COMPARATIVE ECOLOGY AND INTERSPECIFIC COMPETITION BETWEEN THE SYMPATRIC CONGENERS *SEBASTES CAURINUS* (COPPER ROCKFISH) AND *S. MALIGER* (QUILLBACK ROCKFISH)

by

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ABSTRACT

Comparative ecology and interspecific competition were examined between two sympatric congeners, *Sebastes caurinus* Richardson 1845 (copper rockfish) and *S. maliger* (Jordan and Gilbert 1880) (quillback rockfish) in Saanich Inlet, British Columbia, Canada, from 1986-1990. Ecological profiles were constructed through analyses of depth distribution, habitat and species associations, activities, feeding habits, gut allometry, growth, and reproduction. Interspecific competition between copper and quillback rockfish was examined by experimentally manipulating the densities of one or the other species on rocky reefs in Saanich Inlet where they were sympatric.

The *Pisces IV* submersible was used to survey the distribution of rockfish in relatively deep-water (21-140 m) in Saanich Inlet. Copper and quillback rockfish were sympatric in water depths of 21-65 m. They occurred in association with one another the majority of the time (>90%) and their densities were greatest over areas of complex substrate. Size of copper and quillback rockfish was positively correlated with increased depth, primarily due to the absence of small fish in deeper waters. Both species were observed most frequently perched on open substrate or hovering in the water column. Copper rockfish were observed swimming more frequently than quillback rockfish.

Copper and quillback rockfish primarily consumed demersal crustaceans throughout the year. Copper rockfish consumed a greater proportion of pelagic fishes than quillback rockfish, whereas quillback rockfish had a greater proportion of pelagic crustaceans in their diet. Levins' (1968) measure of niche breadth of the diet (by mass), as standardized by Hurlbert (1978), was narrow (0.19-0.20) to moderate (0.32-0.51) for quillback and copper rockfish respectively, during spring, summer, and fall. In the winter it was extremely narrow (0.02) for both species due to their feeding predominantly on one prey type, juvenile herring (*Clupea harengus*). The Simplified Morisita Index of niche overlap (Horn 1966) in feeding habits (by mass) was relatively high (>0.55) throughout the year, and particularly during the winter (0.99). This high niche overlap in the winter occurred when large schools of juvenile herring were available in the environment and were probably not a limited resource. Extensive niche overlap between copper and quillback rockfish may therefore indicate an abundance of a shared resource rather than competition for the resource.

Copper and quillback rockfish consumed the greatest quantity of food during the winter when feeding on juvenile herring, although quillback rockfish consumed significantly less food mass than copper rockfish in the winter. A greater proportion of quillback rockfish were collected with

food in their stomachs during the spring and summer, when the numerically dominant food items were pelagic crustaceans. The importance of fish prey in the diets of both copper and quillback rockfish increased with size.

Copper rockfish had a shorter intestine and larger stomach relative to similar-sized quillback rockfish. This suggested that the gastrointestinal tract of copper rockfish was better suited to holding and digesting fish and larger crustaceans than quillback rockfish, an observation consistent with differences in their feeding habits.

Copper and quillback rockfish had similar growth patterns with no readily identifiable species-specific and sex-specific differences. Both sexes of both species attained asymptotic lengths of 30-31 cm total length and had similar growth coefficients (0.141-0.187). Within each sex, copper rockfish had a smaller increase in mass per unit of body length than quillback rockfish, indicative of a more pelagic lifestyle for copper rockfish.

Estimated lengths at first and 100% sexual maturity for female and male copper and quillback rockfish were similar. Male copper rockfish were ripe, and potentially inseminated females, in January and February. Female copper rockfish were found to be carrying fertilized eggs in April and May, and gave birth to their young primarily in June. The reproductive cycle of quillback rockfish preceded that of copper rockfish by approximately one month, with parturition for quillback rockfish occurring mainly in May. The fecundity of copper and quillback rockfish was similar, with a 30-cm fish giving birth to approximately 90,000 young.

Visceral fat cycles of mature female copper and quillback rockfish were complementary to their cycles of gonad maturation and increases in gonad size, indicating that they use visceral fat stores as a source of energy for maturation of their eggs and nourishment of their developing young. Visceral fat cycles of mature males were mainly coincident with the maturation and size increase of their gonads, indicating that they did not use visceral fat reserves in the maturation of their gonads. Male rockfish secondarily may have used their fat reserves as an energy source during the period when they were ripe, perhaps for mating activities. Visceral fat accumulation and dissipation in immature males and females appeared to be primarily related to periods of feeding.

Interspecific competition between copper and quillback rockfish was asymmetrical, seasonal, and transitory, based on experimental manipulations of the densities of the congeners in natural populations. Copper rockfish did not have a competitive effect on quillback rockfish, but quillback rockfish had a weak competitive effect on copper rockfish. This effect was apparent only during the fall, was strongest in the fall immediately following the density manipulations, and appeared to weaken in the subsequent fall season. The seasonal competitive effect may have been caused by copper rockfish moving onto the study reefs (18-31 m depth) from shallower waters (<20 m) during the fall and winter, creating a short-term 'ecological crunch' in which food or space resources were limited.

Overall, comparative ecological profiles of copper and quillback rockfish exhibited a large degree of overlap. Differences observed between them were small but consistently indicated that copper rockfish had a more pelagic lifestyle than quillback rockfish. The otherwise high degree of similarity between the two congeners, however, did not translate into sustained interspecific competition.

Ecological theory purporting a major role for interspecific competition in structuring fish communities was therefore not supported by experimental manipulations of population densities of deep-subtidal, temperate zone rockfishes. The asymmetrical, seasonal, and transitory occurrence of weak interspecific competition demonstrated that competition between these rockfish species is dynamic, and cannot account for the pattern of species association. Alternative hypotheses based on the importance of intraspecific competition, predation, or environmental variability must therefore be considered.

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This dissertation is dedicated to

my parents

Frontispiece

Quillback rockfish (left) and copper rockfish (right)
at 30 m in Saanich Inlet, British Columbia.

CHAPTER I

GENERAL INTRODUCTION

Ecological theory proposes that interspecific competition is a major contributing factor in structuring natural communities (Schoener 1974, 1982, 1983; Diamond 1978; Pianka 1981; Roughgarden 1983), although debatably so (Wiens 1977; Connor and Simberloff 1979; Connell 1980, 1983; Strong 1980; Simberloff 1983). Interspecific competition occurs when two (or more) species interfere with or inhibit one another, either by direct interference (e.g., fighting) or through exploitative means (e.g., feeding on a common food type). When a shared resource is actually or potentially limiting, the presence of each species reduces the fitness and/or equilibrium population size of the other (Pianka 1981).

Patterns of resource use and partitioning can therefore provide insight into relationships between the ecological niches of coexistent species and aid in assessment of the potential competitive interactions (Schoener 1974). Central to this theme are the concepts of niche breadth and niche overlap. Niche breadth is a measure of the variability of the use of one particular niche dimension (e.g., variation in the size of prey consumed) (Pianka 1981). Niche overlap is the joint use of a resource by two (or more) species

(Colwell and Futuyma 1971). Overlap is complete when the two species have identical niches and absent if the two niches are completely disjunct. The competitive exclusion principle asserts that two species with identical niches will not be able to coexist (e.g., see Gause 1934). A measurement of niche overlap is therefore sometimes used as an estimate of competition for resources (Levins 1968; Schoener 1968). Using overlap to infer competition has recently come under considerable criticism, however, because disjunct niches may be due to competition that has occurred in the past and hence led to the ecological segregation of the species (Connell 1980), or because extensive niche overlap may actually be due to an abundance of a shared resource (Pianka 1981). Hence, niche overlap may be used to either support or refute the presence of competitive interactions (Colwell and Futuyma 1971).

Niche metrics (e.g., breadth and overlap) can, however, provide a thorough ecological profile of potentially competing species. They are most effective when used in conjunction with experimental manipulations to test for the presence of interspecific competition (Pianka 1981). Experimental studies of interspecific competition in natural populations employ direct density manipulations, through selective addition or removal of individuals. The population density of a species is monitored in the presence and in the absence of its potential competitor, in an otherwise unchanged environment (Dunham 1980; Pianka 1981). With removal of a potential competitor, an observed increase in population density of the remaining species, or a niche shift in response to the absence of the competitor, constitutes direct evidence of interspecific competition (Dunham 1980; Pianka 1981). If competition is shown to be a contemporary process in a particular system, then manipulation of specific resource(s), based on quantification of the niche metrics, can be used to elucidate the mechanism of interaction (Dunham 1980).

The presence or absence of interspecific competition in natural fish populations, and its importance in structuring communities in temperate marine ecosystems, have received little consideration relative to investigations of tropical fish and terrestrial vertebrates (Connell 1983; Schoener 1983). According to Schoener's (1983) review of interspecific competition, only 5% (4/80) of the species involved in experimental marine field studies were temperate marine fishes, representing 7% (2/30) of the total number of studies. Studies on surfperches (*Embiotoca*: Embiotocidae) (Hixon 1980) and rockfishes (*Sebastes*: Scorpaenidae) (Larson 1980a) in California, however, have indicated that interspecific competition has significant effects on the life history traits and distributional patterns of these temperate species.

In the Eastern North Pacific Ocean, the genus *Sebastes* contains approximately 65 species and is notable for its numerous sympatric congeners (Chen 1971), making them a valuable group for studying interspecific competition (Pianka 1981). In addition, most species of *Sebastes* are exploited by either sports or commercial fisheries (Love *et al.* 1990). The ecological profiles constructed for rockfish species using niche metrics, while providing insight into any potential competitive interactions, may therefore also prove beneficial in their management.

Two of these congeners, *S. caurinus* Richardson 1845 (copper rockfish) and *S. maliger* (Jordan and Gilbert 1880) (quillback rockfish), were of particular interest because of their abundance in coastal areas of British Columbia and their importance to local fisheries (Hart 1973; Richards 1987; Richards and Cass 1987; Hand and Richards 1991). They are known to occur in benthic areas of rocky habitat (Richards 1987) and are superficially similar in morphology and ecology. This combination of characters suggests that they are probable candidates for interspecific competition when or where populations are sympatric (Pianka 1981).

The purpose of my research was twofold: 1) to establish the degree of ecological similarity between copper and quillback rockfish; and 2) to test empirically if populations of these sympatric congeners are limited by interspecific competition. The study was comprised of two major sections, the first being the construction of ecological profiles of the two species to determine their similarities and differences (Chapters II-IV), and the second (Chapter VII) being the experimental manipulation of sympatric populations of copper and quillback rockfish to test for the presence or absence of interspecific competition.

Voucher specimens of sympatric copper and quillback rockfish collected in Saanich Inlet, British Columbia, have been deposited with the Royal British Columbia Museum for future reference.

CHAPTER II

COMPARATIVE DISTRIBUTIONAL AND BEHAVIOURAL ECOLOGY OF ROCKFISH IN SAANICH INLET, BRITISH COLUMBIA, USING THE *PISCES IV* SUBMERSIBLE

INTRODUCTION

Prior to the advent of submersibles, *in situ* observations of deep-water fish assemblages have been restricted by time-depth limitations of SCUBA. Marine scientists limited to non-decompression diving are therefore restricted to observing fish assemblages above 40 m (130 ft) (Colin 1976; Moulton 1977; Carlson and Straty 1981; Richards 1986; Dennis and Bright 1988; Parker 1990). Distributional studies of fishes inhabiting waters deeper than 30-40 m have therefore had to rely on hook-and-line surveys, box trapping, or net trawling, all of which have known biases and limitations (Westrheim 1970; Uzmann *et al.* 1977). The recent availability of small submersibles for research purposes has allowed direct visual assessment of the depth distribution, density, habitat, and activity of a variety of deep-water fish species (Colin 1974, 1976; Uzmann *et al.* 1977; Carlson and Straty 1981; Richards 1986; Dennis and Bright 1988; Pearcy *et al.* 1989). The use of submersibles to obtain estimates of densities and activities of deep-water fishes is particularly appropriate when observing benthic-oriented fishes inhabiting rocky areas (e.g., rockfishes, *Sebastes* spp.) where trawl net captures are ineffective (Uzmann *et al*. 1977; Dennis and Bright 1988; Pearcy *et al*. 1989).

Rockfish form an important component of the nearshore recreational and commercial fisheries along the northeastern Pacific coast (Hart 1973; Patten 1973; Richards 1987). Many of the inshore rockfish species are believed to be ecologically and morphologically similar, and are primarily benthic, sedentary fishes (Patten 1973; Moulton 1977; Mathews and Barker 1983; Richards 1986, 1987). Distributions of nearshore rockfish may depend on a variety of factors, including depth, habitat, and the presence of con- and heterospecifics. Various species are known to segregate bathymetrically (Larson 1980a; Hallacher and Roberts 1985; Richards 1986, 1987; Pearcy *et al*. 1989), reducing or eliminating possible competitive interactions between otherwise ecologically similar species (Larson 1980a). Using a submersible, it is possible to directly observe species-specific depth distributions, as well as to estimate each species' numerical abundance or density throughout depth. Changes in density with depth may ultimately be related to rockfish size because fish size is often positively correlated with depth (Westrheim 1970; Boehlert 1980; Wilkins 1980; Richards 1986).

Nearshore rockfish are usually found in close association with the bottom or vertical relief (e.g., kelp beds) and their density may therefore be dependent on the type of habitat available (Hart 1973; Patten 1973; Moulton 1977; Richards 1986, 1987; Pearcy *et al*. 1989). In this respect, submersibles provide the unique opportunity to observe not only the type of habitat that various rockfish species frequent, but also their behaviour and, hence, their use of the habitat. To date, there have not been any studies that quantitatively assess the *in situ* behaviour of deep-water rockfish.

In the present study, the *Pisces IV* submersible (Department of Fisheries and Oceans, Canada) was used to observe rockfish inhabiting relatively deep-water regions (21-150 m) in Saanich Inlet, British Columbia, Canada. The objectives of the study were: 1) to determine the species composition and depth distributions of rockfish at depths greater than 20 m; 2) to estimate the density, habitat, and size of rockfish with depth; and 3) to determine the activities of rockfish in a deep-water environment.

METHODS

The *Pisces IV* submersible was used to survey rockfish populations in Saanich Inlet, British Columbia, in December 1986. A comprehensive description of the *Pisces IV* submersible is given in Mackie and Mills (1983). Saanich

Inlet has a steep, rocky slope bottom interspersed with sand-shell valleys. It is 7.2 km at its widest and reaches a maximum depth of 234 m. Physical characteristics of Saanich Inlet have been studied in detail elsewhere (Herlinveaux 1962; Anderson and Devol 1973). Three sites within Saanich Inlet were surveyed: Five transects were traversed at Elbow Point, eight in an area north of McKenzie Bight, and three in an area north of Sheppard Point (Fig. 1). All surveys were conducted between 0930 h and 1600 h. Hydrocasts made in the deep central portion of Saanich Inlet, at depths of 80-220 m, determined that the basin of the Inlet was not anoxic during the survey period. Underwater visibility at the time of the surveys was 5-6 m using the external floodlights.

At the start of each transect the *Pisces IV* submerged to a depth of 100-150 m while in open water. On reaching this depth the submersible would turn on its external floodlights and slowly manoeuvre horizontally towards the cliff face. Once the bottom substrate (cliff) was located, the submersible started a slow ascent ($\sim 5\ m \cdot min^{-1}$), keeping the viewing ports (port, pilot, and starboard) directed perpendicular to and approximately 3 m from the substrate.

On ascent, an audio-record was made of the species, time, depth, size (whenever possible), activity, and habitat for each rockfish observed. Each observer (port and starboard) recorded all rockfish observed in an area

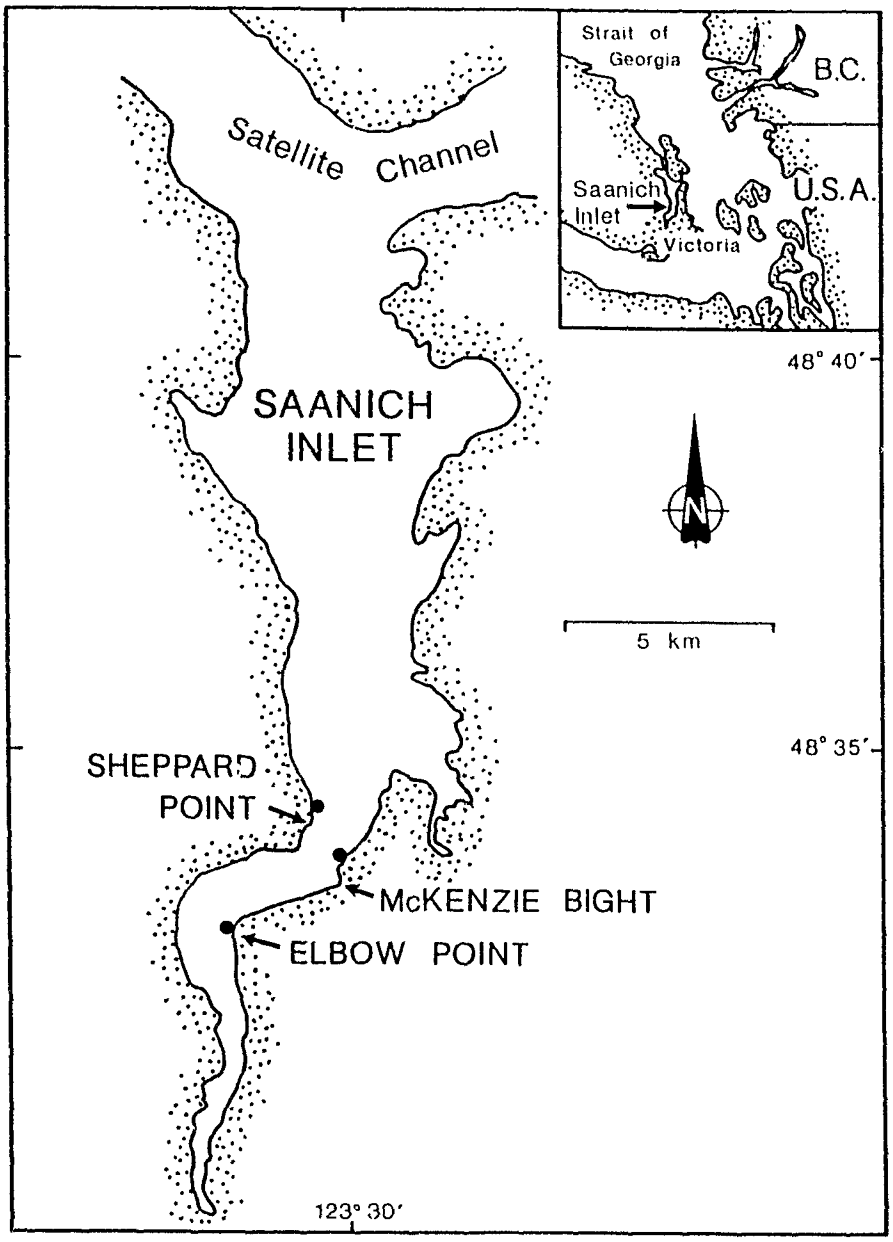

Fig. 1. Location of transect sites (●) in Saanich Inlet, Vancouver Island, B.C. Inset: Location of Saanich Inlet in relation to the mainland of B.C.

extending from the centre of the pilot's viewport outward at an angle of approximately 45° to each side, corresponding to approximately 3 m of horizontal distance across the substrate (i.e., viewing width). Total length of fish (TL, most anterior tip of the longest jaw to the most posterior tip of the caudal fin) was visually estimated (± 5 cm) by comparison of the fish with an externally-mounted, graduated rod. Rockfish were designated as small ($\leq$20 cm TL) and large (>20 cm TL) based on the size at which they enter recreational and commercial fisheries (after Richards 1986). Activity of fish was scored according to whether the fish was perched in the open, positioned in a crevice, occupying a shelter hole, hovering off the substrate, or actively swimming forward. Habitat was categorized as wall, sand/mud, or complex (comprised of broken rock and boulder fields). Any change in the slope of the substrate (± 10°) was estimated and depth noted.

Rockfish density was determined for 20-m depth intervals. The total number of fish recorded by both observers within a 20-m depth interval was divided by the total area of substrate viewed for that depth interval. The area viewed was calculated by multiplying the viewing width of both observers (i.e., 6 m) by the ratio of the change in depth to the sine of the slope.

Activities of each species of rockfish were analyzed using % occurrence, which was calculated by dividing the sum of all individuals observed in each activity by the total number of individuals of the species for which activities were recorded, and multiplying by 100%. Species associations were determined for individual fish within each species by scoring the presence of a conspecific or a heterospecific within ± 3 m. The sum of the number of individuals which were observed in the presence of a con- or heterospecific was then expressed as a percentage of the total number of individuals of the species. Individual rockfish with no other rockfish within 3 m were considered to be 'alone'.

Median ($Q_{0.25}$, $Q_{0.75}$) densities of small and large fish were calculated for each habitat type and 20-m depth interval, with transects pooled for increased sample size. Densities of rockfish among depth intervals and habitats were analyzed using Kruskal-Wallis tests for those species with median densities greater than 1 fish$\cdot$100m^{-2} (SAS 1985). Statistical significance was indicated by $P \leq 0.05$. Analyses for rockfish species with median densities of less than 1 fish$\cdot$100m^{-2} were therefore limited to qualitative comparisons of their depth distributions and numerical abundances. It was nevertheless important to include these comparisons because direct observation for these species has rarely, or never, been documented.

RESULTS

Physical Parameters

In total, an area of 10,521 m^2 was surveyed using the submersible, of which 38% was wall habitat, 47% complex habitat, and 15% sand/mud. The area of coverage among complex and wall habitat types differed with depth (Fig. 2). The area of complex habitat decreased with depth whereas the area of wall habitat increased with depth. Sand/mud habitat was encountered only at depths of less than 60 m and the median area surveyed was zero. Wall habitat was the only habitat type observed at the deepest depth interval (121-140 m). Slope was correlated with depth (Spearman rank correlation: $r_s = 0.37$, $n = 705$, $P < 0.001$) and wall habitat found primarily in deep water provided vertical or near-vertical relief (~70-90° slope), whereas complex and sand/mud habitats in shallower depths provided a graded substrate (~20-70° slope).

The area of each habitat type differed among survey sites (Kruskal-Wallis: P = <0.001, 0.03, <0.001 for wall, complex, and sand/mud habitat respectively). Elbow Point and McKenzie Bight had similar habitats whereas Sheppard Point had less wall and complex habitat and more sand/mud habitat relative to the Elbow Point and McKenzie Bight sites.

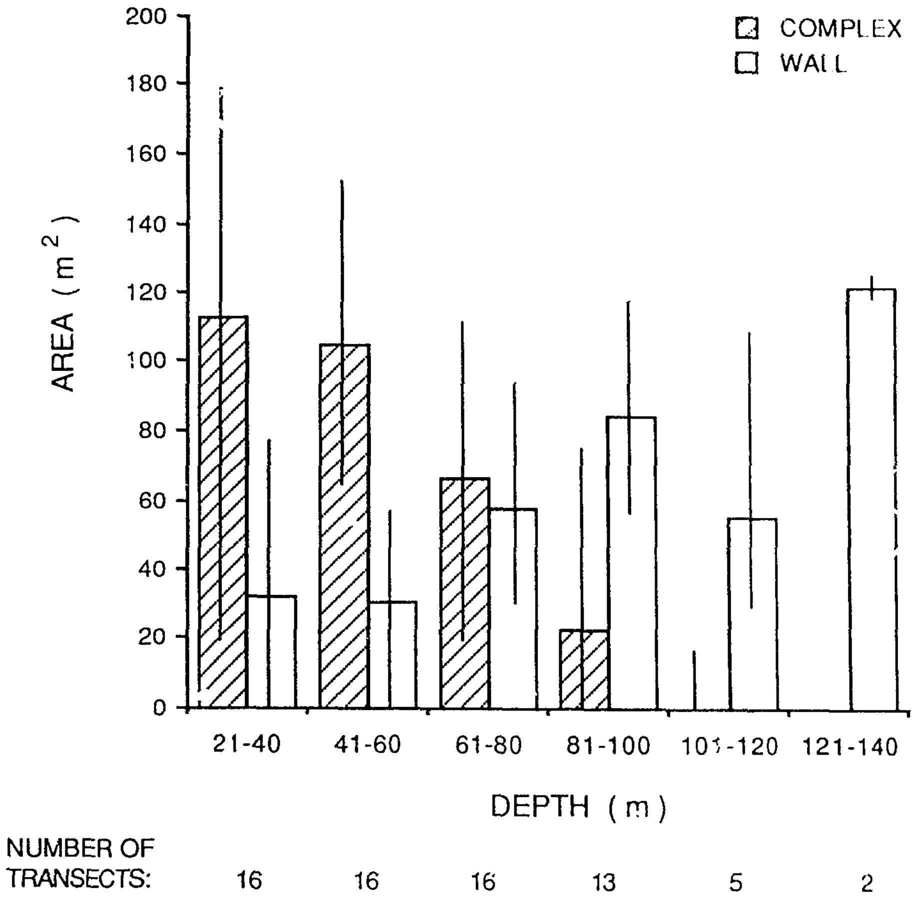

Fig. 2. Median areas of submersible surveys for complex and wall habitats in relation to depth. Vertical bars represent the interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$).

Depth, Size, and Density Distributions

Quillback rockfish (*S. maliger*) represented 88% (681/770) of all rockfish sighted and were observed over a depth range of 21-115 m, with a median depth of 54 m (43 m, 70 m). Overall density of quillback rockfish did not differ among depth intervals between 21-100 m ($P = 0.35$) (Fig. 3a). Density at depths greater than 100 m was negligible with only three quillback rockfish observed. The median size of quillback rockfish was 23 cm (18 cm, 25 cm). Their size was positively correlated with depth ($r^2 = 0.23$, $P < 0.001$, $n = 460$), however, and the density of small and large quillback rockfish therefore varied among depth intervals ($P = 0.01$ and $P = 0.02$ for small and large fish respectively) (Fig. 3b). The density of small quillback rockfish was similar to that of large quillback rockfish at the 21-40 m depth interval ($P = 0.66$), but it was less at depth intervals greater than 40 m (all $P < 0.05$) (Fig. 3b). In contrast, the median densities of large quillback rockfish at depth intervals between 41-100 m increased in relation to their densities at 21-40 m (Fig. 3b).

Tiger rockfish (*S. nigrocinctus*) constituted 4% (28/770) of the rockfish encountered and were observed between 33 and 97 m, with a median depth of 55 m (46 m, 67 m) (Fig. 4a). Tiger rockfish were most abundant at 41-60 m (Fig. 4a) (0.6 fish$\cdot$100m^{-2}), although their median density over 21-140 m was zero. Tiger rockfish were large and had a

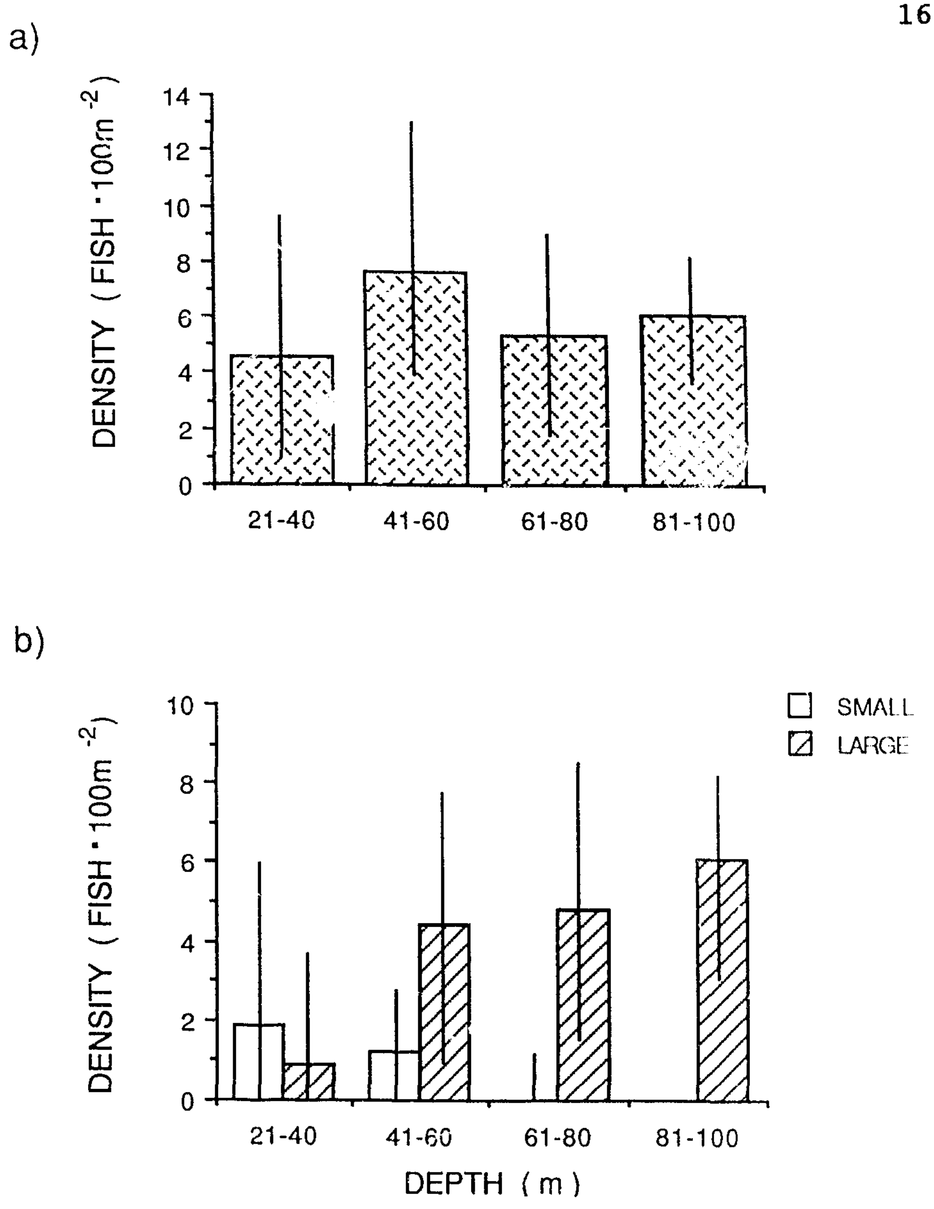

Fig. 3. a) Median densities of all quillback rockfish over depth intervals between 21 and 100 m; b) median densities of small and large quillback rockfish over depth intervals. Vertical bars represent the interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$). Median densities of quillback rockfish at depth intervals >100 m were zero.

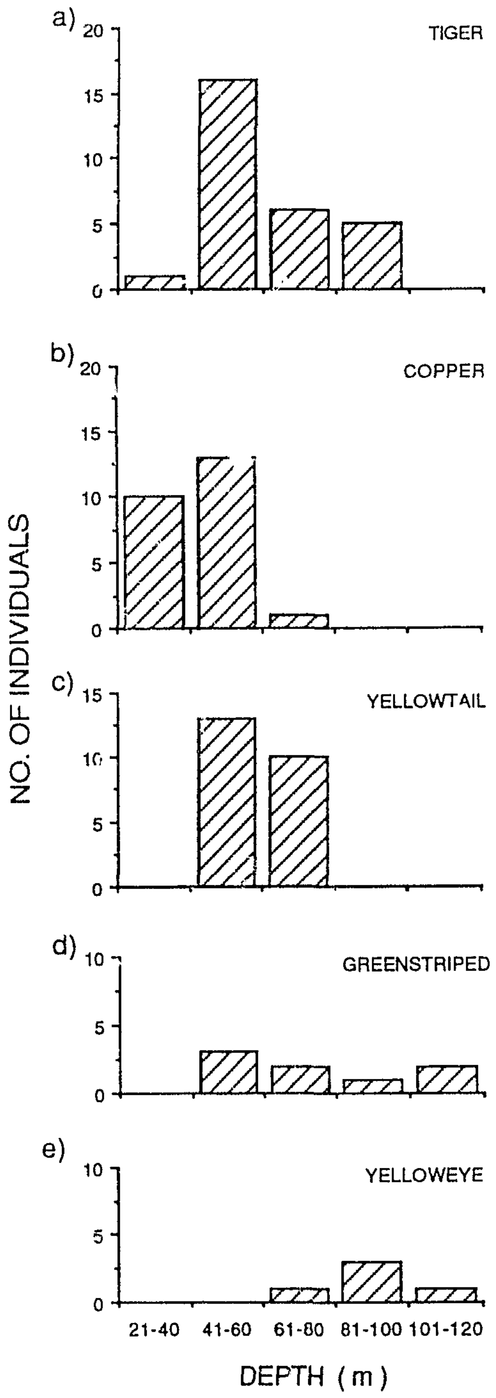

Fig. 4. Numerical abundance of rockfish species (excluding quillback rockfish) over depth, all transects pooled: a) tiger rockfish; b) copper rockfish; c) yellowtail rockfish; d) greenstriped rockfish; and e) yelloweye rockfish.

median size of 28 cm TL (25 cm, 31 cm). The size of tiger rockfish was not correlated with depth ($P = 0.27$, $n = 15$).

Copper rockfish (*S. caurinus*) represented 3% (24/770) of all rockfish observed. They were observed in low abundance (median density of zero) between 21 and 65 m, and had a median depth of 44 m (26 m, 45 m) (Fig. 4b). Median size of copper rockfish was 25 cm TL (18 cm, 28 cm). The size of copper rockfish was positively correlated with depth ($r^2 = 0.36$, $P = 0.02$, $n = 15$), with small copper rockfish ($\leq$20 cm TL) never found at depths greater than 40 m.

Yellowtail rockfish (*S. flavidus*) also represented 3% (23/770) of all rockfish observed on the surveys. They were seen only between 41 and 65 m, and had a median depth of 49 m (49 m, 65 m) (Fig. 4c). They were observed in low abundance (median density of zero) except in 41-80 m depth intervals where their densities reached a maximum of 6.3-6.6 fish$\cdot$100m^{-2}. Yellowtail rockfish were large fish ranging from 20-40 cm TL with a median size of 35 cm TL. The size of yellowtail rockfish was not correlated with depth ($P = 0.46$, $n = 21$).

Greenstriped rockfish (*S. elongatus*) ($n = 8$), yelloweye rockfish (*S. ruberrimus*) ($n = 5$), and one unidentified rockfish each represented less than 1% of all observed rockfish. Greenstriped rockfish occurred from 52 m to 114 m, with a median depth of 65 m (59 m, 89 m) (Fig. 4d). They were observed in low abundance throughout their depth range (median density of zero), with maximum densities of less than 1.0 fish•100m^{-2}. The median size of greenstriped rockfish was 18 cm TL (15 cm, 20 cm).

Yelloweye rockfish were observed between 77 and 103 m, with a median depth of 89 m (83 m, 95 m) (Fig. 4e). Most yelloweye rockfish were observed at 81-100 m, although in low abundance (less than 0.8 fish•100m^{-2}). Their median density over 21-140 m, however, was zero. All juvenile yelloweye rockfish (18-20 cm TL) observed were at depths greater than 95 m. Subadult and adult yelloweye rockfish were 36-46 cm TL and occurred between 80-90 m.

Habitat Distribution

Overall, quillback rockfish density was highest in areas of complex habitat (5.8 fish•100m^{-2}), followed by densities in wall habitat (3.5 fish•100m^{-2}) (Fig. 5). Only four quillback rockfish were observed over sand/mud habitat. Quillback rockfish densities, whether in complex or wall habitat, did not differ among depth intervals $\leq$100 m (P = 0.52 and P = 0.64 respectively) (Fig. 5).

Density of quillback rockfish differed among survey sites (P = 0.00). Elbow Point and McKenzie Bight sites had a median density of 5.7 fish•100m^{-2} (3.3 fish•100m^{-2}, 9.1 fish•100m^{-2}) whereas the median density at Sheppard Point was zero (0 fish•100m^{-2}, 3.0 fish•100m^{-2}).

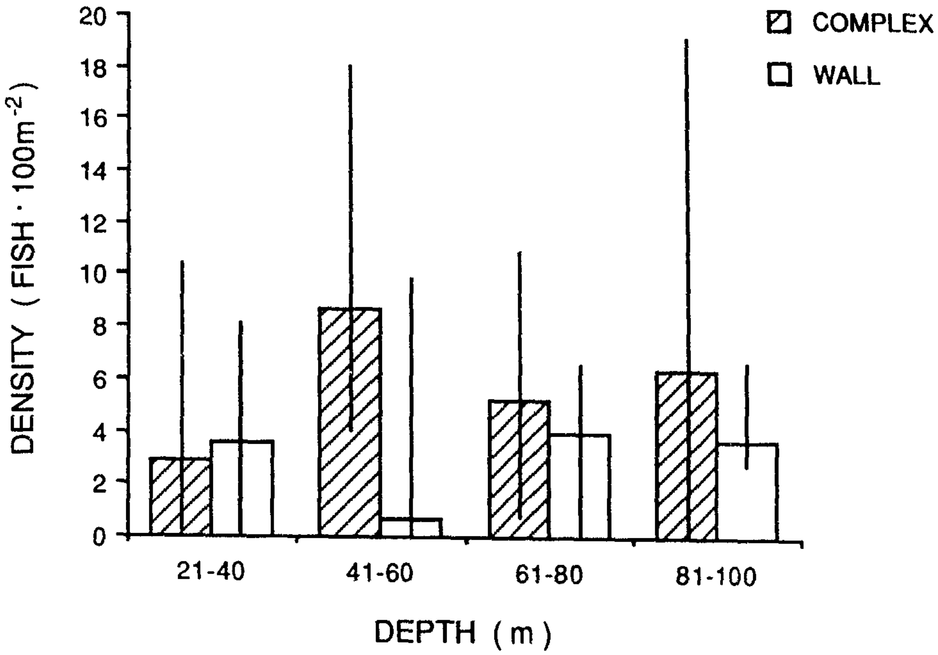

Fig. 5. Median densities of quillback rockfish in complex and wall habitats among depth intervals. Vertical bars represent interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$). Median densities of quillback rockfish over sand/mud habitat were zero.

Tiger, copper, yellowtail, and yelloweye rockfish were observed only over complex or wall habitats. There was no difference in the relative abundance of tiger rockfish in complex and wall habitats (46% and 54% respectively). The relative abundances of copper, yellowtail, and yelloweye rockfish were greater in complex habitat (83%, 91%, and 80% respectively) than over wall habitat. Greenstriped rockfish were observed primarily (80% of abundance) over sand/mud habitat and were never seen over complex habitat.

Activities

The majority of quillback rockfish were observed hovering or perched on substrate in the open (Fig. 6a). Copper rockfish were also observed primarily hovering and perched in the open, but were seen swimming relatively more frequently than quillback rockfish (Fig. 6b). Both species were observed infrequently in crevices and almost never seen in shelter holes. Tiger rockfish were also observed most frequently perched in the open (Fig. 6c). As with yelloweye rockfish (Fig. 6d), however, they were seen relatively frequently in crevices, and to a lesser degree in shelter holes. Both were only occasionally seen either swimming or hovering. Yellowtail rockfish (Fig. 6e) were all observed either hovering or swimming close to the substrate. Greenstriped rockfish (Fig. 6f) were all observed while perched on the substrate in the open.

