

Abstract—Stomach samples from three rockfish species, yellowtail (*Sebastes flavidus*), widow (*S. entomelas*), and canary (*S. pinniger*) rockfish, seasonally collected off the Pacific Northwest in 1998 and 1999, provided quantitative information on the food habits of these species during and after the 1997–98 El Niño event. Although euphausiids were the most common major prey of all three predators, gelatinous zooplankton and fishes were the most commonly consumed prey items during some seasonal quarters. The influence of the El Niño event was evident in the diets. Anomalous prey items, including the southern euphausiid species *Nyctiphanes simplex* and juveniles of Pacific whiting (*Merluccius productus*) frequently appeared in the diets in the spring and summer of 1998. The results of stomach contents analyses, based on 905 stomach samples from 49 trawl hauls during seven commercial fishing trips and from 56 stations during research surveys, were consistent with the timing of occurrence and the magnitude of change in biomass of some zooplankton species reported from zooplankton studies in the northern California Current during the 1997–98 El Niño. Our findings indicate that the observed variations of prey groups in some rockfish diets may be a function of prey variability related to climate and environment changes.

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Dietary variations in three co-occurring rockfish species off the Pacific Northwest during anomalous oceanographic events in 1998 and 1999

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Numerous rockfish species inhabit the waters off California, Oregon, and Washington. At least 69 species are found in the northeast Pacific Ocean (Love et al., 2002). Although many of these species have been an important part of the commercially exploited groundfish in this region, rockfish harvests off the U.S. West Coast have been greatly curtailed in recent years because several stocks were assessed as being severely depleted (Parker et al., 2000). Despite the economic importance of these species, we have limited knowledge of their behavior and ecology, including how the individual species interact within the coastal ecosystem. Detailed knowledge about the ecological behavior of fish species, especially their food habits, is essential for developing ecosystem-based approaches to fisheries management because such information will provide the linkages between the fish species in multispecies stock assessment models (Livingston, 1985; Livingston and Jurado-Molina, 2000).

During the unusual oceanographic events of the 1997–98 El Niño and the subsequent cooling phase called La Niña in 1999, we collected information on the food habits of three commercially important rockfish species, yellowtail (*Sebastes flavidus*), widow (*S. entomelas*), and canary (*S. pinniger*) rockfish. Although the diets of these species off the west coast of the

United States were examined in two previous studies (Brodeur and Pearcy 1984; Adams 1987), neither study was conducted during anomalous oceanographic events such as El Niño and La Niña years as observed in the current study. Most other studies of rockfish food habits have focused on shallow-water species or have been limited in the geographic and temporal range of their sample collections. The current study not only updates our knowledge of rockfish food habits over wide geographic and temporal ranges but also examines their dietary variations during periods of major environmental change.

Since 1950 there have been seven strong El Niño occurrences (<http://www.elnino.noaa.gov>; accessed July, 2009). The recent event (1997–98) is considered the first or second strongest El Niño in the 20th century, comparable to the record 1983 El Niño (McPhaden, 1999). Peterson et al. (2002) reported changes in the species composition and biomass of the copepod community during El Niño of 1997–98 off central Oregon and found that warm-water copepod species dominated the community during this period. Alternations in the zooplankton community and the unusual occurrence of southern zooplankton species were noted in the northern coastal waters off Oregon and British Columbia during the same period

Table 1

The number of rockfish stomach samples collected from commercial fishing trawlers off the Oregon coast by seasonal quarter and from the NMFS 1998 summer survey cruises off the Oregon and Washington coasts. The numbers of nonempty stomach samples are provided in parentheses.

Sampling dates	Fishing vessel	No. of stations	<i>Sebastes flavidus</i>	<i>Sebastes entomelas</i>	<i>Sebastes 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					
16–18 Apr 1999	<i>Pacific</i>	11	54 (45)	48 (46)	27 (6)
13–16 Sep 1999	<i>Pacific</i>	7	18 (13)	47 (32)	8 (0)
Subtotal of quarterly fishery sampling		49	167 (139)	274 (194)	104 (65)
27 Jun–7 Aug 1998 (NMFS survey)	<i>Dominator Vesterallen</i>	56	360 (312)	—	—

(Mackas and Galbraith, 2002; Keister and Peterson, 2003; Keister et al., 2005). With major changes in environmental conditions, and consequent changes in zooplankton abundance and community structure, one would expect to observe changes in the food habits of planktivorous fish species.

The objectives of this study were 1) to describe the food habits of three commercially important rockfish species (yellowtail [*S. flavidus*], widow [*S. entomelas*], and canary [*S. pinniger*] rockfish) over the study period (1998–99), during which the ocean environment underwent considerable changes, 2) to examine the relationship in these rockfish species between dietary variation and extrinsic factors: spatial (depth, latitude), temporal (time of day, season, year), and biological (predator type, sex, fish size), and 3) to compare the diets of *S. flavidus* collected during El Niño year 1998 with the diets reported during 1980, a non-El Niño year (Brodeur and Pearcy, 1984), to examine possible changes between the two periods.

Materials and methods

Data collection

There were two different types of sampling sources for the study: quarterly fishery samplings and U.S. National Marine Fisheries Service (NMFS) summer surveys. These data sets were maintained and analyzed separately. From the quarterly fishery samplings, stomach samples of three rockfish species, *S. flavidus*, *S. entomelas*, and *S. pinniger*, were collected off the Oregon coast during seven fishing trips aboard Oregon trawlers over six consecutive quarters from spring of 1998 to fall of 1999. Each trip consisted of two to four days of fishing. A total of 398 nonempty stomach samples of the three rockfish species were collected from 49 dif-

ferent stations over the six quarters. From the 1998 NMFS summer bottom trawl survey, stomach samples of only one rockfish species (*S. flavidus*) were collected off the Oregon and Washington coasts, and 312 nonempty stomach samples were collected from 56 stations during this survey (Table 1). Additional data on *S. flavidus* were obtained from stomach contents samples collected off Oregon and Washington during the 1980 summer NMFS survey (R. Brodeur, personal commun.¹). The data were made available at the individual stomach level (128 nonempty stomach samples) and were compared with the 1998 summer NMFS survey data on *S. flavidus*.

The NMFS samples were collected at stations allocated by 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 laid across the depth strata, with at least one station assigned to each depth stratum along each trackline segment. Each trawl haul was made for 30 minutes at a given station. In contrast, for the quarterly sampling aboard the commercial fishing boats, the fishermen selected the trawling stations on the basis of sonar detection of large schools of rockfishes on the bottom. These different sampling schemes resulted in different coverage of the study area. The quarterly fishery samplings covered a confined area off the Oregon coast, whereas the NMFS survey covered a wider range of coastal waters (Fig. 1), but only during summer.

