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Comparative feeding ecology of two sympatric rockfish congeners, *Sebastes caurinus* (copper rockfish) and *S. maliger* (quillback rockfish)

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Abstract Feeding ecology was compared between sympatric populations of *Sebastes* congeners, *S. caurinus* (copper rockfish) and *S. maliger* (quillback rockfish), to determine the potential for interspecific competition for food resources. A total of 602 copper rockfish and 285 quillback rockfish were collected from rocky reefs in Saanich Inlet, British Columbia, Canada, from October 1986 to August 1990. All fish were collected in 15 to 40 m depth, where the species are sympatric. Seasonal and size-related differences in diet composition, niche breadth and overlap of diets, diel variation in feeding, and quantity of food consumed were analysed to construct ecological profiles of the species. Overall, these two species had similar diets composed of pelagic and demersal fishes and crustaceans; both species consumed primarily demersal crustaceans throughout the year. Copper rockfish, however, consumed a greater proportion of pelagic fishes than quillback rockfish. Quillback rockfish had a greater proportion of pelagic crustaceans in their diet, especially during the spring and summer. The importance of fish in the diets of both species also increased with size. Copper and quillback rockfish consumed the greatest mass of food during the winter when feeding on juvenile herring (> 90% of the mass of their diets). Copper rockfish also consumed a greater quantity of food than quillback rockfish during the winter. This winter feeding may be significant in the timing of the reproductive cycle in these rockfish. Values for niche overlap in food habits based on the mass of food resources consumed by copper and quillback rockfish were relatively high (> 0.55) throughout the year, and in particular during the winter (0.99). Extensive niche overlap in the winter, however, occurred when niche breadths based on mass contribution were narrow. This was coincident with the presence of large schools of juvenile herring, and it was therefore assumed that herring were not a limited resource. Maximum niche overlap was therefore correlated with an abundance of a shared resource and hence did not indicate the presence of interspecific competition between copper and quillback rockfish.

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Introduction

Despite the diversity and abundance of rockfish in the northeastern Pacific Ocean (≃ 65 species) (Chen 1971), and their importance in sport and commercial fisheries (Hart 1973; Richards and Cass 1987; Love et al. 1990), detailed food habits are known for only ≃ 15 species (e.g. Gotshall et al. 1965; Patten 1973; Prince and Gotshall 1976; Moulton 1977; Hueckel and Stayton 1982; Brodeur and Pearcy 1984; Buckley and Hueckel 1985, Singer 1985; Rosenthal et al. 1988; Reilly et al. 1992). Many of these rockfish species co-occur, have similar morphology and occupy similar habitats, and are therefore potentially overlapping and competing for the use of resources (Larson 1980; Brodeur and Pearcy 1984; Murie 1991; Murie et al. 1994). Quantification of the niches of these sympatric species can provide a basis for determining potential competition over resources. Niche overlap in food resources may be indicative of potential competition if such resources are limited (Schoener 1974; Pianka 1981). Because food resources may be ephemeral, niche overlap may change seasonally and it is therefore important to determine not only the species composition of the diet, but also to assess any temporal changes in food habits and the variation in the use of food resources (niche breadth).

Two sympatric *Sebastes* congeners, the copper rockfish (*S. caurinus*) and the quillback rockfish (*S. maliger*), are of particular interest because of their abundance in nearshore areas of British Columbia (Richards 1987; Murie 1991; Murie et al. 1994) and their use in sports and commercial fisheries (Richards and Cass 1987; Hand and Richards 1991). These two species co-occur in benthic areas of rocky habitat and are morphologically and ecologically similar (Murie 1991). Previous food-habit studies of copper and quillback rockfish have been centered off the coasts of California, Oregon, Washington and Alaska. Feeding ecology of copper rockfish in coastal areas of the USA (Patten 1973; Prince and Gotshall 1976; Moulton 1977; Buckley and Hueckel 1985; Rosenthal et al. 1988) has been examined in more detail than the feeding ecology of quillback rockfish (Hueckel and Stayton 1982; Rosenthal et al. 1988). Seasonal or size-related changes in the feeding ecology of copper and quillback rockfish have been addressed in few of these studies (e.g. Patten 1973; Prince and Gotshall 1976).

The purpose of this study was to compare the feeding ecology of copper and quillback rockfish in Saanich Inlet, British Columbia, Canada, to assess the potential for competition between these sympatric species for food resources. Composition and quantity of food consumed by copper and quillback rockfish were compared on a seasonal and size-related basis. Niche breadth and niche overlap in the diets between species were also examined on a seasonal basis to compare their use of common resources. Finally, niche overlap in food habits between copper and quillback rockfish was related to the availability of the food resources in the environment as a qualitative indication of the potential for interspecific competition.

Materials and methods

Collection

Sebastes caurinus and *S. maliger* were collected from an area north of McKenzie Bight (Latitude 48° 34′ N; Longitude 123° 30′ W) in Saanich Inlet, British Columbia, Canada, from October 1986 to August 1990. In general, quillback rockfish tend to occur at deeper depths than copper rockfish (Murie et al. 1994). In Saanich Inlet, however, densities of both species have been observed to be greatest on discrete rocky reefs in 15 to 40 m (50 to 130 ft) water depth (Murie 1991). A total of 602 copper rockfish and 285 quillback rockfish were collected from these rocky reef areas, where they were sympatric. Fish were head-speared and immediately placed in individual plastic bags at depth to prevent the loss of regurgitated food. Total length (TL), wet body mass, and sex were recorded for each fish. Fish were then frozen and later dissected. The masses of the liver, gastrointestinal tract, gonads, and visceral fat (the fat covering the external surfaces of the viscera) were subtracted from the wet body mass of the fish to give an eviscerated wet body mass (referred to simply as body mass). The stomach was excised at its junction with the pyloric caeca, and its contents were removed for identification. Regurgitated food present in the collection bag and the buccal cavity of the fish was also recovered and included in the stomach-content analysis.

Food habit analyses

Composition of diet

The contents of each stomach were sorted into categories of pelagic or demersal fishes, pelagic or demersal crustaceans, and miscellaneous food items. Debris (e.g. rocks) and parasites were excluded from the analysis. Undigested fish recovered in the stomach contents were used to determine species (Hart 1973), as well as sizes and masses of individual fish whenever possible. Otherwise, fish were identified from their sagittal otoliths using a reference collection and Morrow (1979). Fish size was estimated using calculated regressions relating the length of the vertebral column or the length of the sagittal otolith to the standard length (SL) of the fish, or from calculated regressions relating fish length to fish mass (Murie 1991). Crustaceans and miscellaneous invertebrates were identified from whole or partial specimens using descriptions by Butler (1980), Hart (1982), Kathman et al. (1986), and Kozloff (1987). The number of each crustacean species consumed was determined by counting the total number of carapaces or bodies, or in the case of mostly digested mysids or euphausiids, by counting the total number of eyes and dividing by two. Masses of individual crustaceans were estimated by measuring undigested individuals or from calculated regressions relating carapace width, carapace length, or flexed-body length to whole-body weight (Murie 1991). All measurements were taken using vernier calipers (± 0.1 mm). The total mass of food consumed by each rockfish was estimated by summing the calculated masses for all individual prey items consumed by the fish.

The relative importance of food items in the diet of copper and quillback rockfish was expressed as: (1) percent occurrence of food items in stomachs; (2) percent numerical abundance of items; and (3) percent mass (Hyslop 1980). The presence or absence of food items in the stomachs of copper and quillback rockfish was analysed among seasons [winter (January–March), spring (April–June), summer (July–September), and fall (October–December)] and sexes. The occurrence of different food types in the diet and the presence or absence of food among seasons for different sizes of copper and quillback rockfish were also examined. Both analyses were done using chi-square contingency tables with Yate's correction for continuity (χ^2_c), when $df = 1$ (Zar 1984). Statistical significance was indicated by $P \leq 0.05$.

