-0.167</u> (0.024)
SST	<u>-0.174</u> (0.001)	0.028 (0.611)	<u>0.198</u> (0.001)	0.078 (0.229)	0.138 (0.051)

Table 4.4. *Continued.*

Quarterly					
(df)	DOV (116)	PET (104)	CAN (96)	YEL (81)	WID (68)
MEI	<u>-0.217</u> (0.019)	0.134 (0.168)	0.018 (0.863)	0.079 (0.484)	-0.043 (0.726)
PDO	-0.173 (0.064)	-0.040 (0.681)	-0.009 (0.933)	-0.021 (0.855)	0.031 (0.804)
NPI	-0.164 (0.079)	-0.053 (0.589)	0.018 (0.859)	0.031 (0.784)	<u>0.304</u> (0.012)
SOI	<u>0.216</u> (0.02)	-0.142 (0.143)	0.056 (0.586)	-0.112 (0.32)	0.056 (0.652)
NOI	0.109 (0.242)	-0.017 (0.865)	-0.057 (0.579)	0.042 (0.707)	0.136 (0.269)
UPI	-0.130 (0.165)	-0.087 (0.373)	0.004 (0.972)	0.099 (0.379)	<u>0.420</u> ($<.0001$)
SL	0.094 (0.336)	0.162 (0.111)	0.175 (0.104)	0.051 (0.668)	-0.226 (0.08)
SST	<u>-0.222</u> (0.017)	0.011 (0.913)	<u>0.267</u> (0.009)	0.099 (0.382)	0.154 (0.215)

Table 4.4. *Continued.*

Half-yearly					
(df)	DOV (58)	PET (52)	CAN (48)	YEL (41)	WID (34)
MEI	<u>-0.320</u> (0.014)	0.195 (0.157)	0.040 (0.789)	0.080 (0.62)	-0.033 (0.854)
PDO	-0.204 (0.124)	-0.030 (0.827)	0.018 (0.902)	-0.072 (0.657)	0.048 (0.788)
NPI	-0.070 (0.603)	<u>-0.329</u> (0.015)	<u>-0.310</u> (0.032)	-0.172 (0.283)	-0.261 (0.137)
SOI	<u>0.343</u> (0.008)	-0.223 (0.105)	0.003 (0.983)	-0.104 (0.516)	0.096 (0.589)
NOI	0.265 (0.045)	-0.143 (0.304)	-0.201 (0.171)	0.043 (0.789)	0.210 (0.233)
UPI	-0.011 (0.933)	<u>-0.373</u> (0.005)	-0.104 (0.483)	-0.009 (0.954)	0.196 (0.265)
SL	-0.013 (0.928)	<u>0.448</u> (0.001)	<u>0.407</u> (0.006)	0.083 (0.622)	-0.092 (0.617)
SST	-0.185 (0.164)	0.121 (0.385)	<u>0.382</u> (0.008)	0.056 (0.73)	-0.122 (0.493)

Table 4.4. *Continued.*

(df)	Yearly				
	DOV (29)	PET (26)	CAN (24)	YEL (21)	WID (17)
MEI	-0.332 (0.078)	0.189 (0.344)	0.200 (0.348)	0.095 (0.683)	-0.028 (0.916)
PDO	-0.253 (0.186)	0.009 (0.966)	0.178 (0.407)	-0.017 (0.942)	0.163 (0.532)
NPI	0.019 (0.921)	0.142 (0.481)	-0.400 (0.053)	-0.080 (0.731)	-0.109 (0.677)
SOI	0.361 (0.055)	-0.227 (0.255)	-0.093 (0.667)	-0.131 (0.573)	0.083 (0.751)
NOI	0.233 (0.224)	-0.212 (0.289)	-0.306 (0.146)	0.050 (0.831)	0.224 (0.387)
UPI	0.206 (0.284)	0.189 (0.344)	0.243 (0.252)	0.186 (0.419)	<u>0.612</u> (0.009)
SL	-0.087 (0.661)	0.190 (0.352)	<u>0.452</u> (0.03)	-0.126 (0.595)	-0.452 (0.079)
SST	-0.203 (0.29)	-0.028 (0.888)	<u>0.458</u> (0.024)	-0.008 (0.973)	-0.266 (0.303)

case of the quarterly average. For the yearly averages, there were only a few combinations that were significantly correlated, but the correlation levels were higher than at the short time intervals. The widow rockfish index was fairly well correlated with UPW ($r = 0.612$) and the canary rockfish index (CAN) with SL ($r = 0.452$) and SST ($r = 0.458$). It is interesting to note that CAN was positively correlated with SST, because we would expect growth to be suppressed with higher temperatures, which are generally indicative of poor upwelling and low oceanic productivity in the region. The index for yellowtail rockfish was not correlated with any of the environmental variables at any of the time scales, but this could be due to the larger number of gaps in the data series for this species.

On the whole, it appears that the growth condition index for Dover sole compared to the other species is more closely correlated with environmental variables that are indicators of warming episodes and El Niño events, like MEI and SOI. In contrast, the growth condition for petrale sole, canary rockfish, and widow rockfish are more sensitive to variables associated with local production, like NPI, UPW, and SL.

DISCUSSION

The environmental conditions in the Northeast Pacific Ocean have different temporal scales of fluctuation, from high frequency fluctuations with time scales of a few years to low frequency fluctuations with decade or longer time scales. The El

Niño phenomenon is an example of a relatively high frequency periodic ocean event that occurs with a periodicity of several years (Ware 1995). Decadal alternations of cool and warm conditions in the NE Pacific are an example of a low-frequency variation in the ocean environment. These different scales of climate variation have varying levels and duration of impact on marine biological systems. Studies have shown that in 1976 there was an abrupt regime shift to generally warmer atmospheric and ocean environments in the Pacific (Ebbesmeyer et al. 1991). As mentioned in introduction section, this warming period coincided with decreases in mean length-at-age for some fish species in the Northeast Pacific, including Pacific halibut, Pacific herring, the Pacific salmon species, and Pacific hake. This evidence of changes in growth in terms of length-at-age leads one to expect similar changes in the weight-length relationship (growth condition).

In this study, temporal changes in the growth condition of three rockfish species and two bottom-dwelling flatfish species were examined using existing market sample data. The results showed no particular long-term temporal trend in the growth condition indices, although substantial seasonal and interannual variations were detected. Also, the response of the indices to the unusual oceanographic events of El Niño was inconsistent from species to species and from event to event. A previous study on the growth history of two rockfish species, canary (*S. pinniger*) and splitnose rockfish (*S. diploproa*), covering a period of several decades, did not find any temporal trends in growth (Boehlert et al. 1989). Their study developed information about growth history by examining increments in the fish otoliths.

Significant interannual variations in growth were detected but no clear associations were found, which is similar to the findings in this study. Thus, it is not unusual that growth is maintained for long time periods while being apparently unresponsive to environmental factors.

There could be several possible explanations for the lack of long-term trends in growth condition and for the lack of any close association between the variation of growth condition indices and environmental variables. One is that a decrease in average size does not necessarily reflect a decrease in condition. Fish growth in size is one component in the partitioning of surplus energy. There are other physiological components in the context of a fish's energy budget (Jobling 1994). Energy expenditures are largely divided into three main categories: maintenance metabolism, reproductive growth, and somatic growth. Maintenance metabolism includes basic bodily functions, activity, digestion, and absorption. The energy gained from foods is allocated to different functions according to the priorities of the body's requirements. The intake of energy must at least equal the energy used for maintenance metabolism to sustain the current condition. The reproductive and somatic growth take place when excess energy is available after satisfying body maintenance. Somatic growth may be sacrificed for current reproductive needs. Thus, fish condition could be maintained even when the fish would not be able to spare energy for reproduction or body growth. The loss of body weight does not occur until the previously acquired energy, stored in a form of the body tissues, is metabolized because the energy intake is not sufficient for basic maintenance. This

may explain the lack of temporal trends in growth condition of the examined species, even though there is evidence of decreases in mean length-at-age for other species during the same period. However, long-term changes in the length-at-age of the species considered in the current study have not been reported in the literature or identified in stock assessment documents. It is not possible to state conclusively that reductions in size-at-age occurred in these species as in others.