Individuals of the three targeted rockfish species were randomly selected from the catch and their stomachs were removed at sea. Before a stomach was removed, the buccal cavities were examined for evidence

¹ R. Brodeur. 2001. National Marine Fisheries Service, Northwest Fisheries Science Center, 2030 S. Marine Science Dr., Newport, OR 97365-5296.

of stomach eversion, regurgitation, or feeding in the net. Fish were discarded if they showed signs of any of these actions. Each valid stomach was wrapped in a cloth bag and tied with a tag indicating the species type, sex, fork length (cm), date of sampling, and sampling location, and then preserved in a 10% buffered formalin solution. After arrival at the laboratory, the stomach samples were rinsed with water, and transferred and stored in 70% ethanol for later 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 0.01 gram and recorded.

Data analysis

To quantify and summarize the diets within each of the two data sets, the quarterly fishery data and the NMFS summer survey data, we calculated the percent frequency of occurrence and the percent by weight of each prey item for each fish species over each season in a given year. The frequency of occurrence was calculated by dividing the number of stomachs containing a particular prey item by the number of nonempty stomachs in a given season. The percent by weight was calculated by dividing the total weight of a particular prey item by the total weight of the stomach contents in a given season. Samples in the quarterly fishery data set were grouped into four different seasons: winter (December–February); spring (March–May), summer (June–August), and fall (September–November).

Many factors potentially influence the diet patterns of fish, such as biological factors (species, sex, and length), spatial factors (latitude and depth), and temporal factors (daily, quarterly, and annually). Many methods of quantitative analysis, ranging from univariate to multivariate statistical techniques, have been proposed for examining the variation of diets in relation to extrinsic factors (Hyslop, 1980; Cortés, 1997). However, no single method has been accepted as being the best to represent variability in fish food habits. For food-habit studies individual diet information is often aggregated at a population level or across certain extrinsic factors for a statistical comparison of diets. In most studies there is no attempt to formally evaluate diet variability, except at the level of aggregate mean values. Such data aggregation techniques attempt to overcome the multivariate nature of diet data and the problems associated with the high variability and unequal weighting 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 erroneous conclusions as to the significance of a factor because an analysis based on aggregated data cannot simultaneously account for other factors or assess possible interactions with other factors.

For this study, we employed a multivariate method, principle component analysis (PCA), to examine the patterns of individual diet compositions in relation to sets of extrinsic factors. With the PCA, the measures of diet composition are extracted in a low-dimensional ordination space, based on the individual stomach diet information. We can then relate extrinsic factors to the ordination scores of stomach samples extracted from the PCA to test whether or not the factors are related to dietary variation. We can also gauge the relative

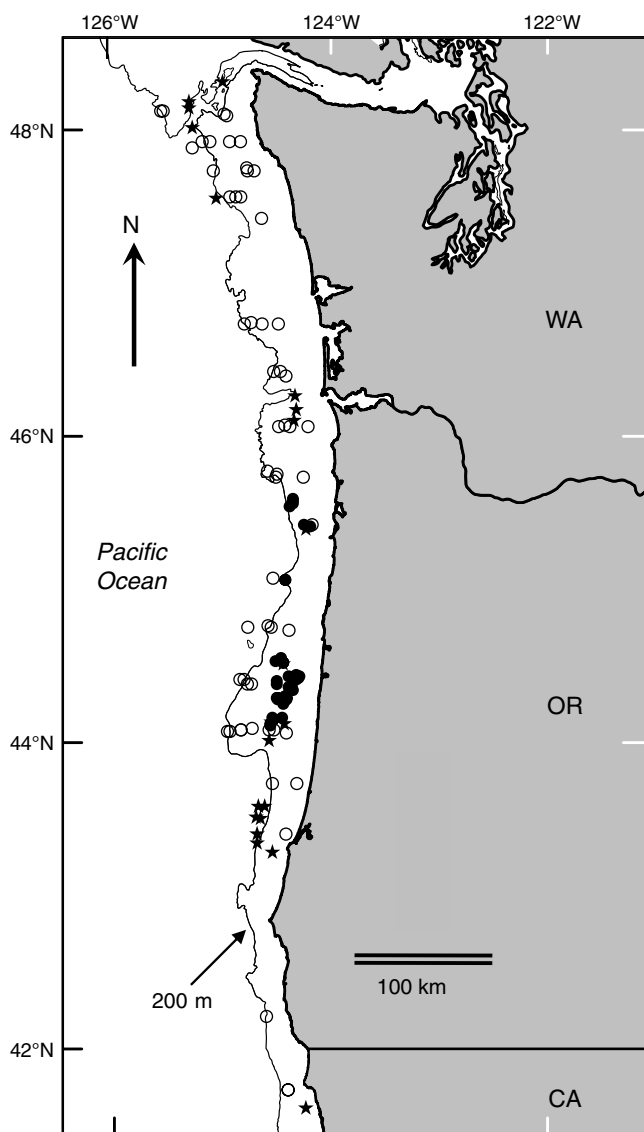


Figure 1

Map of locations sampled for three rockfish species stomachs: *Sebastes flavidus*, *S. entomelas*, and *S. pinniger*. Each symbol represents different sampling collections: solid circles for the seasonal quarterly collections (April 1998 to September 1999); open circles for the 1998 NMFS survey collections; stars for the 1980 NMFS survey collections.

Table 2

Extrinsic factors and their levels that were examined in the analyses of diet variability in rockfish species. Two data matrices were formed for the analyses: quarterly fishery samples (April 1998 to September 1999) and NMFS summer survey samples (1980 and 1998). Given in parentheses are the numbers of nonempty stomach samples for each level of the given factor across all other factors.

Data matrix	Factors	No. of levels	Levels	
Quarterly fishery samples	Predator	3	<i>S. flavidus</i> (139), <i>S. entomelas</i> (194), <i>S. pinniger</i> (65)	
	Season	6	Six seasons (81, 101, 51, 23, 97, 45)	
	Depth	2	<146 m (304), >146 m (94)	
	Time of Day		3	Morning (before 10 a. m.) (90)
				Midday (10 a. m.–5 p. m.) (230)
				Evening (after 5 p. m.) (78)
NMFS summer survey samples	Sex	2	Male (162), Female (236)	
	Fish size	3	<40 cm (136), 40–45 cm (203), >45 cm (59)	
	Year		2	1980 (128), 1998 (312)
		Latitude		4
				45°–47° (137), 47°–49° (99)
	Depth		3	<110 m (113)
				110–165 m (222)
				>165 m (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)		

importance of the factors by variance partitioning in a linear model.