Diel differences in feeding between copper and quillback rockfish were assessed by examining the percentage of stomachs that were empty, and the percentage of body mass represented by the mass of stomach contents, from samples pooled into 2 h intervals. Collection times for individual fish sampled throughout the year were standardized to a day with sunrise at 06.00 hrs and sunset at 18.00 hrs Pacific Standard Time (Brodeur and Pearcy 1984), using sunrise–sunset tables supplied by the Dominion Astrophysical Observatory, Victoria, British Columbia.

The relationship between total mass of food consumed and body mass was examined for copper and quillback rockfish for within- and between-species effects due to season and sex using regression analysis. Dependent and independent variables were $\log_{10}$-transformed to correct for heteroscedasticity based on examination of diagnostic plots of residuals (Larsen and McCleary 1972; Kleinbaum and Kupper 1978). As a preliminary requirement to the use of a two-factor analysis of covariance (ANCOVA), the homogeneity (i.e., equality) of regression coefficients (slopes) of the groups to be analysed (males and females among the four seasons) was tested using a single-factor ANCOVA [Biomedical Computer Programs (BMDP), Program 1V; Dixon et al. 1983] with rockfish body mass as the single covariate (Tabachnick and Fidell 1983). When this preliminary assumption was satisfied, then the effects due to season or sex within each species were analysed using a two-factor ANCOVA (BMDP, Program 4V; Dixon et al. 1983).

Niche breadth and overlap

Niche breadth was estimated using Levins' (1968) measure (B) as standardized (B_A) by Hurlbert (1978). Values of niche breadth are expressed on a scale of 0 to 1; $B_A = 0$ when all the individuals, items, or mass occur in only one food category (maximum specialization), and $B_A = 1$ when the same number of individuals, items, or mass occurs in each of the food categories (no discrimination among food categories, a generalist) (Krebs 1989). For the purpose of estimating niche breadth, food resources were assumed to be equally available to both copper and quillback rockfish because collections were made only in areas where the two species of rockfish were sympatric.

Niche overlap between copper and quillback rockfish was measured using the Simplified Morisita index (C_H) (Horn 1966). Values of niche overlap vary from 0, when the two species share no food resources, to 1, when the two species have the same proportional distribution of use among the food resources (Colwell and Futuyma 1971).

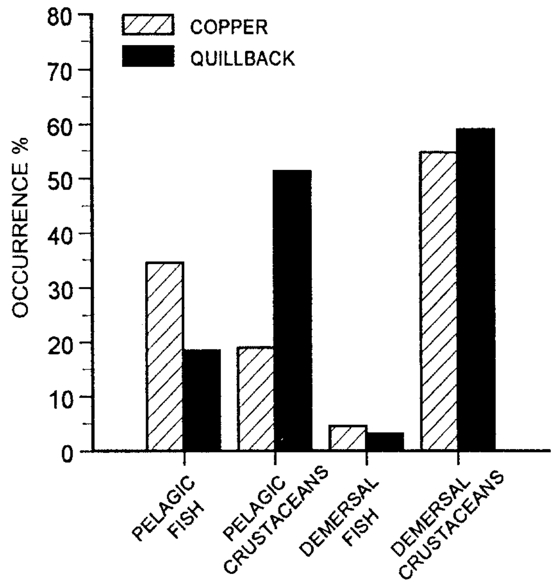

Fig. 1 *Sebastes caurinus* and *S. maliger*. Percent occurrence of different food types in stomach contents of copper and quillback rockfish

Results

General food habits

Overall, 47% (284 of 602) of the *Sebastes caurinus* and 55% (158 of 285) of the *S. maliger* collected had food items in their stomachs. For these rockfish, the type of food consumed (pelagic fishes, demersal fishes, pelagic crustaceans, demersal crustaceans) was species-dependent ($\chi^2_3 = 39.99$, $P < 0.001$) (Fig. 1). The occurrence of pelagic food or demersal food was independent of rockfish species ($\chi^2_c = 1.18$, $P > 0.25$), but the food type (fish or crustacean) was not ($\chi^2_c = 20.60$, $P < 0.001$). Overall, there was a higher occurrence of fishes in the diet of copper rockfish, and a higher occurrence of crustaceans in the diet of quillback rockfish (Fig. 1). Specifically, the majority of copper rockfish had fed on herring (*Clupea pallasi*), squat lobsters (*Munida quadraspina*), coonstriped shrimp (*Pandalus danae*), various small unidentified shrimps (primarily *Heptacarpus* spp.), and to a lesser extent mysids (*Xenacanthomysis pseudomacropsis*) (Table 1). All other species of prey were fed on by < 10% of the copper rockfish. Based on numerical abundance, however, pelagic crustaceans, such as euphausiids (*Euphausia pacifica*) and mysids, were consumed in the greatest numbers. The greatest contribution to the diet of copper rockfish on a mass basis was by pelagic fishes, such as kelp perch (*Brachyistius frenatus*), herring, and pile perch (*Rhacochilus vacca*). Demersal crustaceans [squat lobsters, coonstriped shrimp, and two-spot prawns (*Pandalus platyceros*)] contributed a further 20.3% to the diet's mass. The mass contribution by pelagic crustaceans was negligible (Table 1).

A large proportion of quillback rockfish had also fed on herring, squat lobsters, coonstriped shrimp, and various other unidentified shrimps, as well as pelagic crustaceans (Table 2). Numerically, pelagic crustaceans dominated the diet, and their mass contribution to the quillback diet was greater than for copper rockfish (10.8% vs 1.2%). On a mass basis, however, herring was the most important component in the diet, along with squat lobsters and coonstriped shrimp.

Seasonal changes in food habits

The proportion of copper rockfish that had food in their stomachs did not differ among seasons ($\chi^2_3 = 4.38$, $P = 0.22$) (Fig. 2). As well, the presence or absence of food in the stomachs of copper rockfish within each season was independent of sex of the fish (χ^2_c; all $P > 0.06$). In contrast, the proportion of quillback rockfish that had fed did differ among seasons ($\chi^2_3 = 15.75$, $P < 0.001$). Subdividing the contingency table (Zar 1984) indicated that quillback rockfish were found more frequently with food in their stomachs in spring and summer than in fall and winter ($\chi^2_c = 12.57$, $P < 0.001$) (Fig. 2). As with copper rockfish, the presence or absence of food in the stomachs within each season was independent of sex of the quillback rockfish (χ^2_c; all $P > 0.45$). Differences among seasons in the proportion of individuals with food in their stomachs were also evident between rockfish species ($\chi^2_3 = 27.11$, $P < 0.001$). Subdivision of the contingency table indicated that food was present in a greater proportion of quillback rockfish than copper rockfish during spring ($\chi^2_c = 7.47$, $P < 0.01$) and summer ($\chi^2_c = 6.02$, $P < 0.02$), but was in equal proportions during fall ($\chi^2_c = 0.99$, $P > 0.75$) and winter ($\chi^2_c = 0.07$, $P > 0.90$) (Fig. 2).