Compensatory growth (Nicieza and Metcalfe 1997; Russell and Wootton 1992) is another possible explanation for the lack of a trend in the growth condition and for no clear relationship between condition and environmental factors. When conditions for feeding are poor, the growth trajectory deviates from normal. However, fish growth is restored rapidly on a return to adequate feeding conditions. During this recovery period, the rate of weight gain is faster than the normal growth trajectory of individuals that were able to continually feed. Sometimes, over-compensation in growth results in the maintenance of a high growth rate even after the normal growth trajectory is achieved. In the wild it is not unusual to observe periodic fluctuations in the food supply. Due to the ability for compensatory growth, fish could recover quickly from poor feeding conditions and suffer no long-term damage in growth condition.

The behavior of the fish could also reduce the risk of continued poor growth condition (Jobling 1997). Metabolic and ingestion rates have a close relationship with temperature. When food is available, fish could prefer warmer waters within thermal their range and obtain higher metabolism and ingestion rates and better

growth. However, during periods of limited food supplies, the fish could migrate to colder water where energetic costs are minimized after the completion of feeding. This type of behavioral response to the thermal environment could help the fish maintain their growth condition during the periods of low food abundance (Olla and Davis 1990; Sogard and Olla 1996).

The relative proportions of proteins, lipids, carbohydrates, and water in a fish's body for a given weight varies with feeding conditions and the levels of food supply (Boisclair and Leggett 1989a, 1989b). This aspect of dynamic change in body composition means that the simple measurement of length-specific weight alone as a condition index would not completely represent the status of growth or health condition of the fish because the composition of the fish body might not be constant, even though the fish's weight remains unchanged. Other types of condition indices such as RNA/DNA ratios of the liver and muscle, caloric values of fish tissues, and protein-energy ratio may better represent the growth condition, but they require time-consuming laboratory analysis (Bogler et al. 1989). Furthermore, long-term collection of fish tissue samples is uncommon.

Seasonal variability in growth condition was clearly evident in all the species. Seasonal variability in condition is due to the annual cycle of acquisition and depletion of energy reserves, and it is closely associated with the reproductive cycle (LeCren 1951). The seasonal cycles of fat deposition and depletion in rockfish species are concurrent with the timing of gonad development and spawning seasons (Guillemot et al. 1985). The seasonal cycles of the predicted condition indices of

rockfish species (Figure 4.4) generally agree with the cycles of visceral and gonadal fat volumes reported by Guillemot et al (1985) and the seasonality of reproduction reported by Echeverria et al. (1987). The study of Guillemot et al. on gonad volume also showed that the male gonadal volume peaks in fall and female peaks in winter for yellowtail and widow rockfish. This timing difference between the male and female for yellowtail and widow rockfish was also evident in the seasonal condition indices examined in this current study. Thus, the seasonal changes in condition apparently reflect the seasonal accumulation and elimination of energy as well as development of the gonads. The agreement between the seasonal condition cycles found in this study and the seasonal fat deposition and reproduction cycles found in other studies validates the methodology used in the current study for measuring the condition.

The lack of long-term trends in growth condition based on the length-weight relationship or a historic record in the body parts (e.g., otoliths) does not necessarily imply the stable long-term reproductive condition of the fish. Maintenance of growth condition can occur to the detriment of reproductive growth (Wootton 1979). Thus, it is possible that these rockfish and flatfish species experienced varied reproductive performance, while maintaining long-term growth conditions. When food supplies are low, iteroparous species may not be able to reproduce every year and the spawning proportion of a population may decline (Wootton 1984). The quality of eggs may also be influenced by the poor feeding conditions of the parental stocks. Reduction in egg size and fecundity has been reported for Pacific salmon species,

but monitoring of the fecundity, egg size, and egg quality of the commercial flatfish and rockfish species has not been conducted off the U.S. west coast. These reproductive factors may have important roles in the success and variability of recruitment. The examination of the life history parameters associated with the reproduction system might provide more sensitive indications of growth condition as well as recruitment potentials. For future research, monitoring of long-term growth condition and reproductive condition of commercially important species is recommended.

CHAPTER 5: SUMMARY

Marine organisms continuously face the changes in the environments and have to cope with the those environmental variations that directly and indirectly influence their life history traits; survival, growth, reproduction, etc. In this study food habits and growth condition of some groundfish species off Pacific Northwest were examined to understand the possible oceanographic effects on those life history characteristics of the species. With strong seasonal and interannual variations in the ocean environment of the region, it was expected to observe a certain changes in the food habits and growth condition.

For the food habit study, the stomach samples of three co-occurring rockfish species, yellowtail rockfish (*Sebastes flavidus*), widow rockfish (*S. entomelas*), and canary rockfish (*S. pinniger*), were seasonally collected off Oregon from spring of 1998 to fall of 1999. During the study period, the pacific ocean has experienced anomalous ocean events, El Nino and La Nina. For the growth condition study, the two flatfish species, Dover sole (*Microstomus pacificus*) and petrale sole (*Eopsetta jordani*) along with those three rockfish species were examined. These groundfish are highly valuable commercial species off Pacific Northwest.

S. flavidus and *S. entomelas* showed broader diet spectrums and much greater seasonal variations than *S. pinniger*. The major prey items for *S. flavidus* were euphausiids, fish, and salps. *S. entomelas* prey mostly on jellyfishes and salps but

less on fish species. While *S. flavidus* and *S. entomelas* seasonally changed their diets possibly due to the availability of prey items, interestingly *S. pinniger* preyed almost exclusively on euphausiids species over the seasons. This may indicate that these rockfish species have evolved to segregate themselves from each other by having different feeding habits so that they can co-exist in the same habitat.

Signature of El Nino was found in the diets of all three rockfish species as unusual southern zooplankton species, a euphausiids (*Nyctiphanes simplex*) and juvenile whiting (*Merluccius productus*). *S. flavidus* was more dependent on the jellyfishes during the summer of 1998 (El Nino year) than during the summer of 1980 (Non- El Nino year). The unusual dominance of jellyfishes in the diet of *S. flavidus* during summer of 1998 may be because of the jellyfish blooms caused by El Nino event in 1997/98.

Oregon market sample data were used to develop time series of growth condition indices for the past several decades. Analysis of market sample data required a unique type of non-linear regression to extract the growth condition of fish species based on the length-weight data because the market sampling program measure the length in individual basis but the weight in aggregated basis. Chapter 3 was devoted to test the performance of non-linear regression on the accuracy of estimators from aggregated length-weight data using Monte-Carlo simulation approach. The applicability of the method in detecting the changes in parameter values over time was also investigated. It is found that the accuracy of estimators from

the non-linear regression improve with increase in sample size, and the method is sensitive enough to detect the small changes in parameter values over time.

The time series of growth condition indices for the five groundfish species that were developed based on the market sample and the non-linear regression method did not exhibit a particular long-term trend, though showed substantial seasonal and interannual variations over the time period. The responsiveness to the strong El Nino events in 1983 and 1997 was not consistent from species to species and the synchrony in the condition variations over the study period was not evident even among the similar fish species (e.g., rockfish species). The lack of consistency and the lack of synchrony between the species indicate that each species have different ways of responding to the environmental variations because of different life history characteristics although they co-occur and occupy similar habitats. These differences may be due to the difference in the food habits. As found in chapter 2, each rockfish species seems to have different food preferences. Because of different food preferences and feeding habits, it's possible that changes in the zooplankton populations in a certain time period would not necessarily influence those fish species in a same manner.