For the analysis of dietary variation, we formed two matrices of prey species composition data based on the two sampling schemes: a quarterly fishery sample data matrix for the three rockfish species collected from commercial fishing trips, and a summer survey sample data matrix for the *S. flavidus* stomachs collected during the 1980 and 1998 NMFS summer surveys. Some unique extrinsic factors, as well as shared factors, were associated with each data matrix. The unique extrinsic factors associated with the quarterly fishery sample data matrix were predator type and season. We used this data matrix to examine differences among the three rockfish species and the quarterly patterns in their diets but could not explore a latitudinal effect because of the limited geographic coverage of the samples. The unique extrinsic factors associated with the NMFS summer survey data matrix were year (1980 and 1998) and latitude. Other factors tested for both data matrices were depth, time of day, sex, and fish size. All factors were treated as categorical variables. A summary of the factors, their levels, and the number of corresponding stomach samples for each data matrix are given in Table 2.

For the analysis the prey species were grouped into seven major prey groups: euphausiids; fishes; salps; heteropods; jellyfishes (species other than salps and heteropods in the gelatinous zooplankton group); decapods;

and miscellaneous prey items. To remove the problem of unequal weights across the samples in the PCA, the weights of prey groups were standardized to proportions based on the total stomach contents weight for each individual fish stomach. In the data matrices each row represented an individual fish stomach and each column represented a prey group. The value of each cell in a data matrix is the weight proportion of a particular prey group in a particular fish stomach. Before running the PCA, we transformed the weight proportions (WP) using the angular transformation, $(2/\pi)$ arcsine ($WP^{1/2}$), which is considered an appropriate transformation for proportion data for improving the assumptions of normality and the homogeneity of variance (Sokal and Rohlf, 1994).

After running the PCA we fitted a series of general linear models (GLMs) to the sample scores extracted from the primary PCA axes to relate the diet compositions to the extrinsic factor. Different strategies are available for the selection of independent variables in a GLM: forward selection; backward elimination; stepwise selection; or use of statistical information criteria (e.g., Akaike information criteria) (Ramsey and Schafer, 2002). For our study, which had limited data, we took a parsimonious approach in selecting variables: a forward selection strategy with a constraint on the maximum level of interactions. We did not consider interactions higher than two-way interactions. Given the limited number of samples (Table 2) it seemed unlikely that

we could detect reliably higher-level interactions. Also, this strategy was necessary because the degrees of freedom could become exhausted as higher interaction terms were added to the model. The model was first fitted with the full set of main effects and the most insignificant terms were then eliminated one at a time until all of the remaining variables were significant ($P < 0.05$). The resulting model was then fitted with the selected main effects and all possible two-way interactions of those effects. The model was further refined by removing the most insignificant interaction terms one

at a time until no further terms could be removed at a significance level of 0.05.

Results

Description of the diets

The detailed stomach contents data for these species were summarized in terms of frequency of occurrence and percent by weight over each season and year in tables (not presented because of space limitations, but available from the authors). A general description of the diet of each species follows.

***S. flavidus*—Quarterly fishery samples** Yellowtail rockfish preyed upon diverse groups of pelagic planktonic organisms. Although important prey species or groups varied from season to season, in general euphausiids (mainly *Euphausia pacifica*) were the dominant prey group by both occurrence and weight across the seasons (Fig. 2A). Various fish species frequently were found in the diets and fish comprised an important prey group, although the species types varied over the seasons. Juvenile Pacific whiting (*Merluccius productus*) were found in samples from the 1998 spring and summer collections. They were not an important prey item during spring (0.1% by weight, 17.2% by occurrence), but became the most important item by weight in the diets during summer (37.4% in quarterly fishery sampling, 32.5% in the 1998 summer survey). Slender sole (*Lyosetta exilis*) was the top prey item as a single species by weight (42.2%) during the fall of 1998.

Some prey types dominated the diets during certain quarters. Jellyfish species were important in spring and summer of 1998. However, because of their soft fragile body structure and high digestion rate in the stomach, detailed species identification was not possible. Whitish mucus-like digested material was often encountered in the stomachs and was believed to be the digested remains of either Siphonophora or Ctenophora. This unidentified gelatinous zooplankton prey group constituted the number one prey item both by weight (71.1%) and by occurrence (46.2%) in the diets of *S. flavidus* in fall 1999.

Shrimp species were moderately important by weight and occurrence in the fall of 1998 (*Pandalus jordani*, 7.5%) and 1999 (*Sergestes similis*, 9.8%). *Clione* spp. occurred frequently only in the summer 1998 samples from the quarterly fishery and summer survey collections. This prey group was moderately important (10.7% by weight and 27.8% by occurrence) in the 1998 summer survey sample but was less frequent (3.4%) and did not make up more than 0.1% by weight in the quarterly samples. Salps were the most important