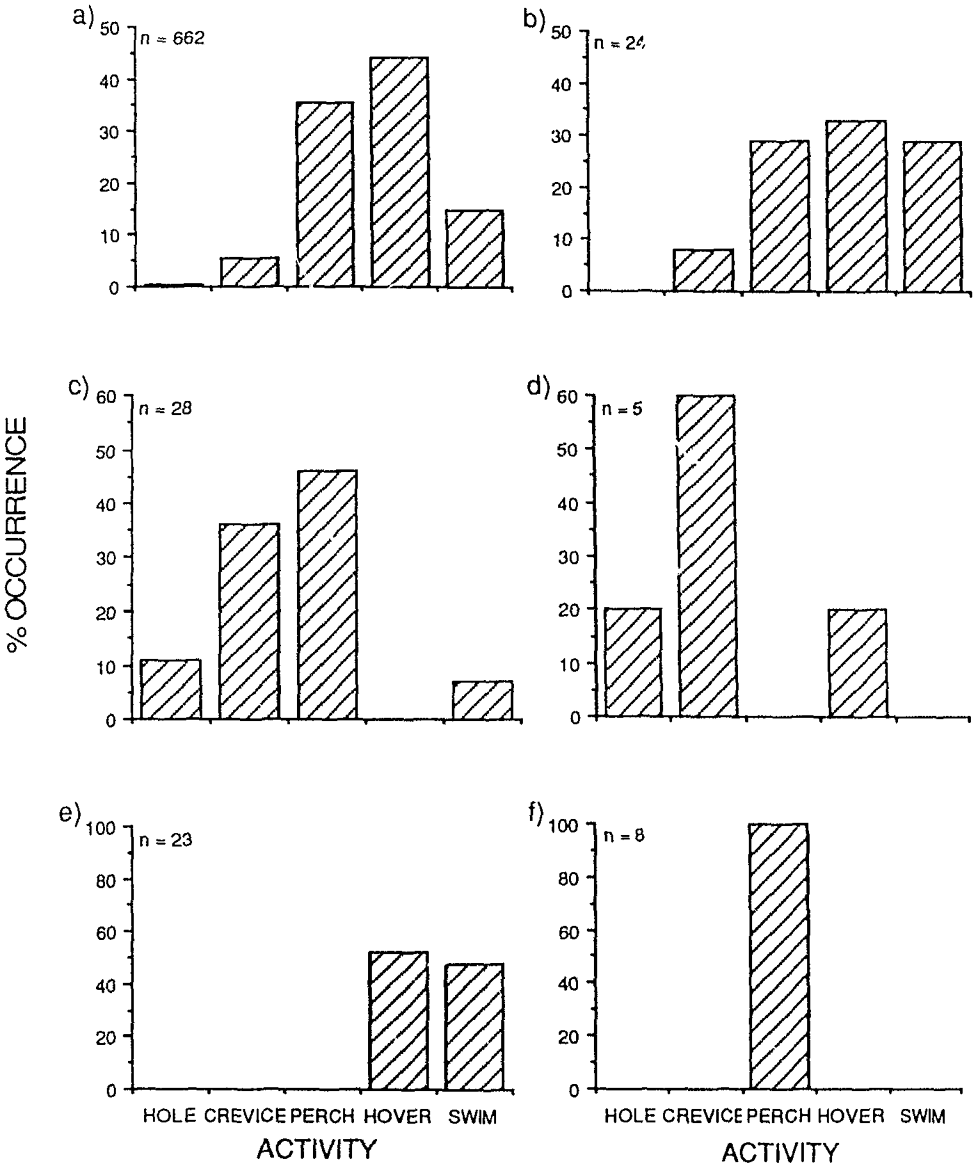

Fig. 6. Percent occurrence of activities for: a) quillback rockfish; b) copper rockfish; c) tiger rockfish; d) yelloweye rockfish; e) yellowtail rockfish; and f) greenstriped rockfish.

Species Associations

The majority of quillback rockfish (94% occurrence) were observed within 3 m of at least one other quillback rockfish (Fig. 7a). Quillback rockfish were almost never observed alone (2%) and were observed in the presence of other species relatively infrequently (~20% occurrence or less). Copper rockfish, although observed within 3 m of quillback rockfish the majority of the time (92%) (Fig. 7b), also tended to occur near other copper rockfish (64% occurrence) and tiger rockfish (32%). They were seldom near greenstriped rockfish (4%) or alone (4%). Tiger rockfish were almost always (96% occurrence) (Fig. 7c) observed near quillback rockfish, and to a much lesser extent, near other tiger rockfish (21%). They rarely were observed alone (4%) or near either copper or yellowtail rockfish. The majority of yellowtail rockfish were observed in proximity to quillback rockfish (96%) and other yellowtail rockfish (91%) (Fig. 7d). All yelloweye rockfish were seen within 3 m of at least one quillback rockfish (Fig. 7e). They were never found in the presence of other rockfish species, including conspecifics. Greenstriped rockfish were observed in association with quillback rockfish (75%), although less frequently than were the other species of rockfish (Fig. 7f). They were otherwise observed with copper rockfish (12%) or alone (25%).

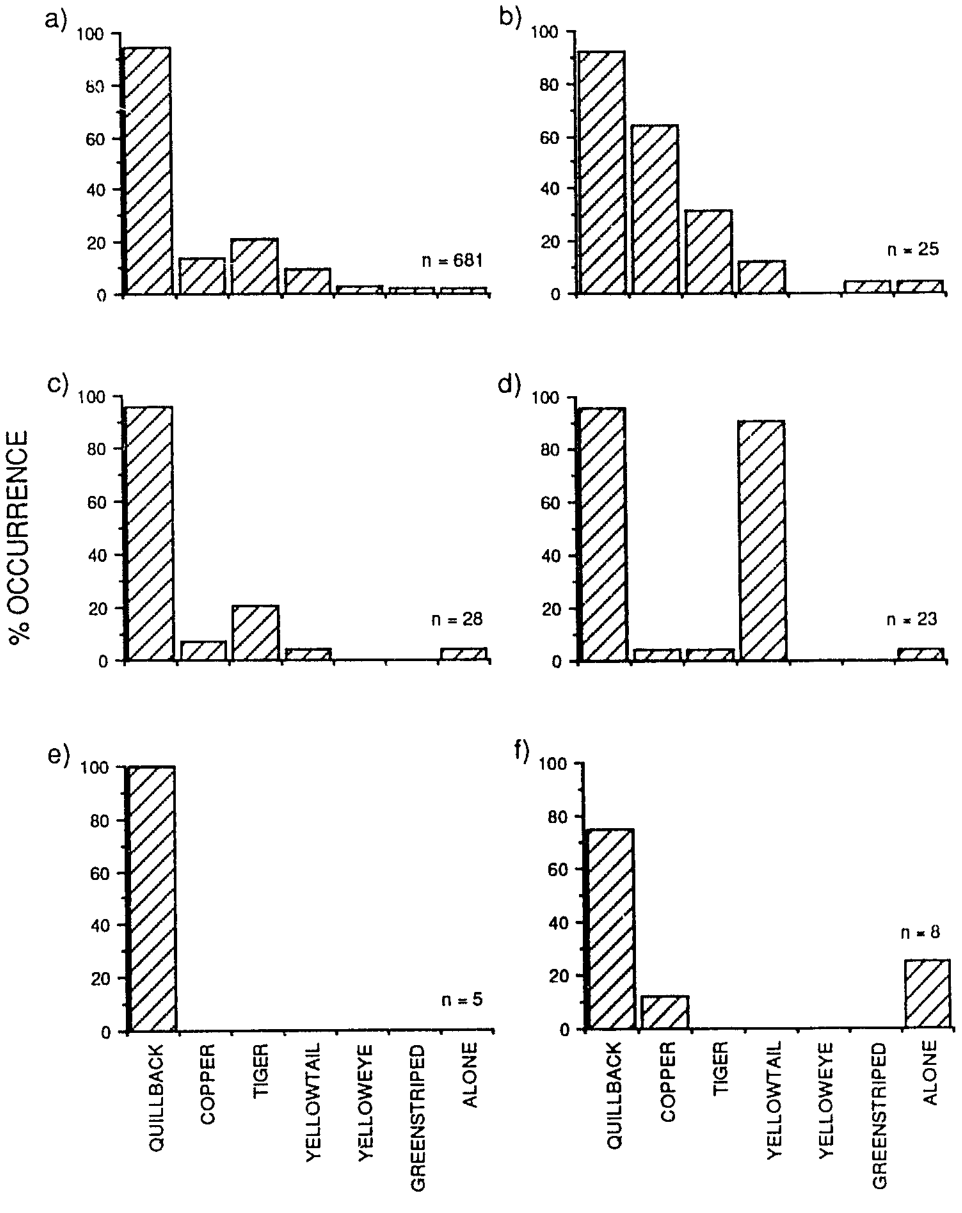

Fig. 7. Percent occurrence of con- and heterospecific rockfish in association with: a) quillback rockfish; b) copper rockfish; c) tiger rockfish; d) yellowtail rockfish; e) yelloweye rockfish; and f) greenstriped rockfish.

DISCUSSION

Quillback rockfish appear to be the numerically dominant rockfish species at depths of 21-100 m in coastal areas of southern British Columbia (this study; Richards 1986). Their depth distribution is centered at 41-60 m (Fig. 3a), and in Saanich Inlet, as well as in the Strait of Georgia (Richards 1986), their density at this depth is eight times greater than that of any other rockfish species observed. In contrast, tiger, copper, yelloweye, and greenstriped rockfish occurred in consistently low abundances (all had median densities of 0 fish•$100m^{-2}$) throughout the depth and habitat range surveyed in Saanich Inlet (Fig. 4). Greenstriped and yelloweye rockfish were also observed in relatively low densities (means of $\leq$ 1.5 fish•$100m^{-2}$) in depths of 21-140 m in the Strait of Georgia, British Columbia (Richards 1986). Yellowtail rockfish were also observed in Saanich Inlet in low abundance but their propensity to form conspecific schools caused periodic maximum densities of ~6 fish•$100m^{-2}$.

The predominance of quillback rockfish throughout the majority of the depth range surveyed in Saanich Inlet (21-100 m) suggested that any segregation among the six rockfish species was based on habitat type and activities rather than strict bathymetry. Despite the low abundance of many of these rockfish species, comparisons of depth, habitat, and behaviour were made because of the relative absence of the documentation of *in situ* observations for these low-density species. However, all of these species form part of sports and commercial fisheries (Love *et al.* 1990) and it was therefore worthwhile to attempt preliminary comparisons.

Tiger rockfish overlapped with quillback rockfish in depth and habitat, and both rockfish species perched in the open frequently. Tiger rockfish were found in shelter holes and crevices more frequently than quillback rockfish, however, and they were never observed hovering over the bottom like quillback rockfish. The close association of tiger rockfish with the substrate was indicative of a relatively sedentary lifestyle which was consistent with its known territorial behaviour (Hart 1973). Tiger rockfish are also considered to be solitary fish (Hart 1973; Kramer and O'Connell 1988) in that they are usually not associated with conspecifics (Keenleyside 1979). In Saanich Inlet, tiger rockfish were not only associated with quillback rockfish (96% occurrence) (Fig. 7c) but were also found within 3 m of other tiger rockfish (21% occurrence) and hence were not strictly solitary. This was in contrast to yelloweye and greenstriped rockfish which were never seen in the presence of conspecifics in Saanich Inlet.

Copper rockfish were observed at shallower depths than quillback rockfish in Saanich Inlet. This was consistent with studies using SCUBA (Moulton 1977; Richards 1987) which, in general, considered copper rockfish to be a shallow-water rockfish species when compared to quillback rockfish. Segregation between copper and quillback rockfish based on habitat and activities, however, was not marked and both species were observed over similar habitat types and had similar activities.

Yellowtail rockfish and quillback rockfish also overlapped in depth and habitat, and the majority of yellowtail rockfish were found in conspecific schools near quillback rockfish (Fig. 7d). Their activities in complex and wall habitats were different from those of quillback rockfish, however, as they were always observed hovering or swimming in the water column over the substrate and never came in direct contact with the bottom. Yellowtail rockfish were, therefore, spatially segregated from quillback rockfish.

Based on limited data available for greenstriped and yelloweye rockfish, depth and habitat segregation among quillback, greenstriped, and yelloweye rockfish in Saanich Inlet was consistent with observations for these species at 21-140 m depths in the Strait of Georgia (Richards 1986). Greenstriped rockfish in Saanich Inlet partially overlapped with quillback rockfish in depth, although greenstriped rockfish were generally distributed at deeper depths than quillback rockfish. In contrast to quillback rockfish, they were observed over sand/mud areas adjacent to the complex and wall areas frequented by quillback rockfish. Yelloweye rockfish overlapped with quillback rockfish in type of habitat but were observed more frequently in shelter holes and crevices (Fig. 6). Greenstriped rockfish overlapped with yelloweye rockfish in depth but were segregated by habitat type.

In addition, most rockfish move to deeper water as they increase in size and reach maturity (Westrheim 1970; Boehlert 1980; Larson 1980a; Wilkins 1980; Hallacher and Roberts 1985). In Saanich Inlet, the increase in quillback and copper rockfish size in relation to increasing depth was primarily due to the paucity of small quillback and copper rockfish in deeper waters rather than an absence of large quillback and copper rockfish in shallower waters. Similar positive correlations between rockfish size and depth have also been observed for quillback, yelloweye, and greenstriped rockfish in the Strait of Georgia (Richards 1986).

The depth distribution of rockfish in Saanich Inlet, and hence any size or species segregation, may be influenced by intermittent anoxia that occurs in the bottom-water of Saanich Inlet during spring and summer (Herlinveaux 1962). During April to August, the zone of anoxia in the bottom-water may intrude up to 125-150 m depths (Burd 1983), causing squat lobsters (*Munida quadrispina*) to migrate vertically *en masse* to avoid the decreasing oxygen levels (Burd 1983). During the *Pisces* transects in December, *Munida* were observed at least as deep as 153 m (start of the transects) and there were no signs of anoxia in the bottom-water based on hydrocasts. In addition, there appeared to be adequate dissolved oxygen in the bottom-water to allow at least the passage of fish since schools of hake (*Merluccius productus*) were observed swimming across the bottom at 230 m (pers. comm., Dr. J. Littlepage, Biology Dept., Univ. Victoria, Victoria, B.C., V8W 2Y2). Although *Munida* can tolerate low oxygen levels (0.10-0.15 $ml \cdot L^{-1}$) (Burd 1983), most invertebrates and fishes cannot inhabit such waters and must move if possible to avoid low oxygen levels. Rockfish may therefore compress or shift their depth distributions towards more shallow waters during the spring and summer when the bottom-water of Saanich Inlet is anoxic. The depth distributions of rockfish species observed in December may therefore not be the same as their distributions in spring-summer.

Regardless of depth, quillback (Fig. 5), tiger, copper, yellowtail, and yelloweye rockfish densities were greatest in complex habitat dominated by broken rock and boulder fields. This type of habitat appeared to be a common feature for the occurrence of most near-bottom rockfish. Based on *Pisces* surveys in the Strait of Georgia, Richards (1986) also observed that quillback and yelloweye rockfish were most abundant in complex habitat. Similarly, Richards (1987) determined that densities of copper and quillback rockfish were highest in complex habitat or in areas of highly irregular relief in water <18 m in depth. Using SCUBA surveys, Matthews (1990a) also found the highest densities of large copper and large quillback rockfish on high-relief rocky reefs. Additionally, submersible observations in the vicinity of Heceta Bank, Oregon, by Pearcy *et al.* (1989) suggested that tiger, yelloweye, and yellowtail rockfish were most frequently encountered over rock and rubble habitat in depths of 67-149 m. The densities of these near-bottom species may be greatest in this type of habitat because of increased protection from predators or increased prey due to the increase in microhabitat structure.

Given the propensity of rockfish to aggregate over complex habitat, the differences in density of quillback rockfish among sites in Saanich Inlet was not surprising. The Sheppard Point site was noticeably different from the Elbow Point and McKenzie Bight sites. It had more sand/mud areas and a shallower slope. It was also the only site where greenstriped rockfish were observed, which was in keeping with the apparent habitat distribution of this species (Richards 1986; Pearcy *et al.* 1989).

It was obvious from observing the activities of quillback, copper, yellowtail, and greenstriped rockfish that they spend the majority of their time, during daylight hours at least, perched in the open, hovering, or swimming

(Fig. 6). These activities potentially expose the fish to predation much more than occupation in crevices or shelter holes. Observations from the submersible were limited in this respect because it was impossible to look into all crevices or into shelter holes under rocks for the presence of fish. Tiger and yelloweye rockfish could be seen in shelter holes and crevices but their size could not always be estimated. Although the *Pisces* approached shelter holes from below (during its ascent), fish in deep shelter holes and crevices may not have been detected. The presence of fish in crevices and shelter holes was therefore probably underestimated. Nevertheless, at present, submersibles and remotely operated vehicles (ROVs) provide the best means of censusing rockfish in complex habitat in deep-water environments.

Rockfish did not appear to be attracted or repelled by the presence of the *Pisces* submersible and its lights. At times, rockfish actively finned to keep in position in the water column or on the rock substrate after the submersible had inadvertently blown water (and hence the fish) at the cliff face. In comparison, obvious attraction to the submersible and its lights was apparent by the behaviour of some ratfish (*Hydrolagus colliei*) and a sixgill shark (*Hexanchus griseus*), both of which swam back-and-forth around the front of the submersible. Carlson and Straty (1981), while observing rockfish in southeastern Alaska using a submersible, also noted that most of the rockfish were neither repelled by, nor attracted to, their submersible and its lights. A notable exception in their study was large (7-10 kg) yelloweye rockfish, which were obviously attracted to the submersible and actually followed it around. Pearcy *et al.* (1989) have also noted that large schools of yellowtail rockfish were attracted to their submersible and followed it over substantial periods of time and depth. The small schools of yellowtail rockfish encountered in Saanich Inlet did not appear to be attracted to the *Pisces* submersible. Although it was therefore evident that estimates of abundance using observations from a submersible involve some bias, direct visual assessment using a submersible can provide unique information on density, habitat, activities, and species associations for nearshore rockfish species that is unattainable by conventional survey techniques used in fisheries.

SUMMARY

As surveyed using the *Pisces IV* submersible, quillback rockfish were the numerically dominant rockfish in Saanich Inlet between depths of 21-100 m where they attained median densities of 5.7 fish·$100m^{-2}$. Copper, tiger, yellowtail, yelloweye, and greenstriped rockfish were all observed in consistently low densities (less than 1 fish·$100m^{-2}$). Segregation among rockfish species was based on a combination of depth, habitat, and behaviour. The greatest densities of rockfish occurred over complex habitat; the exception was greenstriped rockfish which occurred predominantly over sand/mud habitat. The majority (>50% occurrence) of rockfish were observed either perched on open substrate, hovering, or swimming. Tiger and yelloweye rockfish were more frequently observed in shelter holes and crevices compared with other rockfish species. All rockfish species were associated with quillback rockfish (all >75% occurrence). Quillback, copper, and yellowtail rockfish also were associated with conspecifics, indicative of socially interacting fishes. Yelloweye, greenstriped, and to a lesser degree, tiger rockfish, were solitary fishes.

CHAPTER III

COMPARATIVE FEEDING ECOLOGY OF COPPER AND QUILLBACK ROCKFISH

INTRODUCTION

In spite of the diversity and abundance of rockfish in the northeastern Pacific Ocean (approximately 65 species) (Chen 1971), and their importance in sport and commercial fisheries (Hart 1973; Love *et al.* 1990), detailed food habits are known only for approximately 15 species (e.g., Gotshall *et al.* 1965; Patten 1973; Prince and Gotshall 1976; Moulton 1977; Hueckel and Stayton 1982; Brodeur and Pearcy 1984; Singer 1985; Buckley and Hueckel 1985; Rosenthal *et al.* 1988). Many of these rockfish species co-occur, have similar morphology, and occupy similar habitats, creating a large matrix of species that are potentially overlapping and competing for the use of resources (Brodeur and Pearcy 1984).

Quantification of the niches of these potentially competing species can provide a basis for determining potential conflicts over resources. One of the most common resources measured is food (Pianka 1981; Krebs 1989). 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, however, 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 quillback rockfish and the copper rockfish, are of particular interest because of their abundance in nearshore areas of British Columbia (Chapter II; Richards 1987) and their use in local fisheries (Hart 1973; Richards and Cass 1987; Hand and Richards 1991). To date, feeding studies of copper and quillback rockfish have not been carried out in waters of British Columbia; previous studies have been centred off the coasts of California, Oregon, Washington and Alaska. Feeding ecology of copper rockfish in coastal areas of the United States (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 quillback and copper rockfish, however, have been addressed in few of these studies (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, in order to assess potential competition between the species for food resources. Food habits of both species were compared on a seasonal and size-related basis. Niche breadth and niche overlap in the diets between copper and quillback rockfish were examined on a seasonal basis to compare their use of common resources. Niche overlap in food habits between the species was related to the availability of the food resources in the environment in order to indicate, on a qualitative basis, the potential for interspecific competition.

METHODS

During October 1986 to August 1990, 602 copper rockfish and 285 quillback rockfish were collected from an area north of McKenzie Bight in Saanich Inlet, B.C. (Fig. 1). Rockfish were collected in water depths between 15 and 40 m (50-130 ft) from rocky reef areas where they were sympatric. Fish were speared in the head using a modified Hawaiian sling-spear and were placed in individual polyethylene bags at depth to prevent the loss of regurgitated food resulting from the expansion of the air bladder during ascent. Each rockfish was measured for standard length (SL, anterior most tip of upper jaw to the posterior end of the vertebral column), total length, and wet body mass (blotted on paper towel) (Cailliet *et al.* 1987), and was sexed externally according to Moser (1967). Fish were then opened ventrally and the gonads were removed, weighed as a pair, and retained for further analysis (Chapter VI). The remainder of the fish was immediately frozen and later dissected in detail.

In the dissection, the liver and the complete gastrointestinal tract (from esophagus to anus) were removed. When possible, visceral fat (the fat covering the external surfaces of the viscera) was collected. The stomach was then 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 were also recovered for the stomach content analyses.

In conjunction with the processing of the gastrointestinal tract for an allometry study (Chapter IV), the excised intestine and caeca were emptied of any contents and weighed. Wet masses also were obtained for the empty stomach, as well as for the liver and visceral fat of each fish. These masses, along with the mass of the stomach contents and gonads, were then subtracted from the wet body mass of the fish to give an eviscerated wet body mass (referred to simply as body mass).

Food Habit Analyses

Composition of the Diet

Contents of the stomach were sorted into categories of pelagic and demersal fishes, pelagic and demersal crustaceans, miscellaneous food items, and debris and parasites. Debris and parasites were excluded from the analysis.

Fish in stomach contents were identified by any undigested whole fish present in the stomach contents (Hart 1973) or from their sagittal otoliths using a reference collection and Morrow (1979). Size of each fish was initially measured as vertebral column length (VCL), the length of the vertebral column from its point of insertion in the skull to the hypural plate. If the head of the fish was intact then standard length (SL) was also measured. For herring (*Clupea harengus pallasi*) and kelp perch (*Brachyistius frenatus*), VCL was a consistent measure available even in digested fish and VCL was converted to standard length of the fish using calculated VCL-SL regressions. For other fish species represented by only a few individuals, standard lengths were individually measured for relatively undigested fishes, and a mean standard length was calculated for each fish species. Similarly, mass for each fish consumed was estimated from the masses of individual, undigested fish present in the stomachs or from calculated VCL-mass regressions.

All regressions were checked for heteroscedasticity, data outliers, and adequacy of a linear regression model using diagnostic plots of residuals (Larsen and McCleary 1972; Kleinbaum and Kupper 1978). Variables used in regression analyses were $\log_{10}$ transformed where necessary to correct for non-constant variance. Data points were designated as outliers, and deleted, if they were ±3 standard deviations from the regression line and were clearly separated from the other data in residual plots.

Crustaceans and miscellaneous invertebrates were identified from whole or partial specimens using 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. Sizes of crustaceans were estimated by measuring parts of their bodies that were relatively resistant to digestion and therefore consistently available for measuring. All measurements were taken using vernier calipers (± 0.1 mm).

For squat lobsters and shrimps (with the exception of *Pandalus platyceros*), carapace length (CL: the distance from the back of the eye orbit to the posterior edge of the carapace) and, for relatively undigested individuals, flexed body length (FBL) was measured. FBL is the distance from the back of the eye orbit to the posterior edge of the flexed, third abdominal segment. FBL was measured rather than total length (distance from the tip of the rostrum to the tip of the telson) as squat lobsters and shrimps are found in a completely flexed position in the stomachs of rockfish, and measurement of total length is subject to error (Butler 1980). Carapace lengths were converted to FBL using a calculated CL-FBL regression, and masses of individual squat lobsters and shrimps were determined from CL-mass relationships. Due to the small sample size, mean FBL and mass, rather than regression analyses, were used to estimate the size of *P. platyceros* consumed.

All crabs were measured along the axis of the greatest dimension of the carapace. For oval-shaped crabs in the family Cancridae (*Cancer*) and Porcellanidae (*Petrolisthes*), carapace width (CW: distance between the lateral projections of the carapace) was measured. For pear-shaped crabs in the family Majidae (*Chorilia, Hyas, Pugettia*), carapace length (CL: distance between the anterior margin of the rostrum to the posterior edge of the carapace) was measured. Mass of individual *Cancer oregonensis* was estimated using a calculated CW-mass regression. Other crabs were either weighed directly or their mass was estimated from similar-sized, undigested individuals of the same species.

Total length (distance between the back of the eye orbit and the tip of the telson with the animal extended) was measured for euphausiids, mysids, and megalopa larvae of crabs. Total length of amphipods was measured as the distance between the furthest anterior and the most posterior portions of the body. These pelagic crustacean groups were enumerated according to size classes within each group and a mean total length and a mean mass were calculated for each size class based on undigested individuals.

Lengths of miscellaneous food items were either measured as total lengths (tunicates, polychaetes, and pteropods) or as a diameter (fish eggs, disc of brittlestar). Mass was determined from relatively undigested individuals.

Total mass of food consumed by each rockfish was estimated by summing the calculated masses for all individual prey items consumed by the fish. 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 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-hour intervals. Collection times for individual fish sampled throughout the year were standardized to a day with sunrise at 0600 h and sunset at 1800 h PST (Brodeur and Pearcy 1984), using sunrise-sunset tables supplied by the Dominion Astrophysical Observatory, Victoria, B.C.

The relationship between total mass of food consumed and body mass was examined for both copper and quillback rockfish for within-species effects due to sex and season. Dependent and independent variables were $\log_{10}$ transformed to correct for heteroscedasticity based on examination of residuals. 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) (Tabachnick and Fidell 1983), with rockfish body mass as the single covariate. When this preliminary assumption was satisfied, then the effects due to sex or season within each species were analysed using a two-factor ANCOVA (BMDP, Program 4V, Dixon *et al.* 1983).

Similarly, differences between species in the total mass of food consumed in relation to body mass were examined among the four seasons. Differences between copper and quillback rockfish in the size of food consumed were examined using a single-factor ANCOVA for each food type (pelagic fishes, demersal fishes, demersal crustaceans, and pelagic crustaceans).

Niche Breadth

Niche breadth was estimated using Levins' (1968) measure (B) as standardized by Hurlbert (1978) (B_A) (Krebs 1989):

$$[1] \qquad B_A = \frac{B - 1}{n - 1}$$

where: B is $1/\Sigma p_j^2$; p_j^2 is the proportion of individuals found in or using food category j or the proportion of items or mass in the diet that are of food category j (estimated by N_j/Y) ($\Sigma p_j = 1.0$); N_j is the number of individuals, items, or mass found in or using resource state j; Y is ΣN_j, which is the total number of individuals, items, or mass sampled; and n is the number of possible food resources. Values of

B_A 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

Niche overlap between copper and quillback rockfish was measured using the Simplified Morisita Index (C_H) (Horn 1966):

$$[2] \qquad C_H = \frac{2 \Sigma p_{ij}p_{ik}}{\Sigma p_{ij}^2 + \Sigma p_{ik}^2}$$

where: p_{ij} is the proportion that resource i is of the total resources used by species j; and p_{ik} is the proportion that resource i is of the total resources used by species k. Values of C_H 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). The Simplified Morisita Index was used as a measure of overlap because it allows the use of proportions in the calculation of overlap between the diets of the two species based on mass contribution: Morisita's (1959) original measure is independent of sample size and resource diversity (Wolda 1981; Smith and Zaret 1982) but does not allow the use of proportions (Krebs 1989). Comparison of overlap values based on numerical abundance using Morisita's original measure and the Simplified Morisita Index indicated that any differences were negligible (<2%) and, if present, were conservative (i.e., overlap values based on the Simplified Morisita Index were always less than values calculated using Morisita's original measure).

Surveys of Potential Prey Species

Potential invertebrate and fish prey of copper and quillback rockfish were surveyed to assess their relative densities in the environment. Different survey methods were used for pelagic versus demersal prey types. Pelagic crustaceans and fishes were surveyed simultaneously with population surveys for rockfish over three rocky reefs where copper and quillback rockfish were sympatric (Chapter VII). Species and number of perch and the presence and relative size of euphausiid and/or mysid aggregations and schools of "bait fish" (e.g., juvenile herring) were recorded during 121 surveys over these rocky reefs. Demersal crustaceans and fishes were surveyed on the same study reefs using quadrats placed randomly over the reefs' gridded surfaces

(Chapter VII). The survey quadrat was a weighted hula-hoop with a circular area of 0.5 m^2. All invertebrates and demersal fish within the area circumscribed by the hoop were enumerated. Underwater lights were used to illuminate any cracks in rocks, and rocks without buried bases were overturned when possible (e.g., rocks less than ~25 cm diameter) to search for organisms. A total of 48 quadrats were surveyed over 9 days from January to May over the three rocky reefs.

RESULTS

General Food Habits

Overall, 47% (284/602) of the copper rockfish and 55% (158/285) of the quillback rockfish 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. 8). 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 (especially pelagic fishes) in the diet of copper rockfish, and a higher occurrence of crustaceans in the diet of quillback rockfish (Fig. 8).

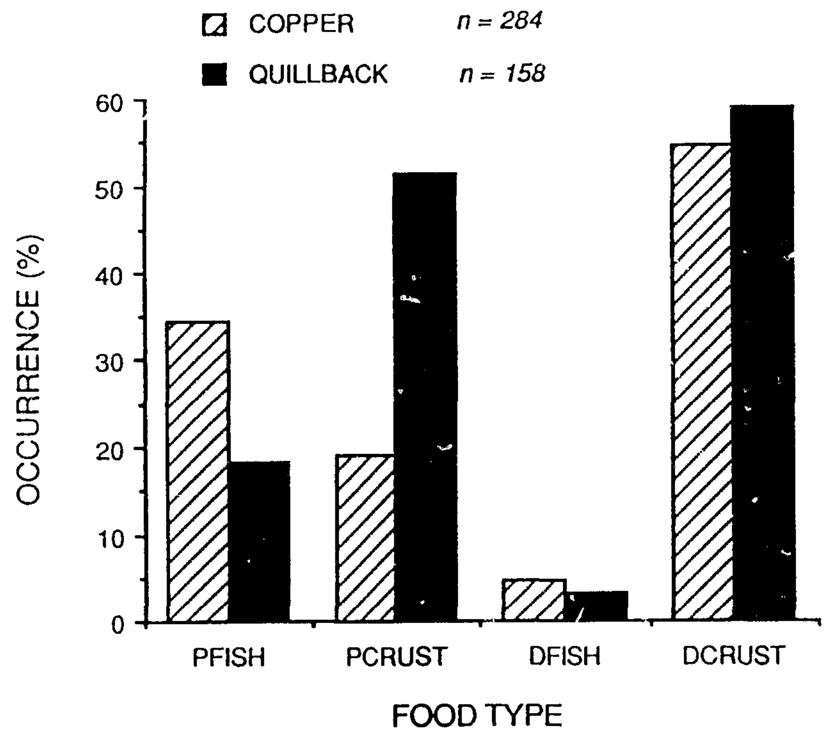

Fig. 8. Percent occurrence of different food types in the stomach contents of copper and quillback rockfish. Food types are: PFISH = pelagic fishes; PCRUST = pelagic crustaceans; DFISH = demersal fishes; and DCRUST = demersal crustaceans.

Specifically, the majority of copper rockfish had fed on herring, 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 less than 10% of the copper rockfish. Based on numerical abundance, however, pelagic crustaceans, such as euphausiids (*Euphausia pacifica*) and mysids, were consumed in greater numbers by copper rockfish than consumption of herring, squat lobsters, coonstriped shrimp, or other shrimps. The greatest contribution to the diet of copper rockfish on a mass basis was by pelagic fishes (73.5%), such as herring, kelp perch, and pile perch (*Damalichthys vacca*). Demersal crustaceans (coonstriped shrimp, two-spot prawns, and squat lobsters) contributed a further 20.3% to the diet's mass. The contribution by pelagic crustaceans, in particular euphausiids and mysids, was negligible (Table 1).

As with copper rockfish, a large proportion of quillback rockfish had fed on herring, squat lobsters, coonstriped shrimp, and various other unidentified shrimps (Table 2). In contrast to the relatively small percentage of copper rockfish having fed on pelagic crustaceans (19.0% occurrence), a large proportion of quillback rockfish had fed on mysids (34.2%) or euphausiids (24.7%). As well, of all the food items consumed by quillback rockfish, the

Table 1. Frequency of occurrence, numerical abundance, and mass of different prey found in stomachs of copper rockfish from Saanich Inlet, B.C.

Prey Taxa	Occurrence (%)	Numerical Abundance (%)	Mass (grams) (%)
PELAGIC FISH	98 (34.5)	128 (11.7)	675.22 (73.5)
Brachyistius frenatus (Kelp Perch)	11 (3.9)	11 (1.0)	80.84 (8.8)
Clupea harengus pallasi (Pacific Herring)	85 (29.9)	115 (10.5)	543.17 (59.2)
Damalichthys vacca (Pile Perch)	1 (0.4)	1 (0.1)	51.21 (5.6)
Fish Larvae	1 (0.4)	1 (0.1)	0.00 (0.0)
DEMERSAL FISH	13 (4.6)	13 (1.2)	42.09 (4.6)
Coryphopterus nicholsii (Blackeye Goby)	5 (1.8)	5 (0.5)	26.78 (2.9)
Cottidae (Sculpins)	2 (0.7)	2 (0.2)	0.59 (0.1)
Pholidae (Gunnels)	6 (2.1)	6 (0.5)	14.72 (1.6)
DEMERSAL CRUSTACEANS	155 (54.6)	236 (21.7)	186.23 (20.3)
Callianassa gigas (Ghost Shrimp)	1 (0.4)	1 (0.1)	3.93 (0.4)
Cancer gracilis	3 (1.1)	3 (0.3)	8.17 (0.9)
Cancer oregonensis	10 (3.5)	11 (1.0)	1.87 (0.2)
Cancer productus (Red Rock Crab)	4 (1.4)	4 (0.4)	8.23 (0.9)
Chorilia longipes (Deepwater Decorator Crab)	2 (0.7)	2 (0.2)	0.29 (0.0)
Hyas lyratus	1 (0.4)	1 (0.1)	1.04 (0.1)
Munida quadraspina (Squat Lobster)	63 (22.2)	85 (7.8)	30.00 (3.3)
Pandalus danae (Coonstriped Shrimp)	61 (21.5)	76 (6.9)	85.94 (9.4)
Pandalus platyceros (Two-spot Prawn)	5 (1.8)	5 (0.5)	29.95 (3.3)
Petrolisthes eriomerus (Porcelain Crab)	2 (0.7)	2 (0.2)	2.30 (0.2)
Pugettia gracilis (Kelp Crab)	2 (0.7)	2 (0.2)	6.44 (0.7)
Shrimp (Unid.)	33 (11.6)	44 (4.0)	8.07 (0.9)

Table 1 (Cont'd). Frequency of occurrence, numerical abundance, and mass of different prey found in stomachs of copper rockfish from Saanich Inlet, B.C.

Prey Taxa	Occurrence (%)	Numerical Abundance (%)	Mass (grams) (%)
PELAGIC CRUSTACEANS	54 (19.0)	703 (64.5)	11.29 (1.2)
Euphausiids (*Euphausia pacifica*)	23 (8.1)	480 (44.0)	8.21 (0.9)
Gammarid Amphipods	3 (1.1)	3 (0.3)	0.04 (0.0)
Hyperiid Amphipods	3 (1.1)	18 (1.7)	0.07 (0.0)
Megalopa of Crabs	1 (0.4)	1 (0.1)	0.01 (0.0)
Mysids (*Xenacanthomysis pseudomacropsis*)	31 (10.9)	201 (18.4)	2.96 (0.3)
MISCELLANEOUS	5 (1.8)	10 (0.9)	3.32 (0.4)
Clavelina huntsmani (Lightbulb Tunicate)	1 (0.4)	6 (0.5)	0.67 (0.1)
Ophiura lutkeni (Brittlestar)	1 (0.4)	1 (0.1)	0.17 (0.0)
Polychaeta (Errantia)	3 (1.1)	3 (0.3)	2.48 (0.3)
TOTALS	284 (100)	1,090 (100)	918.15 (100)

Table 2. Frequency of occurrence, numerical abundance, and mass of different prey found in stomachs of quillback rockfish from Saanich Inlet, B.C.

Prey Taxa	Occurrence (%)	Numerical Abundance (%)	Mass (grams) (%)
PELAGIC FISH	29 (18.4)	45 (1.8)	227.12 (65.1)
Clupea harengus pallasi (Pacific Herring)	27 (17.1)	43 (1.7)	227.12 (65.1)
Fish Larvae	2 (1.3)	2 (0.1)	0.00 (0.0)
DEMERSAL FISH	5 (3.2)	9 (0.4)	12.11 (3.5)
Cottidae (Sculpins)	1 (0.6)	1 (0.0)	0.80 (0.2)
Pleuronectidae (Flatfish)	3 (1.9)	7 (0.3)	8.18 (2.3)
Rhamphocottus richardsonii (Grunt Sculpin)	1 (0.6)	1 (0.0)	3.13 (0.9)
DEMERSAL CRUSTACEANS	93 (58.9)	169 (6.6)	67.02 (19.2)
Acantholithodes hispidus	2 (1.3)	2 (0.1)	1.82 (0.5)
Cancer gracilis	2 (1.3)	2 (0.1)	0.62 (0.2)
Cancer oregonensis	8 (5.1)	9 (0.4)	2.32 (0.7)
Caprellid Amphipod	1 (0.6)	1 (0.0)	0.01 (0.0)
Chorilia longipes (Deepwater Decorator Crab)	2 (1.3)	2 (0.1)	0.30 (0.1)
Munida quadraspina (Squat Lobster)	46 (29.1)	75 (2.9)	28.40 (8.1)
Pandalus danae (Coonstriped Shrimp)	16 (10.1)	22 (0.9)	23.67 (6.8)
Shrimp (Unid.)	33 (20.9)	55 (2.1)	8.44 (2.4)
Telmessus cheiragonus (Helmet Crab)	1 (0.6)	1 (0.0)	1.44 (0.4)

Table 2 (Cont'd). Frequency of occurrence, numerical abundance, and mass of different prey found in stomachs of quillback rockfish from Saanich Inlet, B.C.

Prey Taxa	Occurrence (%)	Numerical Abundance (%)	Mass (grams) (%)
PELAGIC CRUSTACEANS	81 (51.3)	2221 (86.4)	37.71 (10.8)
Euphausiids (*Euphausia pacifica*)	39 (24.7)	1524 (59.3)	27.73 (7.9)
Gammarid Amphipods	1 (0.6)	2 (0.1)	0.03 (0.0)
Hyperiid Amphipods	7 (4.4)	82 (3.2)	0.33 (0.1)
Megalopa of Crabs	2 (1.3)	5 (0.2)	0.09 (0.0)
Mysids (*Xenacanthomysis pseudomacropsis*)	54 (34.2)	608 (23.6)	9.53 (2.7)
MISCELLANEOUS	7 (4.4)	127 (4.9)	5.16 (1.5)
Fish Eggs (*Ophiodon elongatus*)	2 (1.3)	114 (4.4)	1.03 (0.3)
Polychaeta (Errantia)	4 (2.5)	4 (0.1)	3.31 (1.0)
Pteropod Molluscs	1 (0.6)	9 (0.4)	0.82 (0.2)
TOTALS	158 (100)	2,571 (100)	349.12 (100)

majority (83% numerical abundance) were either euphausiids or mysids. On a mass basis, however, herring was the most important component in the diet, along with squat lobsters and coonstriped shrimp. Mass contribution to the quillback diet by pelagic crustaceans was greater than for copper rockfish (10.8% versus 1.2%).