The reduction in the length-at-age of species, pacific halibut, pacific herring, pacific whiting, and pacific salmon species, were reported in other studies corresponding to the warming period since the regime shift in 1976. Although the variation in the length-at-age of the groundfish species examined in this study have not been established, the negative influence of the regime shift on the growth

condition was expected. However, long-term trend in growth condition was not evident over the examined time period. Possible reasons for the lack of long-term trend in growth condition were discussed in chapter 4. The examined fish species in this study are higher trophic level organisms with deepwater habitat and comparatively high longevity. Deepwater condition is more stable than the upper ocean and often is not subject to the influence of the variations in the upper ocean or atmospheric environments. Higher trophic level and long-lived organisms are generally better equipped with life history characteristics to endure the environmental variations than the lower trophic level organisms. These would be the reasons for the lack of long-term trend and the lack of associations with environmental variables of upper ocean. Lack of long-term trend may be solely due to the short time coverage of data. Data for the rockfish species were available after the regime shift in 1976. Thus it's possible that data series were not long enough to reveal the long-term trend associated with regime shift. Also if the nature of long-term growth condition variability has a low frequency, more than several decadal time series data would be needed to detect such a variability. It is recommended to reexamine the growth condition of these species as data are accumulated more in the future. The study on the growth condition of those species that have reportedly undergone the reduction in length-at-age is also suggested.

The differences in the food habits of those examined rockfish species would bear the different sustainability and rebounding ability from the human exploitation and anomalous ocean variations. Although *S. pinniger* had consistent feeding on

euphausiids over the seasons, growth condition in terms of length-weight relationship did not seem to be affected. As mentioned in chapter 2, studies reported the 5-fold decrease in abundance of euphausiids populations off the southwest Vancouver Island since early 1990s. Population level of euphausiids off Oregon is not known during that period. However, stable growth condition of *S. flavidus* may suggest that either the euphausiids populations did not declined off Oregon, or declined to similar level of the northern populations but the declined level did not limit the feeding of the predator species. Further investigation on the food habits of the this fish species along with temporal monitoring on prey species populations is necessary to understand the relationship between food habits and dynamics of prey populations, and its influence on the predator population health condition.

Stable growth condition of a fish species based on the length-weight relationship does not always suggests whether the fish population is in good health as discussed in chapter 4. Other life history components of fish species must be examined; fecundity, proportion of spawning, egg quality, and other types of growth condition indices. Only the long-term data collection on these variables enables the scientists to investigate on the long-term variations in the life history parameters and to understand their relationships with other environmental variables. However, long-term data series collection is time-consuming and expensive. For these reasons, fisheries managers and scientists must closely examine the current existing sampling programs to explore the possibility of adding or modifying the sampling plans to monitor more information on the fish biology, within the boundaries that the

modifications do not hinder the primary purposes of the sampling. Because as our understanding improve on the biology of fish and its interaction with environments, we will be able to develop better fishery management plans.

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APPENDICES

Appendix A. GLM coefficients for PCA axes.

GLM coefficients of PCA Axis 1 from seasonal collections

Factor	Levels	Coefficient
Intercept		1.24184
Predator	Yellowtail	-1.28081
	Widow	-1.04861
	Canary	0.00000
Quarter	Sp/98	-0.66878
	Su/98	-0.57690
	F/98	-0.66687
	W/99	-0.59038
	Sp/99	-0.78574
	F/99	0.00000
Predator*Quarter	Yellowtail Sp/98	0.93364
	Yellowtail Su/98	0.61706
	Yellowtail F/98	0.96094
	Yellowtail W/99	1.28825
	Yellowtail Sp/99	0.35919
	Yellowtail F/99	0.00000
	Widow Sp/98	0.56582
	Widow Su/98	0.10968
	Widow F/98	0.47241
	Widow W/99	0.05572
	Widow Sp/99	0.00000
	Widow F/99	0.00000
	Canary Sp/98	0.00000
	Canary Su/98	0.00000
	Canary F/98	0.00000
	Canary W/99	0.00000
	Canary Sp/99	0.00000

Appendix A. *Continued***GLM coefficients of PCA Axis 2 from seasonal collections**

Factor	Levels	Coefficient
Intercept		-0.21920
Predator	Yellowtail	-0.04283
	Widow	0.33962
	Canary	0.00000
Quarter	Sp/98	0.28884
	Su/98	0.35434
	F/98	0.33996
	W/99	0.35821
	Sp/99	0.34505
	F/99	0.00000
Predator*Quarter	Yellowtail Sp/98	-0.23865
	Yellowtail Su/98	-0.23147
	Yellowtail F/98	-0.09696
	Yellowtail W/99	0.04421
	Yellowtail Sp/99	0.32389
	Yellowtail F/99	0.00000
	Widow Sp/98	-0.67777
	Widow Su/98	-0.96855
	Widow F/98	-0.57042
	Widow W/99	-0.74302
	Widow Sp/99	0.00000
	Widow F/99	0.00000
	Canary Sp/98	0.00000
	Canary Su/98	0.00000
	Canary F/98	0.00000
	Canary W/99	0.00000
	Canary Sp/99	0.00000

Appendix A. *Continued***GLM coefficients of PCA Axis 1 from survey collections**

Factor	Levels		Coefficient
Intercept			-0.17312
Year	1980		0.32832
	1998		0.00000
Latitude	42°		0.69631
	44°		0.60123
	46°		0.24551
	48°		0.00000
Depth	Shallow		-0.25414
	Mid		0.04995
	Deep		0.00000
Year*Latitude	1980	42°	-1.10374
	1981	44°	-0.83828
	1982	46°	-0.41082
	1983	48°	0.00000
	1998	42°	0.00000
	1999	44°	0.00000
	2000	46°	0.00000
	2001	48°	0.00000
Latitude*Depth	42°	Shallow	-0.53735
	42°	Mid	0.00000
	42°	Deep	0.00000
	44°	Shallow	-0.30473
	44°	Mid	-0.30535
	44°	Deep	0.00000
	46°	Shallow	0.50800
	46°	Mid	0.12502
	46°	Deep	0.00000
	48°	Shallow	0.00000
	48°	Mid	0.00000
	48°	Deep	0.00000

Appendix A. *Continued***GLM coefficients of PCA Axis 2 from survey collections**

Factor	Levels		Coefficient
Intercept			-0.16326
Year	1980		0.24349
	1998		0.00000
Latitudes	42°		0.15339
	44°		-0.01066
	46°		0.53299
	48°		0.00000
Depth	Shallow		0.14345
	Mid		0.28268
	Deep		0.00000
Time	Morning		-0.16193
	Midday		-0.06597
	Evening		0.00000
Year*Depth	1980	Shallow	-0.52233
	1980	Mid	-0.40916
	1980	Deep	0.00000
	1998	Shallow	0.00000
	1998	Mid	0.00000
	1998	Deep	0.00000
Latitude*Depth	42°	Shallow	-0.15634
	42°	Mid	-0.09838
	42°	Deep	0.00000
	44°	Shallow	0.12594
	44°	Mid	-0.05275
	44°	Deep	0.00000
	46°	Shallow	0.20462
	46°	Mid	-0.24844
	46°	Deep	0.00000
	48°	Shallow	0.00000
	48°	Mid	0.00000
	48°	Deep	0.00000
Latitude*Time	42°	Morning	0.00000
	42°	Midday	0.07921
	42°	Evening	0.00000
	44°	Morning	-0.27723
	44°	Midday	0.11373
	44°	Evening	0.00000
	46°	Morning	-0.10323
	46°	Midday	-0.56315
	46°	Evening	0.00000
	48°	Morning	0.00000
	48°	Midday	0.00000
	48°	Evening	0.00000

Appendix B. Number of samples by year and month for each fish species (both sexes) that were used for the data analyses. Usually one market sample basket contains both males and females and thus results in two sets of data on total weight and length frequency, one set for the males and another for the females.