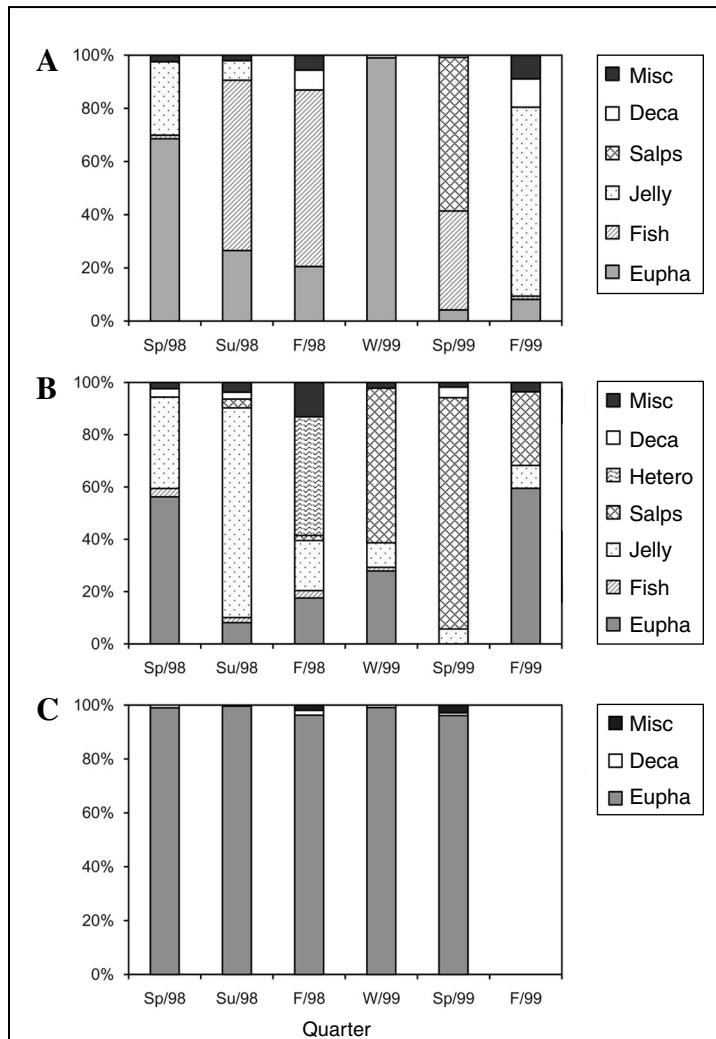


Figure 2

Quarterly variations in stomach contents (percent by weight) of the three rockfish species: (A) *Sebastes flavidus*, (B) *S. entomelas*, and (C) *S. pinniger*. Prey categories contributing more than 1% to the total prey weight in a given quarter were defined as separate prey categories. Trivial prey items, contributing less than 1%, were grouped into the miscellaneous group. The labels for the x axis denote the quarter and year: Sp (spring), Su (summer), F (fall), W (winter), 98 (1998), and 99 (1999). Deca=decapods, Eupha=euphausiids, Hetero=heteropods, Jelly=jellyfishes, Misc=miscellaneous.

prey species both by weight (61.5%) and occurrence (80%) in the spring 1999 samples. The numerous planktonic amphipod species were frequently observed in all seasonal quarters except during the winter of 1999, but there were of minor importance in terms of weight.

***S. entomelas*—Quarterly fishery samples** The prey groups eaten by widow rockfish were as varied as those eaten by *S. flavidus*. However, the importance of the fish prey species group in the overall diet was less than it was for *S. flavidus* (Fig. 2B). Juvenile Pacific whiting were found in the diets during the spring and summer of 1998, but were not an important prey in either quarter (<0.7% in weight, <5.4% occurrence). Euphausiids (mainly *E. pacifica* and *Thysanoessa spinifera*) and jellyfishes were major prey items by both weight and occurrence in most quarters. Salps were prey in all seasons and became the most important prey in 1999. In particular, salps were found in more than 95% of the stomach samples collected during the spring of 1999 and were an exceptional prey source in terms of weight (92.6%). This may account for the absence of euphausiid species in the diets during that season. The heteropods was the highest prey group both in terms of weight (45.3%) and frequency of occurrence (45.8%) in the fall of 1998.

***S. pinniger*—Quarterly fishery samples** The number of prey taxa identified in the stomachs of *S. pinniger* was substantially fewer than those in the stomachs of *S. flavidus* and *S. entomelas*: 22, compared to 45 and 44, respectively. Euphausiid species (mainly *E. pacifica* and *T. spinifera*) were the most dominant (>95%) prey group by weight in the diets over all quarters (Fig. 2C). In some quarters, decapods (shrimps) occurred frequently (around 20%) but with little contribution in weight. Salps did not appear in the diets even during quarters when salps were a major prey item for *S. flavidus* and *S. entomelas*. Nonempty stomachs were not present in the fall quarter samples of 1999, when few stomachs of *S. pinniger* were collected (n=8).

There were considerable quarterly variations in the prey groups by weight in the diets of *S. flavidus* (Fig. 2A) and *S. entomelas* (Fig. 2B). The dominance and the degree of contribution of the prey groups changed from quarter to quarter for these two fish species. In contrast, over all the quarters studied *S. pinniger* (Fig. 2C) maintained a diet consisting almost completely of euphausiids (>96.1%) but the sample sizes for this species were quite small.

***S. flavidus*—NMFS summer surveys in 1980 and 1998** The major differences between the diets of *S. flavidus* in 1980 and 1998 were the occurrence of unusual prey species of southern origin and the dominance of gelatinous zooplankton species in the 1998 samples. The southern prey species were frequently found in 1998 samples, *Nyctiphanes simplex* (euphausiid) and juvenile *M. productus*, with occurrences of 2.2% and 36.8%. These prey species, which are thought to be a

major signature of El Niño in the diets of *S. flavidus*, were not found at all in the stomach samples from 1980. *Merluccius productus* was the single most important prey species by weight (32.5%) in 1998, whereas *E. pacifica* was most important (26.4%) in 1980. Fishes were important prey items in 1980. The major species present was herring (*Clupea harengus pallasii*, 18.4%), which was not observed in the 1998 stomach samples. Various gelatinous zooplankton species frequently occurred in the stomach samples, composing the second most important prey group by weight (33.3%) after the fish group (41.4%). The gelatinous zooplankton species found in the 1980 stomach samples were *Sagitta elegans* and *Limacina helicina*, and they made a minimal contribution with less than 0.1% by weight.

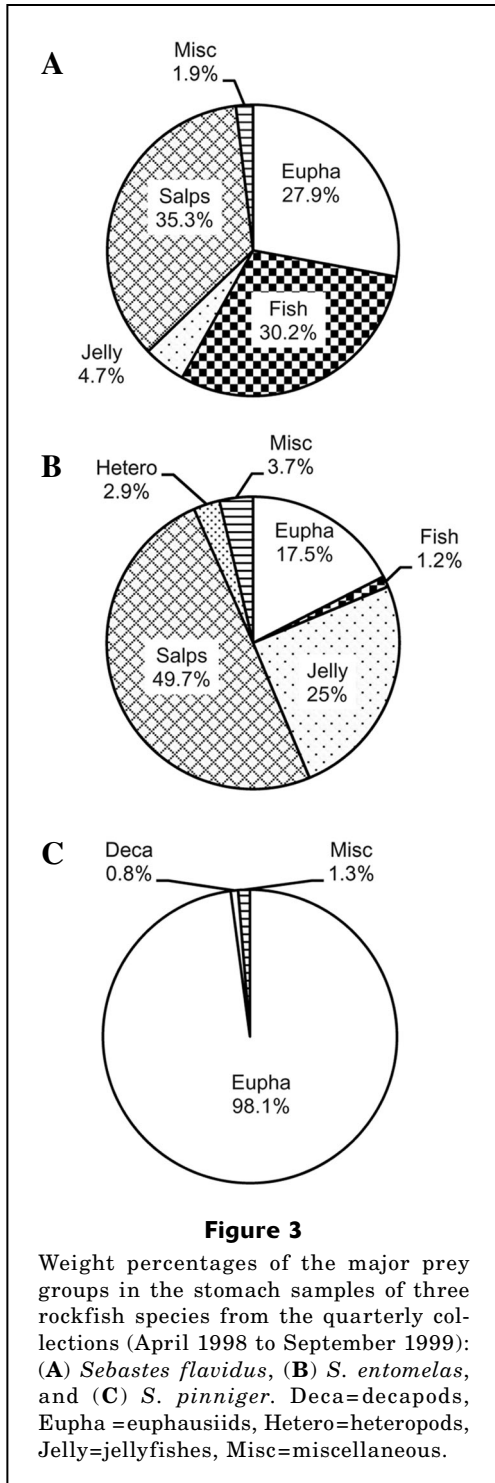
Diet comparison based on major prey groups

The weight proportions (average ratio) of the seven prey groups, calculated across the six quarters, demonstrated overall differences in the diets among the three rockfish species during the study period (Fig. 3). 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 fishes were a major item for *S. flavidus* (30.2%).