Table 1 *Sebastes caurinus*. Frequency of occurrence, numerical abundance, and mass of prey found in stomachs of copper rockfish collected from Saanich Inlet, British Columbia. Values in parentheses are percentages of totals

Prey taxa	Occurrence (%)		Numerical abundance (%)		Mass (g) (%)	
Pelagic fishes	98	(34.5)	128	(11.7)	675.2	(73.5)
Brachyistius frenatus (kelp perch)	11	(3.9)	11	(1.0)	80.8	(8.8)
Clupea pallasi (Pacific herring)	85	(29.9)	115	(10.5)	543.2	(59.2)
Rhacochilus vacca (pile perch)	1	(0.4)	1	(0.1)	51.2	(5.6)
Fish larvae	1	(0.4)	1	(0.1)	0.0	(0.0)
Demersal fishes	13	(4.6)	13	(1.2)	42.1	(4.6)
Coryphopterus nicholsii (blackeye goby)	5	(1.8)	5	(0.5)	26.8	(2.9)
Cottidae (sculpins)	2	(0.7)	2	(0.2)	0.6	(0.1)
Pholidae (gunnels)	6	(2.1)	6	(0.5)	14.7	(1.6)
Pelagic crustaceans	54	(19.0)	703	(64.5)	11.3	(1.2)
Euphausiids (*Euphausia pacifica*)	23	(8.1)	480	(44.0)	8.2	(0.9)
Gammarid amphipods	3	(1.1)	3	(0.3)	0.0	(0.0)
Hyperiid amphipods	3	(1.1)	18	(1.7)	0.1	(0.0)
Megalopa of crabs	1	(0.4)	1	(0.1)	0.0	(0.0)
Mysids (*Xenacanthomysis pseudomacropsis*)	31	(10.9)	201	(18.4)	3.0	(0.3)
Demersal crustaceans	155	(54.6)	236	(21.7)	186.2	(20.3)
Callianassa gigas (ghost shrimp)	1	(0.4)	1	(0.1)	3.9	(0.4)
Cancer gracilis	3	(1.1)	3	(0.3)	8.2	(0.9)
Cancer oregonensis	10	(3.5)	11	(1.0)	1.9	(0.2)
Cancer productus (red rock crab)	4	(1.4)	4	(0.4)	8.2	(0.9)
Chorilia longipes (deepwater decorator crab)	2	(0.7)	2	(0.2)	0.3	(0.0)
Hyas lyratus	1	(0.4)	1	(0.1)	1.0	(0.1)
Munida quadraspina (squat lobster)	63	(22.2)	85	(7.8)	30.0	(3.3)
Pandalus danae (coonstriped shrimp)	61	(21.5)	76	(6.9)	85.9	(9.4)
Pandalus platyceros (two-spot prawn)	5	(1.8)	5	(0.5)	29.9	(3.3)
Petrolisthes eriomerus (porcelain crab)	2	(0.7)	2	(0.2)	2.3	(0.2)
Pugettia gracilis (kelp crab)	2	(0.7)	2	(0.2)	6.4	(0.7)
Shrimp (unidentified)	33	(11.6)	44	(4.0)	8.1	(0.9)
Miscellaneous	5	(1.8)	10	(0.9)	3.3	(0.4)
Clavelina huntsmani (lightbulb tunicate)	1	(0.4)	6	(0.5)	0.7	(0.1)
Ophiura lutkeni (brittlestar)	1	(0.4)	1	(0.1)	0.2	(0.0)
Polychaeta (Errantia)	3	(1.1)	3	(0.3)	2.5	(0.3)
Totals	284	(100)	1090	(100)	918.1	(100)

For copper rockfish, demersal crustaceans were important prey throughout all seasons, increasing in occurrence from winter to fall (Fig. 3A). They were particularly important on a numerical basis during fall (Fig. 3B), but contributed substantial mass to the diet of copper rockfish during spring, summer, and fall (Fig. 3C). The occurrence of pelagic crustaceans in the diet of copper rockfish was common in spring and summer and relatively infrequent in fall and winter (Fig. 3A). Pelagic crustaceans were also important in terms of numerical abundance in spring and summer (Fig. 3B), but contributed little to the mass of food consumed within each season. Pelagic fishes had been eaten by a majority of copper rockfish in winter, and to a lesser extent in the other seasons (Fig. 3A). They contributed ~49% of the food items (Fig. 3B) and 93% of the mass (Fig. 3C) consumed by copper rockfish during the winter season. Pelagic fishes represented < 10% of the numerical abundance of food items and < 50% of the mass consumed by copper rockfish within other seasons. In contrast, demersal fishes were consumed by relatively few copper rockfish throughout the year (Fig. 3A), and represented < 5% of the food items (Fig. 3B) and ≤ 10% of the mass (Fig. 3C) consumed within each season.

Demersal crustaceans also occurred frequently in the diet of quillback rockfish throughout the year, increasing in occurrence from winter through to fall (Fig. 3D). Numerically, demersal crustaceans were important only in fall (Fig. 3E) but their mass contribution was substantial (> 20%) in all seasons except winter (Fig. 3F). Pelagic crustaceans occurred frequently in the diet of quillback rockfish during winter, spring, and summer, and contributed a substantial proportion to the mass of the diet during summer. Conversely, pelagic fishes were a common occurrence in the diet of quillback rockfish only in winter (Fig. 3D), and were relatively unimportant in terms of numerical abundance throughout the year (Fig. 3E). Herring, however, comprised the majority of the mass of the diet of quillback rockfish in winter and, to a lesser extent, in the other seasons (Fig. 3F). Demersal fishes were consumed

Table 2 *Sebastes maliger*. Frequency of occurrence, numerical abundance, and mass of prey found in stomachs of quillback rockfish collected from Saanich Inlet, British Columbia. Values in parentheses are percentages of totals

Prey taxa	Occurrence (%)		Numerical abundance (%)		Mass (g) (%)	
Pelagic fishes	29	(18.4)	45	(1.8)	227.1	(65.1)
Clupea pallasi (Pacific herring)	27	(17.1)	43	(1.7)	227.1	(65.1)
Fish larvae	2	(1.3)	2	(0.1)	0.0	(0.0)
Demersal fishes	5	(3.2)	9	(0.4)	12.1	(3.5)
Cottidae (sculpins)	1	(0.6)	1	(0.0)	0.8	(0.2)
Pleuronectidae (flatfish)	3	(1.9)	7	(0.3)	8.2	(2.3)
Rhamphocottus richardsonii (grunt sculpin)	1	(0.6)	1	(0.0)	3.1	(0.9)
Pelagic crustaceans	81	(51.3)	2221	(86.4)	37.7	(10.8)
Euphausiids (*Euphausia pacifica*)	39	(24.7)	1524	(59.3)	27.7	(7.9)
Gammarid amphipods	1	(0.6)	2	(0.1)	0.0	(0.0)
Hyperiid amphipods	7	(4.4)	82	(3.2)	0.3	(0.1)
Megalopa of crabs	2	(1.3)	5	(0.2)	0.1	(0.0)
Mysids (*Xenacanthomysis pseudomacropsis*)	54	(34.2)	608	(23.6)	9.5	(2.7)
Demersal crustaceans	93	(58.9)	169	(6.6)	67.0	(19.2)
Acantholithodes hispidus	2	(1.3)	2	(0.1)	1.8	(0.5)
Cancer gracilis	2	(1.3)	2	(0.1)	0.6	(0.2)
Cancer oregonensis	8	(5.1)	9	(0.4)	2.3	(0.7)
Caprellid amphipod	1	(0.6)	1	(0.0)	0.0	(0.0)
Chorilia longipes (deepwater decorator crab)	2	(1.3)	2	(0.1)	0.3	(0.1)
Munida quadraspina (squat lobster)	46	(29.1)	75	(2.9)	28.4	(8.1)
Pandalus danae (coonstriped shrimp)	16	(10.1)	22	(0.9)	23.7	(6.8)
Shrimp (unidentified)	33	(20.9)	55	(2.1)	8.4	(2.4)
Telmessus cheiragonus (helmet crab)	1	(0.6)	1	(0.0)	1.4	(0.4)
Miscellaneous	7	(4.4)	127	(4.9)	5.2	(1.5)
Fish eggs (*Ophiodon elongatus*)	2	(1.3)	114	(4.4)	1.0	(0.3)
Polychaeta (Errantia)	4	(2.5)	4	(0.1)	3.3	(1.0)
Pteropod molluscs	1	(0.6)	9	(0.4)	0.8	(0.2)
Totals	158	(100)	2571	(100)	349.1	(100)