Dover sole

	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
1972					8	8	10	8	6				40
1973					8	8	6	7	6				35
1974					4	10	6	4	2				26
1975					4	6	8	8	2				28
1976					2	4	4	6	6				22
1977					2		6	2	2				12
1978							2	6	2				10
1979		2	4	2	4	2	8	8	2	4	4		40
1980			2	6	4	7	7	2	6	4		4	42
1981		8		17	4	6	4	14	9	6	2		70
1982	6	4	9	3	6	6	8	9	4	2	4	4	65
1983	2	4	9	4	4	6	4	5	4	6	6	4	58
1984	1	6	4	10	13	6	8	10	10	2		4	74
1985	3	10	6	8	10	4	8	5	6	4	4	4	72
1986	2	8	10	8	6	6	4	6	10	4	4	2	70
1987	2	6	10	9	4	10		15	6	6		8	76
1988	8	8	8	6	8	4	10	6	9	14	4	12	97
1989	3	8	16	6	14	16	18	14	6	8	6	7	122
1990	8	12	10	9	12	13	21	16	6	8	6	6	127
1991	14	22	18	18	12	24	18	14	16	8	10	8	182
1992	8	20	23	12	12	17	17	15	13	12	12	10	171
1993	11	8	12	4	1	3	4	2	4	4	4	4	61
1994	4	6	10	6	4	8	8	4	6	6	4	4	70
1995	6	6	4	4	4	4	8	4	4	6	6		56
1996	4	2	6	7		2	2	2	6	4	2	7	44
1997	8	4	2	6	10	8	7	4	10	4	2	4	69
1998	6	2	8	11	9	6	10	8	7	14	4	8	93
1999	10	2	6	9	4	6	17	8	2	6	4	10	84
2000	6	8	10	11	8	4	6	5	8				66
Total	112	156	187	176	181	204	239	217	180	132	88	110	1982

Appendix B. *Continued.***Petrale sole**

	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
1971							2	2	2	2			8
1972					6	8	6	6	4				30
1973					6	4	4	4	4				22
1974				2	6	4	2	2	2				18
1975					4	4	6	4	4				22
1976													
1977		2		2	4	4	7	6	2				27
1978	2		4			4	4	8					22
1979			2	2	4	4	6	8	2	4	2	6	40
1980		3	2	2	6	8	4	6	8	6	2	3	50
1981		4	4	6	6	8	5	18	14	3	3	2	73
1982		1	6			8	10	8	2		2		37
1983													
1984													
1985			2	2	2	2	2				2		12
1986		4	4			2		8	2	2	2	4	28
1987	4	2	2	2		8	12	4	2	2		4	42
1988	2	2	2	2	2	2			2	4	4	10	32
1989	2	2	2	4		2	4	8	4	2	2		32
1990	4	2	4		2	4	2	7	2		2	2	31
1991	10	5	2	6			4		2		2		31
1992	2	3	7	1	4		2	2	4		2	8	35
1993	4		2	1	2	2	4	2		1	1	10	29
1994	4	2	3	1	2		2	2	2	4	2	2	26
1995	8	2					2		2			2	16
1996													
1997	6	4	3	4	3		2		6	4		6	38
1998	4		2	10	4		10	4	4	4		6	48
1999	10		2			10	6	1	6	1	3	4	43
2000	7	5			1	2		5	2				22
Total	69	43	55	47	64	90	108	115	84	39	31	69	814

Appendix B. *Continued.*

Canary rockfish		Month												Total
Year		1	2	3	4	5	6	7	8	9	10	11	12	
1977						2	2	4	8					16
1978				2			2	2	4	2	2			14
1979			4					2	2			2		10
1980	4	6	4	2	3	2	6	1	4	4	2	2	2	38
1981			4				2	2	2	2	2	2		16
1982	4	2	2	4	2	4	2	7	1	2	2	6	2	38
1983		4	6	4	13		10	7	6	4			2	56
1984	4		12	6	8	6	2	4						42
1985	4	4	4	4	8	2	6	6	6	6	2	4		50
1986	2		6	8	2	4					4	2	2	30
1987	4	8	2	8	2	4	6	6	10	16				66
1988	6	2	2	8	2	6	2	8	6				4	46
1989	6	8	4	4	4	2	4				4	2		38
1990	2	2	6	2	6	4	6	10	2	3				43
1991		2	2	6	8	6	4	2	2	6	2			40
1992	4	2	3	12	10	4	6	2	6	2	2	2	2	55
1993	4		4		8	4	4	10	6	2	2			44
1994	2	4	2	2	4	8		2	2	4				30
1995	4	2		4	4	4				4	6			28
1996			8	2	6	8	4	2			6		2	38
1997	5	2	2	7	12	14	8	10	8	4	4	2	2	76
1998	2		10	4	18	10	22			4	2			72
1999		4	6	10	8	7	12	6	6					59
2000			1	4	2	3	2	4	11	4				31
Total		57	52	94	103	132	108	116	103	88	77	28	18	976

Appendix B. *Continued.*

Yellowtail rockfish		Month												Total
Year		1	2	3	4	5	6	7	8	9	10	11	12	
1977							4	8	6	2				20
1978					4			2	4	2				12
1979				2	2	2			6	4				16
1980														
1981														
1982		2			4	4	16	8	2	2	2		2	42
1983														
1984		4			4	6	2	2	2				2	22
1985														
1986		4	4	6	2	2	4		2	2	2		4	32
1987		6	12	14	2	2	6	4	4	2	10		2	64
1988		10	10		4	3	2	4	8	10	8	2	6	67
1989		6	15	2	8	6	6	10	8	12	6	1		80
1990		8	10	12	4	10	4	2	8	6	4	2		70
1991		8	13	4	12	6	8	6	2	7	2	2		70
1992		10	18	18	18	10	14	20	4	6	4	10	6	138
1993		8	12	6	8	6	6	6	14	8	20	10	2	106
1994		20	10	16	18	8	14	14	12	8	11	6		137
1995		3	6	8	4	10	8	10	4	6	14	2	10	85
1996		8	2	8	8	8	6	12	6	6	8	2	2	76
1997		8	5	4	11	25	18	22	20	11	18	2		144
1998		6		4	16	26	18	24	8	14	4	2	2	124
1999		8	2	6	10	14	18	14	16	14	2			104
2000		2	2	4	7	16	10	12	6	15	7	6	2	89
Total		121	121	114	146	164	164	180	142	137	122	47	40	1498

Appendix C. GLM coefficients for each species.

Appendix C.1. Dover Sole.

Main Effects : Intercept = -0.3146

Year	Coefficients	Month	Coefficients	Latitude	Coefficients	Sex	Coefficients
1972	-0.1144	1	0.3853	South	-0.2541	Male	0.6402
1973	-0.2896	2	1.1575	Central	0.0964	Female	0.0000
1974	0.4537	3	0.8550	North	0.0000		
1975	0.6652	4	0.7018				
1976	0.1374	5	0.3577				
1977	-1.3855	6	0.3125				
1978	0.4073	7	0.5202				
1979	0.5630	8	0.3469				
1980	1.8293	9	0.4632				
1981	-1.1241	10	-0.5261				
1982	0.0179	11	-0.0076				
1983	-0.4082	12	0.0000				
1984	0.0748						
1985	0.5765						
1986	1.2020						
1987	0.3110						
1988	0.6270						
1989	-0.4436						
1990	0.5071						
1991	0.2033						
1992	0.7695						
1993	-0.5120						
1994	1.2190						
1995	-0.2805						
1996	1.8570						
1997	-0.1188						
1998	0.1452						
1999	0.4140						
2000	0.0000						