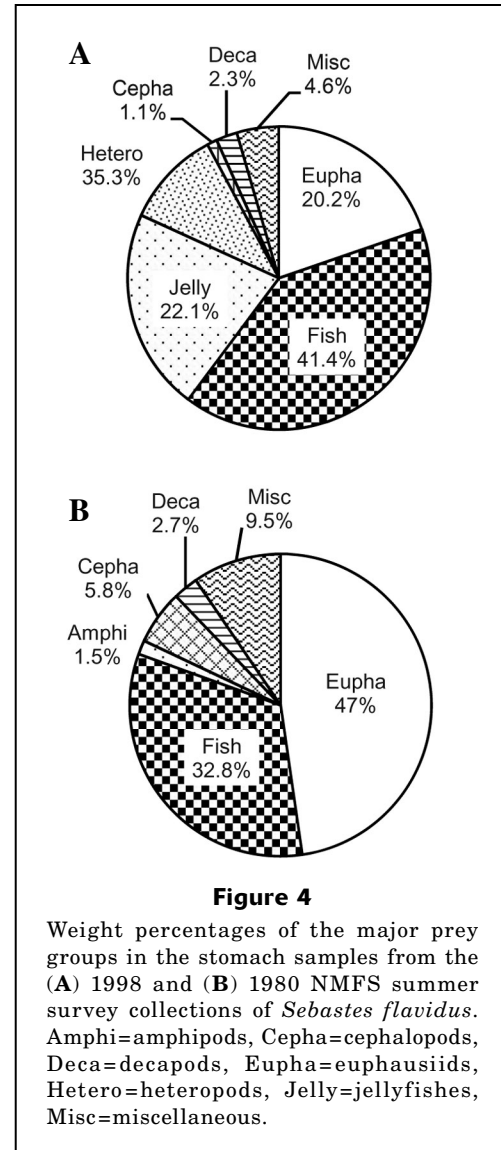
The major difference between the NMFS summer survey samples for *S. flavidus* in 1998 and 1980 was the role of jellyfishes (22.1%) in 1998 as a major prey group. It was the second most important prey group by weight after the fish group (41.4%) (Fig. 4A). In 1980, jellyfishes did not even represent a major prey group (Fig. 4B). When the 1998 NMFS summer survey samples for the diets of *S. flavidus* are compared with the 1998 summer samples from the quarterly fishery sampling, the more geographically restricted quarterly fishery samples show less feeding on jellyfish (7.3%) (Fig. 2A). The importance of euphausiids by weight was less distinctive in 1998 (20.2%) than in 1980 (47%). It appears that *S. flavidus* depended more on euphausiids in 1980 than in 1998. The importance of the fish prey group in 1998 (41.1%) was more than the fish prey group in 1980 (32.8%) because of the major contribution of *M. productus* in 1998.

Diet variability in relation to extrinsic factors

The PCA for the quarterly fishery samples was successful in accounting for 73.6% of the total variability in the prey composition data, with the first two PCA axes explaining 43.5% and 30.1%, respectively. Similarly, the percentage of the total variability in the summer survey data accounted for 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 adequately represent the food habits of the fish species based on individual stomach content information.



The PCA ordination scores for the individual stomach samples are plotted in the ordination space defined by PCA axis 1 and axis 2 (Fig. 5). The ordination scores of the seven major prey species groups obtained from the transposed PCA analysis are overlaid on the graph. The location of each prey species label on the graph represents the association of that prey species in relation



to the surrounding stomach sample points on the graph in terms of its dominance in the diet composition of the stomach samples. For example, the stomach sample points of *S. pinniger* in Figure 5 were tightly clustered around the middle portion of the rightmost side of the graph. When the ordination scores of prey species were overlaid, the score for euphausiids was located very near the stomach samples of *S. pinniger*. This result occurs because the euphausiid group was the dominant prey species group in the diet composition of those stomach samples.

The general linear models for the PCA scores from the quarterly fishery samples 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 to predator type, season, and their interaction, which implies that the food habits differed between

the species and changed differently over the seasons.

The factor "predator type" accounted for most of the variability in the PCA axis 1 scores in terms of mean squares ($MS=10.152$, $df=2$), and season accounted for most of the variability of the axis 2 scores ($MS=1.643$, $df=2$). In other words, PCA axis 1 mostly measured differences between the fish species and PCA axis 2 mostly measured quarterly changes in their food habits. In building the models for the food habits of the three rockfish species from the quarterly fishery collections, we found that the other variables considered (depth, time of day, sex, and fish size) were not significant ($P>0.05$). The two sets of PCA scores predicted by the GLMs summarize the diet variation of species over the six quarters (Fig. 6) and show that the diet of *S. pinniger* was stable over the quarters, whereas the diets of *S. flavidus* and *S. entomelas* were not stable and did not vary in parallel.

Separate groupings of the 1980 and 1998 NMFS summer survey samples were fairly evident in the PCA ordination space (Fig. 7), which had a triangular appearance similar to that of the PCA plot from the quarterly fishery collections. Again, the proportions of euphausiids, fishes, and jellyfishes were the primary prey items determining the shape of the PCA plot; the fish stomachs at the points of the triangle had only one prey-item species of euphausiids, fishes, or jellyfishes. However, there were no 1980 summer survey samples in the upper portion of the scatter plot, which corresponded to samples where jellyfishes and heteropods were major prey species in the 1998 samples. This finding, based on individual stomach sample data, corresponds with the result based on the weight proportions calculated from aggregated samples (Fig. 4), in which a dominance of these prey groups in the diets of *S. flavidus* was found in 1998 but not in 1980.