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. 9). As well, the presence or absence of food in the stomachs within each season was independent of the sex of the fish (Table 3). 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 1985) indicated that quillback rockfish were found more frequently with food in their stomachs in spring and summer (67 and 76% respectively) than in fall and winter (44 and 48% respectively) ($\chi^2_c = 12.57$, $P < 0.001$) (Fig. 9). As with copper rockfish, however, the presence or absence of food in the stomachs within each season was independent of the sex of the quillback rockfish (Table 3). Differences were also evident between rockfish species among seasons in the proportion of individuals with food in their stomachs ($\chi^2_3 = 27.11$, $P < 0.001$). Subdivision of the contingency table indicated that food was present in a greater proportion of

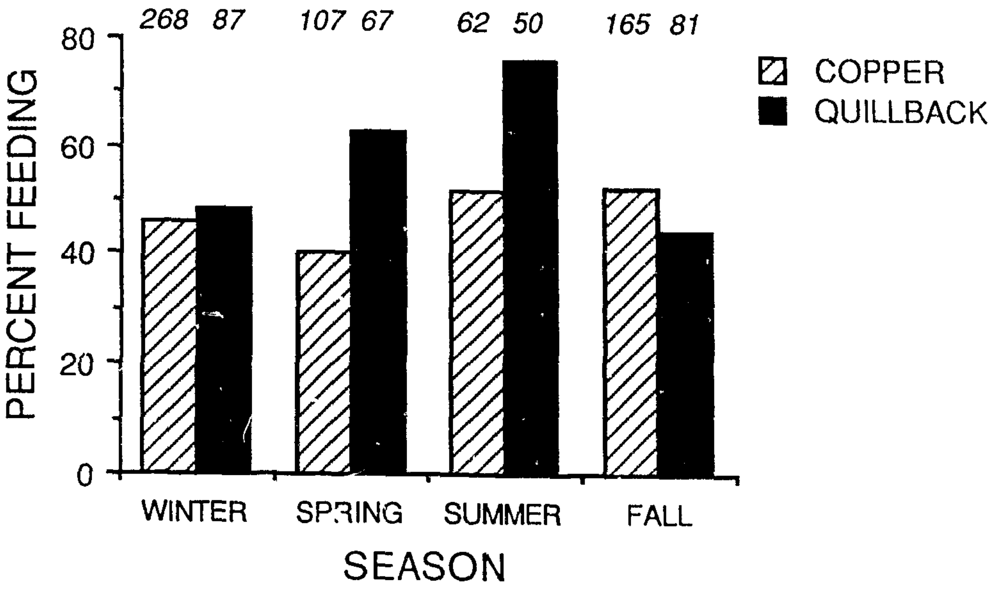

Fig. 9. Percent of copper and quillback rockfish with food in their stomachs within each season of the year. Number of each species collected within each season is given in italics.

Table 3. Chi-square analysis for the independence of the presence or absence of food in the stomachs of copper and quillback rockfish within seasons in relation to their sex.

Species	Season	*n*	χ_c^2	*P*
Copper	Winter	268	0.302	0.58
Rockfish	Spring	107	1.263	0.26
	Summer	62	3.527	0.06
	Fall	165	2.838	0.09
Quillback	Winter	87	0.338	0.56
Rockfish	Spring	67	0.025	0.87
	Summer	50	0.570	0.45
	Fall	81	0.016	0.90

quillback rockfish than copper rockfish during the spring ($\chi_c^2 = 7.47$, $P < 0.01$) and the summer ($\chi_c^2 = 6.02$, $P < 0.02$), but was in equal proportion during the fall ($\chi_c^2 = 0.99$, $P > 0.75$) and winter ($\chi_c^2 = 0.07$, $P > 0.90$) (Fig. 9).

For copper rockfish, demersal crustaceans were important prey throughout all seasons (35-81% occurrence), increasing in importance from winter to fall (Fig. 10a). They were particularly important on a numerical basis during the fall (56%) (Fig. 10b) but contributed substantial mass to the diet of copper rockfish during the summer, spring, and fall (35-64%) (Fig. 10c).

The occurrence of pelagic crustaceans was common in the diet of copper rockfish in the spring and the summer and relatively low in the fall and winter (Fig. 10a). Pelagic crustaceans were also important in terms of numerical abundance in the spring and summer (Fig. 10b), but they contributed little to the mass of food consumed within each season.

Pelagic fishes had been eaten by a majority (64%) of copper rockfish in winter, and to a lesser extent in the other seasons (Fig. 10a). They contributed ~49% of the food items (Fig. 10b) and 93% of the mass (Fig. 10c) 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.

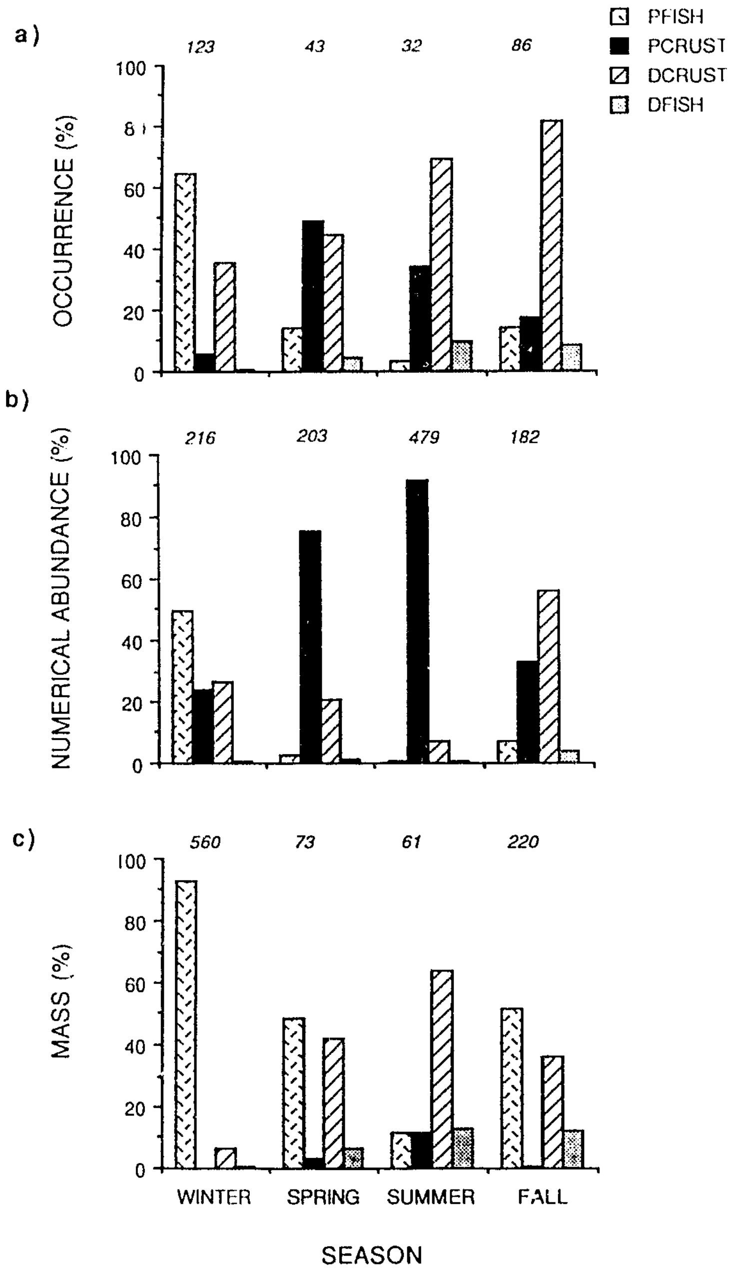

Fig. 10. Summary of food habits of copper rockfish among seasons on the basis of a) occurrence, b) numerical abundance, and c) mass contribution to the diet. Totals for each season are given in italics. Legend as in Fig.8.

In contrast, demersal fishes were consumed by relatively few copper rockfish throughout the year (Fig. 10a) and represented <5% of the food items (Fig. 10b) and $\leq$10% of the mass (Fig. 10c) consumed within each season.

Demersal crustaceans also occurred frequently in the diet of quillback rockfish throughout the year (29-94% occurrence), increasing in prevalence from winter through to fall (Fig. 11a). Numerically, they were important only in the fall when they constituted ~58% of the food items consumed by quillback rockfish (Fig. 11b). The mass contribution to the diet by demersal crustaceans was substantial (>20%) in all seasons except winter (Fig. 11c).

Pelagic crustaceans were also relatively important (>28% occurrence) to quillback rockfish throughout the year, and in particular in the spring and summer (Fig. 11a). Of all the food items consumed within each season by quillback rockfish, pelagic crustaceans were the most prevalent except during the fall (Fig. 11b). They contributed a substantial proportion of the mass consumed by quillback rockfish in summer (36%) (Fig. 11c).

Conversely, pelagic fishes were a common occurrence in the diet of quillback rockfish only in the winter (Fig. 11a) and were relatively unimportant to quillback rockfish in terms of numerical abundance throughout the year (Fig. 11b). As with copper rockfish, however, pelagic fishes were important on a mass basis to quillback rockfish in the

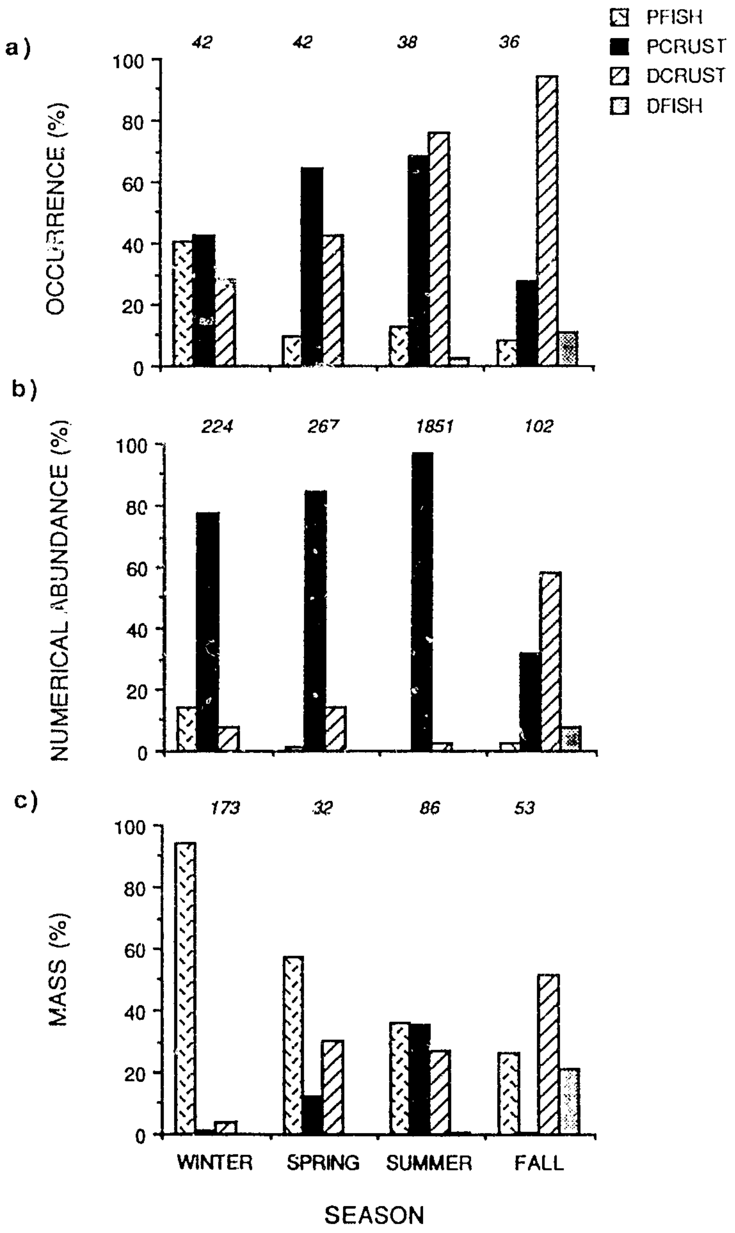

Fig. 11. Summary of food habits of quillback rockfish among seasons on the basis of a) occurrence, b) numerical abundance, and c) mass contribution to the diet. Totals for each season are given in italics. Legend as in Fig.8.

winter (~94%) and to a lesser extent through the other seasons (Fig. 11c).

Demersal fishes were consumed infrequently by quillback rockfish (Fig. 11a), represented few items in the diet (Fig. 11b), and contributed negligible mass to the diet except in the fall (Fig. 11c).

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) ($\bar{X}$ ± 1SD) than quillback rockfish (235 ± 50 mm TL, *n* = 285). To facilitate comparison of diet changes related to rockfish growth, rockfish were partitioned into four relative size categories: extra-small ($\leq$ 150 mm TL), small (>150 to $\leq$200), medium (>200 to $\leq$250), and large (>250 mm TL). Quillback rockfish were assigned to the same categories, except that the two smallest size categories were combined due to the paucity of extra-small ($\leq$150 mm TL) quillback rockfish collected.

Overall, the presence or absence of food in the stomachs of copper rockfish within each size category was independent of the season (Table 4). An exception to this was for extra-small copper rockfish in which stomachs collected in winter and fall had a higher proportion of food present than stomachs collected in the spring and summer.

Table 4. Chi-square analysis for the independence of the presence or absence of food in the stomachs of copper and quillback rockfish within size categories in relation to season.

Species	Size Category	*n*	χ_c^2	*P*
Copper	Extra-Small	85	12.06	0.01*
Rockfish	Small	193	1.15	0.77
	Medium	196	3.68	0.30
	Large	128	1.58	0.66
Quillback	Small	65	4.98	0.17
Rockfish	Medium	108	11.81	0.01*
	Large	112	5.02	0.17

* Significant at $P \leq 0.05$.

The presence or absence of food in the stomachs of quillback rockfish within each size category was independent of the seasons for small and large rockfish only (Table 4). For medium-sized quillback rockfish, the proportion of stomachs with food present was less in the fall than in the other seasons.

The majority of extra-small and small copper rockfish had fed on demersal crustaceans (Fig. 12a). Medium and large 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 (22.5 to 19.4% occurrence), which was slightly greater than the consumption of pelagic crustaceans by large copper rockfish (Fig. 12a).

Demersal crustaceans also represented the greatest numerical abundance of any food item in the diet of extra-small copper rockfish (Fig. 12b). Pelagic crustaceans, in contrast, contributed the greatest numerical abundance of prey for small, medium, and large copper rockfish. Pelagic fishes represented ≤10% numerical abundance of the food items consumed except for large copper rockfish (17%).

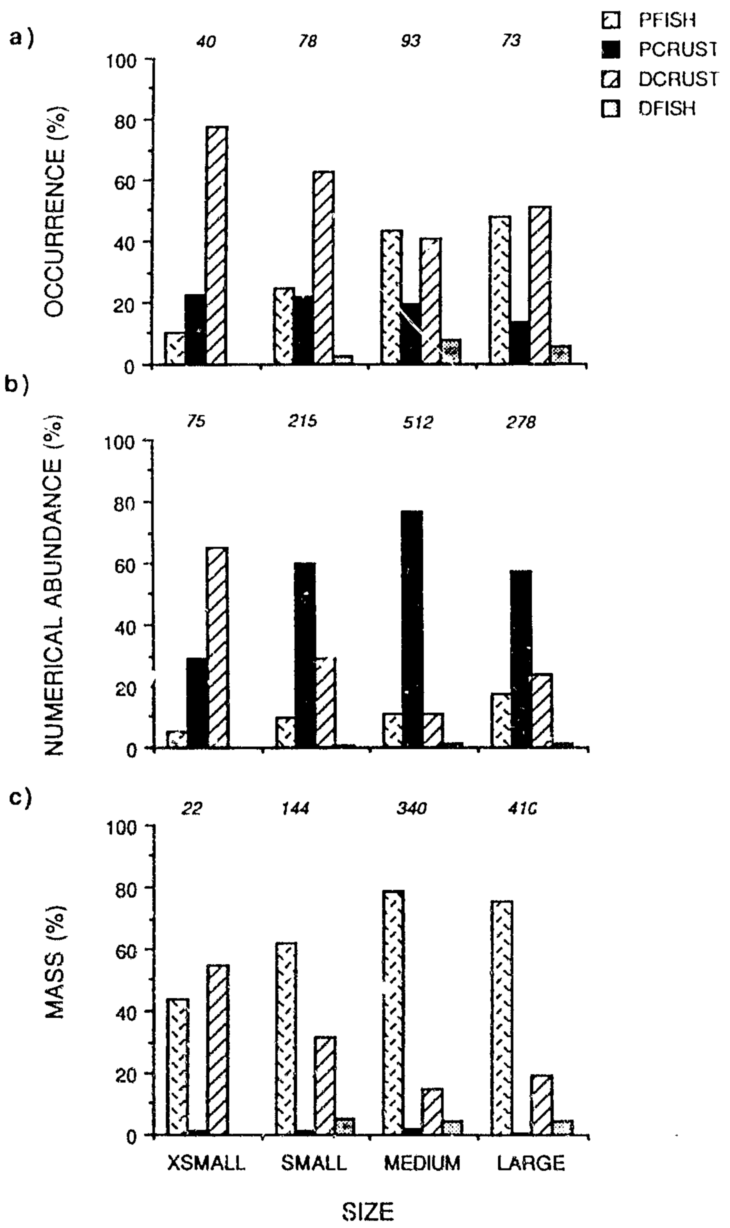

Fig. 12. Summary of food habits of copper rockfish of varying body size on the basis of a) occurrence, b) numerical abundance, and c) mass contribution to the diet. Totals for each size category are given in italics. Legend as in Fig. 8.

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. 12c). Although a substantial portion of the mass in the diet of the extra-small copper rockfish also came from pelagic fishes (43.6%), the majority came from their consumption of demersal crustaceans (54.9%). Demersal fishes and pelagic crustaceans were unimportant to all sizes of copper rockfish (≤5% mass).

The majority of quillback rockfish, regardless of size, fed on demersal crustaceans and pelagic crustaceans (Fig. 13a). Demersal fish were never consumed by small quillback rockfish, and were of only minor occurrence in the diet of medium and large quillback rockfish. Pelagic fishes were of minor importance to small quillback rockfish but were consumed by a substantial number of large quillback rockfish (28% occurrence), although less so than medium and large copper rockfish (≥43%). Pelagic crustaceans contributed the most to the numerical abundance of food items consumed by quillback rockfish, regardless of size (Fig. 13b).

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. 13c). Pelagic fishes contributed the greatest percent mass to the diet of medium and large quillback rockfish. Medium quillback rockfish also consumed

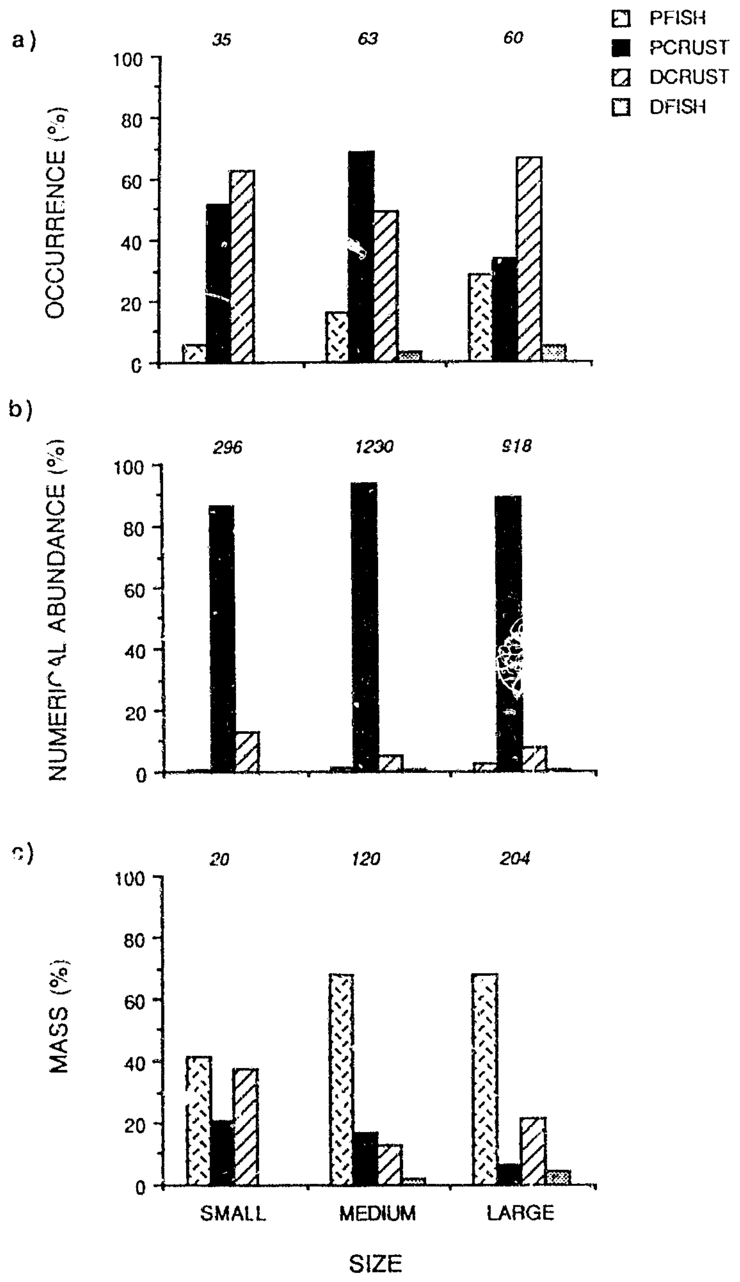

Fig. 13. Summary of food habits of quillback rockfish of varying body size on the basis of a) occurrence, b) numerical abundance, and c) mass contribution to the diet. Totals for each size category are given in italics. Legend as in Fig. 8.

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 (21% mass).

Size of Food Items Consumed

Overall, the fish species consumed by copper and quillback rockfish averaged 64.0 ± 34.2 mm and 8.62 ± 16.14 g (n = 9 fish species) (Table 5), inclusive of mean lengths and masses of herring and kelp perch derived from VCL-SL and VCL-mass regressions (Table 6). Species of demersal crustaceans eaten by rockfish were smaller on average (23.1 ± 18.1 mm and 1.68 ± 1.67 g) (n = 14 species) (Table 5), with mean lengths and masses of squat lobsters, coonstriped shrimp, and shrimp (various) derived from regressions of CL-FBL and CL-mass (Table 6). Pelagic crustacean species consumed by rockfish were consistently smaller than demersal crustaceans species and averaged 8.6 ± 3.8 mm and 0.014 ± 0.007 g (n = 6 species) (Table 5). The size of the miscellaneous prey species consumed by rockfish were within the range of sizes represented by fish and crustacean prey.

The relationship between the length of pelagic fishes consumed and rockfish total length had the same slope (Single-factor ANCOVA: $F_{1,118} = 0.08$, $P = 0.78$) and elevation ($F_{1,118} = 0.02$, $P = 0.89$) for both copper and quillback rockfish. Although the pooled regression (Fig. 14a) was

Table 5. Estimated mean length and mass (± 1SD) of prey species consumed by copper and quillback rockfish.

Species	*n*	Length (mm)	Mass (g)
Fishes[a]			
Brachyistius frenatus[b]	11	58.7 (16.7)	7.35 (5.87)
Clupea harengus[b]	112	79.5 (12.2)	4.88 (1.58)
Coryphopterus nicholsii	5	69.4 (10.9)	5.36 (2.54)
Cottidae	3	35.0 (14.9)	0.46 (0.29)
Damalichthys vacca	1	125.0	51.20
Fish larvae	3	16.0 (9.5)	0.01 (0.02)
Pholidae	4	102.5 (7.4)	2.45 (0.65)
Pleuronectidae (pieces)	3	44.5 (14.8)	2.73 (3.14)
Rhamphocottus richardsonii	1	45.5	3.13
Shrimps and Squat Lobsters[c]			
Callianassa gigas	1	34.0	3.93
Munida quadraspina[b]	109	10.6 (4.5)	0.38 (0.50)
Pandalus danae[b]	77	18.8 (5.7)	1.08 (0.88)
Pandalus platyceros	5	32.4 (2.6)	6.00 (0.95)
Shrimp (Unidentified)[b]	66	10.6 (4.2)	0.19 (0.21)
Crabs (Oval-shaped)[d]			
Cancer gracilis	4	15.0 (19.4)	1.76 (3.52)
Cancer oregonensis[b]	18	8.5 (3.4)	0.21 (0.22)
Cancer productus	4	26.2 (19.7)	2.06 (2.88)
Petrolisthes eriomerus	1	12.0	1.15
Crabs (Pear-shaped)[e]			
Acantholithodes hispidus (leg only)	1	27.0	0.91
Chorilia longipes	4	8.8 (2.6)	0.15 (0.09)
Hyas lyratus	1	15.0	1.04
Pugettia gracilis	2	26.2 (3.6)	3.22 (1.48)
Telemessus cheiragonus (leg only)	1	78.0	1.44

Table 5 (Cont'd). Estimated mean length and mass (± 1SD) of prey species consumed by copper and quillback rockfish.

Species	*n*	Length (mm)	Mass (g)
Amphipods, euphausiids, mysids, and larvae[f]			
Caprellid Amphipod	1	9.6	0.008
Euphausiids:			
small	6	7.6 (0.8)	0.004 (0.001)
medium	11	12.1 (1.3)	0.017 (0.008)
large	20	18.4 (2.7)	0.034 (0.007)
Gammarid Amphipod	2	8.8 (0.5)	0.013 (0.002)
Hyperiid Amphipods:			
small	1	2.0	0.001
medium	8	4.2 (0.6)	0.004 (0.001)
large	6	5.8 (0.7)	0.006 (0.003)
Megalopa of Crabs:			
small	4	2.2 (0.4)	0.012 (0.005)
medium	2	3.9 (0.8)	0.025 (0.007)
Mysids:			
small	7	7.8 (1.6)	0.006 (0.003)
medium	38	12.8 (1.3)	0.015 (0.006)
large	7	16.4 (1.5)	0.027 (0.010)
Miscellaneous[g]			
Clavelina huntsmani	6	16.0	0.112
Fish eggs	12	2.6 (0.3)	0.009 (0.001)
Ophiura lutkeni	1	6.0	0.173
Polychaete	1	113.0	0.828
Pteropod	3	7.3 (2.6)	0.091 (0.036)

[a] Length measured as standard length; [b] Derived from regressions in Table 6; [c] Length measured as body length; [d] Length measured as carapace width; [e] Length measured as carapace length; [f] Length measured as total body length; [g] Length measured as the greatest distance of the body.

Table 6. Relationships for length and mass of common prey species consumed by copper and quillback rockfish in Saanich Inlet, B.C. All relationships are significant at $P = 0.000$.

Prey Species	*n*	Mass (g)[a]	r^2	Length (mm)[b]	r^2
Brachyistius frenatus	8	$M = 4.24 \times 10^{-5} VCL^{3.013}$	0.99	$SL = 1.131 VCL^{1.0059}$	0.99
Clupea harengus pallasi	20	$M = 9.28 \times 10^{-4} VCL^{2.053}$	0.99	$SL = 0.980 + 1.226 VCL$	0.97
Munida quadraspina	70	$M = 9.10 \times 10^{-4} CL^{2.903}$	0.94	$FBL = 1.518 CL^{1.0125}$	0.96
Pandalus danae	54	$M = 2.48 \times 10^{-3} CL^{2.528}$	0.82	$FBL = 1.953 CL^{0.9746}$	0.97
Shrimps (Various spp.)	37	$M = 2.84 \times 10^{-3} CL^{2.392}$	0.80	$FBL = 2.150 CL^{0.9721}$	0.98
Cancer oregonensis	16	$M = 5.52 \times 10^{-4} CW^{2.640}$	0.89		

[a] VCL = vertebral column length; CL = carapace length; CW = carapace width.

[b] SL = standard length; FBL = flexed body length.

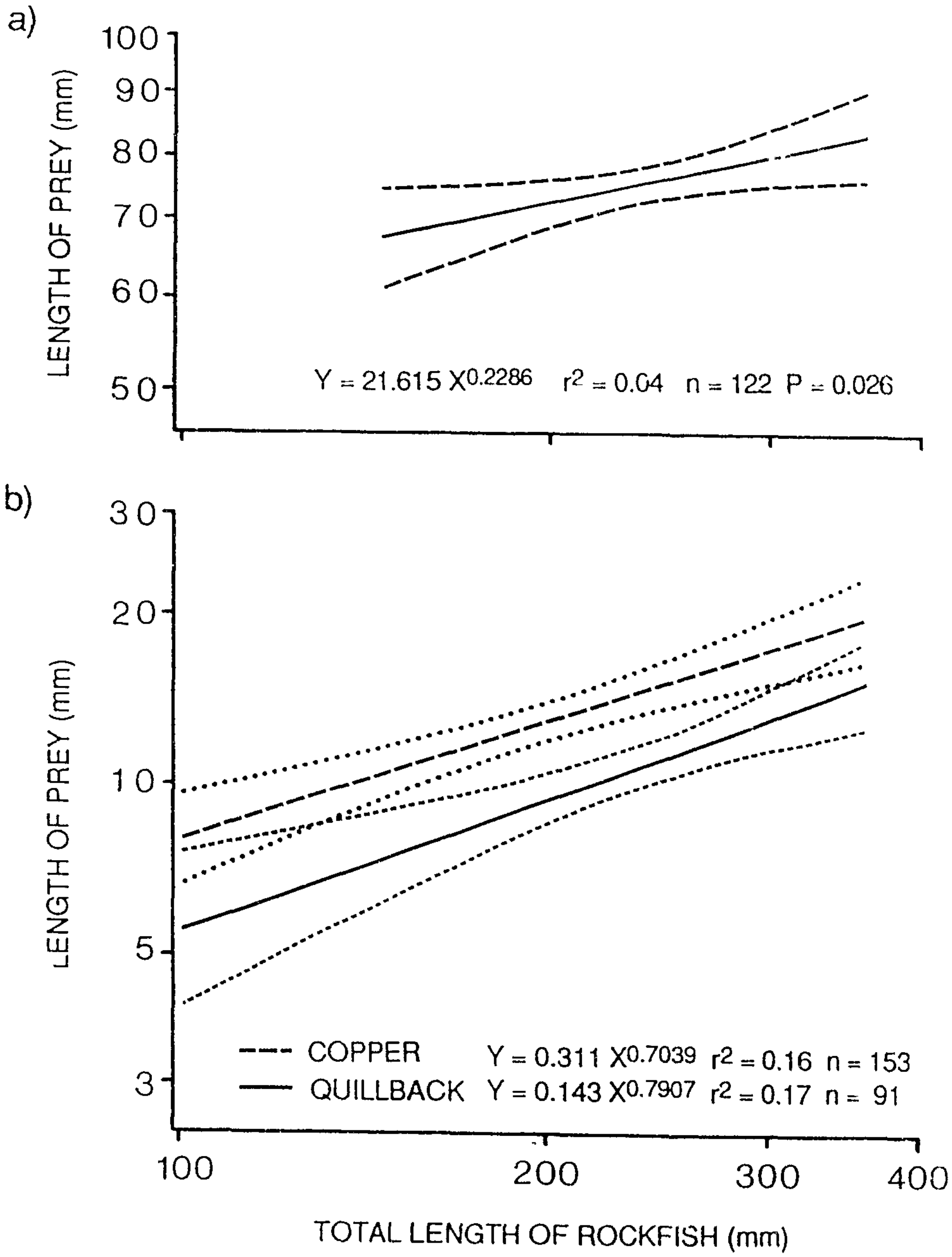

Fig. 14. Length of a) pelagic fishes and b) demersal crustaceans (both $P < 0.0001$) consumed by copper and quillback rockfish as a function of rockfish length. Dashed and dotted curves represent 95% confidence limits around the regression lines.

significant and positive, it explained little of the variation. This may have been due to the majority of pelagic fishes consumed being juvenile herring, all of similar size.

Slopes for the relationship of length of demersal crustaceans consumed to rockfish total length were the same for copper and quillback rockfish ($F_{1,240} = 0.13$, $P = 0.72$), but copper rockfish consistently consumed demersal crustaceans that were larger (i.e., longer) than those consumed by similar-sized quillback rockfish ($F_{1,240} = 25.00$, $P = 0.00$) (Fig. 14b).

The relationship between the length of pelagic crustaceans consumed as a function of rockfish length was nonsignificant for both copper rockfish ($F = 0.80$, $n = 49$, $P = 0.38$) and quillback rockfish ($F = 3.36$, $n = 76$, $P = 0.07$). Pelagic crustaceans were on average 12.3 ± 2.0 mm in length ($n = 135$). Similarly, the size of demersal fishes consumed was not related to rockfish total length for either copper rockfish ($F = 1.39$, $n = 13$, $P = 0.26$) or quillback rockfish ($F = 0.08$, $n = 5$, $P = 0.82$). On average, demersal fishes consumed by copper and quillback rockfish were 70.8 ± 26.6 mm in length ($n = 18$).

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. 15a). The percentage of stomachs that were empty was lowest at sunrise, corresponding to an early morning peak in feeding. The percentage of empty stomachs 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. 15b). 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.

Quantity of Food Consumed

For copper and 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 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 due to season alone was evident when each species was tested for effects due to sex, season, or their interaction (Table 7).

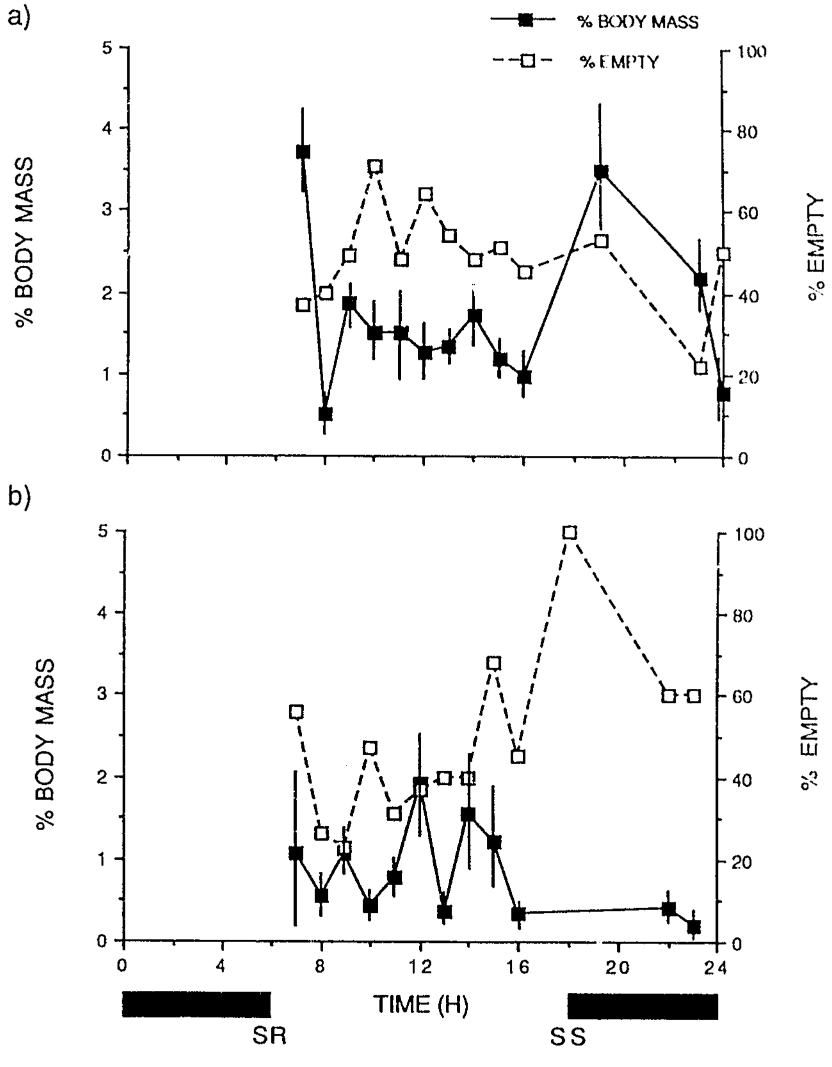

Fig. 15. Diel variation in feeding (± 1SE) of a) copper rockfish and b) quillback rockfish based on % empty stomachs and mass of food consumed as a percentage of body mass. Black bars represent hours of darkness and twilight; SR = sunrise and SS = sunset.

Table 7. Two-factor analysis of covariance statistics for sex and season effects in total mass of food consumed as a function of body mass in copper and quillback rockfish.

Species	Factor	DF	*F*	*P*
Copper	Sex	1,275	1.35	0.25
	Season	3,275	16.17	0.00*
	Interaction	3,275	0.02	0.99
Quillback	Sex	1,148	2.31	0.13
	Season	3,148	8.02	0.00*
	Interaction	3,148	1.31	0.27

* Significant at $P \leq 0.05$.

Between species over the four seasons, however, the regression coefficients were different due to copper rockfish in the winter ($F_{1,432} = 4.87$, $P = 0.03$). The relationship of the food consumption by copper rockfish in the winter, relative to their body mass, was allometric with the slope of the relationship greater than one (*t*-test: $t = 2.79$, DF = 121, $P < 0.01$). The relative rate of food consumption therefore increased as copper rockfish size increased (Fig. 16a). Regression coefficients for copper rockfish for three seasons (winter excluded) and quillback rockfish for all four seasons were not different from one another (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 *t*-test matrix for adjusted group means indicated that food consumption of copper and quillback rockfish in the summer, quillback rockfish in the winter, and copper rockfish in the fall (Fig. 16b), were greater than the food consumption of both copper and quillback rockfish in the spring and quillback rockfish in the fall (Fig. 16c) (all differences at $P \leq 0.05$). The relationships between food consumption and size for these latter two pooled groups was isometric (e.g., slopes = 1) (*t*-tests: $t = 0.13$, DF = 195, $P = 0.50$, and $t = 0.43$, DF = 119, $P = 0.50$, respectively); the relative rate of food consumption was therefore the same regardless of rockfish size.

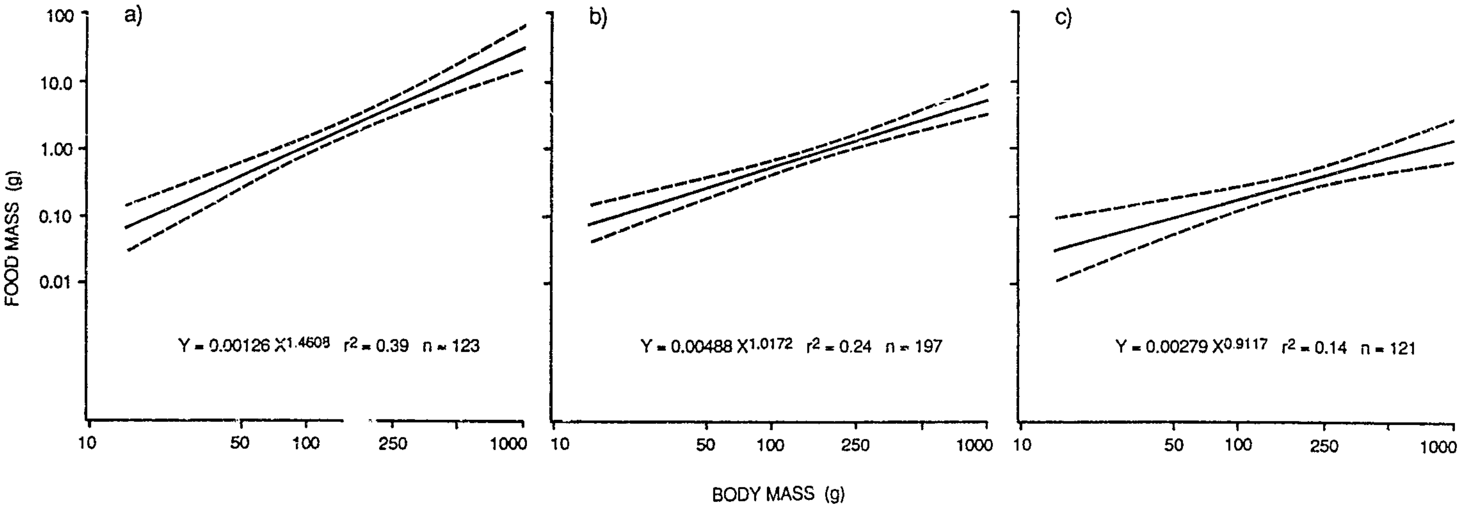

Fig. 16. Mass of food consumed as a function of body mass of copper and quillback rockfish among seasons: a) copper rockfish in winter; b) quillback rockfish in winter and summer, and copper rockfish in summer and fall; and c) quillback rockfish in fall and spring, and copper rockfish in spring. Dashed curves represent 95% confidence limits around the regression lines. All regressions are significant at $P < 0.0001$.

Occurrence and Density of Potential Prey

Squat lobsters were the most abundant demersal crustacean on the rocky reefs based on benthic surveys (Table 8) and represented ~65% of the total density of benthic animals surveyed. Small shrimps of various species were also common, relative to larger shrimps and crabs. Demersal fishes on the rocky reefs occurred in relatively low densities (<0.5 fish·m^{-2}) and were comprised of fishes known to be consumed by rockfish (Table 1 and 2). A variety of benthic, macroscopic invertebrates were also observed on the rocky reefs in relatively low densities (≤ 0.15 individual·m^{-2}) except for the brittle star, *Ophiura*. *Ophiura* was found in the stomach contents of copper rockfish, whereas polychaete worms were components of the diet of both species of rockfish.