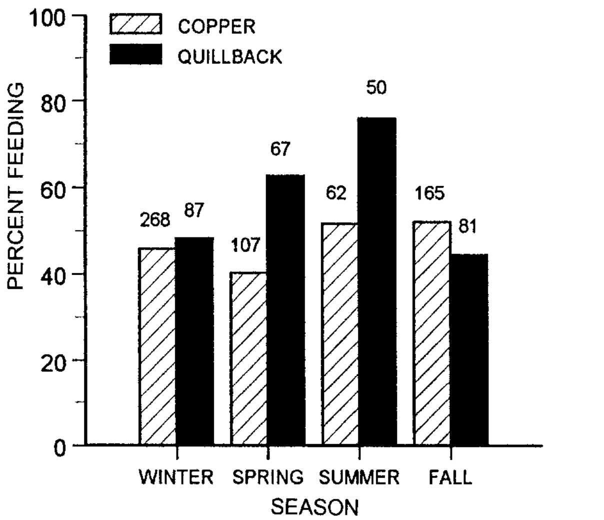

Fig. 2 *Sebastes caurinus* and *S. maliger*. Percent of copper and quillback rockfish with food in stomachs in each season of the year. Number of each species collected within each season is given above bars

infrequently by quillback rockfish, represented few items in the diet, and contributed negligible mass to the diet except in fall.

Size-related changes in food habits

The size distribution of copper rockfish collected was skewed to small fish: copper rockfish collected were on average smaller (212 ± 53 mm TL, $n = 602$) (Mean $\pm$ 1SD) than quillback rockfish (235 ± 50 mm TL, $n = 285$) (Fig. 4). Discrete modes in size frequencies of collected rockfish were not evident, and hence to facilitate comparison of diet changes related to rockfish size, fish were categorized as: extra-small (≤ 150 mm TL), small (> 150 to ≤ 200 mm), medium (> 200 to ≤ 250 mm), and large (> 250 mm TL). The two smallest size categories were combined for quillback rockfish, due to the paucity of extra-small fish. These size categories were also chosen to be consistent with categories employed in concurrent field experiments (Murie 1991).

The presence or absence of food in the stomachs of small, medium, and large copper rockfish was independent of season (χ^2_3; all $P > 0.30$). Stomachs of extra-small copper rockfish collected in winter and fall had a higher proportion of food present than stomachs collected in spring and summer ($\chi^2_c = 12.06$, $P = 0.01$). The presence or absence of food in the stomachs of quillback rockfish within each size category was independent of season for small and large rockfish only

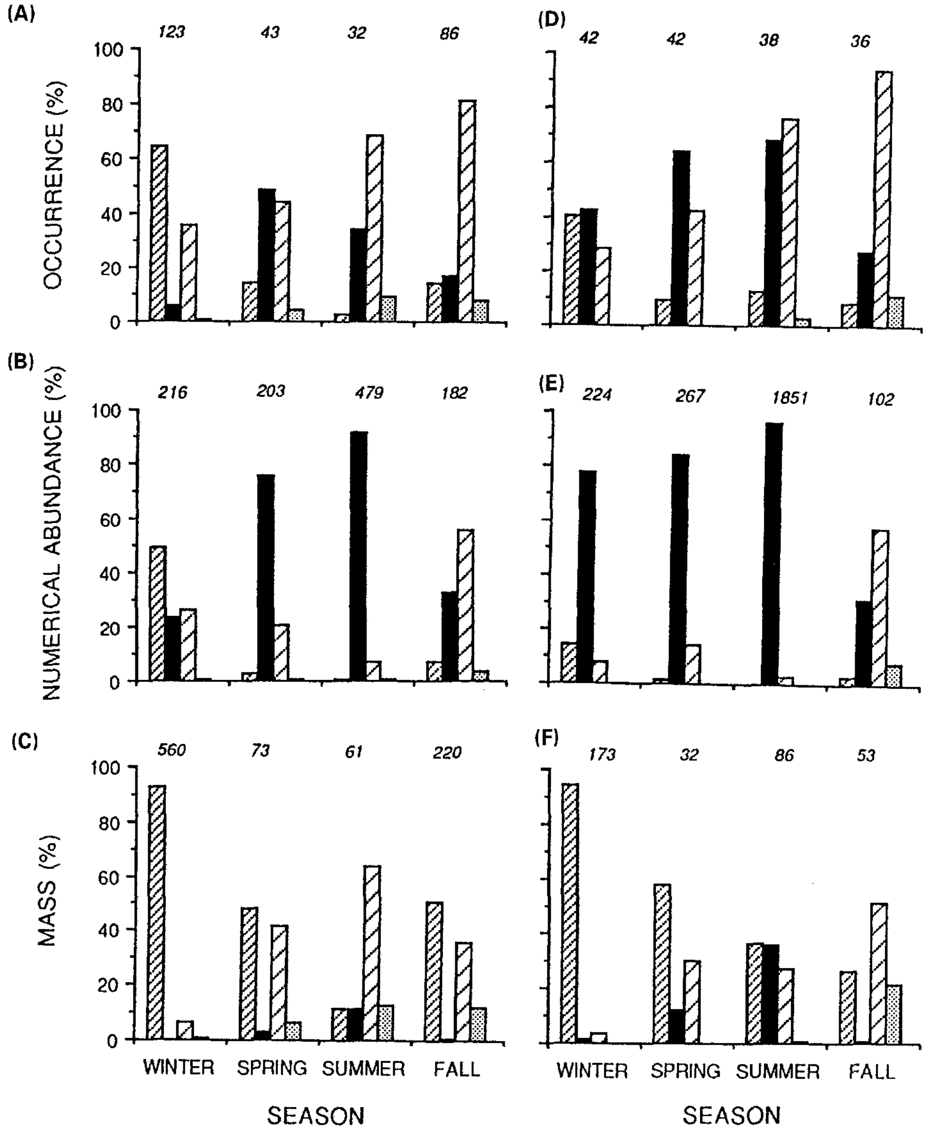

Fig. 3 *Sebastes caurinus* (**A–C**) and *S. maliger* (**D–F**). Summary of food habits of copper rockfish and quillback rockfish among seasons on basis of occurrence, numerical abundance, and mass contribution to diet. Totals for each season are given in italics. Food types are pelagic fishes (*finely hatched bars*), pelagic crustaceans (*black bars*), demersal fishes (*stippled bars*), and demersal crustaceans (*widely hatched bars*)

(χ^2_3; both $P = 0.17$). For medium-sized quillback rockfish, the proportion of stomachs with food present was less in fall than in the other seasons ($\chi^2_c = 11.81$, $P = 0.01$).