Appendix C.1. *continued.*

Year*Month												
Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1972					-0.7110	-0.9502	-0.3849	0.1407	0.0000			
1973					0.0203	-0.3506	-0.0690	-0.2015	0.0000			
1974					-1.1544	-0.8976	-0.3164	-0.3058	0.0000			
1975					-0.8921	-1.0794	-0.4920	-0.3002	0.0000			
1976					0.4322	0.2031	-0.2379	-0.0125	0.0000			
1977					-0.2740		1.3176	-1.9677	0.0000			
1978							-0.3915	-1.2472	0.0000			
1979		-1.6235	-2.0187	-1.0217	-0.9677	0.2612	-1.2507	-0.9754	-0.5186	0.5910	0.0000	
1980			-2.0043	-2.7780	-2.3108	-2.1589	-1.8547	-2.0269	-1.7008	-0.0943		0.0000
1981		1.0571		-0.3681	0.9348	1.2488	0.7508	0.8732	0.5361	2.0623	0.0000	
1982	-0.9836	-0.0273	-0.1147	-0.1983	0.1838	-0.8595	0.5598	-0.4633	0.8974	0.9948	0.8003	0.0000
1983	0.9570	-0.1241	0.2755	-0.6840	-0.7655	-0.6251	-0.3495	-0.2373	-0.0208	0.8485	0.3896	0.0000
1984	-0.7705	-0.4253	-0.7950	-0.5960	-0.6430	-0.5521	-0.1887	-0.4877	0.8710	-0.0229		0.0000
1985	-1.6162	-1.0832	-0.7672	-0.3202	-0.2503	-1.5033	-1.0091	-0.6349	-0.1724	-0.0319	0.0430	0.0000
1986	-0.8452	-1.8051	-0.7680	-1.7837	-0.8853	-1.0631	-1.8246	-1.3992	-1.0217	0.1187	-0.5342	0.0000
1987	-0.4117	-1.5492	-0.5368	-1.2768	-0.6106	-1.1418		-0.1566	0.1544	0.4992		0.0000
1988	-0.4343	-0.9690	-1.0113	-0.9504	-1.5882	-1.0085	-0.6689	-0.7359	-0.4907	0.3790	-0.4277	0.0000
1989	1.2796	-0.0167	0.5934	-0.0665	-0.2672	-0.0172	0.6091	-0.1562	0.8927	0.8314	0.8848	0.0000
1990	-0.7277	-1.2146	-0.7033	-0.5709	-0.2404	-1.3792	-1.1351	-0.0569	-0.9101	0.1802	-0.3422	0.0000
1991	0.2030	-0.7698	-0.1442	-0.1873	-0.4788	-0.7575	-0.6514	-0.0352	-0.4973	0.7704	-0.3728	0.0000
1992	-0.4189	-1.6735	-0.8055	-1.0814	-1.5282	-1.5787	-0.8594	-0.7687	-0.6192	0.6285	-0.2078	0.0000
1993	0.2585	-0.1517	0.3218	0.0347	0.1550	0.6758	-0.6049	-0.1664	0.9760	0.7968	0.8999	0.0000
1994	-1.2697	-2.4949	-1.2431	-1.4449	-2.1548	-1.7849	-0.9038	-1.0972	-1.6238	-1.6195	-1.0875	0.0000
1995	0.0362	-0.5564	-0.1693	-0.0781	-0.2730	-0.7535	0.2021	0.5143	-0.2928	0.6851	0.0000	
1996	-1.8222	-2.6547	-2.0563	-2.7477		-2.3619	-1.0442	-2.9379	-1.4713	-1.6437	-1.9926	0.0000
1997	-0.0383	-0.7284	0.3925	-0.6078	0.1074	0.2095	0.0718	-0.0672	0.6678	1.9589	1.6997	0.0000
1998	0.0695	-2.9471	-0.6571	-1.2612	-0.6287	-0.2680	-0.4406	-0.3637	0.6158	0.5620	-0.8965	0.0000
1999	-0.1107	-0.1032	-0.3397	-0.6372	-0.3889	-0.3799	-0.3927	-0.5739	0.0000	0.0000	0.0000	0.0000
2000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000			

Appendix C.1. *continued*

Year*Latitude

Year	Latitude		
	South	Central	North
1972	0.4429		0.0000
1973	0.3509		0.0000
1974	-0.3845		0.0000
1975	0.0249		0.0000
1976	0.4948		0.0000
1977	1.6775		0.0000
1978			0.0000
1979	0.1566		0.0000
1980	0.1869	2.3608	0.0000
1981	0.8506	0.1142	0.0000
1982	0.4761	-0.8163	0.0000
1983	0.3967		0.0000
1984	-0.1405	1.5307	0.0000
1985	-0.3604		0.0000
1986	-0.2957	-0.8251	0.0000
1987	-0.1215	-0.0871	0.0000
1988	0.0485	-0.1769	0.0000
1989	-0.1279	-0.2844	0.0000
1990	-0.5875	-1.4610	0.0000
1991	-0.5300	-0.8240	0.0000
1992	-0.6423	-0.8526	0.0000
1993	0.6335	-0.0044	0.0000
1994	-0.4802	-1.1270	0.0000
1995	-0.3705	0.0954	0.0000
1996	-0.1030	-1.0994	0.0000
1997	0.1508	-0.2380	0.0000
1998	0.5329	0.2528	0.0000
1999	-0.1966	-0.2963	0.0000
2000	0.0000	0.0000	0.0000

Month*Latitude

Month	Latitude		
	South	Central	North
1	0.2448	1.0182	0.0000
2	0.5562	0.4505	0.0000
3	0.3711	0.6946	0.0000
4	0.7504	0.4776	0.0000
5	0.3731	-0.7426	0.0000
6	0.2658	-0.1292	0.0000
7	0.0605	0.0620	0.0000
8	0.3452	-0.5723	0.0000
9	0.2754	0.7092	0.0000
10	0.2479	0.0197	0.0000
11	0.5680	0.5206	0.0000
12	0.0000	0.0000	0.0000

Month*Sex

Month	Sex	
	Male	Female
1	-0.8143	0.0000
2	-0.9608	0.0000
3	-1.1406	0.0000
4	-1.0661	0.0000
5	-0.3495	0.0000
6	-0.1800	0.0000
7	-0.6522	0.0000
8	-0.5442	0.0000
9	-0.6771	0.0000
10	-0.3015	0.0000
11	-0.6187	0.0000
12	0.0000	0.0000

Appendix C.2. Petrale Sole.

Main Effects : Intercept = 0.3552

Year	Coefficients	Month	Coefficients	Latitude	Coefficients	Sex	Coefficients
1971	-0.1234	1	-0.0941	South	-0.2067	Male	-0.1754
1972	0.4156	2	0.0319	Central	-0.0329	Female	0.0000
1973	0.2040	3	-0.9664	North	0.0000		
1974	0.1257	4	-0.5492				
1975	0.7041	5	-0.9566				
1977	0.8683	6	-0.3049				
1978	0.5803	7	-1.3363				
1979	-0.0334	8	-0.0498				
1980	0.5515	9	-0.3908				
1981	0.0721	10	0.3780				
1982	3.6692	11	0.1122				
1985	0.6312	12	0.0000				
1986	-0.2048						
1987	1.1395						
1988	0.2393						
1989	-0.1074						
1990	-0.2180						
1991	-0.1633						
1992	-0.1638						
1993	0.1507						
1994	-0.4138						
1995	0.2385						
1996	-1.0438						
1997	0.0859						
1998	-0.0937						
1999	-0.0140						
2000	0.0000						