Individuals and schools of various species of surfperches (Embiotocidae) occurred most frequently during surveys for pelagic prey (Table 9). Kelp perch were observed most frequently in the winter and fall (21-75% occurrence) (Table 9). The number of kelp perch observed at any one time ranged from single individuals to schools of up to 43 individuals, and represented the majority of the perch observed in the winter and spring (52-62% numerical abundance of the perches). Shiner perch (*Cymatogaster aggregata*) were observed infrequently over the rocky reefs (<10% occurrence). The majority of shiner perch were

Table 8. Density (Individuals·m^{-2}) of demersal invertebrates and demersal fishes surveyed over rocky reefs in Saanich Inlet, B.C., during winter and spring (*n* = 48 quadrats).

Prey Taxa	Mean	±1*SD*
Demersal Crustaceans		
Munida quadraspina	21.55	8.43
Shrimps (Various Unidentified)	6.19	5.37
Pandalus danae	1.00	1.00
Chorilia longipes	0.78	0.75
Cancer spp.	0.56	0.80
Acantholithodes hispidus	0.21	0.34
Oregonia gracilis	0.02	0.07
Demersal Fishes		
Coryphopterus nicholsii	0.43	0.64
Pholidae/Stichaeidae	0.19	0.20
Cottidae	0.04	0.13
Miscellaneous Invertebrates		
Brittle Stars (*Ophiura lutkeni*)	1.47	2.31
Sea anemones (*Pachycerianthus*)	0.15	0.45
Terebellid worms	0.13	0.28
Sea stars (*Pycnopodia helianthoides*)	0.08	0.16
Polychaete worms	0.04	0.11
Nudibranchs (*Archidoris odhneri*)	0.04	0.11
Sea cucumbers (*Eupentacta*)	0.04	0.11

Table 9. Percent occurrence (%O) and numerical abundance (%NA) of pelagic fishes and pelagic crustaceans among seasons over rocky reefs in Saanich Inlet, B.C.

Prey Taxa	Winter (*n*=24)		Spring (*n*=23)		Summer (*n*=26)		Fall (*n*=48)	
	%O	%NA[a]	%O	%NA	%O	%NA[a]	%O	%NA[a]
Pelagic Fishes								
Clupea harengus	4	84	0	0	15	88	6	96
Brachyistius frenatus	75	8	4	62	4	0	21	0
Cymatogaster aggregata	4	0	0	0	8	11	4	0
Damalichthys vacca	29	4	9	38	38	1	69	3
Embiotoca lateralis	42	4	0	0	4	0	25	1
Pelagic Crustaceans	8		0		19		0	

[a] Approximate values only.

observed in the summer when one school of approximately 500 individuals was observed passing over one of the rocky reefs. Pile perch, besides being relatively common during the winter and fall, were also common during the summer (Table 9). They occurred singly or in schools of up to 53 individuals. In the fall they represented the majority of perch observed (~60% numerical abundance of the perches). Striped perch (*Embiotoca lateralis*) were also observed as single individuals or in schools of up to 44 perch. They were observed primarily in the winter and fall (Table 9).

Schools of juvenile herring were seen most frequently during the summer, and to a lesser extent in the fall and winter (Table 9). Enumeration of fish in these schools was difficult because of the large number of fish and their speed of movement. On a qualitative basis, however, fish schools observed in the winter and fall were larger (>3000 individuals) than the schools seen in the summer (<1000 individuals). These herring schools passed over the rocky reefs within 3-10 m of the bottom and both copper and quillback rockfish were observed striking at fish in these schools. The percent occurrence of schools of perches was greater than for schools of herring. Due to the large size of the herring schools relative to the perch schools, however, the numerical abundance of perches ($\leq$11%) was low compared to herring ($\geq$84%), except during the spring when herring schools were not observed.

Aggregations of euphausiids or mysids were also observed most frequently during the summer, and to a lesser extent in the winter (Table 9). These pelagic crustaceans were seen in very sparse concentrations (~1000-2000 individuals) primarily in the summer, as well as extremely dense concentrations in both winter and summer. Dense concentrations of the crustaceans occurred when the aggregation covered the entire reef area forming a visible "cloud". These aggregations were typically 3-10 m off the reef substrate. However, observations of euphausiids/mysids in the tentacles of burrowing anemones, *Pachycerianthus fimbriatus*, indicated that at times these pelagic crustaceans are in close proximity to the substrate.

Niche Breadth

Niche breadths based on occurrence of different prey species in the diet of copper and quillback rockfish among seasons were similar except in winter (Table 10). The narrow niche breadth observed for copper rockfish during the winter (B_A = 0.167) resulted 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 10).

Table 10. Niche breadth based on percent occurrence (%O), percent numerical abundance (%NA) and percent mass (%M) in copper and quillback rockfish diets among seasons.

	Copper Rockfish				Quillback Rockfish			
Season	No. of prey taxa	%O	%NA	%M	No. of prey taxa	%O	%NA	%M
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

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 the spring and summer (Table 10). The narrow niche breadths, especially in the summer, resulted from copper and quillback rockfish consuming a disproportionate number of euphausiids and mysids.

On a mass basis, niche breadths for copper and quillback rockfish were similar and extremely low (0.023 and 0.019 respectively) in the winter compared with the other seasons (Table 10). This was again due to the disproportionate consumption of herring in the diet 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 was affected seasonally, with overlap at a maximum during spring and summer, and declining during the fall to reach a minimum during the winter (Table 11). 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

Table 11. Niche overlap based on numerical abundance and mass contribution of prey taxa to the 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

contribution by different prey taxa in the diet was high during the winter and only moderate during the rest of the year (Table 11). 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.

DISCUSSION

Diet Composition of Copper Rockfish

Geographical Variation in Diet

Previous studies on the food habits of copper rockfish have been centred in California (Prince and Gotshall 1976), Washington (Patten 1973; Moulton 1977; Buckley and Hueckel 1985), or Alaska (Rosenthal *et al.* 1988). In Puget Sound, Washington, the most common food types in the stomachs of copper rockfish during the year were fish (~50% occurrence), especially embiotocids and cottids, and crustaceans, especially shrimps (*Crangon*, *Heptacarpus*, and *Pandalus danae*; ~54% occurrence) (Patten 1973). Patten also concluded that fish represented a larger percentage of the stomach contents in terms of percent volume than was indicated by their frequency of occurrence, due to their greater size. Similarly, Buckley and Hueckel (1985) documented embiotocids, *Pandalus danae*, lingcod eggs, and brachyuran crabs as the most important prey items consumed by copper rockfish (>19 cm total length) collected from March to December in Puget Sound, Washington.

In contrast, in South Humboldt Bay, California, copper rockfish consumed primarily demersal crustaceans (69% volume), especially juvenile dungeness crab (*Cancer magister*) (Prince and Gotshall 1976). Fishes were consumed relatively infrequently by copper rockfish in Humboldt Bay (<10% occurrence) but represented a substantial proportion of the total volume of prey consumed (23%). The most common fishes consumed were northern anchovy (*Engraulis mordax*) and shiner perch. Prince and Gotshall (1976) attributed the preponderance of demersal crustaceans in the diet of copper rockfish in Humboldt Bay, in part, 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 and spring.

On an annual basis, therefore, the food habits of copper rockfish in Saanich Inlet were most similar to copper rockfish in Puget Sound, with pelagic fish being particularly important on an occurrence and mass basis (Table 1). As with copper rockfish in 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.

Seasonal Variation in Diet

Food habits of copper rockfish collected by Moulton (1977) between April and August (equivalent to spring and summer) from Puget Sound, Washington, were dominated by fish (~32% occurrence, 53% mass), crabs (~45% occurrence, 33% mass), and shrimp (~28% occurrence, 7% mass), similar to their overall annual food habits. Megalopa and zoea larvae of decapods were important in terms of numerical abundance (~44%), but had negligible mass. Euphausiids were not found in the diet of copper rockfish in Moulton's (1977) study.

Rosenthal *et al.* (1988), studying food habits of copper rockfish in the "summer" in the Gulf of Alaska, concluded that the diet was comprised primarily of small fishes (55% volume), especially sand lance (*Ammodytes hexapterus*) and Puget Sound rockfish (*Sebastes emphaeus*), as well as shrimp (8% volume) (e.g., Caridea and *Pandalus* spp.) and crabs (18% volume) (e.g., *Cancer branneri* and *C. oregonensis*). Pelagic crustaceans recorded in the diet were either brachyuran larvae or mysids (56% numerical abundance, 10% volume).

Although the numerical abundance and fish species 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 (Fig. 10), the mass contributions to the diet by the consumption of pelagic fishes were similar. The difference in the numerical abundance of prey items was due to copper rockfish in Saanich Inlet consuming relatively more pelagic crustaceans (75-92% numerical abundance) (Fig. 10b) 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 diets of copper rockfish in the Gulf of Alaska and Puget Sound were similarly comprised of demersal crustaceans, in terms of numerical abundance and mass (approximately equivalent to volume), to copper rockfish in Saanich Inlet.

In summary, the basic food habits of copper rockfish collected in Saanich Inlet, Puget Sound, and the Gulf of Alaska were similar during the spring and summer and, in general, on an annual basis. The species of prey fishes consumed was the most obvious difference between geographic locations and seasons. This 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 in Saanich Inlet). The consumption of small pelagic fishes, regardless of species, was characteristic of copper rockfish, regardless of location of the study.

The 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 (Table 8). Although the geographical distribution of *Munida* extends from Alaska to Mexico, *Munida* occur most often in fjords (like Saanich Inlet) at depths of 22-1463 m (Hart 1982) and hence may not occur in locations sampled in the other studies.

Size-related Variation in Diet

Changes in food habits with an increase in body size have been recognized in many species (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).

Patten (1973) observed that the percentage of rockfish consuming crustaceans decreased as rockfish size increased (98% down to 56% occurrence for rockfish <200 mm fork length versus >200 mm fork length). Conversely, he also found that the consumption of fishes increased as rockfish size increased (13% up to 81% occurrence respectively). Similarly, copper rockfish ≤155 mm TL collected from Humboldt Bay had consumed only small crustaceans and had not fed on fish or larger crabs. Fish were important only in the diet of copper rockfish >172 mm TL (Prince and Gotshall

1976). This general trend was also evident for copper rockfish in Saanich Inlet where a greater proportion of extra-small and small copper rockfish (≤200 mm TL) had fed on crustaceans rather than fishes when compared to medium and large fish (Fig. 12a). This ontogenetic shift of feeding proportionally more on crustaceans when small to feeding proportionally more on fishes when of larger body size was also reflected in the relative proportions of crustaceans and fishes contributing to the numerical abundance and mass of the diet of different sized copper rockfish (Fig. 12b,c).

Diet Composition of Quillback Rockfish

Geographical and Seasonal Variation in Diet

The food habits of quillback rockfish have been studied less than copper rockfish, with all studies centering on quillback rockfish in Washington (Moulton 1977; Buckley and Hueckel 1985) and Alaska (Rosenthal *et al.* 1988). In Puget Sound, Washington, the diet of quillback rockfish during March to December consisted primarily of caridean shrimp, especially *Pandalus danae* and brachyuran crabs (especially *Cancer oregonensis*) (Buckley and Hueckel 1985).

Crabs were also important in the diet of quillback rockfish collected by Moulton (1977) in Puget Sound from April to August, having been fed on by ~54% of the quillback rockfish. Although the numerical abundance of the crabs was low (~3%) their mass contribution to the diet was high (~44%). Fish were also relatively important to quillback rockfish (~25% occurrence, 23% mass) and to a lesser extent, shrimps (~32% occurrence, 8% mass). Consumption of euphausiids by quillback rockfish in Puget Sound contributed greater mass (10%) than any other pelagic crustacean (Moulton 1977).

Crustaceans were also the dominant prey type consumed by quillback rockfish collected during the "summer" in the Gulf of Alaska (~55% volume) (Rosenthal *et al.* 1988). The majority of demersal crustaceans consumed were caridean shrimps and cancroid crabs. Pelagic crustaceans (Mysidae, *Thysanoessa raschii*, and brachyuran crab larvae) were the most numerous prey items consumed but represented only ~9% of the volume of prey. Fishes consumed by quillback rockfish represented a substantial contribution to the mass of the diet (~40%). As with copper rockfish, sand lance comprised the majority of the identified fish prey consumed by quillback rockfish, with herring and Puget Sound rockfish of relatively minor importance. Although quillback rockfish in Saanich Inlet consumed less fish prey in the spring and summer 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 was most likely due to the quillback rockfish in Saanich Inlet having fed on herring, which are relatively heavier than sand lance of similar length because of the herring's greater body depth (Hart 1973).

In general, 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, crustaceans (demersal and pelagic) 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 was substantial on a mass basis because of the relatively larger size of fish prey compared to crustaceans.

Size-related Variation in Diet

Examination of changes in food habits of quillback rockfish with an increase in body size has not been previously undertaken. As with copper rockfish (Fig. 12), however, the importance of fish in the diet increased with size of quillback rockfish and the relative importance of crustaceans decreased with an increase in size of quillback rockfish (Fig. 13). Compared with copper rockfish, however, quillback rockfish of similar size consumed relatively more crustaceans and fewer fish (Fig. 12, 13).

Food Consumption of Copper and Quillback Rockfish: Seasonality and Quantity

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 the winter is solely for the purpose of body maintenance (Keast 1970). This may be reasonable for freshwater systems that undergo a marked decline in water temperature from summer to winter (e.g., 4°C versus 15-20°C), which decreases digestion and feeding stimulus in a majority of freshwater fishes (Keast 1970); however, copper and quillback rockfish in Saanich Inlet at depths greater than 15 m do not experience a substantial lowering of the water temperature during the winter (Fig. 38b, Chapter VII). Rockfish are also reproductively active throughout the winter and into late spring when their young are born (Chapter VI). The requirement of rockfish to feed in the winter, not only for maintenance but also to offset the energetic demands of reproductive activities, was evident in that the proportion of copper rockfish feeding in the winter was the same as for the other seasons (Fig. 9). In addition, the proportion of quillback rockfish feeding in the winter was the same as for quillback rockfish in the fall and the same as for copper rockfish year round (Fig. 9).

The importance of feeding in the winter was also evident from the relationship of mass of food consumed as a function of body mass of the rockfish (Fig. 16). For copper rockfish, food consumption in the 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 (Fig. 16a). In addition, copper rockfish also had an increased rate of food consumption with an increase in body size. The food consumption of quillback rockfish in the winter was equal to their food consumption during the summer (Fig. 16b), and greater than their food consumption in spring and fall (Fig. 16c). The quantity of food consumed in the winter by both copper and quillback rockfish was a function of their consumption of pelagic fishes, specifically juvenile herring (Fig. 10c, 11c).

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

Relative to copper rockfish, a greater proportion of quillback rockfish stomachs were observed to contain food in the spring and summer (Fig. 9). These fish, however, had not consumed a greater quantity of food relative to their body mass (Fig. 16). This was probably due to the greater propensity of quillback rockfish to feed on pelagic crustaceans, rather than demersal crustaceans, during spring and summer (Fig. 10, 11). Pelagic crustaceans occur as aggregating masses of individuals and the size of the aggregation as a whole would allow many quillback rockfish to feed simultaneously. Pelagic crustaceans, however, do not contribute substantially to the mass consumed because of their small size.

In general, food consumption of fishes is usually allometric with a slope of less than one, 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 2-4% of their body mass daily whereas adult fish consumed ~1.5%. For quillback rockfish and copper rockfish food consumption was isometric over the range of body masses sampled (except for copper rockfish in winter) and food consumed ranged from 0.2-1.9% and 0.5-3.7% of their body mass respectively (Fig. 15 b,c). These values were therefore comparable to or greater than values for freshwater fishes feeding at low temperatures in the winter, which range from 0.2-2.0% of the body mass of the fish (Keast 1968).

Diel Variation in Feeding

Copper and quillback rockfish may partition their feeding niche based on diel variations in time of feeding (Fig. 15a,b). The temporal partitioning of feeding appeared to be between primarily crepuscular feeding by copper rockfish (with secondary daytime feeding) and primarily mid-day feeding by quillback rockfish.

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, and 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; pers. obs.) and would therefore be available to quillback rockfish.

Neither copper rockfish 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 (pers. obs.).

Niche Breadth and Overlap in Food Habits

"Summer" values of niche breadth (B_A) based on volume (approximately equivalent to mass) for copper and quillback rockfish in the Gulf of Alaska were 0.318 and 0.314 respectively [recalculated by inserting Simpson's Niche Breadth value from Table 11 in Rosenthal *et al.* (1988), which was equivalent to B, into my Eqn. 1]. Rosenthal *et al.* (1988) concluded that copper and quillback rockfish had less specialized diets than pelagic rockfish species, and that they were intermediate between dietary specialists and dietary generalists. Average niche breadths by mass for copper and quillback rockfish in Saanich Inlet in spring and summer (equivalent to "summer") were 0.505 and 0.198 respectively, indicating 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 of a dietary specialist 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 evident, however, because both copper and quillback rockfish 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 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).

The major factor that appeared to influence food consumption of copper and quillback rockfish in the winter was the presence of juvenile herring in Saanich Inlet. As niche overlap by mass for copper and quillback rockfish during the winter was close to the theoretical maximum, the two species had extremely similar use of the same food resources (Table 11). The use of herring by copper rockfish in the winter was even greater than the use of herring by quillback rockfish. Copper rockfish, although feeding on a greater diversity of prey taxa than quillback rockfish in the winter, fed infrequently on the majority of the prey taxa and concentrated its feeding disproportionately on herring (Table 10).

Assessing whether the disproportionate use of herring by copper rockfish was due to its availability in the environment was difficult. Niche breadth and niche overlap measures which take into account the availability of the prey resources (Hurlbert 1978) could not be used because the survey techniques for pelagic and demersal prey were not comparable. This was a result of the potential prey taxa differing substantially in their distribution in space and time. Demersal organisms were relatively sedentary, usually occurred as single individuals, and did not move into the water column to any extent. These organisms could be enumerated and their densities calculated with some estimate of variability (Table 8). In contrast, methods of estimating the availability of pelagic organisms, such as euphausiids, mysids and herring, were not comparable to methods used for demersal organisms. Pelagic crustaceans and herring occurred in aggregations or schools that were too large for me to adequately estimate their numerical abundance; for example, euphausiids have been known to occur at depth in Saanich Inlet in concentrations estimated at $10{,}000 \cdot m^{-3}$ (Mackie and Mills 1983). These organisms also moved continuously in the water column, adding to the problem of estimating their number and density (volumetric).

The greatest inadequacy of estimating availability of pelagic prey species, especially pelagic crustaceans and herring, was in observing the presence of their aggregations or schools in the environment during the relatively short time period of each survey (approximately 30 min). The preponderance of herring in the environment in the winter, for example, was based on observing a single large school of herring in a total of 23 survey dives. Perhaps the most informative statement that could be made about the availability of pelagic crustaceans and herring in the environment was that, when they did occur, they were very abundant. This may be particularly relevant to the niche breadth and overlap values calculated for copper and quillback rockfish in summer and winter (Table 10, 11).

During the summer, when niche breadths based on numerical abundance were narrow for both copper and quillback rockfish, 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 abundance of pelagic crustaceans (Table 9) would therefore have allowed both species (i.e., high overlap) to feed primarily on pelagic crustaceans (i.e., narrow niche breadths). Similarly, during the winter, niche breadths based on mass contribution, which are 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 the 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.

Comparative food habit analyses on naturally occurring sympatric populations of copper and quillback rockfish can not directly decipher the presence or absence of interspecific competition over food resources. They can, however, provide information on potential conflicts over resources. In general, niche overlap values for copper and quillback rockfish were moderate to high (0.402-0.997) indicating that these species share in 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.

For copper and quillback rockfish in Saanich Inlet, there appeared to be an important period of food consumption in the winter, not only in the mass of food consumed but in the quality of the food consumed (e.g., high caloric density of herring). Without experimentally excluding schools of herring from the study area, it was impossible to know how critical winter feeding was 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 (Chapter VI).

SUMMARY

Copper rockfish consumed a greater proportion of pelagic fishes than quillback rockfish, whereas quillback rockfish had a greater proportion of pelagic crustaceans in their diet. Both species fed on demersal crustaceans. Food consumption by copper and quillback rockfish differed seasonally. Copper rockfish consumed the greatest mass of food during the winter when feeding on juvenile herring. Quillback rockfish also consumed the greatest quantity of food during the winter, but their consumption was less than copper rockfish during the same period. A greater proportion of quillback rockfish were collected with food in their stomachs during the spring and summer when the numerically dominant food items were pelagic crustaceans. The importance of fish in the diets of both species increased with size.

Values for niche overlap in feeding 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 large schools of juvenile herring were available in the environment and hence were presumably not a limited resource. Maximum niche overlap was therefore correlated with an abundance of a shared resource rather than indicative of competition for food resources between copper and quillback rockfish.

CHAPTER IV

COMPARATIVE ALLOMETRY OF THE GASTROINTESTINAL TRACT OF COPPER AND QUILLBACK ROCKFISH

INTRODUCTION

Differences in diet between species that are consistent over evolutionary time may ultimately lead to differences in functional morphology (Karr and James 1975). For fishes, predictable relationships between morphology and feeding ecology have usually involved measurements of the body form (Keast 1970), the mouth [e.g., gape (Alevizon 1975; Singer 1985)] or the gill arches [e.g., length and spacing of the gill rakers (Singer 1985)]. As in other animals, morphology of the gastrointestinal tract in fishes also may be related to their general feeding ecology (Odum 1970; Kapoor *et al.* 1975).

The morphology of the alimentary tract is usually compared among fishes that are characteristically carnivores, omnivores, or herbivores (Kapoor *et al.* 1975). In general, the ratio of the length of the intestine of a fish to its body length is usually less than one in carnivores, 1-3 in omnivores, and >3 in herbivores (Odum 1970). The correlation between the relative length of the intestine and the type of food ingested is a function of the digestibility of the food, with animal matter being more digestible than plant matter (Odum 1970; Fänge and Grove 1979) and fish being more digestible than invertebrates (Kapoor *et al.* 1975). Within broad feeding categories, even finer specializations may exist; for example, microphagous carnivores usually have longer intestines relative to their body length than fish that feed on larger prey (Bryan 1975; Kapoor *et al.* 1975).

Unlike intestine length, the relationship between the presence and size of pyloric caeca in fish species does not appear to be closely related to their feeding ecology (Kapoor *et al.* 1975; Fänge and Grove 1979). The pyloric caeca are thought to have a variety of functions, including digestion, storage, or absorption of nutrients (Kapoor *et al.* 1975). All these functions relate to enlarging the surface area of the alimentary tract (de Groot 1969). In contrast, a clear relationship exists between stomach mass and the size of food items consumed. In general, stomach mass increases, relative to body size, as food size increases. Stomach mass also increases with an increased duration between meals (Kapoor *et al.* 1975; Smith 1982), typical of animals that are gorge-feeders.

The purpose of this study was to determine the allometry of the gastrointestinal tract of copper and quillback rockfish and to relate the gut allometries to the feeding ecology (Chapter III) of these congeners.

METHODS

Copper and quillback rockfish analysed for allometry of the gastrointestinal tract were collected in conjunction with a study of their feeding habits (Chapter III). Total length, body mass, and sex were determined for each fish (Chapter III). In the processing of the excised gastrointestinal tract, the length of the intestine was measured first to minimize stretching it during handling. To do this, the intestinal mesenteries were cut, allowing the intestine to be straightened and measured, unstretched, from its anterior attachment at the pyloric caeca to the anus. After removal of visceral fat, the intestine was excised from its junction with the pyloric caeca and slit longitudinally. The contents of the intestine were discarded and the empty intestine was weighed. Similarly, the stomach was excised at its junction with the pyloric caeca and its contents were removed for identification (Chapter III). The empty stomach was then weighed. The caeca were counted, emptied of any contents, and weighed.

Relationships of stomach mass, intestine mass, and caeca mass to body mass, and intestine length to standard length, were determined for 232 female and 288 male copper rockfish and 130 female and 131 male quillback rockfish. Allometric relationships between portions of the digestive tract and body size were examined using the standard power function recommended by Peters (1983):

[3] $Y = a \cdot X^b$

where: Y is the mass of the stomach, intestine, or caeca, or intestine length; a is a coefficient; X is the body size variable, either body mass or standard length; and b is the power exponent. Data for dependent and independent variables were $\log_{10}$ transformed to linearize and to correct for heteroscedasticity, giving:

[4] $\log Y = \log a + b \cdot \log X$

As a prerequisite to a two-factor ANCOVA, homogeneity of slopes (b) among males and females of both species for each dependent variable was tested by a single-factor ANCOVA with fish body size (body mass or standard length) as the single covariate. Subsequently, effects due to species and sex were analysed using a two-factor ANCOVA with body size as the covariate.

RESULTS

For both sexes of both species, the preliminary requirement of nonsignificant differences in regression coefficients (slopes) among the groups for caeca mass and intestine mass as a function of the covariate (body mass) was not satisfied (Single-factor ANCOVA: $F_{3,759} = 6.12$ and $P = 0.000$, $F_{1,761} = 4.19$ and $P = 0.041$, for caeca and intestine mass respectively). Regression coefficients and intercepts for each of the dependent variables were not different between males and females within each species but were different between the species (Table 12; Fig. 17, 18). Caeca mass was greater in smaller copper rockfish than quillback rockfish, but the rate of increase in mass of caeca with body size was greater in quillback rockfish. Large copper and quillback rockfish therefore had very similar caeca masses (Fig. 17). As with mass of caeca, the rate of increase in the mass of intestine with size was greater in quillback rockfish than in copper rockfish. Small copper and quillback rockfish had similar intestinal masses, but the difference in the rate of change of intestine mass with size between the species resulted in large quillback rockfish having a greater intestine mass than large copper rockfish (Fig. 18).

In contrast, for intestine length and stomach mass as a function of a covariate (standard length and body mass respectively), the preliminary requirement of nonsignificant differences in regression coefficients among groups was satisfied (Single-factor ANCOVA; $F_{3,759}$ = 0.37 and 0.77, P = 0.77 and 0.51, respectively). An effect due to species alone was evident when the groups were tested for effects due to sex, species, or their interaction (Two-factor ANCOVA; Table 13; Fig. 19, 20). Relative to body size, therefore, quillback rockfish had a longer intestine (Fig. 19) and a smaller stomach (Fig. 20) than copper rockfish.

Table 12. Regression statistics for within and between species effects in caeca mass and intestine mass as a function of body mass of copper and quillback rockfish.

Independent Variable ($\log_{10}$)	Dependent Variable ($\log_{10}$)	Factor	DF	*F*	*P*
Within copper rockfish:					
Body mass (g)	Caeca mass (g)	Sex	2,516	0.75	0.47
	Intestine mass (g)	Sex	2,516	1.88	0.15
Within quillback rockfish:					
Body mass (g)	Caeca mass (g)	Sex	2,257	0.46	0.63
	Intestine mass (g)	Sex	2,257	1.41	0.25
Between copper and quillback rockfish:					
Body mass (g)	Caeca mass (g)	Species	2,777	9.16	0.00*
	Intestine mass (g)	Species	2,777	33.70	0.00*

* Significant at $P \leq 0.05$.

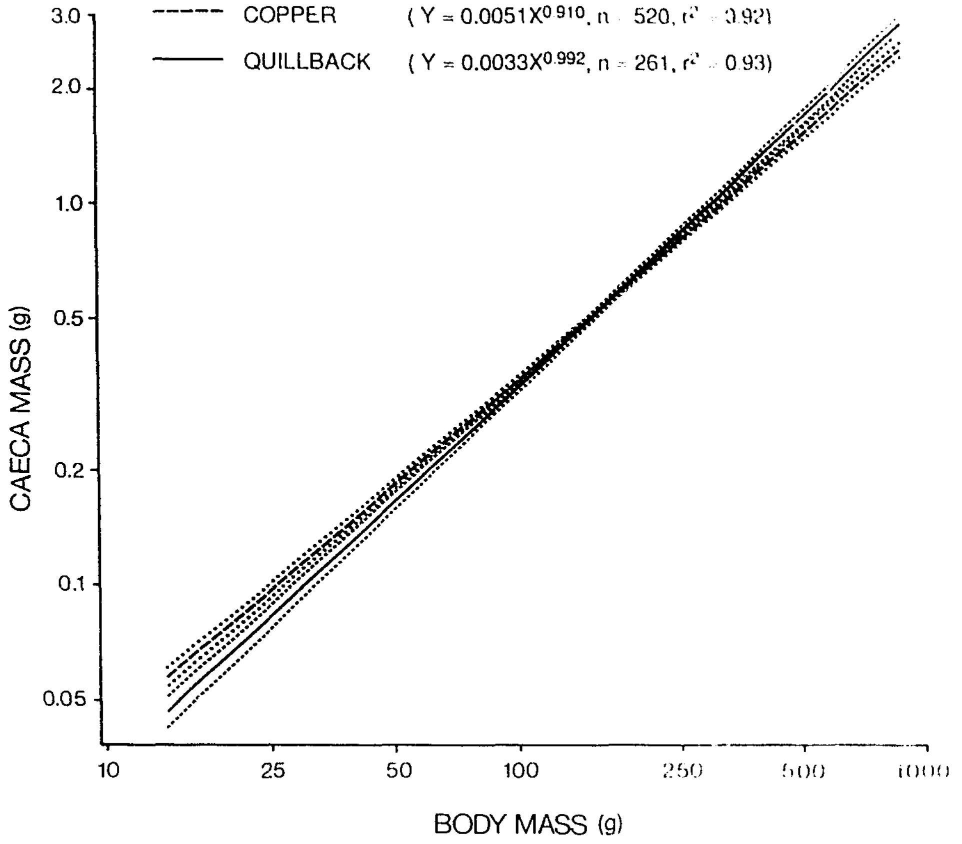

Fig. 17. Mass of caeca (empty) of copper and quillback rockfish as a function of their body mass. Dotted and dashed curves represent 95% confidence limits around the regression lines.

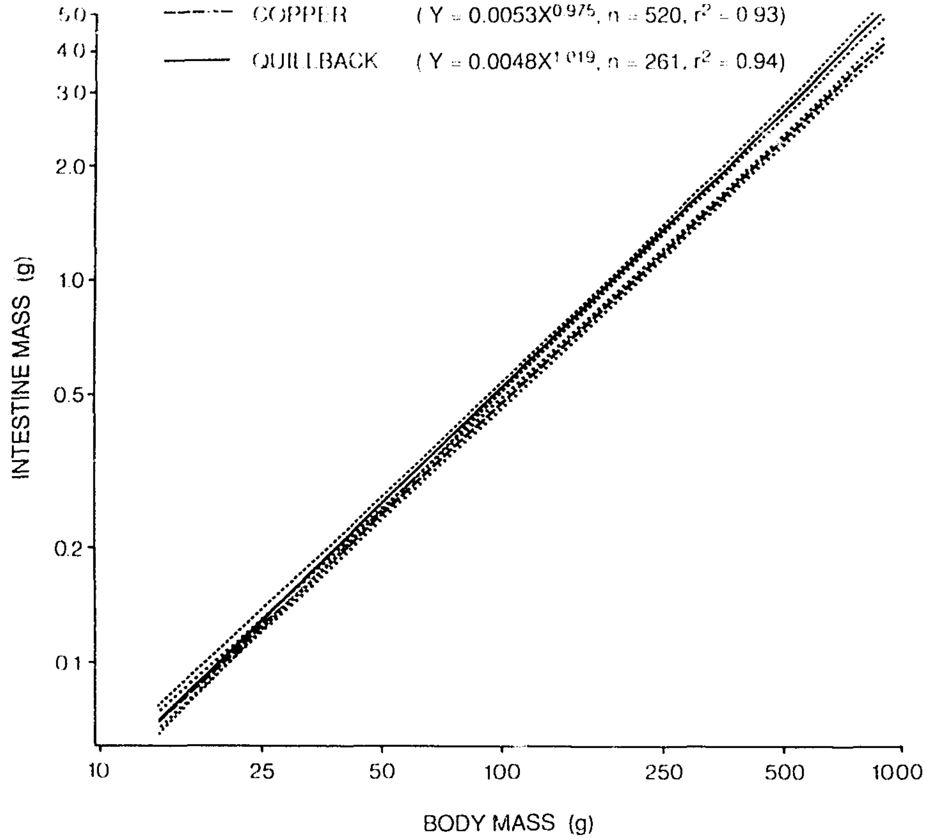

Fig. 18. Mass of the intestine (empty) of copper and quillback rockfish as a function of their body mass. Dotted and dashed curves represent 95% confidence limits around the regression lines.

Table 13. Two-factor analysis of covariance statistics for sex and species effects in stomach mass and intestine length as a function of body size in copper and quillback rockfish.

Covariate ($\log_{10}$)	Dependent Variable ($\log_{10}$)	Factor	*F*	*P*
Body mass	Stomach mass	Sex	2.51	0.11
(g)	(g) (DF=1,762)	Species	222.91	0.00*
		Interaction	0.36	0.55
Standard Length	Intestine	Sex	0.25	0.62
(mm)	Length (mm)	Species	58.94	0.00*
	(DF=1,762)	Interaction	0.32	0.57

* Significant at $P \leq 0.05$.

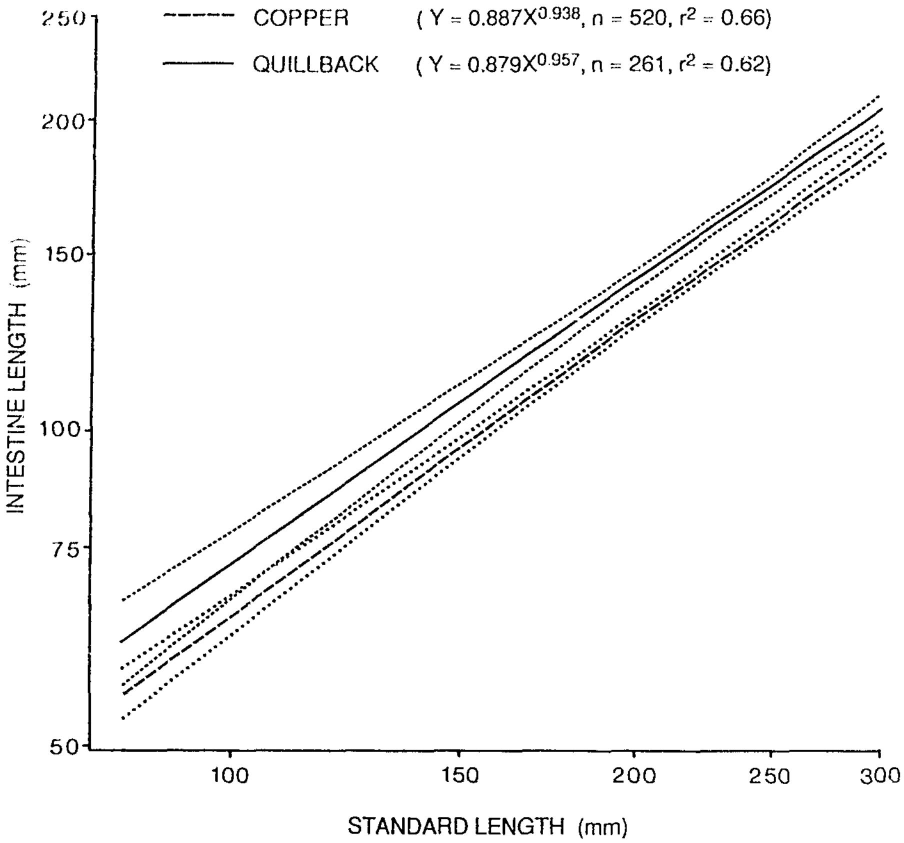

Fig. 19. Intestinal length (unstretched) of copper and quillback rockfish as a function of their total length. Dotted and dashed curves represent 95% confidence limits around the regression lines.

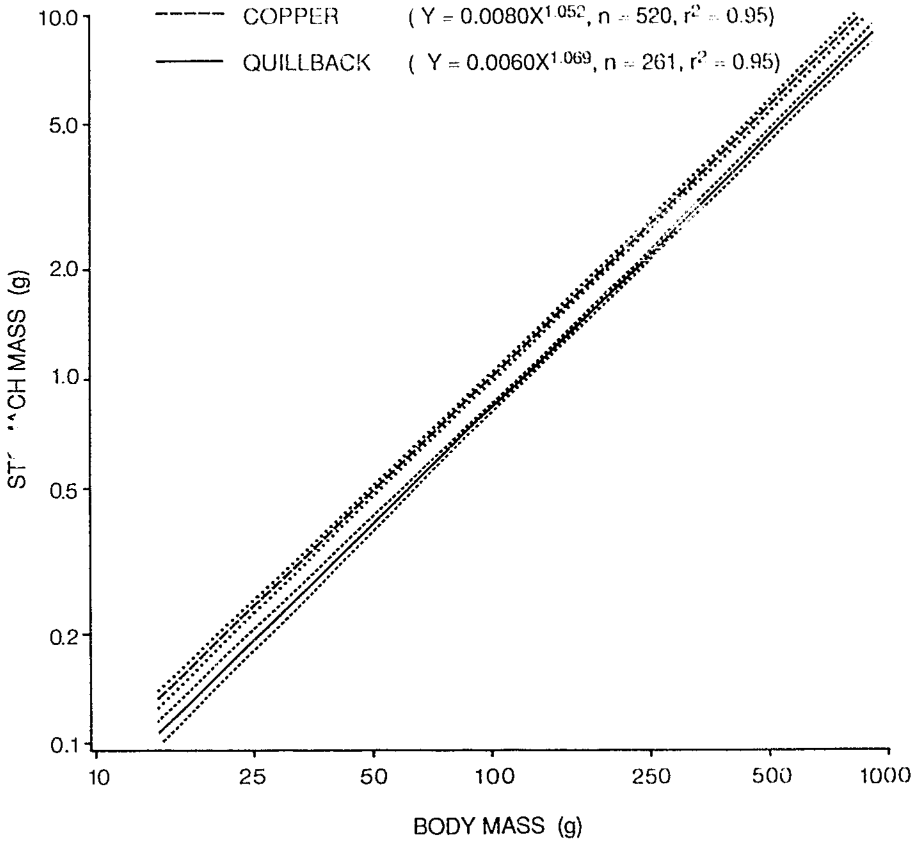

Fig. 20. Mass of the stomach (empty) of copper and quillback rockfish as a function of their body mass. Dotted and dashed curves represent 95% confidence limits around the regression lines.

Unlike gut masses or lengths as a function of body size, which all had significant regression coefficients (i.e., slopes greater than zero), number of caeca was independent of body size for both copper rockfish ($F = 0.16$; $n = 519$; $P = 0.69$) and quillback rockfish ($F = 0.10$; $n = 263$; $P = 0.76$). Regardless of body size, therefore, copper and quillback rockfish had 7-11 caeca, with copper rockfish tending to have a greater number of caeca (9.92 ± 0.04, $n = 519$) ($\overline{X} \pm 1SE$), on average, than quillback rockfish (9.62 ± 0.04, $n = 263$) ($F = 11.78$; $P = 0.00$).

DISCUSSION

Differences in the gut morphology between copper and quillback rockfish varied in a predictable manner based on their general food habits (Chapter III). The relative intestine lengths of both species (< 1, Fig. 19) provided supporting evidence of their carnivorous feeding habits (Table 1, 2). Most notably, the intestine length of copper rockfish, which consumed proportionally more fish and larger crustaceans than quillback rockfish (Chapter III), was shorter and its mass less than the intestine of quillback rockfish (Fig. 18, 19). de Groot (1971) also observed that flatfishes (Pleuronectidae), which consumed fish and larger invertebrates, had smaller relative lengths of the intestine compared to flatfishes, which consumed smaller polychaetes and crustaceans.

In contrast to the lack of a relationship between the number and size of pyloric caeca and the feeding ecology of fishes observed by Kapoor *et al.* (1975) and others , de Groot (1969) found that the number and size of pyloric caeca increased with increased size of prey and indigestible matter in the diet of flatfishes. The relationship between the number and size of caeca and the diet of copper and quillback rockfish, however, was difficult to interpret. On average, copper rockfish tended to have a greater number of pyloric caeca than quillback rockfish, which was consistent with copper rockfish consuming relatively larger food items, especially fish (Chapter III). Caeca mass in quillback rockfish, however, increased at a greater rate than in copper rockfish, and medium and large quillback rockfish had a greater mass of caeca than copper rockfish (Fig. 17). This was also consistent with de Groot's (1969) observation because quillback rockfish consumed relatively more crustaceans (i.e., more indigestible material) than copper rockfish (Chapter III). The number and size of caeca alone, therefore, were not decisive factors in delineating the differences in gut morphology relating to the feeding habits of copper and quillback rockfish.