The majority of extra-small ($n = 40$) and small ($n = 78$) copper rockfish had fed on demersal crustaceans (Fig. 5A). Medium ($n = 93$) and large ($n = 73$) copper rockfish fed more frequently on pelagic fishes than extra-small and small copper rockfish. None of the extra-small copper rockfish had consumed demersal fishes and, as in the general diet, demersal fishes were relatively unimportant in the diet of all sizes of copper rockfish. Extra-small, small, and medium copper rockfish consumed pelagic crustaceans in a relatively constant proportion, which was slightly greater than the consumption of pelagic crustaceans by large copper rockfish (Fig. 5A). Demersal crustaceans also represented the greatest numerical abundance of any food item in the diet of extra-small copper rockfish (Fig. 5B). Pelagic crustaceans, in contrast, contributed the greatest numerical abundance of prey for small, medium, and large copper rockfish. Pelagic fishes represented $\leq 10\%$ numerical abundance of the food items consumed, except for large copper rockfish. On a mass basis, however, the major contribution to the diet for small, medium, and large copper rockfish came from the consumption of pelagic fishes (Fig. 5C). Although a substantial portion of the mass in the diet of the extra-small copper rockfish also came from pelagic fishes, the majority came from their consumption of demersal crustaceans. On a mass basis, demersal fishes and pelagic crustaceans were unimportant to all sizes of copper rockfish (Fig. 5C).

The majority of quillback rockfish, regardless of size, fed on pelagic and demersal crustaceans (Fig. 5D). Demersal fish were never consumed by small ($n = 35$) quillback rockfish, and were of only minor occurrence in the diet of medium ($n = 63$) and large ($n = 60$)

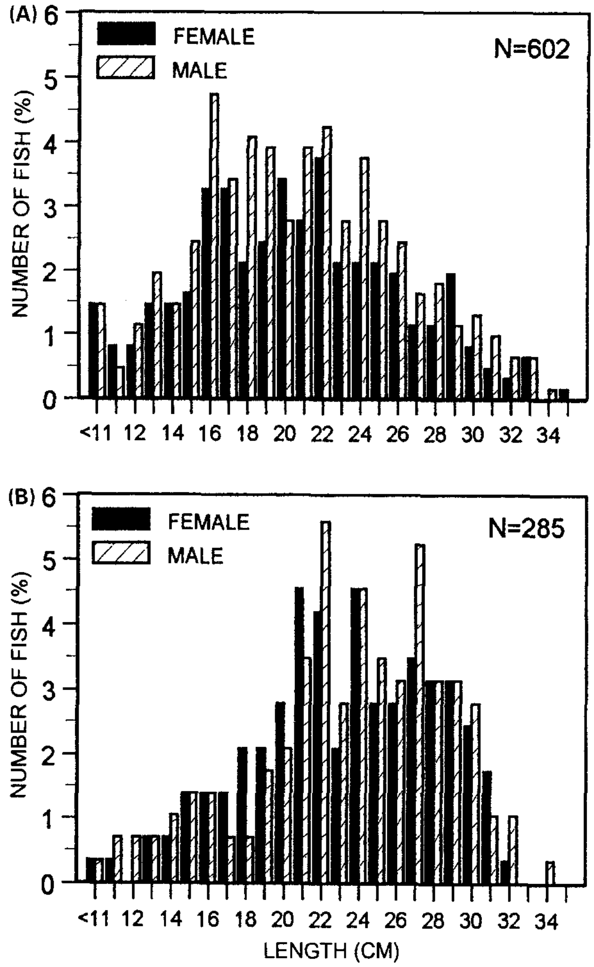

Fig. 4 *Sebastes caurinus* (**A**) and *S. maliger* (**B**). Length frequencies of male and female copper rockfish and quillback rockfish collected for stomach-content analysis

quillback rockfish. Pelagic fishes were of minor importance to small quillback rockfish, but were consumed by a substantial number of large quillback rockfish, although less so than medium and large copper rockfish. Pelagic crustaceans contributed the most to the numerical abundance of food items consumed by quillback rockfish, regardless of size (Fig. 5E). For small quillback rockfish, the consumption of pelagic fishes and demersal crustaceans and, to a lesser extent, pelagic crustaceans, contributed equally to the mass of their diet (Fig. 5F). Pelagic fishes contributed the greatest percent mass to the diet of medium and large quillback rockfish. Medium quillback rockfish also consumed a further 30% mass in pelagic and demersal crustaceans, whereas large quillback rockfish made up the remainder of the mass of prey feeding on only demersal crustaceans (Fig. 5F).

Niche breadth

Niche breadths based on occurrence of different prey species in the diet of copper and quillback rockfish were similar except for the narrow niche breadth observed for copper rockfish during the winter ($B_A = 0.167$) (Table 3), resulting from a disproportionate number of copper rockfish feeding primarily on one resource (herring). Average niche breadths across the seasons (excluding winter) were on average 0.407 ± 0.095 and 0.443 ± 0.088 for copper and quillback rockfish, respectively. Quillback rockfish, however, fed upon fewer prey taxa than copper rockfish (Table 3).

Niche breadths of copper and quillback rockfish based on the numerical abundance of prey items consumed were similar in winter and fall to niche breadths based on occurrence of prey species, but were lower (i.e., narrower) in spring and summer (Table 3). The narrow niche breadths, especially in summer, resulted from copper and quillback rockfish consuming a disproportionate number of small food items (e.g. euphausiids and mysids).

On the basis of mass, niche breadths for copper and quillback rockfish were similar and extremely low in winter (0.023 and 0.019, respectively) compared with the other seasons (Table 3). This was due again to the disproportionate mass attributable to the consumption of herring during the winter by both copper rockfish and quillback rockfish.

Niche overlap

Niche overlap between copper and quillback rockfish based on the numerical abundance of prey in the diet differed seasonally, with overlap at a maximum during spring and summer, declining during fall to reach a minimum during winter (Table 4). Niche overlap (by numerical abundance) was highest, therefore, when niche breadths based on numerical abundance were narrowest. This occurred during the spring and summer, when the diet of both copper and quillback rockfish was numerically dominated by pelagic crustaceans. In contrast, niche overlap based on mass contribution by different prey taxa in the diet was high during winter and only moderate during the rest of the year (Table 4). As with niche overlap based on numerical abundance, niche overlap based on mass was highest when niche breadths based on mass were narrowest. This occurred because both copper and quillback rockfish were consuming the same prey taxon (herring) in disproportionately large amounts.

Diel variation in feeding

Food consumed by copper rockfish represented the greatest percentage of body mass shortly after sunrise and sunset, indicating crepuscular peaks in feeding (Fig. 6A). The percentage of stomachs that was empty was lowest at sunrise, corresponding to an early morning peak in feeding. The percentage of empty stomachs