Appendix C.2. *continued.*

Year*Month												
Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1971							1.3855	0.1490	0.1666	0.0000		
1972					-0.4550	-0.9229	0.0527	-1.2874	0.0000			
1973					0.1813	0.0069	0.8164	-0.6134	0.0000			
1974				0.0322	0.0670	0.2332	0.8479	-0.5590	0.0000			
1975					-0.5336	-0.5772	0.4191	-1.0498	0.0000			
1977		-2.3320		1.3792	1.1857	-1.1435	0.3749	-0.4228	0.0000			
1978	-5.5310		-5.2879			-4.6910	-3.8335	0.0000				
1979			-1.1509	0.1602	-0.1449	0.2756	0.9437	0.2539	1.9292	-0.3811	0.7896	0.0000
1980		0.9550	2.2229	-0.3102	0.3480	-0.3946	-0.3789	-0.6145	-0.1096	-0.4644	-3.7096	0.0000
1981		0.8490	0.1984	-0.0529	0.7439	0.2890	-0.3109	0.0511	0.5076	0.8900	0.6848	0.0000
1982		-9.8802	-2.2900			-2.6438	-1.1937	-2.0717	2.2140		0.0000	
1985			-1.0976	-1.1128	-0.2973	-0.8753	0.5144				0.0000	
1986		0.1733	0.7441			0.2159		0.2411	1.4033	-0.0930	1.0884	0.0000
1987	-1.2227	-1.3276	0.3873	-1.6503		-1.0953	-0.0336	-1.2875	-1.0775	-2.0314		0.0000
1988	-1.0138	-0.0544	0.4138	0.1077	-0.1348	-0.3510			-0.6304	-0.5415	0.0430	0.0000
1989	-0.4896	0.1805	0.8593	-0.3442		-0.3304	1.0244	-0.5578	0.0990	-1.1869	0.0000	
1990	-0.1523	-1.8124	0.9429		1.2020	-0.0288	0.6741	0.1756	0.0970		-0.0072	0.0000
1991	0.0207	-0.4105	-0.1895	-0.1546			0.8845		0.3878		0.0000	
1992	-0.1109	0.2829	0.2199	-0.2745	0.8989		2.2760	-0.1918	0.6122		0.3111	0.0000
1993	0.6084		-0.4740	-0.1510	1.4066	-0.3744	0.7712	-0.6587		1.4906	-0.1311	0.0000
1994	0.3469	-0.2695	0.4945	-0.2173	0.8354		-0.6194	0.8895	-2.6591	0.0142	0.0154	0.0000
1995	-0.0196	-0.5401					1.0094		0.4407			0.0000
1996	0.7841		1.5169					0.0000				
1997	0.5444	-0.1874	0.8921	0.3268	0.5830		1.0661		0.4490	0.8651		0.0000
1998	0.1646		0.1593	0.0000	0.6671		1.0926	-0.2571	0.0978	-0.5883		0.0000
1999	-0.0222		0.0000			0.0546	0.0000	-0.1395	0.0000	0.0000	0.0000	0.0000
2000	0.0000	0.0000			0.0000	0.0000		0.0000	0.0000			

Appendix C.2. *continued*

Year*Latitude			
Year	Latitude		
	South	Central	North
1971	0.0000		
1972	0.3362		0.0000
1973	0.6008		0.0000
1974	-0.3985		0.0000
1975	0.0456		0.0000
1977	-0.5149	-0.4413	0.0000
1978	4.4750		0.0000
1979	-0.2280	0.0000	0.0000
1980	-0.2815	1.8310	0.0000
1981	-0.4525	-1.1397	0.0000
1982	-1.3227		0.0000
1985	0.0000		0.0000
1986	-0.4553	-0.4088	0.0000
1987	-0.0482		0.0000
1988	-0.4470		0.0000
1989	0.2936	0.0000	0.0000
1990	0.1742		0.0000
1991	0.3544	0.0965	0.0000
1992	-0.1656	0.0830	0.0000
1993	-0.5402	0.0000	0.0000
1994	0.2681	0.0000	0.0000
1995	-0.5543		0.0000
1996	-0.4733		0.0000
1997	-0.0592	-0.9284	0.0000
1998	-0.1526	0.4980	0.0000
1999	-0.2296	0.0000	0.0000
2000	0.0000		0.0000

Month*Sex		
Month	Sex	
	Male	Female
1	-0.0730	0.0000
2	-0.4871	0.0000
3	0.5970	0.0000
4	0.0830	0.0000
5	0.1982	0.0000
6	0.0948	0.0000
7	0.1569	0.0000
8	0.2889	0.0000
9	0.1846	0.0000
10	0.4768	0.0000
11	-0.3983	0.0000
12	0.0000	0.0000

Appendix C.3. Canary Rockfish.

Main Effects : Intercept = 0.1358

Year	Coefficients	Month	Coefficients	Latitude	Coefficients	Sex	Coefficients
1977	0.1782	1	-0.2454	South	0.1374	Male	-0.4020
1978	0.2175	2	-0.3176	Central	0.3586	Female	0.0000
1979	-0.2151	3	-0.2610	North	0.0000		
1980	-0.0829	4	-0.5602				
1981	-1.2760	5	-0.2591				
1982	0.7575	6	0.3336				
1983	2.1992	7	-0.5665				
1984	-0.1586	8	0.1599				
1985	-0.9756	9	-0.3742				
1986	0.0941	10	-0.1003				
1987	-0.1497	11	1.2114				
1988	-0.2687	12	0.0000				
1989	-0.7563						
1990	-1.5461						
1991	-1.6138						
1992	-0.0021						
1993	-0.6462						
1994	0.5564						
1995	-0.1652						
1996	-0.4176						
1997	0.0372						
1998	0.1427						
1999	0.2238						
2000	0.0000						

Appendix C.3. *continued.*

Year*Month

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1977					0.1543	0.4993	0.3072	0.0000				
1978				0.5673		-0.2075	0.6473	0.5172	0.6381	0.0000		
1979			0.3207				0.9465	0.4014			0.0000	
1980	1.0540	0.6275	0.3029	0.7032	0.3982	-0.0337	1.4375	-0.3378	0.5127	0.4493	-0.8625	0.0000
1981			1.6385			-0.2778	2.1807	2.8106	1.9503	1.9964	0.0000	
1982	0.1593	-0.5037	-0.4893	-0.4498	-2.7539	-0.8653	0.4703	-0.3220	-4.9182	0.8439	-0.3310	0.0000
1983		-2.9902	-2.1934	-2.3465	-2.1368		-1.2031	-2.0084	-0.7799	-1.6774		0.0000
1984	1.7583		-0.1393	-0.2901	-0.2594	-0.3187	1.1146	0.0000				
1985	0.7685	0.4746	-0.6152	0.1835	0.3485	1.1259	0.5586	0.0545	0.9054	0.5511	0.0000	
1986	0.5268		-0.5366	0.0026	-0.1385	-0.1937				-1.3091	-1.1596	0.0000
1987	-1.0522	-0.4463	-0.1655	-0.0204	-0.9866	-0.4814	0.8567	0.4252	0.5908	0.0000		
1988	0.6864	0.8092	-1.4974	0.9096	1.5765	-0.0301	0.9238	0.1687	0.9861			0.0000
1989	1.1271	0.5450	0.4269	0.1585	0.8423	-0.4921	2.1952			-0.0123	0.0000	
1990	1.6128	2.1502	0.6185	0.4940	0.8911	0.5153	1.7944	1.1721	2.0241	0.0000		
1991		0.4572	0.9205	1.2993	1.5440	0.5819	1.7386	1.3971	0.7461	1.3514	0.0000	
1992	0.5776	-0.0953	-1.6598	0.0531	0.0923	-1.0488	1.2590	-0.3585	0.0347	-0.7676	-0.8154	0.0000
1993	0.6852		-0.3916		0.4826	-0.2006	0.4049	-0.2422	0.1902	0.0475	0.0000	
1994	-0.8870	-0.9996	-0.7471	-0.4535	-0.1145	-0.4549		-1.0958	-0.4493	0.0000		
1995	0.3110	0.0412		0.3910	0.4075	0.1203			0.5860	0.0000		
1996			-0.2150	-0.0557	-0.1875	-0.3806	0.9393	-0.3691		0.2968		0.0000
1997	0.4977	0.1718	-0.2049	0.1434	-0.0638	-1.3340	0.5787	-0.4794	0.6618	0.0000	0.0000	0.0000
1998	0.0000		-0.5983	-0.2280	-0.9338	-1.2043	0.0905		-0.0639	0.0000		
1999		0.0000	-0.0885	-0.9838	-0.7973	-0.3175	-0.0744	-0.7688	0.0000			
2000			0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		

Month*Sex

Month	Sex	
	Male	Female
1	-0.2432	0.0000
2	0.4577	0.0000
3	0.8203	0.0000
4	0.7087	0.0000
5	0.7636	0.0000
6	0.2976	0.0000
7	0.3822	0.0000
8	0.3569	0.0000
9	0.2264	0.0000
10	0.5181	0.0000
11	-0.2986	0.0000
12	0.0000	0.0000

Appendix C.4. Yellowtail Rockfish.