In contrast, the presence of a greater stomach mass in copper rockfish compared to quillback rockfish (Fig. 20) indicated that copper rockfish had a diet comprised of relatively larger food items. Pelagic and demersal fishes consumed by both copper and quillback rockfish were of similar length (Chapter III). Copper rockfish, however, also consumed embiotocids, which have a greater body depth and mass than herring (Table 5). In one unusual case, a copper rockfish had consumed a pile perch which was 56% of the rockfish's length and ~10% of its body mass. The entire caudal peduncle and caudal fin of the pile perch was protruding out the buccal cavity of the copper rockfish (pers. obs.). In addition, the size of demersal crustaceans consumed by copper rockfish were larger than for similar-sized quillback rockfish (Fig. 14b). This was exemplified by the observation that the largest crustaceans (*Callianassa, Pandalus platyceros, Cancer productus, Pugettia gracilis*) (Table 5) had been eaten by only copper rockfish (Table 1). In addition, the consumption by quillback rockfish of only the long, thin legs of large crabs (*Acantholithodes* and *Telemessus*) indicates that whole crabs could not be captured or ingested by quillback rockfish.

The combined traits within copper rockfish of a shorter intestine and larger stomach, compared with quillback rockfish, indicated that the food habits of copper rockfish consisted of a greater proportion of fish and larger food items, in general, than quillback rockfish. This generalization based on gut morphology was supported by the food habit analysis (Chapter III).

SUMMARY

Species-specific differences were evident in the gut allometry of copper and quillback rockfish. Copper rockfish had a shorter intestine and a larger stomach relative to similar-sized quillback rockfish. This suggested that the gastrointestinal tract of copper rockfish was better suited to holding and digesting fish and larger crustaceans than the tract of quillback rockfish. The differences in gut allometry between the species were consistent with observed differences in their diets.

CHAPTER V

COMPARATIVE GROWTH OF COPPER AND QUILLBACK ROCKFISH

INTRODUCTION

Rockfish species of the genus *Sebastes* vary greatly in their maximum size, maximum age, and rate of growth. Maximum total length of rockfish range from 18 cm in Puget Sound rockfish (Moulton 1977) to 97 cm in rougheye rockfish (*S. aleutianus*) (Hart 1973). The maximum ages recorded are equally as variable, ranging from 6 yrs for Puget Sound rockfish (Moulton 1977) to 140 yrs for rougheye rockfish (Chilton and Beamish 1982). In addition, growth coefficients (*K*, the rate at which a species approaches its asymptotic length) for rockfishes, in general, are low (0.1 to 0.3) (Love *et al.* 1990) compared with other fishes (e.g., salmonids, gadoids) (0.3 to 1.0) (Beverton and Holt 1960). Growth coefficients do, however, vary substantially within the genus, ranging from 0.015 in female widow rockfish (*S. entomelas*) (Westrheim and Harling 1975) to 0.789 in Puget Sound rockfish (Moulton 1977). This large degree of variability necessitates the determination of species-specific growth patterns not only to understand the life history characteristics of rockfish species (e.g., age of sexual maturity) but also to efficiently manage rockfish species (Chen 1971; Wyllie Echeverria 1987; Love *et al.* 1990). This is particularly important as this genus is speciose (at least 65 species are recognized in the northeastern Pacific Ocean) and many species in the genus are sympatric with one or more congeners (Chen 1971). Management plans for rockfish species may therefore be more complicated than the single-species management strategies of some other fisheries. The high degree of congeneric sympatry, however, provides an opportunity to compare growth patterns in similar species which can be related to the general ecology of the species.

This chapter compares the growth of two sympatric *Sebastes* congeners, copper and quillback rockfish, to determine the degree of similarity in their patterns of growth. Relationships between age and length were determined using growth models. It was especially pertinent to study the age-length relationships of copper and quillback rockfish because the majority of age data for these species has, to date, been obtained by viewing the external surfaces of sagittal otoliths (Patten 1973; Moulton 1977; Barker 1979; Gowan 1983), rather than viewing cross-sections of broken-and-burnt otoliths (Richards and Cass 1987; Hand and Richards 1991). In the last decade the former method of aging rockfish has been shown to be unreliable for older fish, resulting in serious underestimations of ages (Beamish 1979). Reading broken-and-burnt cross-sections of sagittal otoliths has now become the standard procedure (Chilton and Beamish 1982). This latter method has been validated for a few rockfish species and has demonstrated that large discrepancies can exist between techniques. For ocean perch (*S. alutus*), surface and cross-section ages agree up to the age of 22-24 yrs. After 25 yrs of age, surface readings may underestimate the age in this rockfish species by 50 yrs (Beamish 1979). For copper and quillback rockfish, the two techniques give similar ages only up to approximately 10 yrs (pers. comm., L. Richards, Pacific Biological Station, Nanaimo, B.C.). In general, surface readings of otoliths overestimate the size of fish at a given age if the ages have been underestimated (Archibald *et al.* 1981). Not surprisingly, these different aging techniques are known to affect estimates of growth coefficients and mortality rates (Archibald *et al.* 1981; Wilson and Boehlert 1990).

A second objective of this study was to investigate differences in growth of male and female copper and quillback rockfish to determine whether the sexes are monomorphic in size, and whether differences were evident within sexes between the species. Externally, rockfish do not exhibit sexual dimorphism, other than the presence of a large urogenital papilla in the male (Moser 1967). Differences exist between some females and males in fin and jaw characteristics (Chen 1971), and eye and fin size

(Wyllie Echeverria 1986), but they are not readily apparent without detailed measurement. Length and mass differences between males and females, however, have been reported in some species of rockfish (Chen 1971; Archibald *et al.* 1981; Wyllie Echeverria 1986; Love *et al.* 1990). Chen (1971) suggested that male rockfish should grow faster than female rockfish because the annual cost of reproduction in males is less, and hence more of their energy can be invested in growth. In many species, however, there is no size difference between the sexes or it is the female that attains the greatest size (Archibald *et al.* 1981; Wyllie Echeverria 1986; Love *et al.* 1990).

In addition, growth of copper and quillback rockfish in Saanich Inlet was compared with growth information for these species from other geographical locations. Growth of fish in more northern, cooler waters has been shown to be slower than for the same species from more southern, warmer waters, with the observation that northern fishes live longer and grow larger (Chen 1971: Ricker 1979). This geographical comparison was preliminary, however, because the techniques used for aging the fish differed between studies.

Finally, length-mass relationships were also used to determine the growth patterns of copper and quillback rockfish. Typically, solitary, benthic species of rockfish have a greater increase in mass per unit of body length than schooling, pelagic species (Moulton 1977). Although copper and quillback rockfish are both considered to be solitary, sedentary species (Moulton 1977; Barker 1979; Gowan 1983), copper rockfish appear to be more pelagic than quillback rockfish in Saanich Inlet (Chapters II and III) and this ecological difference may be reflected in their length-mass relationships.

METHODS

Age-Length Relationships

Sagittal otoliths were removed, cleaned, and placed in a storage solution of glycerin:water (1:1), with a small amount of thymol to prevent growth of fungus (Chilton and Beamish 1982). Otoliths were broken through the nucleus and the cross-section of the broken otolith was burnt using an alcohol flame. The otolith half was embedded in plasticine to position the cross-sectional surface for viewing, and the burnt surface was then brushed with a small amount of vegetable oil. Otoliths were viewed under reflected light using a Zeiss 80X-zoom dissecting microscope. Ages of fish were estimated directly by counting the number of annuli present (Chilton and Beamish 1982). Annuli in otoliths correspond to translucent growth zones in the otolith, which represent a reduced rate of growth in winter, and which appear as dark bands when burnt and viewed under reflected light. This is in contrast to the opaque zones, which correspond to the faster growth rates in summer, and which appear as light bands (Chilton and Beamish 1982).

Patterns of growth of male and female copper and quillback rockfish were described by applying a von Bertalanffy (1938) growth model (after Ricker 1975) (BMDP, Program PAR, Dixon *et al.* 1983) to length-at-age data:

$$[5] \qquad l_t = L_{inf}\ [1 - e^{-K(t-t_o)}]$$

where l_t was length at age t, L_{inf} was the theoretical asymptotic length, K was the growth coefficient, and t_o was the theoretical age at which $l_t = 0$.

Length-mass Relationships

The relationship between total length and mass for each species and sex was described using the allometric relationship:

$$[6] \qquad M = a \cdot L^{b}$$

where M was mass, L was total length, and a and b were constants (intercept and slope, respectively) determined from fitting a least-squares regression to the $\log_{10}$ transformed data. Data were $\log_{10}$ transformed to correct for heteroscedasticity and to linearize. Differences in length-mass relationships were tested between sexes and species using ANCOVAs.

RESULTS

Age-Length Relationships

Female and male copper rockfish exhibited monomorphic growth patterns (Fig. 21a), with both sexes attaining asymptotic lengths around 30-31 cm total length (Table 14). Growth coefficients (*K*) were also similar between sexes (Table 14).

Male and female quillback rockfish also appeared to have monomorphic growth patterns (Fig. 21b), with both sexes also attaining asymptotic lengths at 30-31 cm total length (Table 14). Growth coefficients were also similar between sexes (Table 14).

Overall, species-specific or sex-specific differences between copper and quillback rockfish were not evident based on their growth curves (Fig. 21). Both sexes of both species attained asymptotic lengths of 30-31 cm and had similar growth coefficients (0.141-0.187) (Table 14). Although the maximum observed lengths of copper and quillback rockfish were similar, the oldest copper rockfish sampled were only 19-20 years of age. In contrast, the oldest quillback rockfish collected were 30-35 years (Table 14).

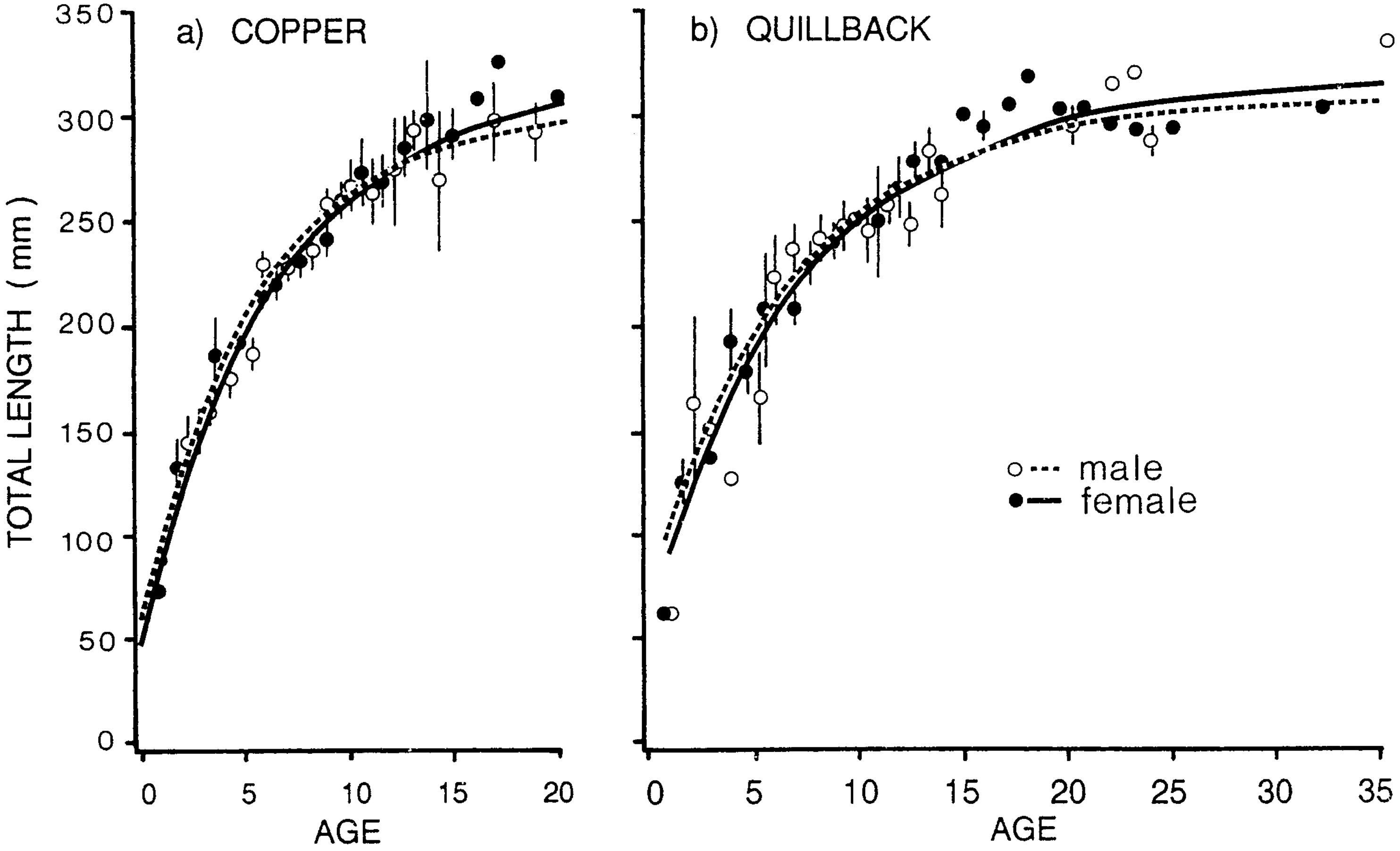

Fig. 21. von Bertalanffy growth curves for a) copper rockfish and b) quillback rockfish. Mean lengths (± 1SE) at age for females and males are offset for clarity where necessary.

Table 14. Parameters (± SD) of the von Bertalanffy growth models for copper rockfish and quillback rockfish collected in Saanich Inlet.

Species	Sex	*n*	L_{inf} (mm)	SD	*K*	SD	t_o	SD	Maximum Observed Age (yr)	Maximum Observed Length (mm)
Copper	Female	110	313.2	13.6	0.162	0.021	-0.886	0.318	20	327
	Male	132	300.5	9.5	0.187	0.020	-0.926	0.286	19	327
Quillback	Female	83	313.7	10.6	0.141	0.020	-1.394	0.617	30	315
	Male	68	306.8	10.9	0.150	0.025	-1.592	0.841	35	336

Length-mass Relationships

The slopes for the regressions of body mass in relation to length for females and males of both species were different (ANCOVA: $F_{3,844} = 5.16$, $P = 0.02$). Slopes for males within each species were slightly greater than slopes for conspecific females ($F_{1,552} = 4.04$ and $P = 0.04$, $F_{1,278} = 3.85$ and $P = 0.05$, copper and quillback rockfish respectively). Slopes for length-mass regressions within sexes between species, however, were not different ($F_{1,385} = 0.10$ and $P = 0.75$, $F_{1,445} = 0.46$ and $P = 0.50$, females and males respectively). In addition, within each sex, the adjusted means (the elevations of the regressions) for copper and quillback rockfish were not the same ($F_{1,385} = 10.25$ and $P = 0.00$, $F_{1,445} = 23.75$ and $P = 0.00$, females and males respectively). For both females and males then, quillback rockfish were slightly heavier at a given body length than copper rockfish (Fig. 22, 23).

DISCUSSION

Previous studies have indicated that copper and quillback rockfish usually differ, to some extent, in their growth patterns (Moulton 1977; Gowan 1983; Hand and Richards 1991). Asymptotic lengths of copper and quillback rockfish can differ between 5 and 14.6 cm, with quillback rockfish

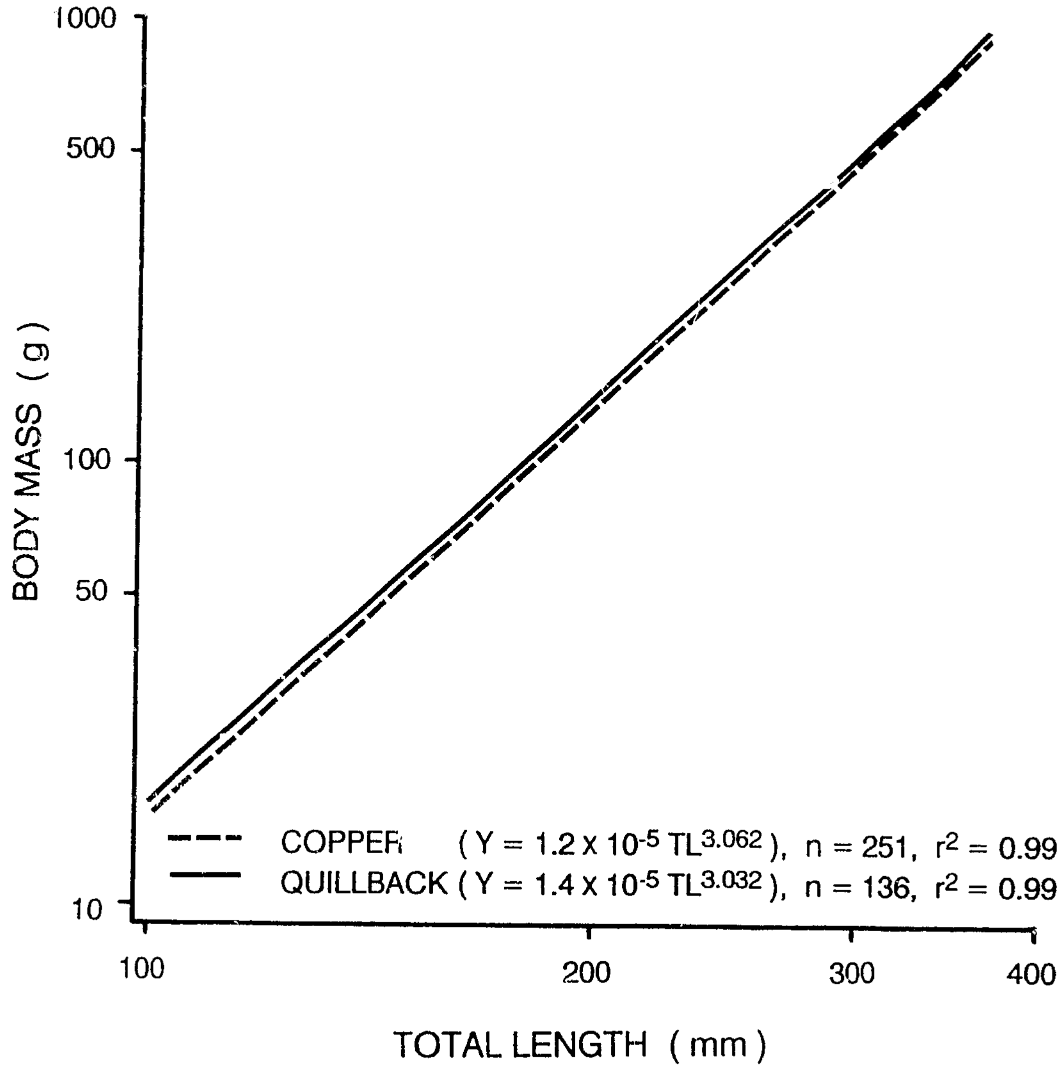

Fig. 22. Length-mass relationships for female copper rockfish and female quillback rockfish.

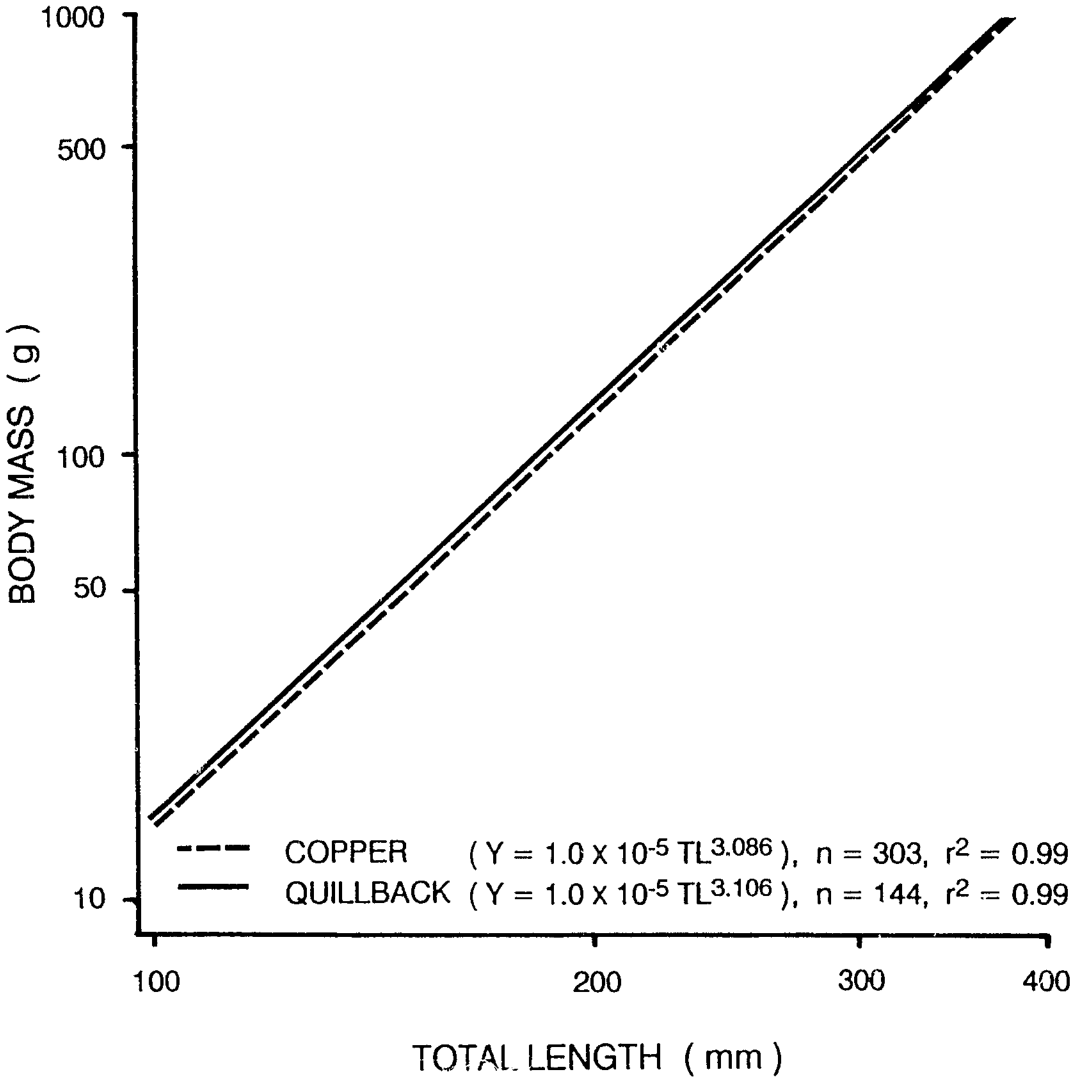

Fig. 23. Length-mass relationships for male copper rockfish and male quillback rockfish.

attaining the larger size (with the exception of male rockfish in Central Puget Sound) (Moulton 1977; Table 15, 16). Growth coefficients (*K*) have also been observed to differ between the species, with copper rockfish attaining their asymptotic lengths faster (e.g., $K > 0.10$) than quillback rockfish (e.g., $K \leq 0.10$) (Moulton 1977; Table 15, 16). Based on aging rockfish using the break-and-burn method, Richards and Cass (1987) have also reported that the maximum observed age of copper rockfish in the Strait of Georgia (Fig. 1) is lower than for quillback rockfish.

In contrast to studies in the Puget Sound and the Strait of Georgia, there were no readily identifiable differences in the growth patterns between copper and quillback rockfish in Saanich Inlet, other than potential differences in their maximum observed ages (Table 14). The similarities in the growth of copper and quillback rockfish in Saanich Inlet can be placed into perspective by considering the relationships between maximum observed ages, growth coefficients, and mortality rates.

A negative correlation between the maximum age of a rockfish species and the rate of approach to its asymptotic length (*K*) has been observed by Archibald *et al.* (1981), suggesting that species with shorter life spans tend to have higher *K*-values. In addition, Archibald *et al.* (1981) suggested that a positive correlation also exists between the estimated mortality rates of rockfish species and their

Table 15. Parameters of the von Bertalanffy growth models for female and male copper rockfish collected in Puget Sound (PS), Washington, and in Campbell River (Strait of Georgia) and Saanich Inlet, British Columbia.

Sex	Collection Location	L_{inf} (mm)[a]	K	t_o	Maximum Observed Age (yr)[b]	Maximum Observed Length (cm)[a]	Reference
Female	Central PS	460	0.16	-1.3	18		Gowan (1983)
	Campbell River	394	0.10	-5.0	38[c]		Hand and Richards (1991)
	Saanich Inlet	313	0.162	-0.9	20	33	This study
Male	Central PS	520	0.12	-1.9	16		Gowan (1983)
	Campbell River	318	0.41	1.5	21[c]		Hand and Richards (1991)
	Saanich Inlet	301	0.187	-0.9	19	33	This study

[a] Lengths were total lengths.

[b] All fish collected from Puget Sound were aged using surface readings of otoliths.

[c] from Richards and Cass (1987).

Table 16. Parameters of the von Bertalanffy growth models for female and male quillback rockfish collected in Puget Sound (PS), Washington, and in Campbell River (Strait of Georgia) and Saanich Inlet, British Columbia.

Sex	Collection Location	L_{inf} (mm)[a]	K	t_o	Maximum Observed Age (yr)[b]	Maximum Observed Length (cm)[a]	Reference
Female	Central PS	540	0.041	-9.8	14		Gowan (1983)
	Northern PS	470	0.092	-1.5	38	45	Barker (1979)
	Campbell River	450	0.054	-6.5	48[c]		Hand and Richards (1991)
	Saanich Inlet	314	0.141	-1.4	30	32	This study
Male	Central PS	450	0.075	-5.9	14		Gowan (1983)
	Northern PS	450	0.100	-1.1	30		Barker (1979)
	Campbell River	410	0.070	-5.5	55[c]		Hand and Richards (1991)
	Saanich Inlet	307	0.150	-1.6	35	34	This study

[a] Lengths were total lengths.

[b] All fish collected from Puget Sound were aged using surface readings of otoliths.

[c] from Richards and Cass (1987).

K-values, indicating that species with high mortality rates also have larger *K*-values. Observations of copper and quillback rockfish in the Strait of Georgia appear to support these correlations since copper rockfish have a greater *K*-value, shorter life span, and greater mortality rate relative to quillback rockfish (Richards and Cass 1987; Hand and Richards 1991).

Similarly, the relatively higher *K*-value, smaller asymptotic length, and younger maximum observed age of quillback rockfish in Saanich Inlet, relative to quillback rockfish in Campbell River (Table 16), may be due to a relatively greater mortality rate for quillback rockfish in Saanich Inlet. This mortality can occur as a result of exploitation by commercial and sports fisheries, or by predation (e.g., marine mammals, piscivorous fishes). Fishing mortality has been directed primarily towards quillback rockfish, which typically comprise 85% of the commercial handline/troll fishery for rockfish and 36% of the rockfish sport catch (Hand and Richards 1991). In Saanich Inlet, the commercial\handline fishery for rockfish between 1954-1985 was low (<10 t) (Hand and Richards 1991). The sport catches for Saanich Inlet and Campbell River prior to 1982 are unknown, although from 1983-1989 the sport catch in Saanich Inlet was equal to, or greater than, the sport catch in the Campbell River area. The commercial handline\troll fishery for rockfish in the Campbell River area, especially for quillback rockfish, began increasing in 1977 and escalated in 1981-1982 (doubled to 106.3 t) (Hand and Richards 1991). Although this is a relatively recent development of an extensive fishery, quillback rockfish stocks in Campbell River have already exhibited signs of exploitation (e.g., decrease in mean size) (Hand and Richards 1991). Increased growth rate (Ricker 1979) and a shifting of the population to a smaller mean size (Hand and Richards 1991) with a truncated age range (Leaman 1991) are common results of fishing mortality.

Moulton (1977) has also indicated that schooling, pelagic species of rockfish have greater rates of growth than solitary, benthic species. He and Barker (1979) have further shown that schooling, pelagic species of rockfish have smaller increases in mass per unit of body length than solitary, benthic rockfish species. Growth coefficients of copper rockfish are generally greater than quillback rockfish (Table 15, 16), although in Saanich Inlet any difference in *K*-values between the species is marginal (Table 14). Copper rockfish in Saanich Inlet, however, have a smaller increase in mass per unit of length compared to quillback rockfish, suggesting that copper rockfish are adapted to a more pelagic lifestyle than quillback rockfish. This was consistent with activity (Chapter II) and feeding (Chapter III) observations.

Analyses of growth patterns of copper and quillback rockfish need to take into account differences between the sexes. Wyllie Echeverria (1986) and Love *et al.* (1990) have observed growth differences between the sexes for various rockfish species, the majority with female rockfish surpassing the asymptotic lengths of their male counterparts (e.g., female *S. elongatus* 7.6 cm longer than males; Love *et al.* 1990). The propensity of female rockfish to attain larger asymptotic lengths is presumably due to the advantages that increased size has for increased fecundity (Chapter VI; Love *et al.* 1990).

Comparative growth studies in Puget Sound and the Strait of Georgia indicate that asymptotic lengths of male and female copper rockfish differ by 6-7.6 cm (Table 15). Asymptotic lengths of male and female quillback rockfish are also known to differ by 2-9 cm, with females attaining larger size than males (Table 16). The sexual monomorphism exhibited by copper and quillback rockfish in Saanich Inlet may be related to increased mortality or low food availability, based on the observation that both species are substantially smaller and have a younger maximum age in Saanich Inlet than in the Strait of Georgia. For example, maximum observed lengths of copper and quillback rockfish in Saanich Inlet were 32-34 cm (Table 14) whereas in the Strait of Georgia this size would represent close to the minimum observed length of rockfish sampled in the commercial fishery (Schnute and Richards 1990), with the mean (rather than the maximum) length of quillback rockfish around 34-35 cm (Hand and Richards 1991). With increased fishing mortality there may be coincident increases in growth rate, earlier maturation, and increased early reproductive effort (Wootton 1990; Leaman 1991). In particular, female rockfish with increased early reproduction would probably have a decreased asymptotic size because rockfish are viviparous and the energetic investment in their developing young (Boehlert and Yoklavich 1984; Boehlert *et al.* 1986) may substantially detract from energy available for growth.

It may also be relevant to consider the growth coefficients by males and females rather than absolute asymptotic sizes (Chen 1971). Based on Barker (1979), Gowan (1983), Love *et al.* (1990), Hand and Richards (1991), and general trends in the present study (Table 14), it was apparent that when any difference existed between the growth coefficients of males and females of each of the species, the growth coefficient tended to be greater for males 78% of the time (*n* = 69 male-female pairs compared). Irrespective of whether or not males obtain a larger asymptotic size than females, they apparently approach their asymptotic lengths relatively faster than females. If the onset of sexual maturity in male rockfishes is attained at a specific size rather than a specific age (Love 1970), then it would be advantageous for males to reach the minimum size at which they can become sexually mature relatively fast, given that they have enough energy to produce gametes once that size has been attained. Indeed in the majority of rockfish species showing differences between the sexes in length at which 50% of them are sexually mature, the difference is due to males maturing at a smaller size than females (Wyllie Echeverria 1987; Love *et al*. 1990).

The observation that rockfishes grow more slowly and to larger sizes, and live to greater ages, in northern waters compared with the same species from southern waters, was equivocal. Studies used in this qualitative analysis were not totally comparable due to different aging methods employed. Nevertheless, where comparisons have been made, 50% showed no latitudinal difference in growth rates (Love *et al*. 1990). Of the 50% of the species which did show differences, the northern group grew faster than the southern group (Love *et al*. 1990), exactly the opposite of that expected. Comparison of the growth of copper and quillback rockfish between Saanich Inlet and Puget Sound also supported this trend, with rockfish from Saanich Inlet having growth coefficients equal to, or greater than, rockfish from Puget Sound (Table 15, 16). The asymptotic lengths that copper and quillback rockfish attained in Saanich Inlet, however, were much smaller than those attained by copper and quillback rockfish in Puget Sound (Table 15, 16). Again, the observed differences may be due to differences in rockfish mortality between Puget Sound and Saanich Inlet.

Ultimately, it would be preferable to compare life-history parameters of copper and quillback rockfish, as well as other rockfish species, from southern and northern waters in which extrinsic factors could be taken into account. For example, differences in fishing pressure or food availability among different geographical areas significantly affect the population structure and the parameters of a growth model (Ricker 1975; Archibald *et al.* 1981; Leaman 1991). Since the majority of rockfish species are now exploited in either sport or commercial fisheries (Love *et al.* 1990), however, it will become increasingly difficult to study natural trends in the life-history variations within this genus.

SUMMARY

In general, copper and quillback rockfish in Saanich Inlet had similar growth patterns with no readily identifiable species-specific and sex-specific differences. Both sexes of both species attained asymptotic lengths at 30-31 cm total length and had similar growth coefficients (0.141-0.187). Within each sex, quillback rockfish had a greater increase in mass per unit of body length than copper rockfish, indicative of the more sedentary lifestyle of quillback rockfish.

CHAPTER VI

COMPARATIVE REPRODUCTIVE BIOLOGY OF COPPER AND QUILLBACK ROCKFISH

INTRODUCTION

Rockfish are viviparous: they retain their eggs within the ovaries after internal fertilization and give birth to live young (DeLacy *et al*. 1964; Moser 1967; Chen 1971). Maternal contribution to the nourishment of developing young is derived either from yolk reserves (lecithotrophy, as in *S. marinus*) (Wourms *et al*. 1988) or from postzygotic nutrition through modification of the hind-gut of the embryos (trophodermy, as in *S. caurinus*, *S. melanops*, and *S. schlegeli*, Boehlert and Yoklavich 1984; Boehlert *et al*. 1986). The mode of maternal nourishment in *S. maliger* is presently unknown.

The majority of *Sebastes* give birth to their young in either winter or spring-summer (Phillips 1964). The reproductive cycle of males differs temporally from the cycle of females, with the testes of males maturing months earlier than the gonads of females. Copulation occurs before the females have completed vitellogenesis and females store the sperm until ovulation (DeLacy *et al*. 1964; Moser 1967; Wyllie Echeverria 1987). The overall reproductive cycle therefore consists of three primary phases that are temporally demarcated: insemination, fertilization, and parturition. The timing of this reproductive cycle is known to vary markedly among rockfish species, as well as within a species from different geographical locations (DeLacy *et al.* 1964; Westrheim 1975; Wyllie Echeverria 1987).

The size (or age) of sexual maturity and fecundity also varies considerably within the genus *Sebastes* but, overall, rockfish mature at a relatively old age and large size, and have relatively high fecundity for a viviparous fish (Wyllie Echeverria 1987; Love *et al.* 1990). Ultimately, maturity is related to the growth of the fish, which in turn may be influenced by environmental conditions (e.g., temperature) (Ricker 1979), food availability (Peter 1979; Love 1980), resource competition, predation, or fishing pressure (Ricker 1979), and genetic constraints (Westrheim 1975; Stearns and Crandall 1984). Within a rockfish species, the size (or age) of maturity and fecundity may therefore differ geographically (e.g., localized areas) (Wyllie Echeverria 1987), latitudinally (Westrheim 1975), bathymetrically (Westrheim 1975), or annually within a localized area (Wyllie Echeverria 1987).

Coincident with changes in the stages of reproduction of many fishes is a complementary cycle of lipid reserves, suggesting that fish use the lipid stores in reproduction (Hoar 1957; Roberts 1979; Love 1980). Alternatively, fish use lipid reserves for body maintenance during periods of food scarcity, and for concurrent maintenance and reproduction (Shul'man 1974; Peter 1979; Wootton 1985). In fishes, lipid reserves obtained during periods of the year when food is abundant or rich in energy are stored primarily in muscle, liver, or depots surrounding the viscera (Ince and Thorpe 1976; Brett and Groves 1979; Cowey and Sargent 1979; Peter 1979; Love 1980; Wootton 1985). The fat from these depots may be mobilized during maturation of the gonads and either transported to the developing eggs or used directly as an energy source (Love 1980; Wootton 1985). Ultimately, the quantity of fat reserves may determine the success of reproduction either directly, through influencing the size or age of sexual maturity, the fecundity, or the yolk contribution to the eggs, or indirectly, by allowing the fish to live through periods of food scarcity and hence reproduce in the future (Love 1980).

For rockfish, Roberts (1979), Guillemot *et al.* (1985), and Lenarz and Wyllie Echeverria (1986) suggested that the cycle of visceral fat deposition and utilization was related primarily to the abundance of food and to a lesser extent reproduction. In the majority of the species studied (5 of 7), however, the relationships among visceral fat reserves, reproduction, and food availability were variable in both timing and quantity in fish of different sex and maturity (Guillemot *et al.* 1985). In addition, the three available studies on visceral fat cycles in rockfish have been carried out in California, and two of the three studies involved offshore rockfish species (Guillemot *et al.* 1985; Lenarz and Wyllie Echeverria 1986). To date, the relationship between reproduction, visceral fat reserves, and periods of feeding have not been elucidated for any rockfish in waters north of California, and have not included benthic inshore rockfish, such as copper and quillback rockfish.

The objectives of this study were: 1) to compare the timing of the reproductive cycles between female and male copper and quillback rockfish; 2) to compare size and age at maturity between the sexes and species; 3) to determine the fecundity of the two species; 4) to examine the relationship between the mass of the gonads in relation to fish size, and the temporal synchronicity of gonad production by females and males; and 5) to relate visceral lipid reserves to the seasonal development of the gonads and periods of feeding (Chapter III).

METHODS

Copper and quillback rockfish analysed for reproductive characteristics and fat reserves were collected and processed in conjunction with a study of their feeding ecology (Chapter III) and gut allometries (Chapter IV). Total length, mass, and sex of each fish were determined. In addition, wet mass of the gonads (pair) was obtained for each fish. Fat removed from the viscera (Chapter III) was dissected over ice to prevent liquefaction at room temperature and its wet weight was determined. Body mass used was total mass less gonadal mass (Erickson *et al.* 1985), mass of stomach contents, and visceral fat.

Maturity

Gonads of male and female copper and quillback rockfish were classified to their stage of maturity according to the criteria of Moser (1967), Gunderson (1971), Westrheim (1975), and Wyllie Echeverria (1987), with modifications based on personal observations (Tables 17, 18).

Gonads for females and males in stages 1 and 2 were classified as immature, and in stages 3 to 7 as mature (Tables 17, 18). Length at maturity was then estimated by plotting the percentage of mature fish for each 5-mm length category. Lengths at which fish first attained maturity, and at which 50% and 100% of the fish were mature, were estimated directly from the maturity graphs.

Fecundity

For female rockfish in maturity stages 4 and 5 (fertilized ova or eyed-larvae), one gonad of each pair was fixed in Bouin's solution and then transferred to 70% ethanol for storage. The ovarian membrane of the preserved

Table 17. Description of maturity stages of female copper and quillback rockfish based on external morphology of the ovaries.

Maturity		Description
Code	Stage	
1	Immature	Small, string-like, translucent pink.
2	Maturing	Small, sac-like, opaque or translucent yellow with small ova (<0.2 mm diameter), ovarian wall thin.
3	Mature	Large, orange-yellow, opaque, ova $\geq$ 0.2 mm diameter, ovary firm and ovarian wall noticeably thicker than in stages 1 and 2.
4	Fertilized	Large, yellow-orange, translucent, ovary not firm.
5	Gravid	Large, translucent, yellow-grey to dark green-grey, eyed embryos or larvae visible, ovary soft, ovarian wall fragile and easily broken.
6	Spent	Large, flaccid, grey-red, may have a few retained larvae visible, ovarian wall thick and tough.
7	Resting	Ovary relatively small, firm, pink-grey, a few black spots within the ovary (from resorped larvae), ovarian wall thick.

Table 18. Description of maturity stages of male copper and quillback rockfish based on external morphology of the testes.

Maturity		Description
Code	Stage	
1	Immature	Small, string-like, translucent, tan.
2	Maturing	Small, ribbon-like, translucent tan-white, translucent sperm ducts.
3	Mature	Ribbon-like, white-tan, opaque, large sperm ducts.
4	Swollen	Large and swollen, rounded in cross-section, white, opaque, fragile, maximal spermatogenesis, spermatozoa present throughout testes.
5	Ripe	Testes not as obviously swollen and rounded as stage 4 testes, cream or tan and periphery of testes darker, spermatozoa visibly pooled into sperm ducts, firm.
6	Spent	Tan, sperm ducts without spermatozoa or spermatozoa only in posterior portion of median sperm duct, testes triangular in cross-section, firm.
7	Resting	Ribbon-like, dark tan-brown, tough and rubbery, sperm ducts narrow (collapsed).

gonad was removed and the eggs or larvae were loosened from the ovarian and connective tissues. The fertilized eggs or larvae were then sieved and washed to remove any remaining debris, and gravity filtered to remove excess water. The total mass of eggs or larvae was then weighed and three subsamples were taken and individually weighed. Eggs or larvae in each subsample were counted and the number of eggs or larvae per gram of subsample was calculated. Mean number of eggs or larvae per gram of subsamples (n = 3) was then multiplied by the total mass of the eggs or larvae and doubled to account for the second gonad of the pair.