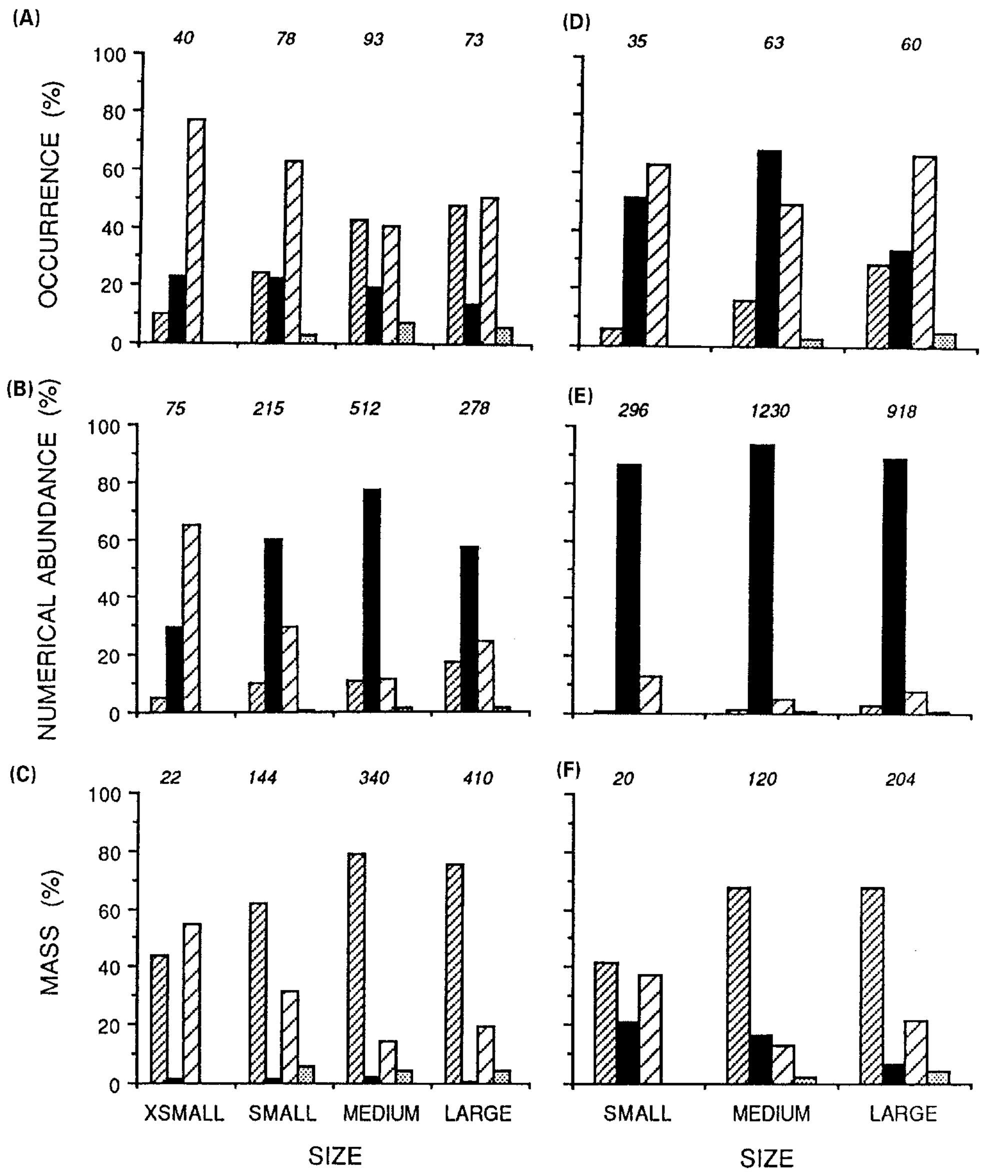

Fig. 5 *Sebastes caurinus* (**A–C**) and *S. maliger* (**D–F**). Summary of food habits of copper rockfish and quillback rockfish of varying body size on basis of occurrence, numerical abundance, and mass contribution to diet. Totals for each size category are given in italics. (*XSMALL* extra-small) (Further details as in legend to Fig. 3)

Table 3 *Sebastes caurinus* and *S. maliger*. Niche breadth based on percent occurrence, percent numerical abundance, and percent mass in diets among seasons

Season	Copper rockfish				Quillback rockfish			
	No. of prey taxa	Occurrence	Numerical abundance	Mass	No. of prey taxa	Occurrence	Numerical abundance	Mass
Winter	13	0.167	0.218	0.023	9	0.496	0.367	0.019
Spring	11	0.475	0.166	0.512	9	0.414	0.127	0.203
Summer	18	0.447	0.043	0.498	17	0.333	0.043	0.192
Fall	21	0.298	0.248	0.318	11	0.529	0.586	0.364

also declined during the feeding peak at sunset, increasing later (approximately midnight) when the percentage of body mass of food consumed decreased.

In contrast, the high percentage of empty stomachs of quillback rockfish at sunrise and sunset suggested that they did not feed during crepuscular periods, but instead fed primarily during mid-day (Fig. 6B). In addition, the majority of quillback rockfish collected after sunset had empty stomachs, and for those rockfish that had any stomach contents the contents represented a low percentage of their body mass.

Table 4 *Sebastes caurinus* and *S. maliger*. Niche overlap based on numerical abundance and mass contribution of prey taxa to diets of copper and quillback rockfish in Saanich Inlet

Season	Total no. of prey taxa	Niche overlap	
		numerical abundance	mass
Winter	15	0.402	0.996
Spring	14	0.982	0.574
Summer	25	0.997	0.558
Fall	25	0.704	0.570

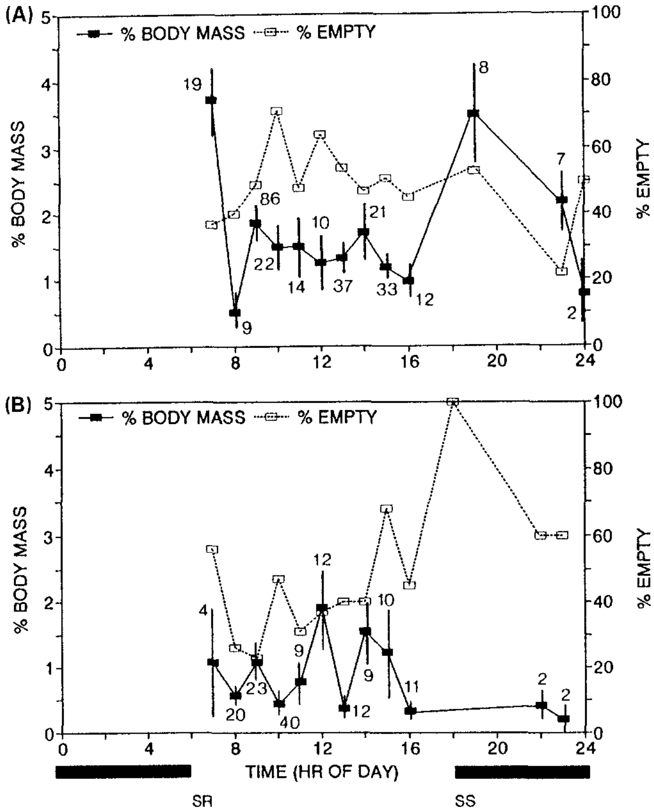

Fig. 6 *Sebastes caurinus* (**A**) and *S. maliger* (**B**). Diel variation in feeding (mean ± 1SE) of copper rockfish and quillback rockfish based on percentage empty stomachs and mass of food consumed as percentage of body mass (*Black bars* hours of darkness and twilight; *SR* sunrise; and *SS* sunset)

Quantity of food consumed

Within copper rockfish and within quillback rockfish, differences among slopes in mass of food consumed by both sexes among all four seasons were nonsignificant (Single-factor ANCOVA; $F_{7,268} = 1.54$ and $P = 0.15$, $F_{1,141} = 0.70$ and $P = 0.67$, for copper and quillback rockfish, respectively), and hence differences in food consumption between the sexes and among the seasons could be tested within each species. An effect in total mass of food consumed due to season was evident for both copper rockfish ($F_{3,275} = 16.17$, $P = 0.00$) and quillback rockfish ($F_{3,148} = 8.02$, $P = 0.00$). There was no effect of food consumed due to sex or the interaction between season and sex (all $P > 0.13$).

Between species over the four seasons, however, the regression coefficients were different due to the food consumption relationship for copper rockfish in winter ($F_{1,432} = 4.87$, $P = 0.03$). Food consumption by copper rockfish in winter, relative to their body mass, was allometric with the slope of the relationship > 1 (Student's *t*-test: $t = 2.79$, $df = 121$, $P < 0.01$). The relative rate of food consumption therefore increased as copper rockfish size increased (Fig. 7A). Regression coefficients for copper rockfish for three seasons (winter excluded) and quillback rockfish for all four seasons were not different from each other (single-factor ANCOVA: $F_{6,305} = 0.79$, $P = 0.58$), although their adjusted means (elevations) were different ($F_{6,305} = 7.19$, $P = 0.000$). The Student's *t*-test matrix for adjusted group means indicated that food consumption of copper rockfish in summer and fall and quillback rockfish in summer and winter (Fig. 7B) was greater than the food consumption of copper rockfish in spring and quillback rockfish in fall and spring (Fig. 7C) (all differences at $P \leq 0.05$). The relationships between food consumption and size for these latter two pooled groups were isometric (e.g. slopes = 1) (Student's *t*-tests: $t = 0.13$, $df = 195$, $P = 0.50$, and $t = 0.43$, $df = 119$, $P = 0.50$, respectively), indicating that the relative rate of food consumption was the same regardless of rockfish size.