Main Effects : Intercept = 0.2561

Year	Coefficients	Month	Coefficients	Latitude	Coefficients	Sex	Coefficients
1977	1.5482	1	0.0012	South	0.2475	Male	-0.3938
1978	-0.5344	2	0.1552	Central	0.6290	Female	0.0000
1979	0.4511	3	-0.2404	North	0.0000		
1982	0.1629	4	-0.8102				
1984	0.6830	5	-0.6090				
1986	0.4696	6	0.1118				
1987	-0.3750	7	-0.2800				
1988	0.0456	8	-0.0251				
1989	0.3037	9	-0.0691				
1990	-0.1168	10	0.0410				
1991	-0.1048	11	0.1123				
1992	-0.2532	12	0.0000				
1993	-0.4602						
1994	-0.1426						
1995	-0.0433						
1996	0.0359						
1997	-0.2689						
1998	-0.6831						
1999	-0.8407						
2000	0.0000						

Appendix C.4. *continued.*

Year*Month

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1977						-0.9055	-0.1384	-0.5043	0.0000			
1978				1.6685			0.9745	0.0357	0.0000			
1979			0.1753	0.5532	-0.1550			-0.1533	0.0000			
1982	-0.4512			-0.1551	-0.4837	0.1008	-0.3431	-0.4370	1.5106	0.4209		0.0000
1984	-1.0019			-0.1571	-0.3325	-0.6514	0.5993	-0.2550				0.0000
1986	-0.9915	-0.6751	-0.2189	-0.8301	0.4207	-0.0452		-0.3102	-0.3126	0.6067		0.0000
1987	0.8707	0.7438	0.1437	-0.4756	-1.4110	-0.4407	1.9271	0.4833	1.5895	0.2161		0.0000
1988	-0.2323	0.0510		0.2029	-3.0503	-0.8964	0.3395	0.5575	0.5627	0.9161	-0.2450	0.0000
1989	-0.6270	-0.6290	-1.9124	-0.5659	-0.2020	-1.0070	-0.4635	-0.4615	-0.1249	-1.1017	0.0000	
1990	0.6124	-0.0157	-0.4476	0.1948	-0.2055	-0.9030	-0.0805	0.4903	0.5129	-0.4352	0.0000	
1991	-0.2445	-0.2151	-0.8459	0.6041	0.2838	-0.0777	0.6466	0.2681	0.2657	0.2359	0.0000	
1992	0.8868	-0.3070	0.4324	1.4004	1.0118	0.0859	0.4861	0.4860	0.2525	0.0625	0.3842	0.0000
1993	0.8605	0.2411	-0.0332	0.4702	0.5743	-0.2542	0.0574	-0.6450	-0.3267	-0.2098	0.1260	0.0000
1994	-0.7765	-0.6546	-0.6052	0.3774	0.6120	-0.3794	0.1293	0.0415	-0.6004	0.2371	0.0000	
1995	-0.6261	-0.3350	-0.4879	-0.1140	0.3799	-0.3632	-0.4730	0.2209	-0.7729	-0.3696	0.1264	0.0000
1996	-0.0106	-1.3621	-0.4801	-0.0164	-0.1883	-0.8332	0.1548	-0.6184	-0.4419	-0.1952	-0.5394	0.0000
1997	0.2087	0.1824	-0.8041	-0.1112	-0.2659	-0.9333	0.1923	0.1274	0.0757	0.0032	0.0000	
1998	0.5277		0.8103	1.1962	0.9793	-0.2646	0.3041	-0.2027	-0.0112	0.8264	1.1500	0.0000
1999	0.4221	0.0610	0.3098	0.7557	-0.1438	0.1775	0.0494	0.4718	0.2460	0.0000		
2000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Appendix C.4. *continued.*

Year*Latitude

Year	Latitude		
	South	Central	North
1977	0.8742		0.0000
1978			0.0000
1979			0.0000
1982	0.0453		0.0000
1984	-0.5849	-0.8944	0.0000
1986	-1.3366		0.0000
1987	0.1294	-0.0446	0.0000
1988	-0.6357	0.2900	0.0000
1989	0.0704	0.2025	0.0000
1990	-0.2193	-0.5969	0.0000
1991	-0.6334	-0.2083	0.0000
1992	-0.6556	-1.0953	0.0000
1993	-0.3643	-1.0941	0.0000
1994	-0.1784	-0.3814	0.0000
1995	0.1686	0.0516	0.0000
1996	-0.1113	-0.3700	0.0000
1997	0.2857	0.1691	0.0000
1998	-0.3026	0.3680	0.0000
1999	0.2766	-0.1266	0.0000
2000	0.0000	0.0000	0.0000

Month*Sex

Month	Sex	
	Male	Female
1	-0.1145	0.0000
2	-0.1216	0.0000
3	0.5810	0.0000
4	0.6918	0.0000
5	0.5694	0.0000
6	0.4269	0.0000
7	0.7121	0.0000
8	0.5599	0.0000
9	0.5457	0.0000
10	0.1347	0.0000
11	-0.3212	0.0000
12	0.0000	0.0000

Appendix C.5. Widow Rockfish.

Main Effects : Intercept = 1.3334

Year	Coefficients	Month	Coefficients	Latitude	Coefficients	Sex	Coefficients
1984	1.1858	1	-1.7268	South	0.5243	Male	-0.8105
1985	-0.4405	2	-1.7438	Central	0.8942	Female	0.0000
1986	-0.7122	3	-2.0430	North	0.0000		
1987	1.0230	4	-2.0804				
1988	0.3410	5	-1.3779				
1989	-0.7497	6	-1.4585				
1990	0.7353	7	-1.2831				
1991	-0.2773	8	-1.4566				
1992	-2.0710	9	-1.2467				
1993	-3.4828	10	-1.6070				
1994	-2.2376	11	-1.3456				
1995	-1.1054	12	0.0000				
1996	-1.9401						
1997	-0.4917						
1998	-0.3295						
1999	0.2052						
2000	0.0000						

Appendix C.5. *continued.*

Year*Month

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1984	-1.1458	0.3284	0.1872	-1.5011	-2.0628	-1.5057	-1.3304	-0.8122	-0.9587	0.0000		
1985	1.2745	0.6124	0.4674	1.1378	1.0112	0.3208	-1.4851	0.8996	1.3905	1.5072	0.6546	0.0000
1986	1.5002	0.7733	1.1044	1.4818	0.6243	1.4930	1.4935	0.6440	1.5230	1.6167	2.2422	0.0000
1987	-0.6639	-0.4762	-0.5524	-0.5046	-1.1446	0.2722	0.1512	-0.1508	-0.6489	0.2694	0.0000	
1988	-0.1926	-0.2752	-0.5438	-0.2651	-0.6119	0.2557	0.6785	-0.2153	0.5451	1.7178		0.0000
1989	1.7939	1.3203	0.7643	1.1378	0.6021	0.7853	0.8330	0.9089	-0.5964	1.5388		0.0000
1990	0.2469	-0.4591	-0.3994	-0.7188	-1.2499	-0.0142	-0.2320	-0.0601	-0.6262	0.0986	0.0000	
1991	0.1666	0.1714	0.1298	0.2585	0.3201	0.8362	0.6012	0.7986	0.9685	0.7986		0.0000
1992	2.4708	2.1639	2.1086	2.7810	3.2316	2.4395	2.1941	2.5186	1.9539	1.7603	2.4071	0.0000
1993	3.3560	3.4340	3.5644	4.4650	3.2800	2.8491	2.6100	2.9755	2.5056	3.6595	3.0340	0.0000
1994	2.4231	2.1219	1.8257	1.9208	1.8470	2.0424	1.7326	2.0497	1.6316	2.5864	2.7856	0.0000
1995	1.1337	0.9812	1.6445	2.1464	0.9571	0.9999	1.5654	1.8794	1.1288	1.8899	1.5427	0.0000
1996	1.7154	1.8882	1.8626	1.7766	1.1691	1.5148	1.7017	2.6130	2.1300	1.6660	1.5549	0.0000
1997	1.9144	0.9861	0.3982	1.3847	-0.3175	1.2445	-0.3105	0.3571	0.5645	2.4983	0.5033	0.0000
1998	-0.1161	-0.2130	-0.4284	0.9029	0.2742	0.9003	0.4525	0.0957	0.6191	0.1965	0.0000	0.0000
1999	0.0000	0.1783	0.0511	0.3703	-0.1142	-0.1356	0.0257	-0.2275	-0.6354	0.3069	0.0000	
2000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Appendix C.5. *continued.*