According to the general linear model for the PCA scores, the diet composition of *S. flavidus* from the summer survey collections was related with extrinsic factors in a more complicated fashion than was apparent in the quarterly fishery samples ($F_{14, 425}=18.28$, $P<0.0001$, coefficient of determination (r^2)=0.376 for axis 1; $F_{21, 418}=30.43$, $P<0.0001$, $r^2=0.395$ for axis 2). Year, latitude, and depth were significant main effects for the first PCA component scores. The significant interaction terms were year by latitude and depth by latitude. The most influential variable was the interaction between year and latitude ($MS=3.714$, $df=2$). The model for the axis-2 scores included terms for time of day and the interaction between time of day and latitude, along with those factors that were significant in the model for axis 1. The interaction between time of day and latitude was the most influential term in the model ($MS=1.646$, $df=5$). In general, PCA axis 1 was mainly associated with differences in the food habits between the years

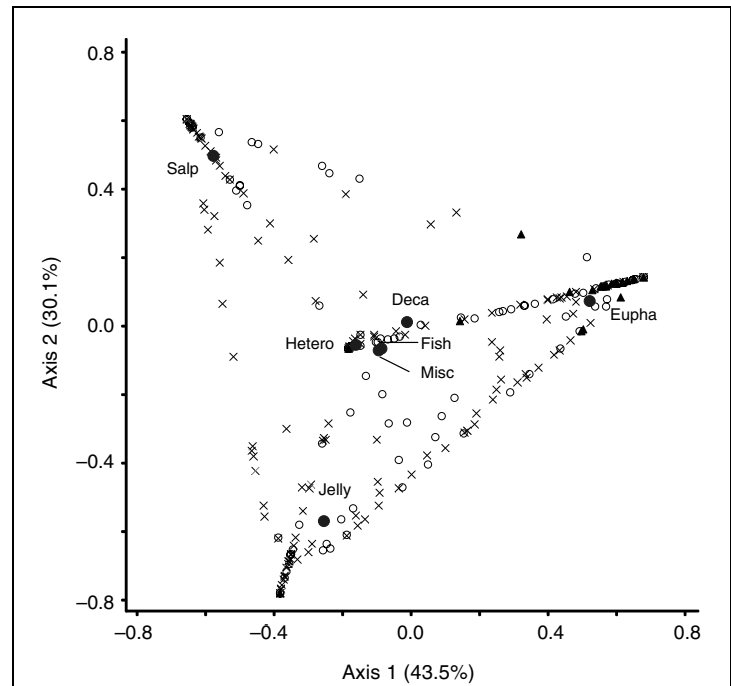


Figure 5

The principle component analysis (PCA) plot for diet compositions of the seasonal quarterly collections of three rockfish stomach species samples: *Sebastes flavidus* (crossed hatch), *S. entomelas* (open circle), and *S. pinniger* (closed triangle). Each point represents an individual stomach sample. In parentheses on the axis labels are the percentages of the total variance in the data explained by each axis. The prey species groups (large closed circles) are overlaid in the same ordination space according to a weighted average of the individual PCA scores: Deca=decapods, Eupha=euphausiids, Hetero=heteropods, Jelly=jellyfishes, Misc=miscellaneous.

and PCA axis 2 with latitudinal effects. The predicted values of the PCA-1 scores for each year and over latitude illustrated that the diets of *S. flavidus* were different in 1998 and 1980, and had different trends with latitude (Fig. 8). Similarly, the predicted PCA-2 scores for time of day and over the latitude showed that the diet pattern differed with the time of feeding and the geographic location of feeding. The complicated models, with significant interactions between temporal and geographical factors, indicate that the *S. flavidus* food habits are not determined by single factors alone. Interestingly, as in the case of the quarterly fishery collections, the fish characteristics (sex and fish size) were not significant explanatory variables for the food habits of *S. flavidus* from the summer survey collection.

Discussion

The three rockfish species examined in this study, which covered a period of unusual oceanographic events (El Niño and La Niña), mostly preyed upon pelagic

macrozooplankton. This finding generally concurred with that from other studies of the diets of rockfish species during normal ocean conditions (Pereyra et al., 1969; Lorz et al., 1983; Brodeur and Pearcy, 1984). However, the dominant prey species differed from previous studies.

The results from the PCA on the diet composition of the rockfish species indicate that patterns in their diets are associated with geographical components (latitude, depth), temporal components (annual, seasonal, diel), and their interactions. The complicated interactions between the geographical and temporal variables in the model for *S. flavidus* from the NMFS summer survey collections, in particular, indicate that the predation pattern for this species was very temporally localized and thus that *S. flavidus* is an opportunistic feeder. An opportunistic feeder in fish ecology refers to a fish species that takes advantage of transitory food sources that are normally outside of its usual diet. The term also describes disproportionately high feeding on food sources that are unusually abundant in a given time frame (Gerking, 1994).

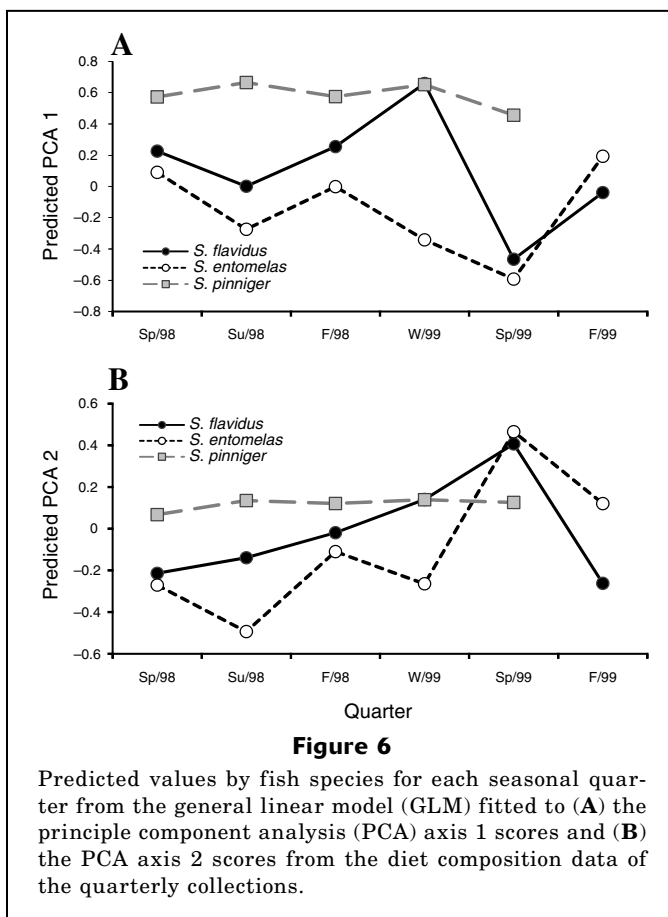
The study by Reilly et al. (1992) on the diets of the pelagic stages of five juvenile rockfish species (*S. flavidus*, *S. entomelas*, *S. goodei*, *S. jordani*, and *S. paucispinis*) off central California found strong annual variation, as well as spatial variation (latitude, depth,

and interaction) in the diets, but no significant variation with fish size-class. Even though the life stage of the samples was different from that in our study (adults), there was a strong similarity in terms of significant extrinsic factors related to dietary variability. The opportunistic feeding pattern during the juvenile stage was also consistent with our finding for adult stage of *S. flavidus* and *S. entomelas*. From the finding of high interannual variability in the diet with low intraspecific dietary overlap, they deduced that some pelagic juvenile *Sebastes* spp. had an opportunistic feeding strategy.