Discussion

Variation in diet of copper rockfish, *Sebastes caurinus*

Previous studies on the food habits of copper rockfish have been centred in Alaska (Rosenthal et al. 1988), Washington (Puget Sound) (Patten 1973; Moulton 1977; Buckley and Hueckel 1985), and California (Prince and Gotshall 1976). On an annual basis, the food habits of copper rockfish in Saanich Inlet (Table 1) were most similar to copper rockfish in Alaska and Washington, with pelagic fish being particularly important on an occurrence and mass basis. As with copper rockfish in Alaska and Puget Sound, demersal crustaceans also occurred in the diet of the majority of copper rockfish in Saanich Inlet, but contributed only 20% to the mass of their diet. In contrast, copper rockfish in California (South Humboldt Bay) consumed primarily demersal crustaceans, especially juvenile dungeness crab (*Cancer magister*) (Prince and Gotshall 1976). Prince and Gotshall attributed the preponderance of demersal crustaceans in the diet to the use of Humboldt Bay as a nursery ground for juvenile dungeness crab. The abundance of juvenile dungeness crab in the diet of copper rockfish was therefore seasonal, being more abundant during summer and fall rather than winter

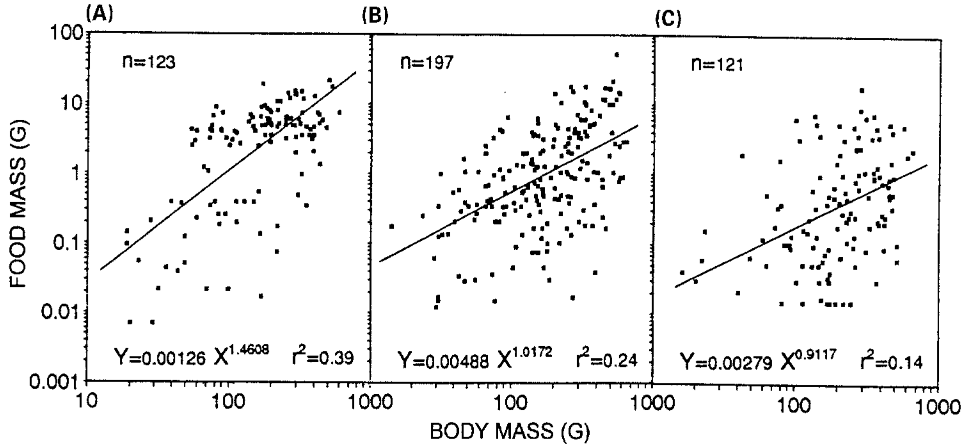

Fig. 7 *Sebastes caurinus* and *S. maliger*. Mass of food consumed as a function of body mass. **A** copper rockfish in winter; **B** quillback rockfish in winter and summer and copper rockfish in summer and fall; **C** quillback rockfish in fall and spring and copper rockfish in spring. All regressions significant at $P < 0.0001$

and spring. Fishes [e.g. northern anchovy (*Engraulis mordax*) and shiner perch] were consumed relatively infrequently by copper rockfish in Humboldt Bay, although they represented a substantial proportion of the total volume of prey consumed.

Although the numerical abundance and species of fishes consumed by copper rockfish in the summer in the Gulf of Alaska and Puget Sound were different from those of copper rockfish in Saanich Inlet, the mass contributions to the diet by the consumption of pelagic fishes were similar. The numerical difference was due to copper rockfish in Saanich Inlet consuming relatively more pelagic crustaceans (Fig. 3B) than copper rockfish in the Gulf of Alaska or Puget Sound. However, the mass contribution to the diet by pelagic crustaceans was low for copper rockfish irrespective of collection location. The consumption of small pelagic fishes, regardless of species, appears to be characteristic of copper rockfish, regardless of location of the study. Hence, Pacific herring was common in the diet of copper rockfish in Saanich Inlet, and Pacific sand lance (*Ammodytes hexapterus*) and Puget Sound rockfish (*Sebastes emphaeus*) were dominant in the stomachs of copper rockfish in the Gulf of Alaska (Rosenthal et al. 1988). Differences in fish species consumed by copper rockfish in different geographical locations may have been due to prey selection (preferences), relative availability of prey, or the geographical distribution of the prey species (e.g. Puget Sound rockfish do not occur within the study site in Saanich Inlet) (own personal observations).

Prey taxa of the most common demersal crustaceans in the diet of copper rockfish were also consistent among all the food-habit studies, except that squat lobsters were consumed only by copper rockfish in Saanich Inlet. Squat lobsters occur in concentrations in Saanich Inlet on rocky reefs below 20 m (own personal observations). Although the geographical distribution of *Munida quadraspina* extends from Alaska to Mexico, *M. quadraspina* occur most often in fjords (like Saanich Inlet) at depths of 22 to 1463 m (Hart 1982), and hence may not occur in locations sampled in the other studies.

Variation in diet of quillback rockfish, *Sebastes maliger*

The food habits of quillback rockfish have been studied less than those of copper rockfish, with studies centered in Alaska (Rosenthal et al. 1988) and Washington (Moulton 1977, Buckley and Hueckel 1985). In comparison with diets examined in the Gulf of Alaska and Puget Sound, a greater proportion of the diet of quillback rockfish in Saanich Inlet was comprised of pelagic crustaceans (by occurrence and numerical abundance; Table 2). Overall, however, pelagic and demersal crustaceans were important (by occurrence and numerical abundance) in the diet of quillback rockfish regardless of geographical location. The proportion of fishes in the diet of quillback rockfish from the various locations was substantial on a mass basis because of the relatively larger size of fish prey compared to crustacean prey. Specifically, sand lance comprised the majority of the identified fish prey consumed by quillback rockfish in Alaska, with herring and Puget Sound rockfish of relatively minor importance. Although quillback rockfish in Saanich Inlet consumed less fish than quillback rockfish in the Gulf of Alaska, fish represented a greater proportion of the total mass of the diet of quillback rockfish in Saanich Inlet. This difference was most likely due to quillback rockfish in Saanich Inlet having fed on herring, which have a greater body depth (and hence are heavier) than sand lance of similar length.

Niche breadth and overlap in food habits

Comparative food habit analyses on naturally occurring sympatric populations of copper and quillback rockfish can not directly infer the presence or absence of interspecific competition over food resources (Colwell and Futuyma 1971). To test quantitatively for the presence of interspecific competition between copper and quillback rockfish it would be necessary to experimentally manipulate the density of their food resources. This would be an arduous task and, at present, experimental field studies have been restricted to manipulating population densities of these two species (Murie 1991). Comparative food habits can, however, provide information on potential conflicts over food resources. Copper rockfish consumed proportionally more fish prey than quillback rockfish. The niche-overlap values for food habits of copper and quillback rockfish , however, were still moderate to high (0.402 to 0.997), indicating that these species share their use of food resources to a large extent. This overlap may be of no consequence to their obtaining their food requirements when the shared resources are abundant (Pianka 1981). If the shared resources become unavailable or limited, however, the rockfish would either have to shift their feeding habits to procure different food resources, or compete for the limited resources, to satisfy their dietary requirements.