Year*Latitude

Year	Latitude		
	South	Central	North
1984	-0.3639	-2.1289	0.0000
1985	0.2177	-0.6375	0.0000
1986	0.0022	-1.5191	0.0000
1987	1.8286	-0.6558	0.0000
1988	-0.1341	-1.7265	0.0000
1989	1.6523	-0.1234	0.0000
1990	-0.7027	-0.8423	0.0000
1991	-1.0040	-1.2598	0.0000
1992	1.0741	0.3158	0.0000
1993	-0.8789	-1.1397	0.0000
1994	-1.2174	-0.7839	0.0000
1995	-0.5863	-0.8658	0.0000
1996	0.2345	-0.3669	0.0000
1997	-1.6813	-1.8027	0.0000
1998	0.3395	-0.2666	0.0000
1999	-0.2131	-1.0090	0.0000
2000	0.0000	0.0000	0.0000

Year*Latitude

Year	Sex	
	Male	Female
1984	0.3574	0.0000
1985	0.0720	0.0000
1986	-0.1798	0.0000
1987	-0.1222	0.0000
1988	0.1550	0.0000
1989	-0.1181	0.0000
1990	-0.2118	0.0000
1991	0.0674	0.0000
1992	0.1068	0.0000
1993	0.2558	0.0000
1994	0.2452	0.0000
1995	0.2020	0.0000
1996	-0.0571	0.0000
1997	-0.3609	0.0000
1998	-0.3265	0.0000
1999	0.0365	0.0000
2000	0.0000	0.0000

Month*Sex

Month	Sex	
	Male	Female
1	0.2099	0.0000
2	0.4811	0.0000
3	1.0046	0.0000
4	1.0226	0.0000
5	1.2570	0.0000
6	0.9899	0.0000
7	1.2049	0.0000
8	1.1193	0.0000
9	0.9168	0.0000
10	0.3470	0.0000
11	0.0418	0.0000
12	0.0000	0.0000

Appendix C.5. *continued.*

Year*Month*Latitude (Latitude = South)

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1984	0.8304	0.7079	-1.3433	0.7943	0.1279	0.0164	0.0000	0.0000	0.0000			
1985	-0.8905	-0.6881	-0.5428	-0.6201	-1.0061	0.2309	2.0050		0.0000			0.0000
1986	-0.2750	0.3386	-0.8580	-0.7367	0.0951	-0.1249	-0.4913	0.7200	0.0000			
1987	0.4327	-2.0398	-1.3327	-1.4360	-2.2959		-1.9193		-0.8699	0.0000		
1988	0.6403	0.2822	0.9772					0.2224	0.0000			
1989	-6.3744	-2.0301	-1.5472	-1.6317	-2.5621	-1.8506	-1.0777	-1.4685	0.0000			
1990	-0.0557	0.1275	-0.4461	0.5090	0.9875	-0.3831	0.2339	0.1356	0.5052	0.7610	0.0000	
1991	1.3254	1.0754	0.5287	1.1288	0.6284	0.4994	0.1831	0.1424	0.0554	0.0000		
1992	-1.0468	-1.4220	-0.8798	-1.4401	-2.5284	-2.1871	-2.1069	-1.4626	-1.1393	-0.5795	-0.9167	0.0000
1993	2.0227	0.3851	0.5498	-0.4549	-0.2038	-0.1660	0.1908	-0.5675	-0.1165	-0.4631	0.0000	
1994	0.5727	0.9248	0.4169	1.0976	1.0074	0.8040	1.0679	2.3443	1.4276	1.1797	0.0000	
1995		-0.1034	-0.0046	0.3306	1.1927		0.4856	-0.1616		-0.7168	0.0000	
1996	-0.4100		-0.9178	-0.8157			-0.0285					0.0000
1997		1.4126	1.4020	1.9050	2.3709	0.6726	2.2087	2.1075	1.4415	0.0000	1.7814	0.0000
1998		-0.6639	-0.0253	-0.6736	-0.6166		-1.3428	0.3372	-1.3559	0.0000	0.0000	
1999	0.1221	0.0000		-0.7472	0.0000	0.4387	-0.3308	-0.0133	0.1611	0.0000		
2000		-0.3883	-0.6008	-0.1433	-0.4665	-0.0849	-0.5595	-0.3638	-0.3945	1.0928	0.0000	

Appendix C.5. *continued.*

Year*Month*Latitude (Latitude = Central)

Year	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
1984	1.8191	0.0000	0.0000	1.9273	2.3432	1.1885	0.0000					
1985	-0.7631	1.0512	-0.9168	0.0472	-0.5044	0.3621	2.3804			0.0000	0.0000	
1986	0.3130	1.2344	0.8818	0.3335	-0.5275		-1.1574	0.3020	0.0000	0.0000		
1987	0.6566	-0.3850	-0.2535	-0.2217	0.3779		-0.4791	-0.6269	0.4957	0.0000	0.0000	
1988	0.9481	0.8797	1.8419	1.3504	1.1682	1.5497		1.4771	1.5249	-0.9865		0.0000
1989	-1.2264	-1.4285	-0.3988	-0.4840	-0.7168		-0.8777		0.4241	0.0000		
1990	-0.4193	-0.1128	-0.7381	-0.2403			0.1015	0.0000				
1991	0.8235	0.6784	0.6211	-0.0695	0.8338	1.4386	1.0817	-0.3706	0.0000			0.0000
1992	-0.8309	-0.5469	-0.8496	-1.0594	-2.4626	-1.8922	-1.1864	-1.5473	-0.9281		0.0000	0.0000
1993	0.7333	1.1331	-0.4966	-0.7823	0.4761	-0.2208	0.4788	-0.2488	-0.1394	-0.4928	0.0000	
1994	-0.2439	-0.0924	0.2367	0.3450	0.0183	0.0652	0.6180	0.5659	0.5667	0.0673	0.0000	
1995	0.4010		0.4643	0.6351	0.9689	0.1066	0.3398	-0.3414	0.1802	-0.4016	0.0000	0.0000
1996	-0.3962	-0.6217	-0.9465	0.0000	-0.0442	-1.1342	-0.1179	-1.7847	-0.9059	0.1312	0.0000	0.0000
1997	0.0000	1.3211	1.4613	0.6862	2.2270	1.6220	1.0662	1.4841	1.5559		2.0232	0.0000
1998	0.0000	0.0000	0.9268	-1.3698		-0.4528	-0.8430		-0.9160		0.0000	
1999	0.3239		-0.4408			0.4968		0.4520	1.1048	0.0000		
2000			-0.7000	0.5063		-0.3670	-0.7250		-0.7704	-0.2451	0.0000	

* North latitude is the reference level.