One noteworthy finding in our study was that the early juvenile stage of *M. productus* often occurred in the stomachs of *S. flavidus* and *S. entomelas* in the spring and summer of 1998, but then disappeared from both species diets later in the year. Previous studies have not reported Pacific whiting as prey of *S. flavidus* in the northeast Pacific. Pacific whiting are generally known to spawn off southern California during winter (Bailey et al., 1982). However, Phillips et al. (2007) provided evidence that since 2003 there have been northward shifts in the nursery areas of Pacific whiting juveniles into southern Oregon. The appearance of whiting in the diets of *S. flavidus* in our study may be due to the anomalous effects of the 1997–98 El Niño or may reflect a more persistent change.

Another unusual southern species in the diets was the euphausiid species, *N. simplex*. This prey species was commonly observed in the stomach samples of all three rockfish species during the spring of 1998. Brodeur (1986) found this southern species in the stomachs of some fish species off the Pacific Northwest during the 1983 El Niño. Brodeur and Pearcy's (1984), during the non-El Niño year of 1980, did not report *N. simplex* in the diet of either *S. flavidus* or *S. pinniger*. Studies of zooplankton off Oregon and Vancouver Island, farther north of the sampling locations in our study, confirmed the appearance of some southern zooplankton species, including *N. simplex*, during the 1997–98 El Niño years (Mackas and Galbraith 2002; Peterson et al., 2002; Tanasichuk and Cooper 2002; Keister et al., 2005).

Another noteworthy finding of our study was that jellyfish species were the dominant prey for *S. flavidus* and *S. entomelas* in some quarters. The amount and the occurrence of jellyfish species in the diets of *S. flavidus* from the 1998 summer survey collection were much higher than reported by Brodeur and Pearcy (1984). The importance of euphausiids as prey for many planktivorous fish populations, including rockfish species in the northeast Pacific Ocean, has been established in previous studies. However, jellyfish species (gelatinous zooplankton) were ordinarily regarded as minor food sources for most rockfish species. Raskoff (2001) reported detecting changes in the species composition and abundance of jellyfish species off Monterey Bay in California during the El Niño events of 1991–92 and 1997–98. Considering the rapid growth rate



and turnover times of jellyfishes, it may have been possible for them to become a dominant component of the ecosystem during the period of our study, when it was disturbed first by El Niño and then again by a transition to La Niña (Lavaniegos and Ohman, 2003). In general, quantitative measures of jellyfish in fish diets are likely to be underestimates because jellyfish are rapidly digested and are difficult to identify due to the damage they suffer when consumed and digested (Arai et al., 2003).

Sebastes flavidus and *S. entomelas* exhibited substantial seasonal variations in their diets, as has also been reported in other studies (Brodeur and Pearcy, 1984; Adams, 1987). Interestingly, although the diets of these two species varied from season to season, possibly responding to changes in the prey field, *S. pinniger* continued to prey almost exclusively on euphausiids during all six quarters of our study. This extreme and seasonally constant dominance of euphausiids agrees with the Brodeur and Pearcy (1984) study. Compared with *S. flavidus*, *S. entomelas* seems to have a greater preference for gelatinous prey organisms, such as jellyfishes and salps, which is intriguing because these rockfish species tend to co-occur in the fishery and are considered to occupy the same habitat. The difference between the species does not appear to be an artifact of sampling. For the quarterly fishery collections in 1998 and 1999 all three species were caught concurrently in 15 out of 49 trawl hauls. The proportions by weight of the major prey groups (based on only the data from these 15 hauls) were very similar to the proportions by weight (based on all 49 stations) (Table 3).

The similarity between the results from the subset and overall data set is important in terms of regurgitation. Although fishes were thoroughly examined for signs of regurgitation, it was still possible that partially regurgitated samples were included as valid intact samples. If that is the case, the data in our study would not provide an unbiased view of the feeding habits of fishes. However, the similarity between the subset and overall set would suggest that the regurgitation issue, even if it existed, did not affect the results of stomach content analyses that were based on proportions. As long as equal proportions of prey items by species and size were lost through regurgitation, then it would not influence the resultant stomach contents analyses. The assumption of loss of equal proportion through

Table 3

Percentages by weight of the major prey groups for the rockfish species (*Sebastes* spp.) that collected in the same trawling hauls during the quarterly collections from April 1998 to September 1999. There were 15 hauls out of a total of 49 hauls in which all three rockfish species were collected concurrently.

Prey groups	<i>S. flavidus</i>	<i>S. entomelas</i>	<i>S. pinniger</i>
Euphausiids	25.8	7.8	99.4
Fishes	32.1	0.4	0.1
Jellyfishes	1.4	24.8	0.3
Salps	39.5	63.6	—
Heteropods	<0.1	1.7	—
Decapods	0.6	0.5	0.2
Miscellaneous	0.6	1.2	<0.1
No. of nonempty stomachs	87	104	42

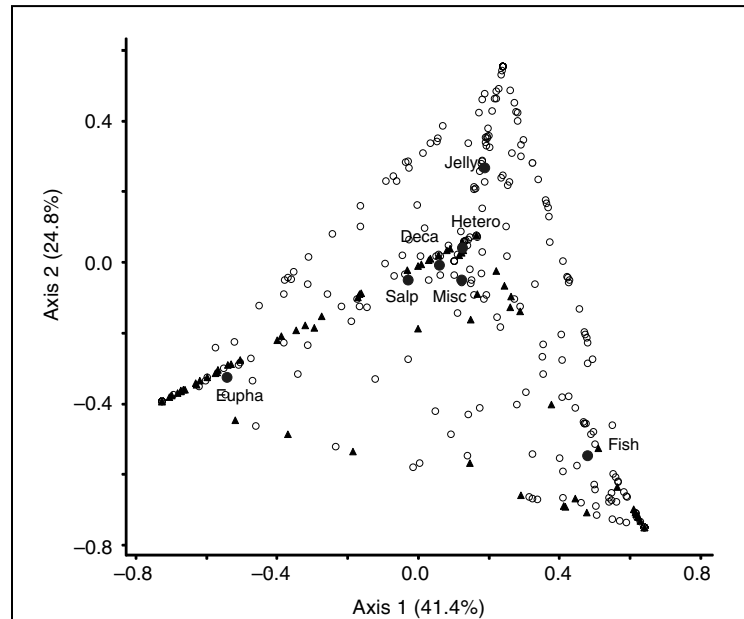


Figure 7

The principle component analysis (PCA) plot of the NMFS summer survey collections: 1980 samples (closed triangle) and 1998 samples (open circles). Each point represents an individual stomach sample. In parentheses on the axis labels are the percentages of the total variance in the data explained by each axis. The prey species groups (large closed circles) are overlaid in the same ordination space according to a weighted average of the individual PCA scores: DeCa=decapods, Eupha=euphausiids, Hetero=heteropods, Jelly=jellyfishes, Misc=miscellaneous.

regurgitation, however, needs to be validated by alternate methods, possibly by using an underwater trapping device to capture the fish.