The relationship between fecundity (F) and total length (L) in female copper and quillback rockfish was examined using the power function (Wootton 1979; Love *et al.* 1990; DeMartini 1991):

$$[7] \qquad F = a \cdot L^b$$

where a and b were the intercept and slope, respectively, of the least-squares regression on the $\log_{10}$ transformed data.

Reproductive Cycle

Seasonal timing of reproduction in female and male rockfish was examined by calculating the percentage of mature fish that occurred in each of maturation stages 3 through 7 for each month sampled, with years pooled for adequate sample size.

In addition, reproductive timing and gonadal condition were examined using monthly changes in gonad mass. Gonad mass was indexed using the Relative Gonadal Index (RGI) (Erickson *et al.* 1985):

$$\text{[8]} \qquad \text{RGI} = \frac{\text{G}}{\text{M}^b}$$

where G was the mass of the gonads (g), M was body mass (g), and *b* was the exponent of the power function:

$$\text{[9]} \qquad \text{G} = a \cdot \text{M}^b$$

equivalent to the $\log_{10}$ transformed model:

$$\text{[10]} \qquad \log \text{G} = \log a + b \cdot \log \text{M}$$

where *b* was the slope of the $\log_{10}$ transformed model for gonadal stage *i*, and log *a* was the intercept of the $\log_{10}$ transformed model for gonadal stage *i*. RGI was used rather than the more common gonadosomatic index (GSI = G/M·100%) because RGI corrects for body mass when the slope (*b*) of the $\log_{10}$ transformed gonad to body mass equation differs significantly from unity, indicative of an allometric rather than an isometric relationship between gonad mass and body mass (Erickson *et al.* 1985).

The RGI was valid to use only when the slopes among gonadal stages were not significantly different from one another (Erickson *et al.* 1985). Initially, therefore, differences in slopes among gonadal stages were assessed using ANCOVAs. When these slopes were not significantly different, then the RGI was calculated using the pooled regression coefficient (*b*). When slopes among gonadal stages were significantly different, comparisons were restricted to evaluating the estimated parameters of the least-squares regression of the $\log_{10}$ transformed model (Erickson *et al.* 1985; Cone 1989).

Visceral Fat Reserves

In a similar manner to the RGI, a relative fat index (RFI) was developed to examine the changes in visceral fat mass between mature and immature rockfish, males and females, and seasons:

$$[11] \qquad RFI = \frac{F}{M^{b}}$$

where F was the visceral fat mass (g), M was body mass (g), and b was the slope of the $\log_{10}$ transformed equation for visceral fat mass as a function of body mass for each gonadal stage. Differences in slopes and intercepts for the regressions were tested using ANCOVAs under the same conditions as for the RGI.

RESULTS

Maturity

All female copper rockfish <195 mm total length were immature (stage 1 or 2) (Fig. 24). The size interval at which 50% of the collected female copper rockfish were mature was between 215 and 235 mm total length. All female copper rockfish were mature when >260 mm in length.

Female quillback rockfish <205 mm total length were all immature (Fig. 24). Fifty percent of female quillback rockfish were mature when ≥240 mm, and all were mature when greater than 265 mm in length.

Male copper rockfish matured when as small as 145 mm total length (12%), but the majority of males <175 mm were immature (Fig. 25). Fifty percent of male copper rockfish reached sexual maturity between 190 and 210 mm total length, and 100% of males were mature when >260 mm in length.

All male quillback rockfish ≤185 mm in total length were immature (Fig. 25). Males reached 50% maturity between 190 and 250 mm in length. All male quillback rockfish >260 mm in length were mature.

Estimated lengths of first and 100% maturity for female and male copper and quillback rockfish were therefore similar, with the possible exception of some male copper rockfish that were able to attain sexual maturity at a relatively small size (Fig. 24, 25).

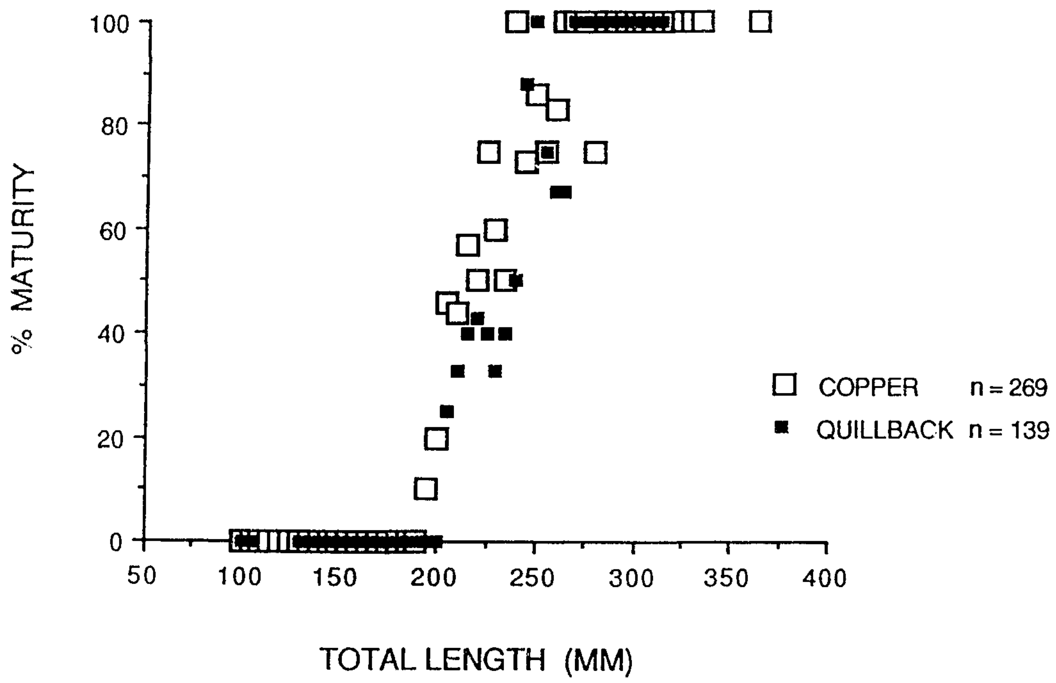

Fig. 24. Relationship between length (5-mm categories) and percent of fish that were mature for female copper and quillback rockfish.

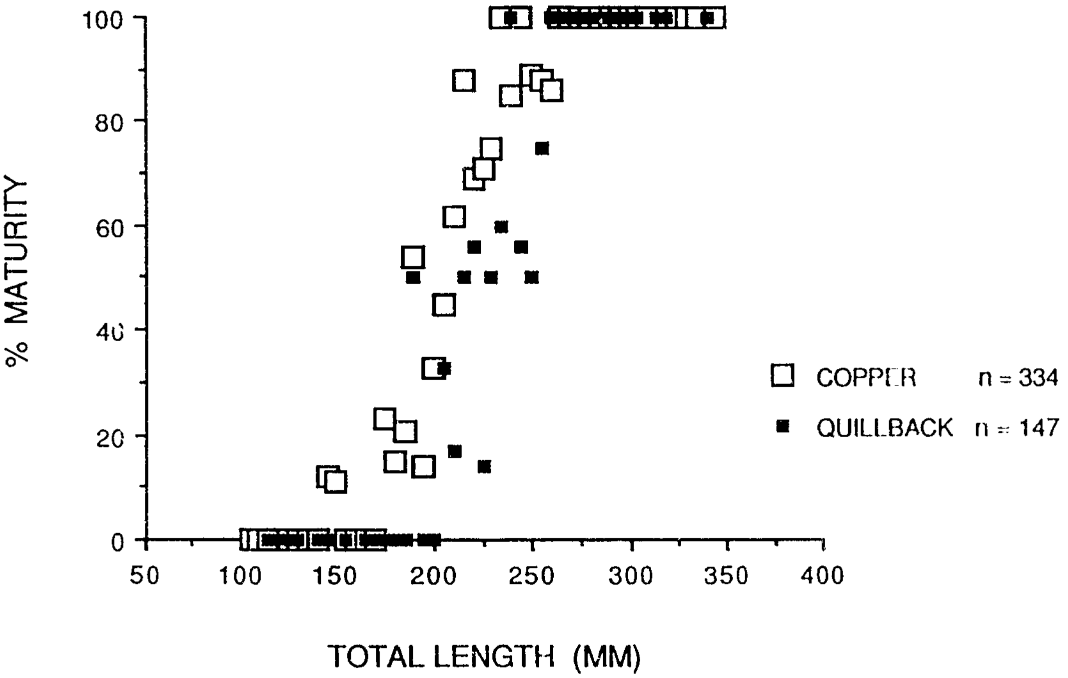

Fig. 25. Relationship between length (5-mm categories) and percent of fish that were mature for male copper and quillback rockfish.

Fecundity

The slope for the relationship between fecundity and total length was not significantly different between copper and quillback rockfish (ANCOVA: $F_{1,21} = 0.28$, $P = 0.60$). Although adjusted means between copper and quillback rockfish were also not statistically significant ($F_{1,21} = 3.64$, $P = 0.07$) (Fig. 26), copper rockfish tended to have slightly lower fecundity compared with similar-sized quillback rockfish. Minimum observed fecundities were 11,600 and 19,000 eggs, and maximum fecundities were 103,000 and 143,000 eggs, for copper and quillback rockfish respectively.

Timing of the Reproductive Cycle

Females

Most sexually mature female copper rockfish (57%) had ovaries with eggs in a mature stage by December, with >90% in a stage 3 of maturity in January, February, and March (Fig. 27a). By April, 50% of the females had fertilized eggs. The majority of females had eyed-larvae present one month later in May, and by June, over 50% of the females had given birth. Gonads of females were in a spent or resting stage from July to November.

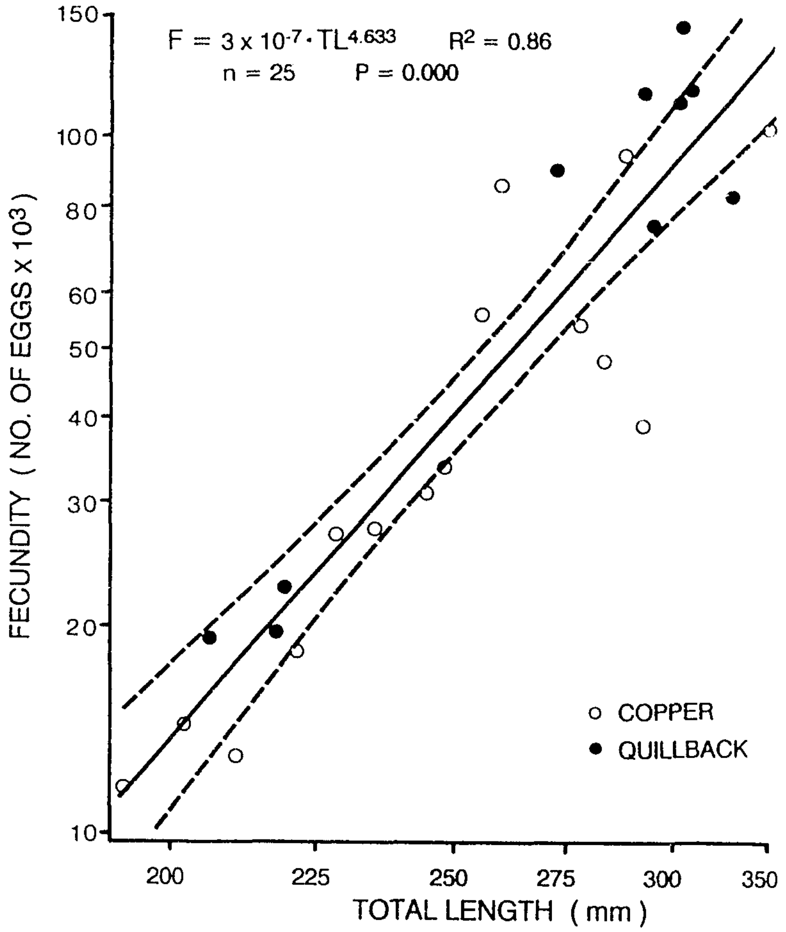

Fig. 26. Relationship between fecundity and female body mass for copper and quillback rockfish. Dashed curves represent 95% confidence limits around the regression.

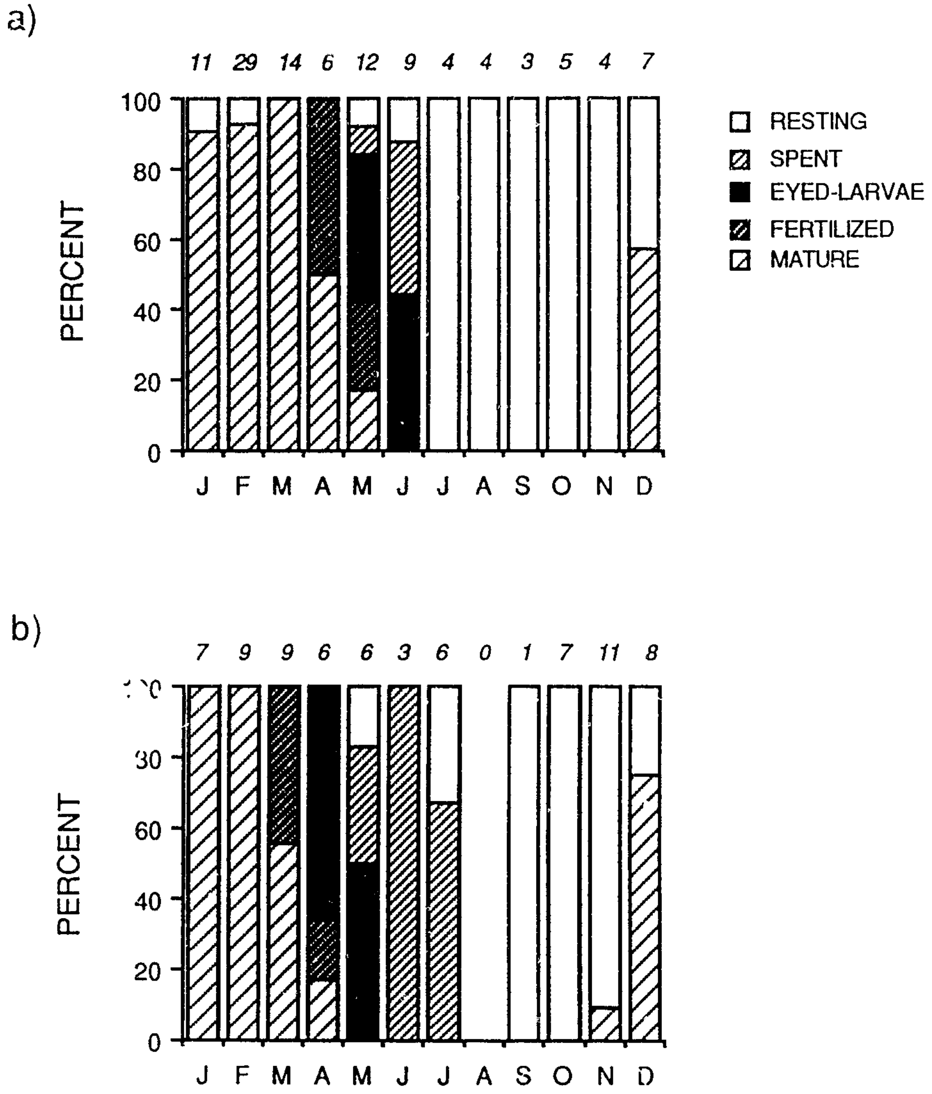

Fig. 27. Monthly percentages of a) female copper rockfish and b) female quillback rockfish in maturity stages 3 (mature), 4 (fertilized), 5 (eyed-larvae), 6 (spent), and 7 (resting). Sample sizes are given in italics.

Maturation of the ovaries in female quillback rockfish (stage 3) was one month earlier than in female copper rockfish (Fig. 27b). A few female quillback rockfish (9%) had ovaries with mature eggs as early as November, although the majority were in stage 3 of maturation during December, January, and February (Fig. 27b). By March, however, a large proportion (44%) of quillback rockfish had fertilized eggs, and by April the majority had eyed-larvae. In May, 50% of females had spent or resting ovaries, indicating that they had already given birth to their young. Female quillback rockfish spent June to November recovering from parturition.

Males

Male copper rockfish had testes in a mature stage as early as July, with the majority of males with swollen testes (stage 4) in November and December (Fig. 28a). Testes of copper rockfish were typically ripe in January and February, and to a lesser extent in March, indicating a relatively prolonged reproductive season in males. A few males had ripe testes as late as April and May. Spent (stage 6) males were collected as early as February, and the majority of copper rockfish had spent testes by April. Male copper rockfish collected from April to August had testes primarily in spent or resting stages.

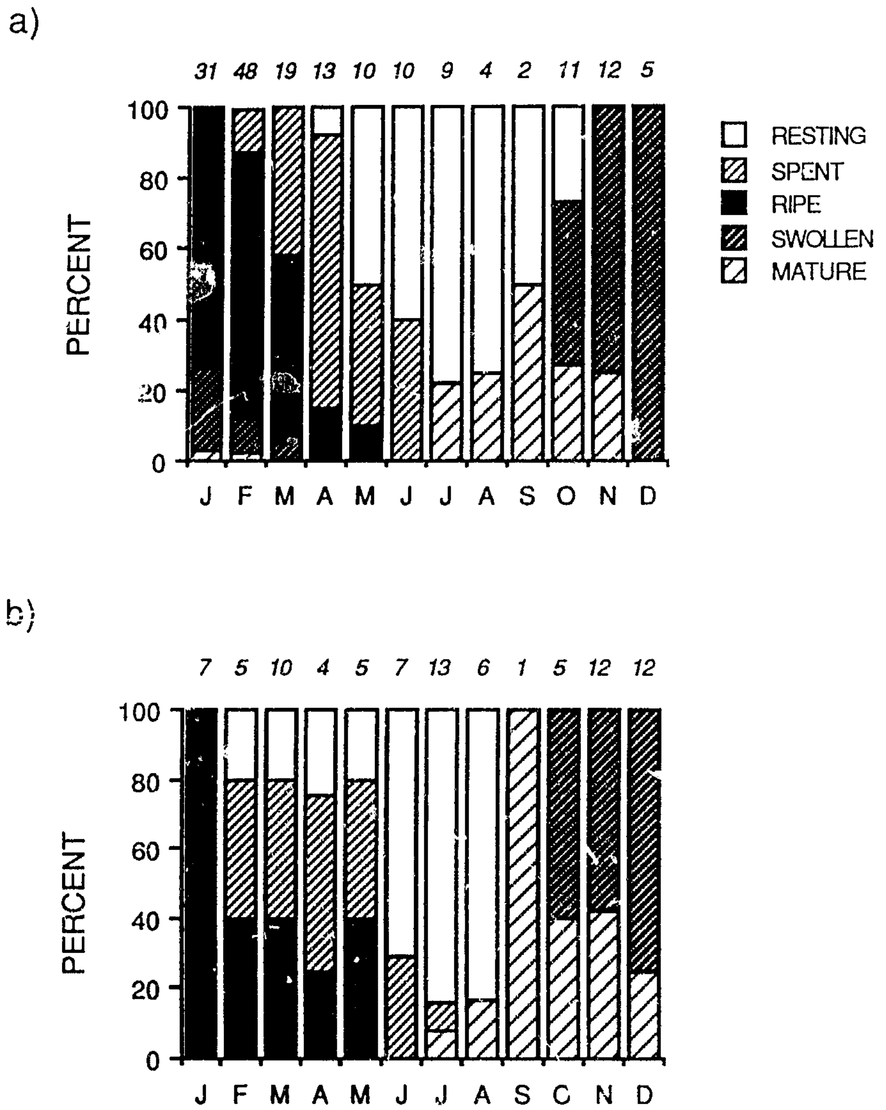

Fig. 28. Monthly percentages of a) male copper rockfish and b) male quillback rockfish in maturity stages 3 (mature), 4 (swollen), 5 (ripe), 6 (spent), and 7 (resting). Sample sizes are given in italics.

Paralleling the reproductive cycle of female quillback rockfish, the cycle of male quillback rockfish also appeared to precede the cycle of male copper rockfish by at least one month (Fig. 28b). Mature male quillback rockfish had testes in a mature stage as early as July and the majority of males with swollen testes (stage 4) were collected in December (Fig. 28b). Unlike copper rockfish, there were no males in stage 4 of maturity collected in January; instead, all males were ripe (stage 5). In addition, 25-40% of males were ripe throughout the period of February to May, again indicating a potentially protracted reproductive season in males. By February, however, the majority of male quillback rockfish collected had spent or resting testes. The majority of male quillback rockfish collected from February to August had testes in either a spent or resting stage.

Gonadal Condition

Females

Slopes (*b*) for the regressions of gonad mass on body mass for female copper and quillback rockfish for each of the gonad maturity stages were not significantly different (ANCOVA: F = 0.60, *P* = 0.82) (Table 19). The pooled regression coefficient ($b = 1.687 \pm 0.056$ (SE), $n = 12$) was different greater than one (*t*-test: $t = 12.26$, DF = 386, $P < 0.001$), however, indicating that the percentage of gonad

Table 19. Least-squares regression parameters for gonad mass($\log_{10}$) versus body mass($\log_{10}$) for female copper and female quillback rockfish in each maturity stage.

Species	Maturity Stage	*n*	Intercept		Slope		r^2	*P*
			Estimate	SE	Estimate	SE		
Copper	1	144	-4.203	0.249	1.687	0.079	0.76	0.00
	3	60	-3.468	0.325	1.709	0.261	0.42	0.00
	4	6	-3.080	0.157	1.928	0.388	0.86	0.01
	5	9	-2.615	0.169	1.793	0.313	0.82	0.00
	6	5	-3.725	0.129	1.774	0.604	0.74	0.01
	7	28	-3.200	0.161	1.315	0.137	0.78	0.00
Quillback	1	65	-4.321	0.211	1.667	0.105	0.80	0.00
	3	27	-4.173	0.290	1.994	0.383	0.52	0.00
	4	5	-2.344	0.083	1.604	0.217	0.95	0.01
	5	7	-3.289	0.150	2.044	0.268	0.92	0.00
	6	9	-4.643	0.227	1.943	0.472	0.71	0.01
	7	23	-5.750	0.144	2.300	0.304	0.73	0.00

mass to body mass increased as female body mass increased. The pooled regression coefficient was used to calculate RGI values for all females.

For female copper rockfish, RGI's for females with mature ovaries (stage 3) increased from December to March and did not reach a maximum until April (Fig. 29a). The maximum RGI for stage 3 females corresponded to the appearance of females with fertilized eggs (Fig. 27a). Females carrying eyed-larvae reached a maximum RGI two months later in June (Fig. 29a), the primary month of parturition for copper rockfish (Fig. 27a). Females with spent or resting ovaries had low RGI's over the period of May to February (Fig. 29a). Values for RGIs were also consistently low for immature female copper rockfish over all months of the year (RGI = 0.073 ± 0.004, *n* = 144).

Similarly, the majority of mature, female quillback rockfish collected in January and February had stage 3 ovaries (Fig. 27b), although RGI's for these females did not peak until February and March, again coincident with the occurrence of females with fertilized eggs (Fig. 29b). RGI values for females with stage 5 ovaries (eyed-larvae) reached a maximum two months later in May (Fig. 29b), the primary month of parturition for quillback rockfish (Fig. 27b). As with copper rockfish, RGI values for spent and resting female quillback rockfish were low over all months sampled (Fig. 29b). In addition, RGI values were

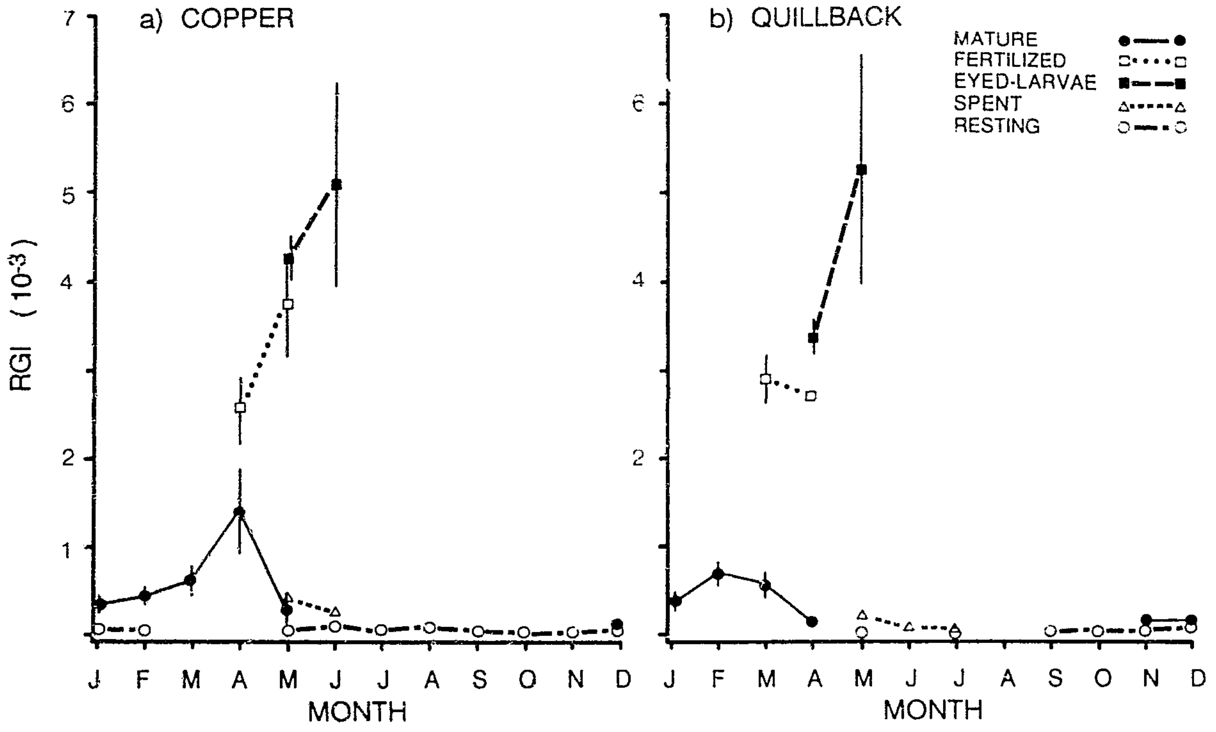

Fig. 29. Monthly changes in the mean (± 1SE) Relative Gonadal Index (RGI) for a) mature female copper rockfish and b) mature female quillback rockfish.

consistently low for immature female quillback rockfish throughout the year (RGI = 0.050 ± 0.004, $n = 65$).

Overall, the allocation to gonad mass, relative to body mass, was similar between female copper and female quillback rockfish for maturity stages 3, 4, 5, and 7 (ANCOVA's: $F_{1,83} = 0.01$ and $P = 0.93$, $F_{1,7} = 0.24$ and $P = 0.63$, $F_{1,12} = 0.60$ and $P = 0.45$, $F_{1,47} = 0.40$ and $P = 0.53$ respectively) (Fig. 30). Gonad masses were highest in females with stage 5 (eyed-larvae) and stage 4 (fertilized) ovaries. Ovaries in this stage of maturity represented up to 48% of the gonadectomized body mass of individual females. Female copper rockfish had a greater gonad mass, relative to body mass, than female quillback rockfish when immature or spent (ANCOVA's: $F_{1,205} = 18.44$ and $P = 0.00$, $F_{1,10} = 16.73$ and $P = 0.00$ respectively) (Fig. 30).

Males

Slopes for the regressions of gonad mass as a function of body mass for male copper and male quillback rockfish for each of the gonad maturity stages were significantly different (ANCOVA: F = 2.22, $P = 0.01$) (Fig. 31, Table 20); hence RGI values could not be calculated based on a pooled regression coefficient (*b*) for both species combined.

Within male copper rockfish, the slopes of the regressions of gonad mass as a function of body mass for each of the gonad maturity stages were different due to the

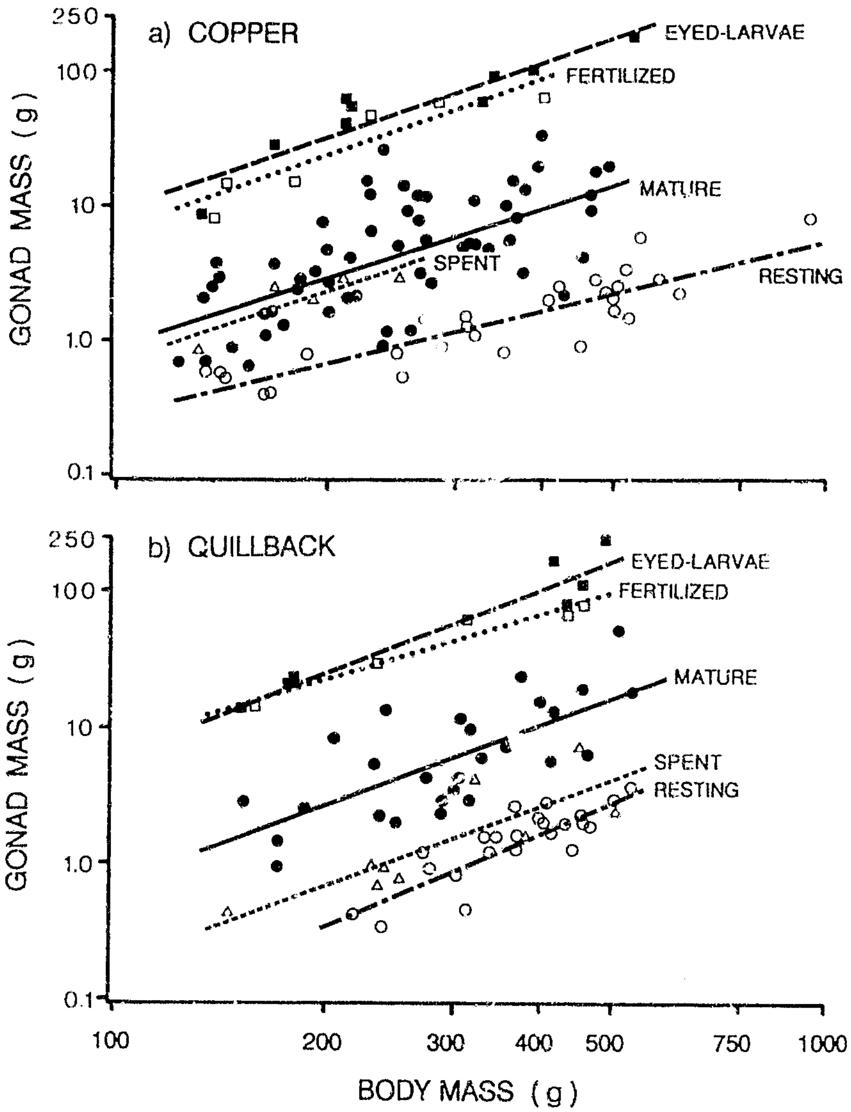

Fig. 30. Relationship between mass of ovaries and body mass for a) female copper rockfish and b) female quillback rockfish, for females in maturity stages 3 through 7. Parameters for all regressions are given in Table 19.

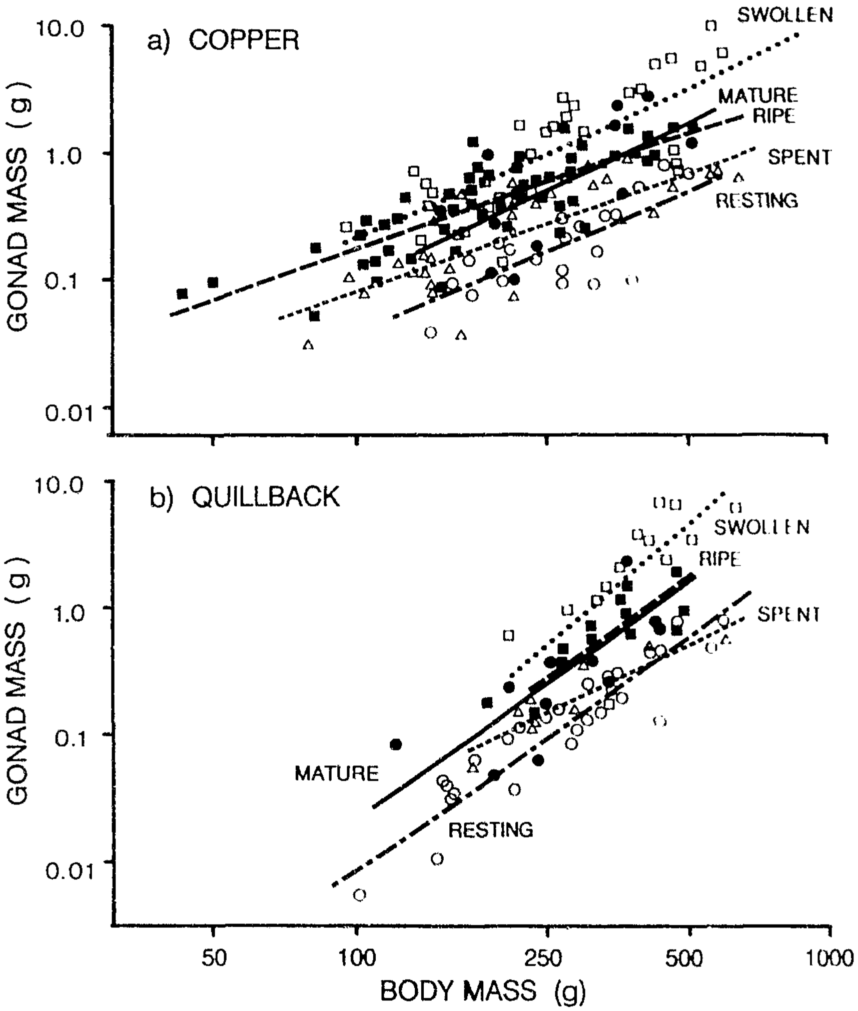

Fig. 31. Relationship between mass of testes and body mass for a) male copper rockfish and b) male quillback rockfish, for maturity stages 3 through 7. Parameters for all regressions are given in Table 20.

Table 20. Least-squares regression parameters for gonad mass($\log_{10}$) versus body mass($\log_{10}$) for male copper and male quillback rockfish in each maturity stage.

Species	Maturity Stage	*n*	Intercept		Slope		r^2	*P*
			Estimate	SE	Estimate	SE		
Copper	1	132	-5.544	0.366	2.101	0.130	0.67	0.00
	3	12	-4.494	0.402	1.738	0.636	0.43	0.02
	4	32	-4.193	0.309	1.736	0.248	0.62	0.00
	5	71	-3.443	0.204	1.332	0.108	0.69	0.00
	6	31	-3.766	0.255	1.331	0.193	0.62	0.00
	7	25	-4.589	0.227	1.578	0.310	0.53	0.00
Quillback	1	56	-4.880	0.335	1.594	0.150	0.68	0.00
	3	13	-6.410	0.354	2.391	0.604	0.59	0.00
	4	19	-7.716	0.321	3.074	0.671	0.55	0.00
	5	16	-6.849	0.232	2.616	0.656	0.53	0.00
	6	13	-5.127	0.124	1.783	0.228	0.85	0.00
	7	26	-6.921	0.194	2.443	0.201	0.86	0.00

inclusion of immature (stage 1 and 2) fish (ANCOVA: $F_{1,295}$ = 17.54, P = 0.00). When the data for immature males were deleted the heterogeneity of slopes within male copper rockfish was nonsignificant (ANCOVA: $F_{4,161}$ = 0.94, P = 0.44) (Fig. 31a). Within mature, male copper rockfish then, a pooled regression coefficient (b = 1.450) was used to calculate RGI values. This pooled regression coefficient was significantly different from unity (t-test: t = 4.94, DF = 169, $P < 0.001$), indicating that the relationship of gonad mass to body mass was allometric in male copper rockfish.

Similarly, within male quillback rockfish, the slopes of the regressions of gonad mass on body mass for each of the gonad stages were different (ANCOVA: $F_{5,133}$ = 9.56, P = 0.00), again due to the inclusion of immature males. With the exclusion of immature fish, the slopes for the regressions for mature males were not different (ANCOVA: $F_{4,77}$ = 0.86, P = 0.49) (Fig. 31b). Within mature male quillback rockfish, therefore, a pooled regression coefficient (b = 2.419) was used to calculate RGI values. As with male copper rockfish, the pooled regression coefficient for mature male quillback rockfish was significantly different than one (t-test: t = 7.77, DF = 85, $P < 0.001$).

For mature, male copper rockfish, RGI values for stage 3 (mature) testes peaked in October and November (Fig. 32), in tandem with the first occurrence of males in stage 4

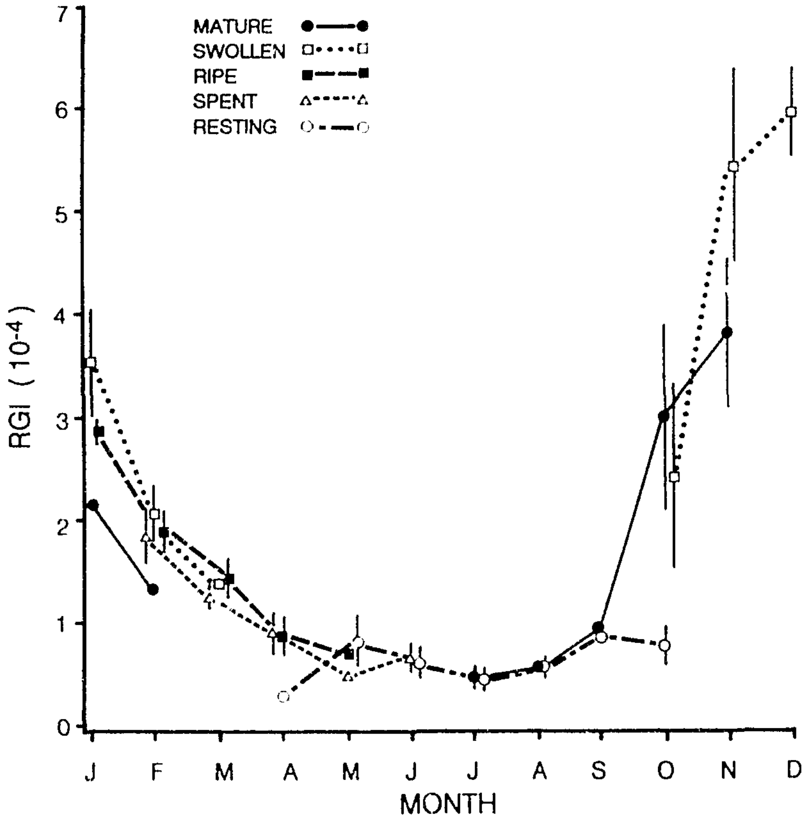

Fig. 32. Monthly changes in the mean (± 1SE) Relative Gonadal Index (RGI) for mature male copper rockfish.

maturity. Males with swollen testes undergoing maximum spermatogenesis (stage 4) reached maximum RGI values in November and December. Males in stage 4 gonadal condition had the highest RGI values of male copper rockfish sampled. RGI values for stage 4 males decreased in January and February, indicative of the decrease in spermatogenesis and the transition to a ripe condition. Males in a ripe condition were present throughout January, February, and March (Fig. 28a), suggesting the potential at this time for insemination. They had maximum RGI values in January, however, with RGI's decreasing in the following months. Male copper rockfish with spent and resting testes had relatively low RGI values throughout February to October.