During the summer, when niche breadths based on numerical abundance were narrow for both copper and quillback rockfish in Saanich Inlet, overlap based on numerical abundance was high (almost unity). In this respect, niche breadths calculated from numerical abundance are biased towards prey taxa comprised of small-sized individuals. An observed abundance of pelagic crustaceans during the summer (Murie 1991) would therefore have allowed both rockfish species (i.e., high overlap) to feed primarily on pelagic crustaceans (i.e., narrow niche breadths). Similarly, during the winter when juvenile herring are abundant (Murie 1991), niche breadths based on mass contribution (biased towards prey taxa comprised of large-sized individuals) were narrow for both copper and quillback rockfish while overlap was at a maximum. Niche overlap, therefore, appeared to be greatest when food resources were abundant. This supports Pianka's (1981) contention that extensive niche overlap may actually indicate an abundance of a shared resource rather than indicate competition for a resource.

Rosenthal et al. (1988) concluded that copper and quillback rockfish in the Gulf of Alaska during the summer had less specialized diets than pelagic rockfish species, and that they were intermediate between dietary specialists and dietary generalists. By recalculation[1], "summer" values of niche breadth (B_A) based on volume for copper and quillback rockfish in the Gulf of Alaska were 0.318 and 0.314, respectively. Average niche breadths by mass (approximately equivalent to volume) for copper and quillback rockfish in Saanich Inlet for spring and summer combined (equivalent to Rosenthal et al.'s "summer") were 0.505 and 0.198, respectively. This indicated that copper rockfish were not only more generalist than quillback rockfish in Saanich Inlet in the spring and summer, but also more generalist than both copper and quillback rockfish in the Gulf of Alaska. Conversely, quillback rockfish in Saanich Inlet were more dietary specialists compared to copper rockfish in Saanich Inlet and both quillback and copper rockfish in the Gulf of Alaska in summer. Seasonality in the degree of dietary specialization was also evident in that both copper and quillback rockfish in Saanich Inlet in the winter had narrower niche breadths (by mass) than any pelagic rockfish species in the summer in the Gulf of Alaska (Rosenthal et al. 1988), or than offshore pelagic rockfish from the Northeastern Pacific Ocean (Brodeur and Pearcy 1984). These latter fish had been considered to have more specialized diets than demersal species of rockfish (Brodeur and Pearcy 1984; Rosenthal et al. 1988).

[1] Simpson's niche breadth value (equivalent to B) from Table 11 in Rosenthal et al. (1988) was inserted into Hurlbert's (1978) equation of standardization

Size-related variation in diet

Changes in food habits with increasing body size have been recognized in many species of fish (Keast 1970). In carnivorous fishes, in general, younger and smaller fish consume smaller food items and feed on a less diverse array of prey than older and larger fish (Nikolsky 1963; Keast 1970). Size-related differences in food habits have been studied previously for copper rockfish (Patten 1973; Prince and Gotshall 1976) but not for quillback rockfish. As in these previous studies, an ontogenetic shift of feeding proportionally more on crustaceans when small to feeding proportionally more on fishes when of larger body size was evident in the diets of different sized copper and quillback rockfish in Saanich Inlet (Fig. 5). Compared with copper rockfish, however, quillback rockfish of similar size consumed relatively more crustaceans and fewer fish. This general difference between the diets of copper and quillback rockfish was also supported by differences in the allometric growth of their gastrointestinal tract (Murie 1994) and in their activity patterns in relation to habitat (Murie 1991; Murie et al. 1994).

Diel variation in feeding

The temporal partitioning of feeding by copper and quillback rockfish appeared to be between primarily crepuscular feeding by copper rockfish (with secondary daytime feeding) and primarily mid-day feeding by quillback rockfish (Fig. 6). The differences in time of feeding between copper and quillback rockfish may be related to the type and availability of prey consumed. Epipelagic species of euphausiids, in particular, undertake diurnal vertical migrations, usually at dawn and dusk (Kathman et al. 1986). Pelagic fishes, such as herring, feed on these pelagic crustaceans primarily during crepuscular periods when they are in transit. Herring, in turn, could be fed upon by pelagic predators, such as copper rockfish, during these crepuscular periods. During the daytime, however, euphausiids are concentrated at depth (Mackie and Mills 1983; own personal observations) and would therefore be available to quillback rockfish.

Neither copper nor quillback rockfish appear to feed at night. Although collection of copper and quillback rockfish was limited through periods of darkness, those fish sampled indicated little if any nocturnal feeding. This was also supported by the observation that most of the rockfish observed during night dives were inactive and sheltering in holes and crevices (own personal observations).

Food consumption: seasonality, quantity, and size-related differences

To date, feeding by rockfishes in the winter, in particular, has received little or no attention. Besides the physical hardships of field sampling during the winter in north-temperate ecosystems, it is also generally assumed that feeding by fishes in winter is solely for the purpose of body maintenance (Keast 1970). This may be reasonable for fishes in freshwater systems that undergo a marked decline in water temperature from summer to winter (e.g. 15 to 20 °C down to 4 °C) with a concomitant decrease in digestion and feeding stimulus in the fishes (Keast 1970). Copper and quillback rockfish in Saanich Inlet at depths between 15 m and 40 m, however, do not experience a substantial lowering of the water temperature during the winter (11 °C down to 9 °C) (Murie 1991). Rockfish are also reproductively active throughout winter and into late spring, when their young are born (Murie 1991). The requirement of rockfish to feed in winter, not only for maintenance but also to offset the energetic demands of reproduction, was evident in that the proportion of copper rockfish feeding in winter was the same as for the other seasons (Fig. 2). In addition, the proportion of quillback rockfish feeding in winter was the same as for quillback rockfish in fall and the same as for copper rockfish year-round (Fig. 2). The importance of feeding in winter was also evident from the relationship of mass of food consumed as a function of body mass of the rockfish (Fig. 7). For copper rockfish, food consumption in winter was not only greater than for similar-sized quillback rockfish in winter, but it was also greater than at any other time of the year.

Mass contribution to the diet may be particularly relevant to rockfish since it is proportionally equivalent to the gross energy obtained by the fish, depending on the caloric density of the prey. Pelagic fishes in general, and herring in particular, have a high caloric density (e.g. 1.93 kcal g^{-1} wet mass) (Cummins and Wuycheck 1971) compared to euphausiids (0.96 kcal g^{-1}) (Tyler 1973) and shrimps (1.32 kcal g^{-1}) or crabs (1.08 kcal g^{-1}) (Cummins and Wuycheck 1971). Thus, on a gross-energy basis, the reliance on herring in the winter approaches 100% for copper and quillback rockfish.

In general, food consumption of fishes is usually an allometric relationship with a slope of < 1, and hence food consumption usually decreases relative to an increase in body mass (Table V in Fänge and Grove 1979). For example, Keast (1970) observed that juvenile freshwater fishes in the summer consumed 2 to 4% of their body mass daily, whereas adult fish consumed ~ 1.5%. In contrast, the relationship between food consumption and body mass for quillback rockfish and copper rockfish (except during winter) was isometric, and food consumption was therefore directly proportional to body size (0.2 to 1.9% and 0.5 to 3.7% of body mass for quillback and copper rockfish, respectively). Of greater significance, the positive allometric relationship (i.e., slope > 1) for food consumption of copper rockfish during winter, and the almost total reliance of both copper and quillback rockfish on juvenile herring during winter, emphasize that the composition and quantity of food consumed by rockfishes need to be investigated throughout the winter, and not just during the summer. Without experimentally excluding schools of herring from the study area during winter, it is impossible to assess how critical winter feeding is for these rockfish. Seasonal consumption of herring, however, may be tied into the seasonal fattening cycle of rockfish, especially females in readiness for gestation and birth of their young (Murie 1991).

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