The diet analyses in our study indicate that although these three rockfish species may occupy similar geographical habitat, they have evolved to occupy differ-

ent feeding guilds and they differ in their trophic adaptability (Dill, 1983). *Sebastes flavidus* and *S. entomelas* seem to be more opportunistic in their feeding habits and have a greater feeding plasticity in response to changing prey environments, whereas *Sebastes pinniger* is a specialist and has very limited feeding plasticity. The diverse rockfish species complex off Oregon seems to share some common physical features for feeding, but each species still holds distinctive features. *Sebastes flavidus* and *S. entomelas* are characterized as having small mouths with low protrusibility and a relatively long intestine, whereas *S. pinniger* has a high number of long and slender gill rakers that may facilitate its specialized feeding on euphausiids (Pequeño, 1984; York, 2005). Although it is not easy to pinpoint exactly which morphological characteristics are responsible for differences in the diets of the examined rockfish species, the subtle but distinctive dissimilarity in features, which would have been developed through evolutionary adaptations, could in part explain the differences in their diets.

It is challenging to infer which feeding habits are more advantageous to these three rockfish species. But in an environment where food resources are scarce, fish species with specialized feeding habits would generally have a harder time finding adequate prey. It is not known whether euphausiids species are a limiting food resource for these rockfish species or for other fish species in the region. Tanasichuk (1998a, 1998b) noted that euphausiid populations (*E. pacifica* and *T. spinifera*) have decreased fivefold in abundance since the early 1990s near Barkley Sound, a southwest Vancouver Island coastal embayment. It is not clear whether there has been a similar decrease in abundance of the euphausiid populations off Oregon during that time period, but it could be hypothesized that a similar decrease may have caused *S. flavidus* and *S. entomelas* to shift to other available prey resources, whereas *S. pinniger* suffered from the decreased availability of euphausiids. These hypotheses, however, are difficult to test given the lack of information on the trends in macrozooplankton abundance in the area and on rockfish food habits during that time period.

Mackas et al. (2001; 2004) reported observing seasonal and interannual changes in zooplankton biomass and community composition off Oregon and southern Vancouver Island, and reasoned that the changes were responses of the zooplankton community to ocean climate fluctuations and changing current patterns. The waters off California, Oregon, and Washington are subject to broad disturbances by El Niño events, which result in increased surface and near-surface water temperature, elevated coastal sea level, a deeper thermocline, anomalous coastal currents, reduced coastal upwelling, reduced nutrient concentrations and abundance of phytoplankton and zooplankton (Huyer et al., 2002). Keister and Peterson (2003) sampled the zooplankton community off the central Oregon coast

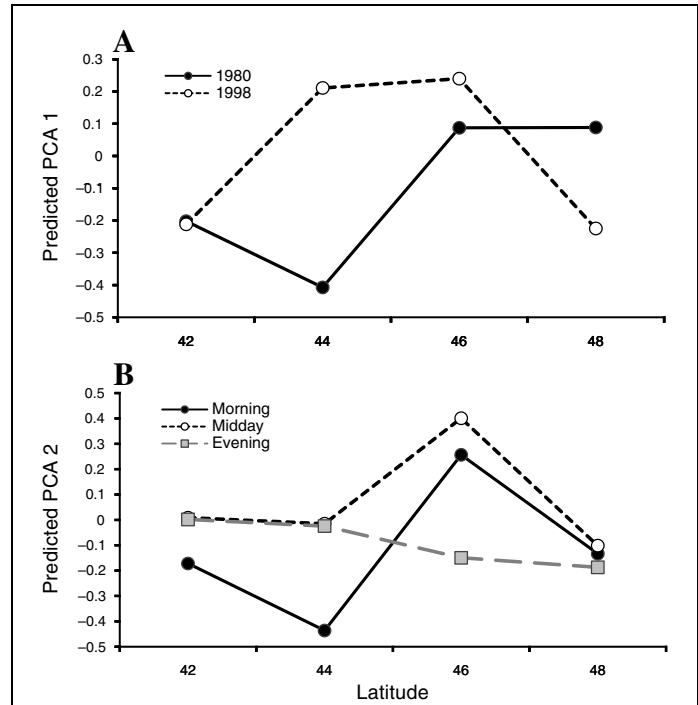


Figure 8

Predicted values from the general linear model (GLM) fitted to the principle component analysis (PCA) axes scores from the *S. flavidus* diet composition data of the NMFS summer survey collections. (A) PCA axis 1 predicted values by year for each latitude zone and (B) PCA axis-2 predicted values by time of day for each latitude zone.

over the time period of 1998–2000 and found that there were zonal and seasonal variations in the zooplankton community and that the 1997–98 El Niño played a significant role in structuring the zooplankton community. The effect of the 1997–98 El Niño on zooplankton was noted to have lasted far longer than its physical effects. It is clear from these studies that organisms at lower trophic levels in the coastal ecosystem are strongly influenced by long-term and short-term environmental perturbations. Many rockfish species are bottom oriented but feed on pelagic macrozooplankton species. One would expect these rockfish to be influenced by changes in zooplankton populations or community structure because they feed heavily upon species that are sensitive to environmental changes. However, findings regarding the diets of the three rockfish species in our study indicate that rockfish species do not all respond in the same way to such changes. A given species' response will largely depend upon its evolutionary traits, which govern how it can adapt to changing food environments. It is not known whether strong seasonal variations and the frequent dominance of gelatinous zooplanktons in the diets of *S. flavidus* and *S. entomelas* were just a short-term response to changes in the zooplankton community caused by anomalous oceanic events, El Niño and La Niña, or if these reflect a more

chronic phenomenon caused by long-term and large-scale climate change.

Although we have attributed the diet variability observed in this study to oceanographic changes, with supporting evidence from other studies, it should be noted that, because of the limited sampling coverage, we could not address the question of how much variability would be due to inherent interannual variability in the diets of these species. Also the prey partitioning and diet variability of these species could be a phenomenon localized only in the study area. Further monitoring of these rockfish species, as well as other fish species in the region, coupled with parallel investigations of the macrozooplankton community would provide a better understanding the relationship between the different trophic levels and the potential consequences of diet changes to the physiology and population biology of these fish species.

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