For mature, male quillback rockfish, testes in stage 3 condition (mature) also reached maximal RGI values in October and November, and this corresponded to the occurrence of stage 4 males (Fig. 33). RGI values of stage 4 testes (swollen) peaked in November, with a slight decrease occurring as early as December, indicative of a shift to the ripe condition. As with male copper rockfish, male quillback rockfish in stage 4 of maturity had the highest RGI values of male quillback rockfish sampled. In January, all males collected were in a ripe condition; none were found with testes still undergoing spermatogenesis (Fig. 28b). RGI values for stage 5 (ripe) males were at a maximum in January, indicating that males could potentially

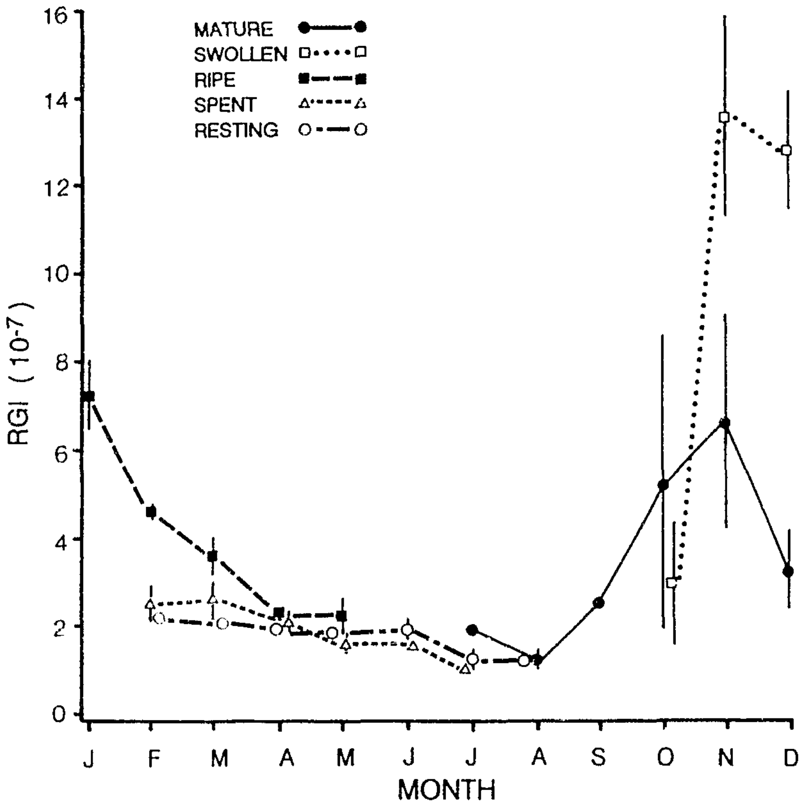

Fig. 33. Monthly changes in the mean (± 1SE) Relative Gonadal Index (RGI) for mature male quillback rockfish.

inseminate females at this time. As with male copper rockfish, RGI values for spent and resting male quillback rockfish were consistently low over the months sampled.

Due to the heterogeneity of slopes among at least some of the regressions of gonad mass on body mass for males in different stages of maturity, separate ANCOVAs were used to compare the mass of the gonads between male copper rockfish and male quillback rockfish for each maturity stage. The regressions for gonad mass as a function of body mass for males with mature (stage 3) or swollen (stage 4) testes did not differ significantly between copper and quillback rockfish and had similar slopes between species ($F_{1,20}$ = 0.88 and P = 0.36, $F_{1,47}$ = 3.63 and P = 0.06, for mature and swollen testes respectively) and similar adjusted means between species (F = 3.65, 0.82; P = 0.07, 0.37 respectively) (Fig. 31). For immature and spent males, slopes for the gonad mass to body mass relationships between the two species were homogeneous ($F_{1,178}$ = 1.93 and P 0.1[illegible] $F_{1,40}$ = 1.00 and P = 0.32, for copper rockfish and quillback rockfish respectively). For both immature and spent males between species, however, the adjusted means were different (F = 41.39, 9.49; P = 0.00, 0.00 respectively) and for both maturity stages, copper rockfish had larger testes relative to body mass than quillback rockfish (Fig. 31). In addition, the gonad mass to body mass regressions between species with testes in ripe or resting stages differed significantly in slopes ($F_{1,84}$ = 4.25 and P = 0.04, $F_{1,47}$ = 5.73 and P = 0.02, for ripe and resting testes respectively). Although male quillback rockfish had the greater rate of increase in the mass of ripe or resting testes with body size (i.e., greater slopes), male copper rockfish in a ripe or resting condition still had larger gonads than male quillback rockfish over the majority of sizes of male fish sampled (Fig. 31).

In general, there was a trend for male quillback rockfish to increase the mass of the testes at a greater rate relative to body mass than male copper rockfish, as reflected in the pooled regression coefficients for each species (b = 2.419 and 1.450 for quillback and copper rockfish respectively). Male copper rockfish, however, had greater testicular mass for any given body size for the majority of maturity stages (Fig. 31).

Visceral Fat Reserves

Mature Females

Slopes for the regressions of visceral fat mass against body mass for mature female copper and quillback rockfish for gonad maturity stages 3 through 7 were homogeneous (ANCOVA: $F_{7,160}$ = 0.42, P = 0.89) and the pooled regression coefficient (b = 1.363) was therefore used to calculate RFI values for mature females. The pooled regression coefficient was significantly different from one (*t*-test: $t = 2.94$, DF = 174, $P < 0.01$), indicating that the relationship between fat mass and body mass in females was allometric.

Values for RFIs for mature female copper rockfish consistently indicated that females in maturity stages 3 (mature) and 7 (resting) had higher fat indices than females in maturity stages 4, 5, and 6 (fertilized through to spent) (Fig. 34a). RFI values were high in stage 3 females in January, February, and March, and did not decrease until April, coincident with the occurrence of females with fertilized eggs (Fig. 34a). RFIs remained low for females during April to June, corresponding to events of fertilization, development of eyed-larvae, and parturition. With the onset of the resting stage in females, the RFI values increased, fluctuating at intermediate levels throughout July to December (Fig. 34a).

On a seasonal basis, regressions for fat mass versus body mass among seasons within mature female copper rockfish had similar slopes but significantly different adjusted means (Table 21). Mature female copper rockfish were fatter, relative to body mass, in winter (January to March) than in summer and fall (July to December), and fatter in the summer and fall compared with the spring (April to June) (Table 21).

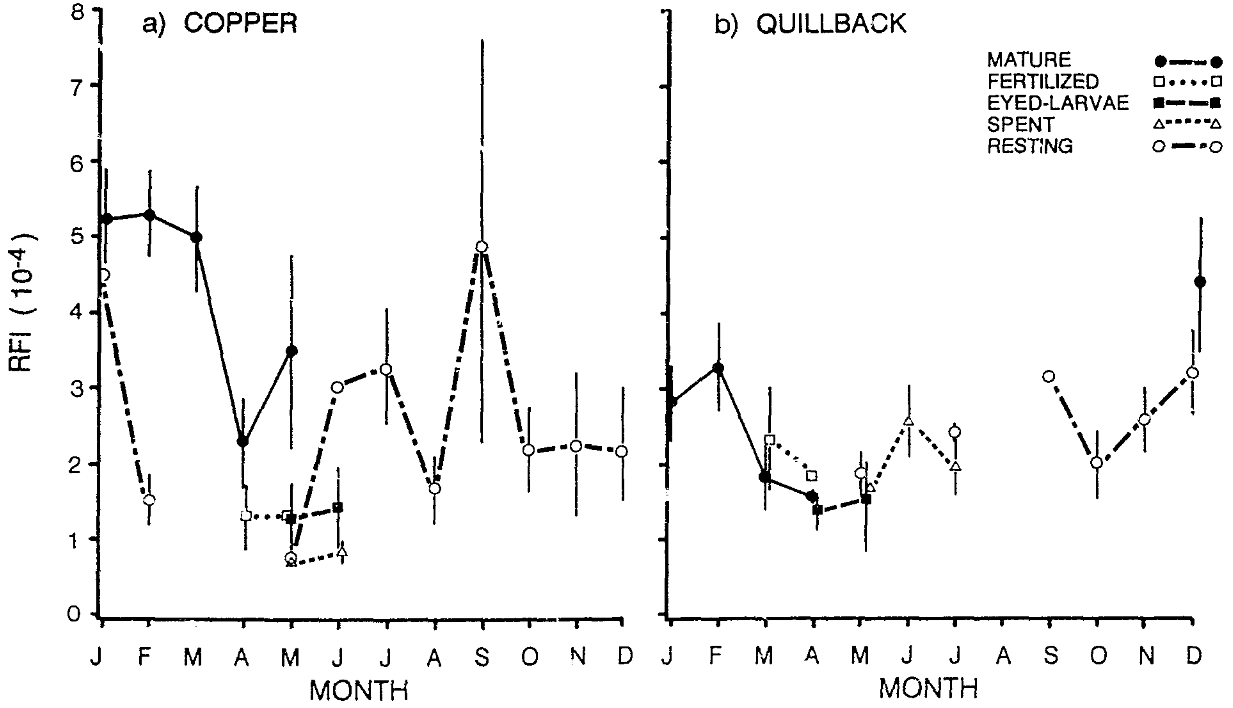

Fig. 34. Monthly changes in the mean (± 1SE) Relative Fat Index (RFI) for a) mature female copper rockfish and b) mature female quillback rockfish.

Table 21. Summary statistics for ANCOVAs for seasonal differences in fat mass–body mass relationships for mature female and mature male copper and quillback rockfish. Horizontal lines between seasons indicate that the seasons did not differ significantly ($P \leq 0.05$). (W = winter; SP = spring; SU = summer; and F = fall).

		Equality of Slopes		Slope Contrasts	Equality of Adjusted Means		Intercept Contrasts[a]
Species	Sex	F	*P*	High to Low	F	*P*	High to Low
Copper	Female	1.05	0.38	W SP SU F	28.95	0.00	W SU F SP
Quillback	Female	1.23	0.31	W SP SU F	2.49	0.07	F W SU SP
Copper	Male	0.96	0.41	W SP SU F	16.56	0.00	F W SU SP
Quillback	Male	0.13	0.94	W SP SU F	3.74	0.01	F SU SP W

[a] Contrasts were based on a *t*-test matrix for adjusted group means from the ANCOVA.

The relationship between RFI and maturity stage in mature female quillback rockfish was not as marked as in mature female copper rockfish. In quillback rockfish, RFIs for stage 3, 4, 6, and 7 females were higher than for stage 5 females (Fig. 34b), but the amplitude of the differences was much smaller than for female copper rockfish. Mature female quillback rockfish in stage 3 of maturity had relatively high RFI indices from December to February. RFI values decreased in March, coincident with the occurrence of females with fertilized eggs (Fig. 34b). RFI values were at a low in April and May, coincident with females with developing larvae and spent females. Females with spent and resting ovaries had increased RFIs that fluctuated at levels comparable to pre-fertilization RFIs.

The relationships for fat mass to body mass within mature female quillback rockfish were similar among seasons, and had homogeneous slopes and similar adjusted means (Table 21). As suggested in Fig. 34b and by the position of the adjusted means in Table 21, however, there was a trend for the fat mass-body mass relationships to be lowest in the spring for female quillback rockfish.

Seasonal comparisons of fat mass to body mass relationships between mature female copper rockfish and mature female quillback rockfish indicated that the major difference between the species occurred in winter (Table 22). During that season, mature female copper rockfish were

Table 22. Summary statistics for ANCOVAs for seasonal differences in fat mass as a function of body mass between mature female copper and quillback rockfish and between mature male copper and quillback rockfish. Nonsignificant differences in slopes or adjusted means are denoted by "=" and significant differences ($P \leq 0.05$) by "< or >".

Sex	Season	Equality of Slopes		Slope Contrasts	Equality of Adjusted Means		Intercept Contrasts[a]
		F	*P*		*F*	*P*	
Within Females	Winter	0.04	0.84	C = Q	16.83	0.00	C > Q
	Spring	0.43	0.51	C = Q	3.21	0.08	C = Q
	Summer	0.42	0.52	C = Q	0.31	0.58	C = Q
	Fall	4.22	0.05	C < Q			
Within Males	Winter	0.05	0.87	C = Q	3.52	0.06	C = Q
	Spring	0.60	0.44	C = Q	7.28	0.01	C < Q
	Summer	2.90	0.10	C = Q	1.70	0.20	C = Q
	Fall	5.75	0.02	C < Q			

[a] Contrasts were based on a *t*-test matrix for adjusted group means from the ANCOVA.

fatter, relative to body mass, than mature female quillback rockfish. During spring and summer, both species had similar fat mass to body mass relationships. In the fall, however, the slopes for the fat mass-body mass relationships were not the same between species, and female quillback rockfish had a greater increase in fat mass with body mass than copper rockfish (Table 22).

Mature Males

Slopes for the regressions of visceral fat mass against body mass for mature male copper and quillback rockfish for gonad maturity stages 3 through 7 were not different (ANCOVA: $F_{7,228} = 1.56$, $P = 0.11$). The pooled regression coefficient ($b = 0.877$) was therefore used to calculate RFI values for mature males. The pooled regression coefficient was not significantly different from one (*t*-test: $t = 1.09$, DF = 242, $P > 0.20$), however, indicating that the relationship between fat mass and body mass in mature males was isometric.

RFI values for mature male copper rockfish were at a maximum in stage 4 males in October through to February (Fig. 35a). Ripe males (stage 5) had lower RFI values and reached a maximum in February. RFIs for ripe, spent, and resting males reached lows in March to May. RFIs increased for resting males after May and were similar to stage 3 males from July to October.

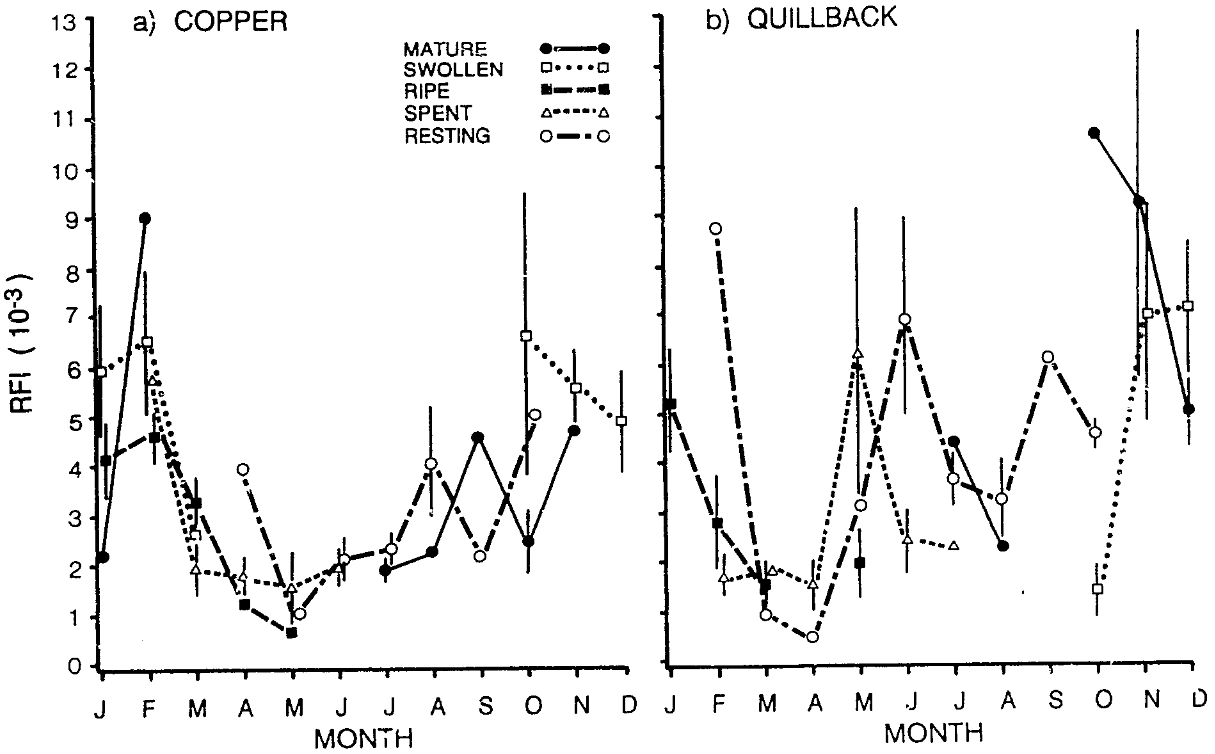

Fig. 35. Monthly changes in the mean (± 1SE) Relative Fat Index (RFI) for a) mature male copper rockfish and b) mature male quillback rockfish.

Seasonally, the relationships for fat mass and body mass among seasons for mature male copper rockfish had similar slopes but different adjusted means (Table 21). Graded differences were observed among seasons and male copper rockfish were, on average, fatter in the fall and winter, with winter fat levels being similar to summer levels (Table 21). Fat mass, relative to body mass, however, was lowest during the spring in mature male copper rockfish.

RFI values for mature male quillback rockfish were at a maximum during October and November in stage 3 males (Fig. 35b). Males with swollen testes (stage 4) had relatively high RFIs during November and December, just prior to the appearance of ripe males in January. Ripe males had maximum RFI values in January and their RFI values were lowest during March to May. Spent and resting males had low RFIs from February to April, with values increasing thereafter to relatively high levels (Fig. 35b).

On a seasonal basis, the relationships for fat mass and body mass among the four seasons for mature male quillback rockfish had similar slopes but different adjusted means (Table 21). Similar to male copper rockfish, there was a graded difference among seasons, with mature males in fall and summer, in general, being fatter than males in spring and winter (Table 21).

Seasonal comparisons of fat mass to body mass relationships between mature male copper rockfish and mature male quillback rockfish indicated that copper and quillback rockfish males were of similar "fatness" in the winter and summer (Table 22). During the spring, however, male quillback rockfish were fatter than male copper rockfish, on a body mass basis. As with mature females, mature male quillback rockfish in the fall demonstrated a greater increase in fat mass relative to body mass when compared to mature male copper rockfish (Table 22).

Immature Females

Slopes for the fat mass to body mass relationships for immature (maturity stages 1 and 2) female copper rockfish and immature female quillback rockfish were not different (ANCOVA: $F_{1,192} = 1.68$, $P = 0.20$) and the pooled regression coefficient ($b = 1.550$) was used to calculated RFI values for immature females. The pooled regression coefficient was significantly different from one (t-test: $t = 4.27$, DF = 194, $P < 0.001$), indicating that the fat mass versus body mass relationship for immature females was allometric.

RFI values for immature female copper rockfish peaked in September and October (Fig. 36a) and were otherwise relatively low throughout the year. On a seasonal basis, the slopes for the fat mass-body mass relationships within immature female copper rockfish were different (Table 23).

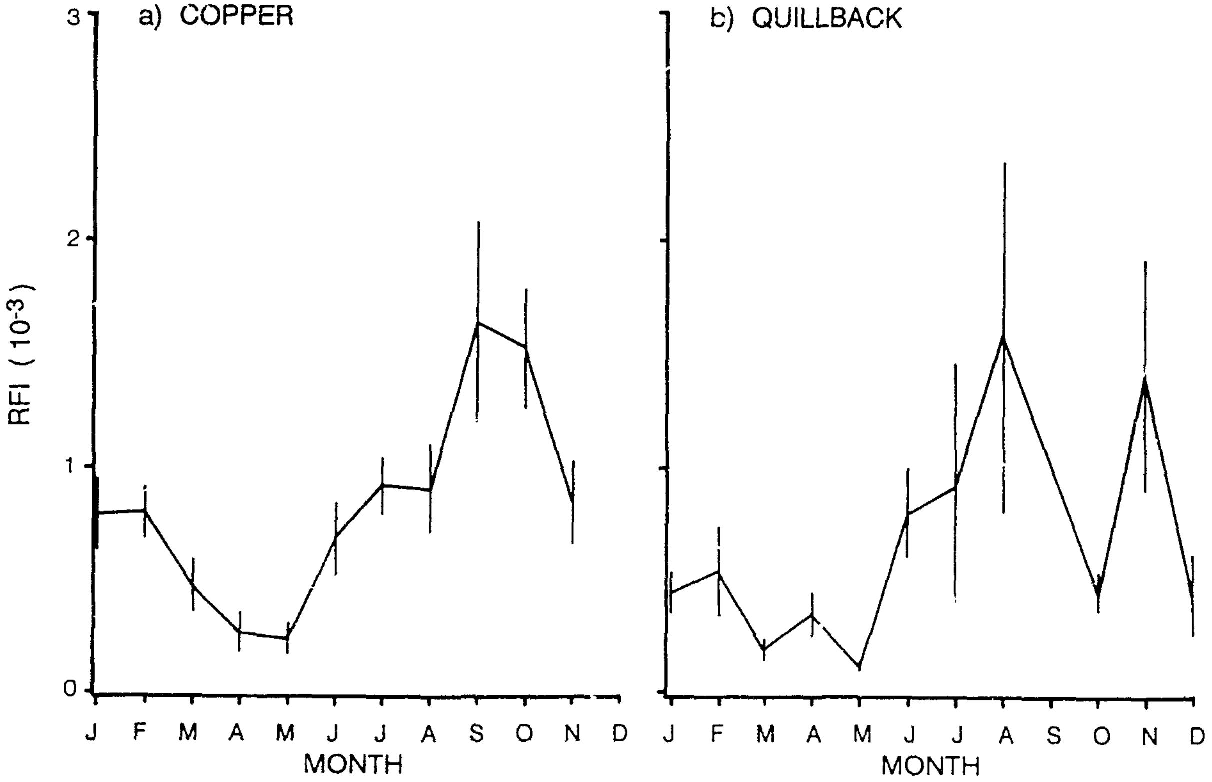

Fig. 36. Monthly changes in the mean (± 1SE) Relative Fat Index (RFI) for a) immature female copper rockfish and b) immature female quillback rockfish.

Table 23. Summary statistics for ANCOVAs for seasonal differences in fat mass-body mass relationships for immature female and immature male copper and quillback rockfish. Horizontal lines between seasons indicate that the seasons did not differ significantly ($P \leq 0.05$). (W = winter; SP = spring; SU = summer; and F = fall).

		Equality of Slopes		Slope Contrasts	Equality of Adjusted Means		Intercept Contrasts[a]
Species	Sex	F	*P*	High to Low	F	*P*	High to Low
Copper	Female	4.15	0.01	SP W F SU			
Quillback	Female	0.21	0.89	SP W F SU	10.83	0.00	F SU SP W
Copper	Male	0.91	0.44	SP SU F W	8.53	0.00	SU F W SP
Quillback	Male	0.92	0.44	W SP SU F	2.21	0.10	SU F SP W

[a] Contrasts were based on a *t*-test matrix for adjusted group means from the ANCOVA.

Immature females had a greater rate of increase of fat mass relative to body mass in the spring when compared to the slopes for winter and fall, which were in turn greater than the rate of fat increase in the summer (Table 23). Despite the differences in slopes, it was apparent that RFIs peaked in the summer-fall (Fig. 36a).

For immature female quillback rockfish, RFI values were intermediate throughout the year with the exception of March to May when RFIs were relatively low (Fig. 36b). The presence of a peak in RFI values in September and October, similar to immature female copper rockfish, could not be evaluated clearly in immature female quillback rockfish because of small sample size. However, the limited data for this time period do not indicate a peak. On a seasonal basis, however, the slopes for the fat mass versus body mass relationships were similar but the adjusted means were different (Table 23). Similar to immature female copper rockfish, therefore, immature female quillback rockfish were fatter in the fall and summer than in the spring and winter (Table 23).

Seasonal comparisons of fat mass to body mass relationships between immature female copper rockfish and immature female quillback rockfish suggested that copper rockfish were fatter than quillback rockfish in the winter (Table 24). Immature female copper and quillback rockfish had similar fat mass relative to body mass in the spring and

Table 24. Summary statistics for ANCOVAs for seasonal differences in fat mass as a function of body mass between immature female copper and quillback rockfish and between immature male copper and quillback rockfish. Nonsignificant differences in slopes or adjusted means are denoted by "=" and significant differences ($P \leq 0.05$) by "< or >".

		Equality of Slopes		Slope Contrasts	Equality of Adjusted Means		Intercept Contrasts[a]
Sex	Season	F	*P*		F	*P*	
Within Females	Winter	0.68	0.41	C = Q	21.55	0.00	C > Q
	Spring	0.85	0.36	C = Q	3.46	0.07	C = Q
	Summer	5.52	0.03	C < Q			
	Fall	0.92	0.34	C = Q	0.01	0.92	C = Q
Within Males	Winter	1.34	0.25	C = Q	7.35	0.01	C > Q
	Spring	1.25	0.27	C = Q	0.00	0.96	C = Q
	Summer	0.01	0.96	C = Q	2.19	0.15	C = Q
	Fall	1.95	0.17	C = Q	1.13	0.29	C = Q

[a] Contrasts were based on a *t*-test matrix for adjusted group means from the ANCOVA.

fall. In the summer, however, the slopes for the fat mass to body mass relationships between copper and quillback rockfish were not the same, and immature quillback rockfish had a greater rate of fat increase relative to body mass than immature female copper rockfish (Table 24).

Immature Males

Slopes for the fat mass to body mass regressions for immature male copper rockfish and immature male quillback rockfish were homogeneous (ANCOVA: $F_{1,175} = 0.02$, $P = 0.88$), and the pooled regression coefficient ($b = 1.199$) was used to calculate RFI values for immature males. The pooled regression coefficient was not significantly different than one (*t*=test: $t = 1.59$, DF = 177, $P > 0.10$), indicating that the fat mass to body mass relationship in immature males was isometric.

Values of RFI for immature male copper rockfish reached a maximum in September and October (Fig. 37a), similar to immature female copper rockfish (Fig. 36a). RFI values for immature male copper rockfish decreased in November to intermediate levels and RFIs remained at this level until March (Fig. 37a). RFI values in immature male copper rockfish reached a low during April and May. Differences in monthly RFI values were supported on a seasonal basis in which immature male copper rockfish were found to be fatter

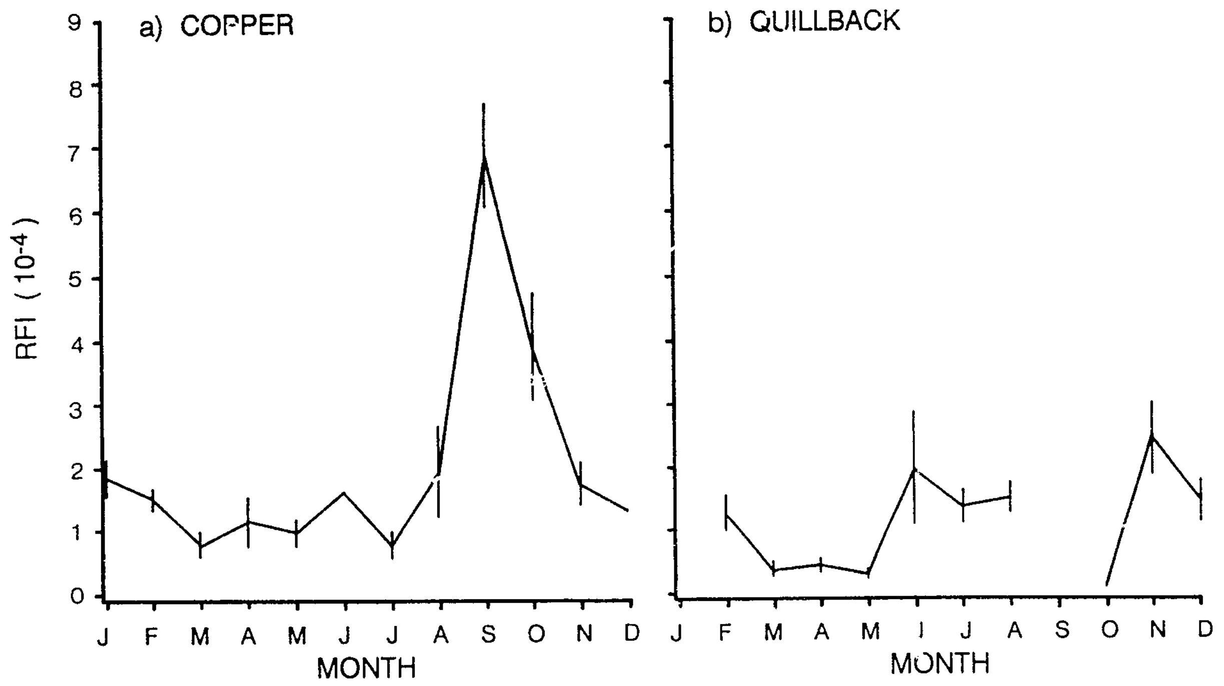

Fig. 37. Monthly changes in the mean (± 1SE) Relative Fat Index (RFI) for a) immature male copper rockfish and b) immature male quillback rockfish.

in the summer and fall than in the winter, and fatter in the winter than in the spring (Table 23).

RFIs for immature male quillback rockfish appeared to be more variable than for immature male copper rockfish, possibly due to the smaller sample size (Fig. 37b). As in immature male copper rockfish, however, RFI values were highest for immature male quillback rockfish during June to November. RFI values did not appear to reach maximum values during September and October, however, as observed for immature copper rockfish. RFIs decreased in immature male quillback rockfish in December and remained at relatively low levels until February (Fig. 37b). In March, RFI values decreased and remained low until May, when minimum values were observed. Among seasons, there were no differences in the fat mass to body mass relationships for immature male quillback rockfish (Table 23).

Comparisons among seasons for fat mass to body mass relationships between immature male copper rockfish and immature male quillback rockfish indicated that copper rockfish were fatter than quillback rockfish in the winter (Table 24). Immature males of both species had similar fat mass to body mass relationships in spring, summer, and fall (Table 24).

DISCUSSION

Maturity

Life history characteristics of rockfish species, such as size (or age) of sexual maturity, are known to be vary among species, as well as within species and between sexes, depending on a wide range of environmental and ecological factors (e.g., latitude, temperature, fishing pressure) (Westrheim 1975; Wyllie Echeverria 1987; Love *et al.* 1990; Wootton 1990; Leaman 1991). In general, when differences exist between sexes in the size of maturity, it is usually due to males maturing at a smaller size than females (Hoar 1957; Westrheim 1975; Wyllie Echeverria 1987; Love *et al.* 1990). Love (1980) speculated that attaining sexual maturity at a smaller size in male fish is reasonable because of their smaller gonad size, requiring a relatively smaller body. Although this may have been the trend for male quillback rockfish in Central California, where males matured at a slightly smaller size (3-4 cm) than conspecific females (Wyllie Echeverria 1987), the general trend was not evident for the majority of copper and quillback rockfish (Table 25). In general, males and females of either sex matured at a similar size, within 0-2 cm of each other (Table 25). In addition, the reverse trend can occur as evidenced by male copper rockfish collected in Puget Sound

Table 25. Estimated total length at first, 50%, and 100% maturity for female and male copper and quillback rockfish in relation to geographic location. Results from the present study are capitalized.

Species	Sex	Sample Location	Maturity 1st	50%	100%
Copper	Female	Central California[a]	310	340	410
		Washington[b]	225		
		Puget Sound, WA[c]	275		
		Central Puget Sound[d]	226	226	343
		Northern Puget Sound[e]	179		267
		SAANICH INLET, B.C.	195	220	260
	Male	Central California[a]	300	320	400
		Puget Sound, WA[c]	297		
		Northern Puget Sound[e]	245		281
		SAANICH INLET, B.C.	145	190	260
Quillback	Female	Central California[a]	260	260	280
		Central Puget Sound[d]	211	211	267
		Northern Puget Sound[e]		224	269
		Campbell River, B.C.[f]	215	292	330
		SAANICH INLET, B.C.	205	240	265
	Male	Central California[a]	220	220	310
		Northern Puget Sound[e]		242	267
		Campbell River, B.C.[g]		295	
		SAANICH INLET, B.C.	190	190	260

[a] Wyllie Echeverria 1987; [b] DeLacy *et al*. 1964; [c] Patten 1973, fork length converted to total length using Echeverria and Lenarz 1984; [d] Gowan 1983, age at maturity converted to total length using Gowan's Tables 4 or 7; [e] Barker 1979, age at maturity converted to total length using Barker's Tables A-1 or A-2; [f] Schnute and Richards 1990; [g] Richards and Cass 1987.

being larger than females at first maturity (Patten 1973; Barker 1979) and at 100% maturity (Barker 1979) (Table 25).

On a latitudinal basis, copper rockfish collected in more southern waters (e.g., Central California) matured at a larger size than fish collected in Saanich Inlet (e.g., the present study) (Table 25). Although this was most noticeable in the length of first and 100% maturity, it also supported Westrheim's (1975) suggestion that size at 50% maturity within a rockfish species varies inversely with latitude. There were exceptions to this trend, however, the most marked being for female and male quillback rockfish collected near Campbell River, British Columbia (Richards and Cass 1987; Schnute and Richards 1990). In particular, 50% maturity in these fish occurred at a much larger size than quillback rockfish from southern waters and from Saanich Inlet (Table 25). This may be a result of any latitudinal comparisons being obscured by differences in fishing pressure or food availability among the different locations. A comparative analysis of maturity for copper and quillback rockfish was confounded by these factors because the maturity information was collected from rockfish populations that were exploited by either sports or commercial fisheries to some unknown level (based on methods reported). While it is generally accepted that increased fishing pressure causes density-dependent changes in an exploited population and, most notably, a coincident increase in growth rate and earlier maturation (Beverton 1963; Wootton 1990), it is debatable whether earlier maturation is dominated by size or age effects (Roff 1982; Stearns and Crandall 1984; Mayo *et al.* 1990; Leaman 1991).

Fecundity

Fecundity in rockfish species appears to increase allometrically with increasing body size (Fig. 26, DeLacy *et al.* 1964; Love *et al.* 1990). Data on fecundity for 16 species of *Sebastes* (DeLacy *et al.* 1964; Love *et al.* 1990), one of which was *S. caurinus*, demonstrated that in all but one species (*S. hopkinsi*, the squarespot rockfish), the regression coefficient (*b*) for the relationship between fecundity and length (log-transformed data) was greater than three, and averaged 4.060 ± 0.715 (± 1 SD, $n = 18$). This indicated that fecundity increased proportionally more in larger females.

Fecundity of rockfish, however, varies enormously over the size range of reproductively active females of different species. Love *et al.* (1990) have noted a significant relationship between maximum fecundity and maximum length of 16 species of *Sebastes*. They give estimates of maximum fecundity ranging from 18,000 eggs in *S. dalli* (calico rockfish, 15.5 cm length) to 2,683,800 eggs in *S. miniatus* (vermillion rockfish, 68.0 cm length) (Love *et al.* 1990). Maximum fecundity estimates for copper and quillback rockfish in Saanich Inlet fit within this generalized pattern.

In general, fecundity is thought to decrease in a species in the northern portion of its range (Hoar 1957; Hislop and Hall 1974; Love 1980). This is equivocal for rockfish species: Love *et al.* (1990) have noted greater egg production in three species of rockfish in southern California versus central and northern California, but Gunderson et al. (1980) found that chilipepper rockfish (*S. goodei*) were less fecund in the southern portion of their study site compared with the northern area.

To date, fecundity estimates for copper rockfish are limited to DeLacy *et al.* (1964) and Schrute and Richards (1990). In the former, the relationship between fecundity and length for copper rockfish collected in Washington translated into a 30-cm fish having a fecundity of approximately 45,770 eggs (DeLacy *et al.* 1964). In comparison, copper rockfish collected in British Columbia had greater fecundities for similar-sized fish: 30-cm copper rockfish collected from Saanich Inlet (Fig. 26) and the Strait of Georgia (Richards and Schnute 1990) had fecundities of approximately 89,870 and 96,000 eggs respectively.

Fecundity estimates for quillback rockfish have also been obtained for fish collected in the Strait of Georgia (Richards and Schnute 1990). For a 30-cm quillback rockfish, fecundity ranged from approximately 92,000 to 116,000 eggs, depending on the area of collection in the Strait. As with copper rockfish, a 30-cm quillback rockfish collected in Saanich Inlet had an estimated fecundity of 89,870 eggs (Fig. 26). Fecundities were therefore similar between similar-sized copper and quillback rockfish and between locations within British Columbia. The majority of copper and quillback rockfish collected in the Strait of Georgia were larger than rockfish in Saanich Inlet, however, and the maximum fecundities observed for both species in the Strait of Georgia were concomitantly much greater (~400,000 and ~648,000 eggs for copper and quillback rockfish respectively) (Richards and Schnute 1990).

Timing of the Reproductive Cycle

Another life history characteristic that varies considerably within *Sebastes* is the timing of the reproductive cycle. Phillips (1964) broadly categorized rockfish as either having an early (winter) or late (spring-summer) reproductive season. Reproductive season, in this sense, refers to the time when the majority of mature females are carrying eyed-larvae (stage 5). Although most rockfish species give birth to their young from January through to May, some give birth throughout the year (Love *et al.* 1990).

Love *et al*. (1990) found no relationship between the reproductive season (duration or peak months) and the ecology or size of rockfish species. Wyllie Echeverria (1987) and Love *et al*. (1990) did suggest, however, that peak months of the reproductive season for closely-related species appeared to be similar. This was supported by data from copper and quillback rockfish in Saanich Inlet, where there was a one month difference between the species in the peak times of parturition and spermatogenesis (Fig. 27, 28).

It was also evident that both copper and quillback rockfish give birth to their young later in the year in more northern locations (Table 26). The progressively later reproductive season as one moves north has also been observed for whiting (*Merlangius merlangus*) (Hislop and Hall 1974) and Atlantic cod (*Gadus morhua*) (Love 1970). For rockfish, Love *et al*. (1990) suggested that the availability of prey associated with coastal upwelling, which proceeds in a northerly direction, was related to the earlier reproductive season of a rockfish species in the southern portion of its range. The occurrence of a later reproductive season with increased latitude in rockfish species could also be a response to decreased temperature or photoperiod (Mann *et al*. 1984).

Table 26. Primary month(s) of parturition in copper and quillback rockfish in relation to geographic location. Results from the present study are capitalized.

Species	Sample Location	Month(s) of Parturition
Copper	Central California	February[a]
	Washington	April[b,c]
	Puget Sound, Washington	March[d]
	Northern Puget Sound	April[e]
	SAANICH INLET, B.C.	JUNE
Quillback	Central California	April[a]
	Northern Puget Sound	April[e]
	British Columbia	April[f,g]
	British Columbia	May[c]
	SAANICH INLET, B.C.	MAY
	Gulf of Alaska	May-July[h]

[a] Wyllie Echeverria (1987); [b] DeLacy *et al.* (1964); [c] Washington *et al.* (1978); [d] Patten (1973); [e] Moulton (1977); [f] Westrheim (1975); [g] Love and Westphal (1981); [h] Rosenthal *et al.* (1981).

Interrelationships among Reproduction, Fat, and Feeding

The relationship between reproduction, visceral fat deposits, and feeding is complex in fishes (Love 1980). In general, the maturation of the gonads of the female results in a greater depletion of energy reserves than maturation of the testes of the male (Love 1980; Wootton 1985), if it is assumed that there are no differences between the sexes in activity. Love (1980) estimated that the total lipid content of the testes are one-tenth that of ovaries, and females generally store lipids in order to transfer the energy to the ovaries during development of the eggs. In rockfishes, the energy costs of reproduction involve supplying the developing young with an extensive vascular network for respiration (Moser 1967), as well as supplying the embryos with nutrition (Boehlert and Yoklavich 1984; Boehlert *et al.* 1986).

Mature Females

For mature female copper and quillback rockfish, cycles of visceral fat deposition and utilization (Fig. 34) were complementary to, rather than coincident with, their reproductive cycles (Fig. 29). This indicated that mature female copper and quillback rockfish use visceral lipid reserves to fuel reproduction. Overlain on the cycles of reproduction and fat accumulation, however, were periods of feeding.

Food consumption by female copper rockfish was greatest in the winter (Fig. 16a), coincident with the greatest fat reserves (RFIs) (Fig. 34a), and relatively low gonad mass (RGIs) for females with maturing eggs (Fig. 29a). Similarly, feeding by quillback rockfish in winter was also at a relatively high level (Fig. 16b), again coincident with high RFI values (Fig. 34b) and relatively low RGIs. The quantity of food consumed by females in the winter was also of relatively high quality (i.e., high caloric density) because rockfish were consuming primarily juvenile herring at this time (Fig. 10, 11). Mature female rockfish were therefore able to accumulate fat stores during relatively intensive feeding in the winter, during time when their ovaries were beginning to mature eggs for the upcoming reproductive season.

During late winter and spring (March to June), however, RFIs decreased for both female copper and quillback rockfish (Fig. 34) concomitant with a large increase in gonad size (Fig. 29). Visceral fat stores in females may have also been used for body maintenance, however, because the lowest level of food consumption for both copper and quillback rockfish occurred during the spring (Fig. 16c), also coincident with a decrease in their RFI values (Fig. 34). It was evident, however, that female copper rockfish recovering from parturition (stage 7) and female quillback rockfish in either stage 6 or 7 (spent and resting) had greater RFIs during the late spring (April) than females of both species in stage 5 (eyed-larvae) (Fig. 34). This indicated that females that had finished giving birth began to accumulate visceral fat reserves even though food consumption was relatively low during the spring. This provided additional indirect support for the major use of lipid reserves by females for reproduction.

Although reduced food consumption during the spring may be due to reduced food availability (especially herring and pelagic crustaceans, Table 9), in females it may also be a result of gestation. Some fishes reduce their food intake during the latter part of the reproductive season because of the large bulk of the ovaries in their abdomen (Love 1980). In copper and quillback rockfishes, the mass of the ovaries relative to the body size of the female can be enormous (i.e., 48%) during the months of gestation (spring). Pregnant female rockfish are sometimes unable to fit into shelter holes which easily accommodate nonpregnant fish of similar body length (pers. obs.). It is reasonable to assume that these pregnant females would also be at a disadvantage and prone to predation if caught in the open while attempting to feed. Reduced feeding in females during gestation may therefore be a selectional response to an "anti-risk" lifestyle.

Overall, mature female copper and quillback rockfish accumulated fat reserves during the summer, fall, and to a greater extent, winter (Fig. 34), when feeding levels were intermediate to high (Fig. 16). Fat reserves decreased, however, when mature (stage 3) females approached their maximum RGI values, indicating that fat reserves were being used in maturation of the ovaries. Visceral fat reserves were lowest in females with fertilized, eyed-larvae, or spent ovaries, indicating that the energy expended by pregnant females in producing a batch of young was significant. The complementary cycle of visceral fat reserves in relation to ovarian development in mature female rockfish was supported by physiological experiments that determined that approximately 70% of the energy required by the developing young during gestation was derived from maternal nutrition (Boehlert and Yoklavich 1984; Boehlert *et al.* 1986).

Guillemot *et al.* (1985), however, indicated that the visceral fat reserves and gonad maturation patterns were coincident, rather than complementary, for females of five species of offshore rockfishes. They concluded that fat reserves accumulated during the summer and fall, concurrent with the main period of vitellogenesis (stage 3), and hence were not being used in the maturation of the ovaries. In addition, visceral fat deposits decreased in the winter, coincident with an increase in gonad volume and a decrease in food availability. They interpreted this decrease in fat volume during the winter as a response to decreased food availability (and therefore a presumed decrease in food consumption). Although they suggested briefly that the decrease may also be due to nutrition of the developing embryos, they concluded that the use of visceral fat reserves in mature females was primarily related to decreased food availability in the winter and the use of the fat reserves for maintenance during this time period. It was difficult to compare data between their study and mine because they did not give gonad and visceral fat relationships for each individual maturity stage of females (they pooled their data). Based on my study, however, it is reasonable to suggest that the decrease in visceral fat reserves of females in the winter, as observed by Guillemot *et al.* (1985), was primarily due to their using fat reserves in gestation of their young, in addition to using some of the fat reserves for maintenance during the winter food scarcity. This is further supported by Guillemot *et al.*'s own data because two of three species of immature females they studied had increased fat volume in the winter relative to the other seasons, rather than a decreased fat volume as was observed in mature females in the winter.

Mature Males

In contrast, the monthly patterns of visceral fat reserves in mature male copper rockfish and quillback rockfish (Fig. 35) were mostly coincident with, rather than complementary to, their reproductive cycles (Fig. 32, 33). As RFI values for mature male copper and quillback rockfish were greatest during the same time period that RGI values were at their maximum, male rockfish, for the most part, were not using visceral fat reserves as an energy source to mature their gonads (stage 3) or for spermatogenesis (stage 4). Guillemot *et al.* (1985) also observed that the deposition of visceral fat in mature male rockfishes was concurrent with gonad maturation although, to date, only a few rockfish species have been studied.

During the winter, however, RFI values for copper and quillback rockfish that were in a ripe condition were lower than for males in stage 4 maturity (peak spermatogenesis), indicating that there was some reduction in visceral fat reserves with ripening of the testes (Fig. 35). Thus RFI values decreased in ripe males during the winter even though this was a period of relatively intensive feeding. In addition, mature male quillback rockfish, in particular, showed an increase in RFIs during low-level feeding in the spring (May and June), indicating that lows in RFIs do not necessarily correspond to reduced periods of feeding in males.

Overall, the accumulation and deposition of visceral fat reserves in mature males was in phase with their reproductive and feeding cycles. Although visceral fat reserves may not be required in males for gonad maturation and spermatogenesis, males evidently use visceral fat reserves in the winter when their gonads are in a ripe condition. This presumably was not due to production of testicular material because spermatogenesis was complete by stage 5 of maturation (Moser 1967). The use of fat reserves in the winter may be related to increased activity of males attempting to court and inseminate females. The prolonged period (3-4 months) over which males were collected in a ripe condition (Fig. 28) suggested that males may mate more than once (Wyllie Echeverria 1987). Alternatively, males may not all be reproductively active at the same time (e.g., smaller males may develop ripe testes later than large males). This is speculative, however, because courtship behaviour (not mating) has been observed only once in rockfish (Helvey 1982).

In both mature females and mature males of both species there also seemed to be a variable amount of deposition of fat primarily during the summer (Fig. 34, 35), coincident with an intermediate level of feeding for copper rockfish and high-level feeding for quillback rockfish (Fig. 16). At that time of year, however, both species and both sexes are resting from reproductive activities (Fig. 29, 32, 33) and their energy requirements for reproduction are concomitantly low.

Immatures

Immature female copper and quillback rockfish had relatively high RFI values in the summer, similar to mature females (Figs. 34, 36). However, visceral fat mass in immature females decreased during the fall and winter, and remained relatively low until late spring and summer (Fig. 36), contrary to the build-up of visceral fat mass in mature females during the winter (Fig. 34).

In general, the monthly pattern of visceral fat reserves for immature male copper and quillback rockfish (Fig. 37) tracked the pattern observed for mature males (Fig. 35), despite the absence of testicular build-up in immature males. The similarities between immature and mature RFI patterns further supported the contention that the visceral fat reserves of males (immature and mature) were mainly coincident with the level of feeding, and secondarily related to reproduction.

The suite of life history traits that contribute to the ultimate reproductive fitness of copper and quillback rockfish, i.e., age of maturity and fecundity, exhibit considerable variation both within and between species. This apparent flexibility in reproductive characteristics appears to be a common feature of the genus *Sebastes* (Chen

1971; Guillemot *et al.* 1985; Wyllie Echeverria 1987; Love *et al.* 1990) and undoubtedly contributes to the success of the genus in the North Pacific Ocean. High fecundity in rockfish despite viviparity may reflect low survivorship of their pelagic larvae. Being relatively long-lived species (Chapter V), however, copper and quillback rockfish have the advantage of accruing offspring over many years (iteroparous reproduction), and the disadvantage of producing a brood in a year unfavourable to offspring is therefore relatively small compared to a fish which is semelparous. The ability of females to store sperm before complete maturation of their eggs, and to delay fertilization, provides an additional avenue of flexibility in the timing of the rockfish reproductive cycle. Sympatric congeners, such as copper and quillback rockfish, may have similar energy requirements for brood production, but any potential reproductive competition was reduced by differences in the timing of their reproductive cycles, in particular, parturition.

SUMMARY

Female and male copper and quillback rockfish attained sexual maturity at a similar size, with the possible exception of some male copper rockfish that are able to mature at a relativley smaller size. Male copper rockfish were ripe, and potentially inseminated females, in January and February. Female copper rockfish carried fertilized eggs in April and May, and gave birth to their young primarily in June. The reproductive cycle of quillback rockfish preceded that of copper rockfish by approximately one month, with parturition of quillback rockfish occurring mainly in May. Fecundity of copper and quillback rockfish was similar and relatively great with, for example, a fish of 300 mm total length giving birth to approximately 90,000 young.

Visceral fat cycles of mature female copper and quillback rockfish were complementary to their cycle of gonad maturation and gonad mass increase, and indicated that female rockfish use visceral fat stores as a source of energy for maturation of their eggs and nourishment of their developing young. Visceral fat cycles of mature male copper and quillback rockfish were mainly coincident with the maturation and increase in the mass of their gonads. This indicated that male rockfish did not use visceral fat reserves in the maturation of their gonads (spermatogenesis) but they may have used the fat reserves as an energy source during the period when they were ripe, perhaps for mating activities. The pattern of visceral fat accumulation and dissipation in immature male and female copper and quillback rockfish appeared to be primarily related to periods of feeding.

CHAPTER VII

INTERSPECIFIC COMPETITION BETWEEN SYMPATRIC POPULATIONS OF COPPER AND QUILLBACK ROCKFISH

INTRODUCTION

There is considerable debate in current ecological theory over the importance of interspecific competition in structuring natural communities (Schoener 1974, 1982, 1983; Connell 1975, 1980, 1983; Wiens 1977; Diamond 1978; Sale 1978; Connor and Simberloff 1979; Strong 1980; Pianka 1981; Roughgarden 1983, 1986; Simberloff 1983; Sale and Douglas 1984). Interspecific competition between two species occurs when their populations reach a level for which resources shared by both become limiting (i.e., the supply of the common resource is not adequate for all individuals of both species) (Dunham 1980; Pianka 1981). The debate ensues because support for the presence and the importance of interspecific competition comes mainly from comparative, observational studies based on niche partitioning (MacArthur 1972; Schoener 1974; Diamond 1978). Patterns of niche differentiation in sympatric populations are usually interpreted as being due to competition arising from the presence in the same environment of ecologically similar species (Dunham 1980; Pianka 1981). The comparative method therefore infers the presence of competition, but offers no direct evidence of competition as a causative factor in producing the patterns of species' distributions and abundances in natural populations (Schoener 1983).

A direct test for the presence of interspecific competition between two species is best gained by an experimental approach involving manipulation of the densities of natural populations or relevant resources (Dunham 1980; Pianka 1981; Connell 1983). In this approach, competition is demonstrated to exist when a reduction in the population density of one species allows the population density of its potential competitor to increase, or allows its potential competitor to expand its niche ('ecological release') (Pianka 1978, 1981; Connell 1983). The reciprocal population manipulation must also be performed because when interspecific competition does occur, it typically is asymmetrical with one species having a greater competitive effect than the other species (Lawton and Hassell 1981; Connell 1983; Schoener 1983).

Field studies of competition have been centred in tropical, rather than temperate, ecosystems primarily because niche partitioning in the species-rich tropics has historically been viewed as extensive (e.g., Darwin 1859; Wallace 1878; Steere 1894). For tropical reef fishes, therefore, competition was thought to be an important structuring force in their communities (i.e., the observational approach) (e.g., Randall 1967; Jones 1968; Smith and Tyler 1973; Anderson *et al.* 1981). Relatively recently, the presence and importance of competition in structuring marine fish communities has been more rigorously examined using experimental approaches, again primarily in the tropics. The majority of these studies examine whether competition is a determining factor in the species composition of fishes on coral reefs by manipulating fish densities or habitat (e.g., Sale and Dybdahl 1975; Sale 1978a,b; Sale and Williams 1982). Based on these types of experiments, the evidence for the existence or importance of competition in these tropical fish communities has become equivocal (Roberts 1991).

In temperate fish communities, experimental studies on the presence or absence of interspecific competition have focused on freshwater species, most notably, sunfishes (Centrarchidae) inhabiting lakes (e.g., Werner and Hall 1976, 1977) or on the economically important salmons and trouts (Salmonidae) in either lakes or streams (e.g., Hartman 1965; Hearn 1987). These studies have demonstrated that interspecific competition significantly affects the distributional patterns and ecology of fish species in temperate freshwater ecosystems.

The few studies of competition between fish species in temperate marine ecosystems have also demonstrated that interspecific competition can have significant effects on the distribution and population dynamics of temperate marine fishes. For example, Hixon (1980) demonstrated asymmetrical competition between striped surfperch (*Embiotoca lateralis*) and black surfperch (*E. jacksoni*) by experimentally manipulating their food resources. Larson (1980a), through manipulating the densities of gopher rockfish (*S. carnatus*) and black-and-yellow rockfish (*S. chrysomelas*), established that the bathymetric segregation of the species was due to interspecific competition.

Members of the rockfish genus *Sebastes* may be particularly amenable to studies of interspecific competition because they are numerous (approximately 65 species in the Northeastern Pacific Ocean) and many occur as sympatric congeners (Chen 1971) with similar morphology and ecology. Two of these species, *S. caurinus* (copper rockfish) and *S. maliger* (quillback rockfish), occur in nearshore waters of British Columbia where they are accessible for *in situ* experimental studies. The apparent ecological and morphological similarities between copper and quillback rockfish (Hart 1973; Moulton 1977) initially suggested the potential for interspecific competition when they were sympatric.

The purpose of this study was to test for the occurrence of contemporary interspecific competition between sympatric copper and quillback rockfish through experimental manipulations of their population densities. The population densities and activities of fish were examined before and after removal of one or the other species from rocky reefs where the species co-occur. An interspecific competitive effect of copper rockfish on quillback rockfish will have been demonstrated if the population density or the activity niche (occurrence of behavioural activities) of copper rockfish increases in the absence of quillback rockfish (Dunham 1980; Pianka 1981). Conversely, a competitive effect of quillback rockfish on copper rockfish will have been demonstrated if the population density or the activity niche of quillback rockfish increases in the absence of copper rockfish.

METHODS

Study Sites

Sympatric populations of copper and quillback rockfish were located in an area north of McKenzie Bight, in Saanich Inlet, British Columbia (Fig. 1). This area consisted of a number of rocky reefs, each with a relatively high degree of habitat relief due to boulder piles, pinnacle rocks, and cliff faces. From general SCUBA surveys it was apparent that copper and quillback rockfish were sympatric in this area between 15 and 40 m (60-130 ft). The presence of copper rockfish with a concomitant absence of quillback rockfish above 10 m was confirmed by SCUBA diving, whereas the absence of copper rockfish with a concomitant presence of quillback rockfish below ~40 m was determined through a study using the *Pisces IV* submersible (Chapter II).

Three reefs were chosen from this general area to act as study sites for the experimental manipulations: Log Reef, Arbutus Reef, and Beach Reef. Criteria for choosing the reefs were accessibility, similar depth range and terrain, similar composition of reef flora and fauna, and distinctiveness of reef boundaries. Although each of the three reefs was within swimming range of other suitable rockfish habitat, the reefs themselves were bounded by flat, smooth bedrock or sand-shell substrate offering little relief or shelter.

The distance between reefs was approximately 250-300 m (straight-line distance). Water depths of the reefs ranged from 18-20 m at the shallowest to 25-31 m at the deepest. All reefs had one or two large boulders (~3-4 m diameter) and a vertical reef face. The basic substrate of all reefs otherwise consisted of rocks and crevices, interspersed with small areas of open bedrock. Cover provided by algae was minimal and was principally the large brown alga, *Agarum fimbriatum* (one to three fronds). Other flora on the reefs were primarily small, foliose or encrusting red algae. Large resident fish or invertebrates on the reefs, other than copper and quillback rockfish, were tiger rockfish (0-1 per reef), lingcod (*Ophiodon elongatus*: 0-2 per reef), octopus (*Octopus dofleini*: 1-3 per reef), and wolf eels (*Anarichthys ocellatus*: 1-2 per reef). Various other smaller fishes and invertebrates were found on the reefs (Tables 8, 9), as well as larger fish and marine mammals that occasionally passed by the reefs.

Reef Preparation

Each reef was prepared for censusing by laying an underwater grid over its entire area. This procedure was initiated by laying a 5-mm diameter yellow polypropylene rope at the base of the reef (approximately north-south) while maintaining a constant bearing using a compass. The rope was marked every 3 m (10 ft) with a red brick coded with a numbered tag and flagged with florescent survey tape. The numbered, flagged bricks allowed the divers to recognize grid lines on the reef without directly approaching the bottom. Once this baseline had been laid, a second reference bearing was taken half-way along the baseline and perpendicular to it (approximately west-east). Bricks were placed every 3 m on this second reference bearing until the top of the reef was reached. The 3-m placement of the bricks in all cases was based on the horizontal plane, using plumb lines, in order to account for changes in reef topography. At each of these bricks placed perpendicular to the baseline, additional bearings were taken that were parallel to the baseline bearing, and bricks were laid every

3 m along these parallel bearings. Upon completion, a grid comprised of 3-m by 3-m cells was superimposed on the entire reef area. Hence, the area between parallel bearings was 3 m wide and of various lengths depending on the reef. Each of these 3-m-wide strips was considered to be a transect.

The total surface area of each reef was calculated by summing the surface areas of the individual 9-m^2 cells. The surface area of each grid was determined by estimating its slope, and then multiplying the width (3 m) by the ratio of the change in depth to the sine of the slope. This was only a gross indication of surface area, because it did not take into account additional surface area afforded by broken and complex habitat.

Tagging Fish

Fish were anaesthetized underwater using metomidate hydrochloride (Marinil). The concentration of the stock solution was 0.2 $g \cdot L^{-1}$; this was rapidly diluted when exposed to open sea water when applying the anaesthetic following the procedure of McElderry (1979). The stock anaesthetic solution was held in a collapsible 4-L water bag. A 1-m piece of flexible rubber tubing was attached to the spigot and a 1-m piece of hollow Plexiglas tubing was attached to the end of this rubber tubing. The collapsible water bag was held under the arm of the diver with the Plexiglas wand extended towards the mouth of the fish. By controlling the pressure exerted on the collapsible bag, in conjunction with opening the spigot, a squirt of anaesthetic could be directed towards the fish on the inhalation portion of its ventilation cycle. After 3-5 well directed inhalations the anaesthetic would become effective and the fish would sit passively on the bottom, but its righting reflex was not necessarily disrupted. The fish was then approached and captured by hand. Anaesthetized fish were then measured for total length and tagged. Although fish were sexed externally when possible (Moser 1967), it was impossible to sex all fish with consistent reliability, especially smaller fish. Tags were inserted into the dorsal musculature of the dorsal fin using a tagging gun (Model FDM-68, Floy Tag & Mfg, Inc., Seattle, WA). Tags were constructed of numbered FD-68BC anchor spaghetti tags (Floy Tag & Mfg., Inc., Seattle, WA) with a 1-cm square of 1-mm thick white styrene attached to the end (McElderry 1979). The white square was marked with the same number as appeared on the spaghetti tag and increased the visibility of the tag number to divers. The spaghetti portion of the tag was also labelled with information on where to report any tag recoveries. Fish were then placed in a large bucket with holes drilled in it to allow water flow, and the bucket was attached to structures on the reef at the depth at which the fish was captured. The fish were released from the bucket after a minimum of 4 hr. This holding of anaesthetized fish was necessary to protect them from predation by other fish while they were unaware of their surroundings due to the effect of the anaesthetic. In total, 18 copper rockfish and 26 quillback rockfish were tagged on Beach Reef during August and September 1986, 25 quillback rockfish were tagged on Arbutus Reef during July and August 1986, and 39 copper rockfish and 4 quillback rockfish were tagged on Log Reef during June and July 1986.

Fish less than 15 cm in total length were not tagged using spaghetti tags due to the large size of the tag relative to the fish size. Small fish on Beach Reef (8 copper rockfish and 15 quillback rockfish) were tagged alternatively by clipping the spines in the dorsal fin using dog-toe clippers. In this tagging, a maximum of 4 out of the possible 13 spines were clipped, with never more than 2 spines clipped in a series so that the protection afforded to the fish by the spines was assumed not to be reduced. These spine-clipped fish, although visible to divers, proved to be too time-consuming to enumerate because it was necessary to view an erect dorsal fin to accurately decipher the identity of the fish.

Population Censuses

Population censuses were taken weekly, depending on weather conditions, for 5 months prior to reef manipulations (October 1986 to February 1987). After reef manipulations

(March 1987), populations were censused one to two times per month for a period of 21 months (April 1987 to Dec 1988). In addition, the populations were censused in May and June of 1990 as a follow-up on the population densities and recruitment. Rockfish populations were analysed on a seasonal basis: winter (January-March), spring (April-June), summer (July-September), and fall (October-December).

On each survey, water temperature was recorded at the surface and at 21 m. Underwater visibility was measured by the supervising diver as the straight-line, horizontal distance between the position of the diver and the furthest distinguishable survey marker (brick). Distinguishability was determined by the observation of a clear outline of the red brick against the rock substrate of the reef, not the coloured flagging tape tied to the bricks. The former measure of visibility was more realistic than the latter, because copper and quillback rockfish are relatively dark coloured against a dark-coloured substrate. Population surveys were taken only when horizontal water visibility was $\geq$6 m (20 ft).

Diving safety precautions prevented the randomization of the starting transect; population censusing therefore began on the two deepest, adjacent transects. The starting direction of the first transects (north or south) and the divers assigned to the transects, however, were randomized.

For consistency in censusing, only I and two other divers were involved in the actual population censuses.

A census began with each observer hovering 3-4 m above the substrate in the central area of a transect, the two observers being in adjacent transects. Each observer was therefore responsible for recording fish within a 3 m transect width (i.e., between two lines of bricks). Observers would begin by hovering ~3 m outside the first transect while observing fish within the first 3-m by 3-m grid. This allowed us to observe fish before actually passing over them. After a record was made of the fish immediately visible in the grid, the observer would swim forward very slowly in order to count any other fish less visible in the grid. Observers checked the substrate systematically for fish, sweeping their vision back-and-forth between the grid lines for the transect as they proceeded forward, even if fish were apparently absent. This was necessary because stationary rockfish are well camouflaged and might otherwise be overlooked. Crevices and shelter holes were checked using underwater flashlights for illumination. Observers checked with one another (using hand-codes) on any fish occupying a position close to or swimming over a grid-line to avoid multiple counts.

When the length of the first adjacent pair of transects was surveyed, the observers would turn 180° and return over the reef to do the next adjacent pair of transects (shallower). The observer doing the shallowest transect of the first pair always did the deeper transect of the second pair. This aided the observers in eliminating or reducing any repeated counts of fish that had been close to the top grid-line on their first pass.

For each fish, the species, size, and activity was recorded. Size was based on comparison of the fish to a scale placed on the edge of the Plexiglas recording slates. Size categories were: Size 1 (<10 cm total length), Size 2 (≥10 - <15 cm), Size 3 (>15 - ≤20 cm), Size 4 (>20 - ≤25 cm), Size 5 (>25 - ≤30 cm), and Size 6 (>30 cm). Observers frequently were able to check their estimates of fish size against the actual size of the fish by aligning the slate, with the scale, immediately next to the fish. A record was also made of the activity of the fish in relation to the habitat (activity niche) at the time it was first sighted. Activity was ranked (1-5) according to the fish's proximity to, and association with, the substrate, and included: 1) sheltering, occupying a hole with at least one entrance/exit but surrounded by substrate on all other sides, including over the dorsum; 2) occupying a crevice, sitting in a manner such that the fish was surrounded by substrate on at least one side; 3) perched, sitting in the open with only the ventrum in contact with the substrate; 4) hovering, maintaining a relatively stationary position off the substrate; and 5) swimming, positioned off the substrate and actively moving forward. The presence of a tag on the fish was also noted, and when possible, the tag number was recorded.

Observations from both divers were pooled over all transects on the reef to give a population census for the reef. A direct count was therefore made of all fish on each reef. Population numbers for each species on each reef were then divided by the surface area of the appropriate reef to give an estimate of their density.

Reef Manipulations

Reefs were initially randomly assigned to one of three experimental treatments: quillback removal, copper removal, or no treatment (control). Log Reef was initially assigned to the Quillback Removal Treatment. However, an apparently large increase (qualitatively) in the number of copper rockfish on Log Reef in the pre-manipulation period, from October to November, 1986, superficially demonstrated that the existing quillback rockfish population on Log Reef was probably not immediately limiting the copper rockfish population. For this reason, Log Reef was reassigned the reverse treatment, the Copper Removal Treatment, to see if copper rockfish were limiting the quillback rockfish population. During the month of March 1987, then, all copper rockfish were permanently removed by spearing from Log Reef. Arbutus Reef was assigned to the Quillback

Removal Treatment and all quillback rockfish were initially removed from the reef in March 1987. Beach Reef was assigned to be the reef receiving no treatment. Sham manipulations on Beach Reef were performed (fish were purposely missed with the spear) to simulate any potential disruption that was occurring on the other two reefs due to the activities of divers removing fish.

Fish were permanently removed from Log and Arbutus Reefs by using a modified two-prong, serrated-tip, Hawaiian sling-spear. With these modifications of the spear, all sizes of rockfish could be easily captured, whether perched in open areas or hiding in crevices, without noticeably disturbing other nearby fish (i.e., within approximately a 1-m radius). It was necessary to permanently remove the rockfish in this experiment because rockfish are known to exhibit homing behaviour (Hallacher 1977; Carlson and Haight 1972; Matthews 1990b) and probably would have returned repeatedly to their home reef, negating the effect of any treatment. The removals of quillback or copper rockfish, depending on the reef treatment, were maintained throughout the post-manipulation survey period. This was done by removing the fish as soon as possible following each census. Removed rockfish were used for analyses of food habit, gut allometry, growth, and reproduction (Chapters III-VI). Experimental manipulations and population surveys continued until November 1988, 20 months following the start of removals (March 1987).

Differences in population densities, sizes, and activities of copper and quillback rockfish on each reef before and after manipulations were analysed by Kruskal-Wallis tests followed by Dunn's Multiple Contrast tests where appropriate (Dunn 1964; Conover 1980; Zar 1984).

Immigration (recruitment) or emigration of individuals (N) following population manipulations was assessed by censusing the number of rockfish on the reef from one month to another, relative to the number of fish removed, as:

$$[12] \qquad N_t = \text{Census}_{t+1} + \text{No. Removed}_t - \text{Census}_t$$

Positive numbers of individuals indicated a gain from census_t to census_{t+1} (immigration), whereas negative numbers of fish indicated that fish had left the reef (emigrated or died).

Movement of rockfish from reefs (emigration or death) in relation to time was investigated by estimating the percentage of tagged fish resighted on the reef at which they had been tagged. In addition, the location of any tagged fish resighted off the reefs was noted, as well as any inter-reef movements.

RESULTS

Physical Properties of the Study Sites

Surface areas of the reefs were similar: 206 m^2 for Beach Reef, 301 m^2 for Arbutus Reef, and 346 m^2 for Log Reef. Visibility on the reefs during the population censuses was minimally 6 m, and mostly between 10-14 m (Fig. 38a). Water temperature at 21 m was fairly constant and ranged between 8-12 °C throughout the year (Fig. 38b). Temperature of the water at the surface, however, changed depending on the month. From December to February, the surface water was colder than water at depth. Surface and deeper waters were the same temperature during March and November. From April to October, however, surface temperatures of the water were higher than the temperature of the water at 21 m, and averaged ~16 °C throughout July, August, and September (Fig. 38b).

Reef Population Censuses

Beach Reef (Non-manipulated)

The densities of quillback rockfish on Beach Reef (the "control" reef) (Fig. 39a) did not differ between the two pre-manipulation seasons (fall 1986 and winter 1987) (Table 27). Although the densities of copper rockfish were also not significantly different between the two pre-manipulation

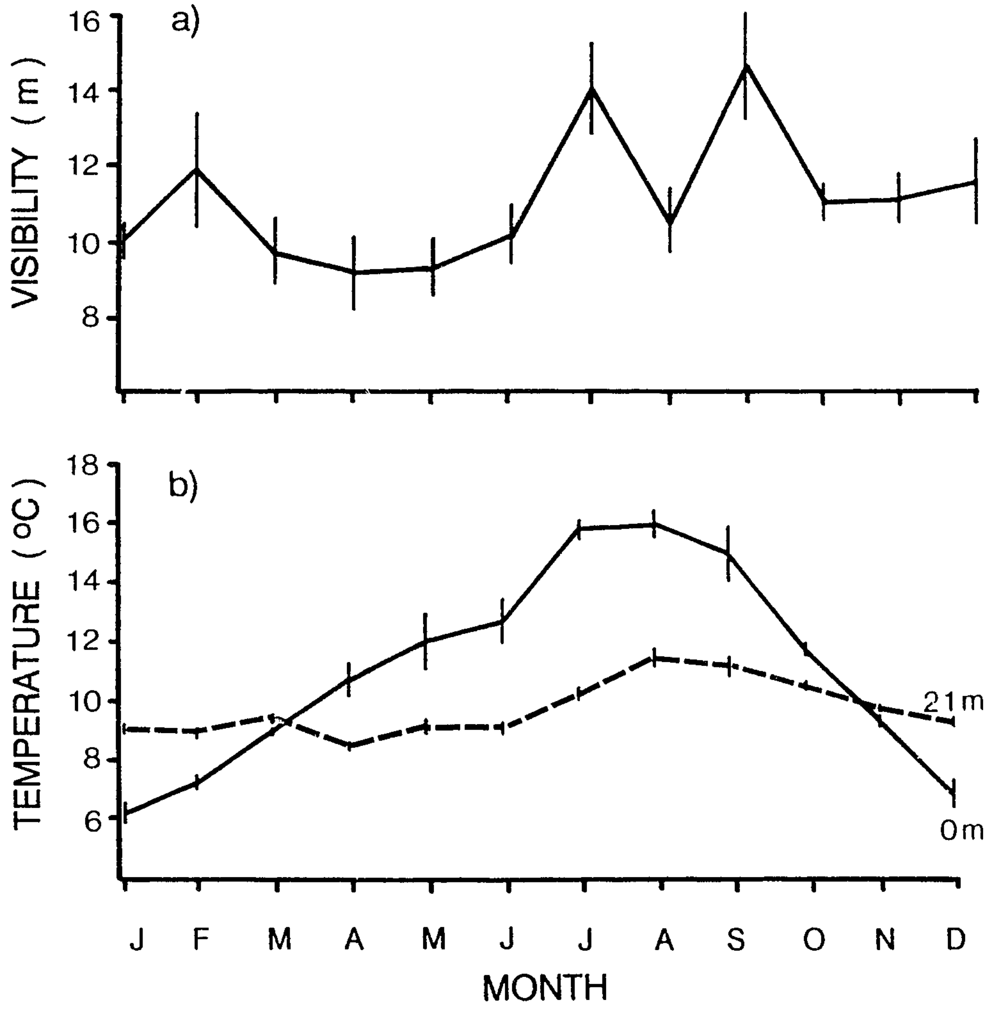

Fig. 38. a) Mean (± 1SE) monthly visibility during population censuses in Saanich Inlet, B.C.; and b) mean (± 1SE) monthly temperature of the surface water and water at 21 m during population censuses.

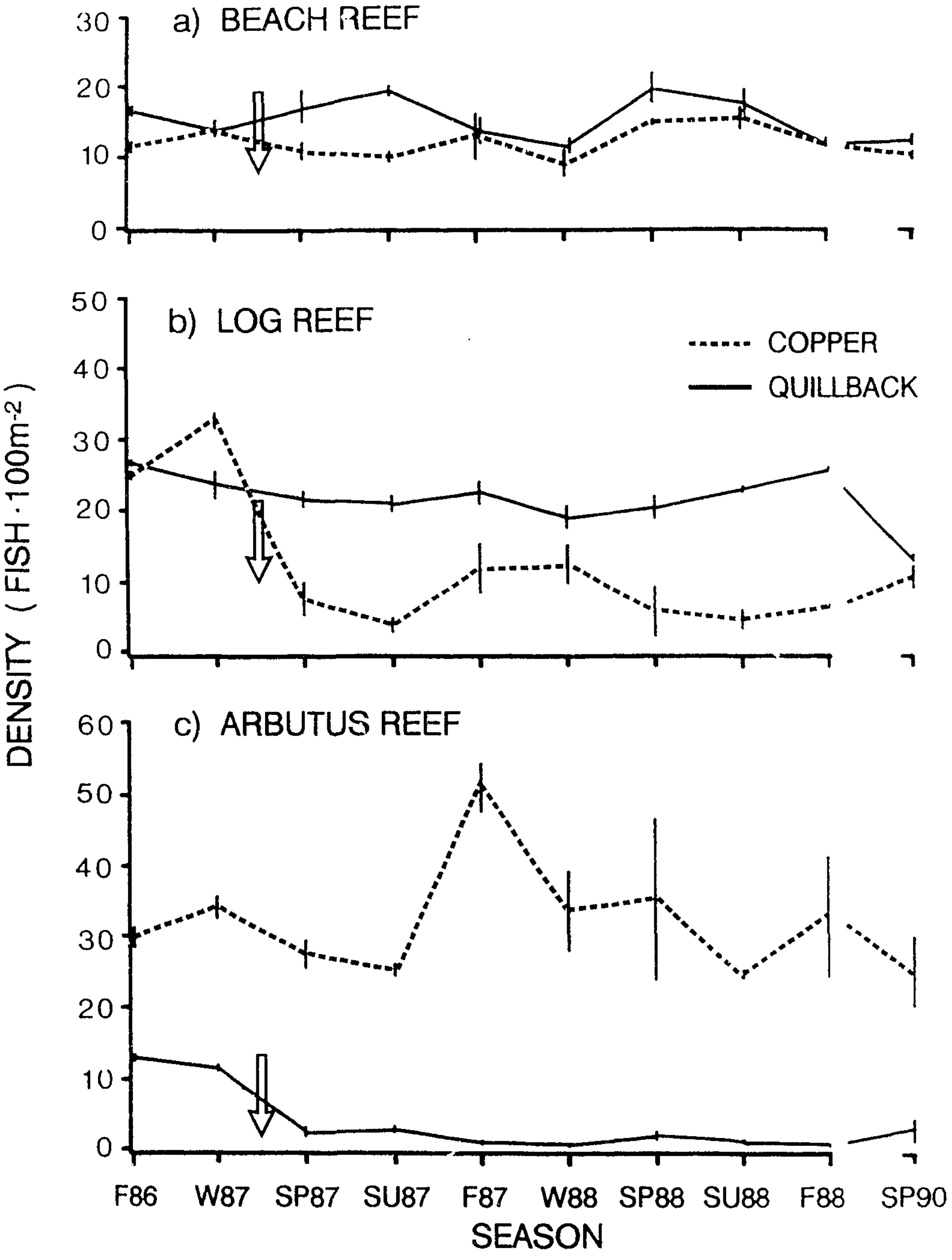

Fig. 39. Mean densities (± 1SE) of copper and quillback rockfish on a) Beach Reef, b) Log Reef, and c) Arbutus Reef, during fall 1986 to spring 1990. Arrows indicate the start of the manipulation period.

Table 27. Kruskal-Wallis summary statistics in testing for differences in density of copper and quillback rockfish between fall and winter seasons in pre- and post-manipulation periods.

		Pre-manipulation		Pre- versus Post-manipulation			
Reef	Species	Fall vs Winter		Fall		Winter	
		χ^2_1	P	χ^2_1	P	χ^2_1	P
Beach	Copper	3.64	0.06	0.53	0.77	3.18	0.07
	Quillback	2.46	0.12	4.41	0.11	2.04	0.15
Log	Copper	1.25	0.26				
	Quillback	2.21	0.14	2.76	0.25	3.87	0.05*
Arbutus	Copper	1.29	0.26	6.95	0.03*	0.56	0.45
	Quillback	1.30	0.25				

seasons (Table 27), the low *P*-level (0.06) indicated that their densities tended to be greater during the winter. Relative to the densities of the pre-manipulation seasons, the post-manipulation densities of quillback rockfish were not different in the fall (fall 1986 versus fall 1987 versus fall 1988) or in the winter (winter 1987 versus winter 1988) (Table 27). Densities of copper rockfish in the pre- and post- manipulation fall and winter periods were not statistically different (Table 27), although the low *P*-level (0.07) indicated that copper rockfish densities tended to be greater in the pre-manipulation winter period.

Overall, the densities of copper and quillback rockfish on Beach Reef on an annual basis were not different among years (χ^2_2 = 0.69, 4.33; P = 0.71, 0.11, for copper and quillback rockfish respectively). Three years after the sham manipulations on Beach Reef (spring 1990), the densities of copper and quillback rockfish on Beach Reef were similar to previous levels (Fig. 39a). This indicated that copper and quillback rockfish populations on Beach Reef were, on an annual basis, in equilibrium. Equilibrium, in this instance, referred to the temporal constancy of the species composition and relative abundance (i.e., persistence) (Connell 1978; Sale 1980).

The density of copper rockfish on Beach Reef also did not differ significantly on an overall seasonal basis (χ^2_3 = 0.21, P = 0.98). In contrast, a seasonal effect on quillback rockfish density on Beach Reef was significant (χ^2_3 = 8.98, P = 0.03) and densities of quillback rockfish were greater on Beach Reef during the spring and summer than the fall, or to a greater extent, the winter (Fig. 39a). This indicated that the perceived equilibrium for quillback rockfish on an annual basis was dynamic and changed on a finer-scale (seasonal) basis.

Log Reef (Copper Rockfish Removed)

On Log Reef (Fig. 39b), the densities of copper rockfish in the two pre-manipulation seasons were the same (Table 27). After the initial removal of copper rockfish from Log Reef (late winter 1987), the density of copper rockfish fluctuated at relatively low levels until the fall of 1987. Maintaining a complete removal of copper rockfish from Log Reef in the fall was difficult due to recruitment (discussed below). In the spring of 1990, 19-20 months after the cessation of copper rockfish removals, the density of copper rockfish had increased only to the levels found in the fall and winter immediately following the manipulation and had not regained the pre-manipulation density level (Fig. 39b). This indicated that the copper rockfish population on Log Reef was not stable under prolonged perturbation (continuous removals): the population could not return to its presumed equilibrium state (i.e., pre-manipulation density) following the perturbation (Connell 1978; Sale 1980).

The density of quillback rockfish on Log Reef was also similar between the two pre-manipulation seasons (Table 27) and the fall season before and after manipulation (Table 27). In the winter, however, the density of quillback rockfish prior to the manipulation was greater than after the manipulation (Table 27).

In general, the density of quillback rockfish on Log Reef was different among years ($\chi_2^2 = 8.17$, $P = 0.02$) and among seasons ($\chi_3^2 = 16.42$, $P = 0.00$). On average, density of quillback rockfish was greatest in the fall, when compared to the other seasons, and greatest in 1986 when compared to 1987-88 (Fig. 39b). Additionally, in the spring of 1990, 45 months after the start of the experimental reef study, the density of quillback rockfish had decreased to approximately one-half of its level prior to the fall of 1988.

It was therefore evident that reducing the density of copper rockfish on Log Reef did not result in an increase in the density of quillback rockfish on Log Reef. Copper rockfish did therefore not have an interspecific competitive effect on quillback rockfish.

Arbutus Reef (Quillback Rockfish Removed)

Density of quillback rockfish on Arbutus Reef (Fig. 39c) was not different between the fall and the winter prior to manipulation (Table 27). After the initial removal of quillback rockfish from Arbutus Reef in March of 1987, the density of quillback rockfish was negligible and was maintained at levels near zero density (Fig. 39c). In the spring of 1990, quillback rockfish density was still near zero. The quillback rockfish population on Arbutus Reef was apparently not stable under continual perturbation as it did not regain the pre-manipulation density following cessation of the perturbation.

Density of copper rockfish on Arbutus Reef prior to manipulations was similar for the fall and the winter seasons (Table 27). In addition, the density of copper rockfish in the winter of the post-manipulation period was the same as in the pre-manipulation period (Table 27).

In contrast, the densities of copper rockfish in fall of the post-manipulation years (1987 and 1988) were significantly different than their density in the fall of the pre-manipulation period (1986) (Table 27) (Fig. 39c). Specifically, the density of copper rockfish in fall 1987 following the manipulation was greater than their density in fall 1986 prior to the removals (Dunn's test: $Q = 3.10$, $P < 0.01$). Two years after the initial removals, in fall 1988, their density was the same as in fall 1987 ($Q = 1.67$, $P = >$

0.20). This response was graded, however, because the density of copper rockfish in the fall of 1988 was not significantly different from their density in the fall of 1986 ($Q = 0.24$, $P > 0.50$). Three years after the manipulation (spring 1990), the density of copper rockfish on Arbutus Reef was the same as for previous spring periods (Fig. 39c).

Overall, the density of copper rockfish on Arbutus Reef was not different among years of the study ($\chi^2_2 = 0.08$, $P = 0.65$) but was different among seasons ($\chi^2_3 = 10.73$, $P = 0.01$). Density was greater in the fall and winter compared to the summer ($Q = 2.74$, $P < 0.05$). Spring densities were intermediate and were not significantly different from either the fall/winter highs or the summer low ($Q = 1.36$, $P > 0.50$). The variability of the population censuses on Arbutus Reef increased noticeably beginning in the fall following the beginning of the manipulation, relative to the population censuses prior to the manipulation of quillback rockfish (Fig. 39c). This indicated that the density of copper rockfish on Arbutus Reef was fluctuating, and that at least a portion of the copper rockfish population was moving on and off the reef. The degree of variability noted in the densities of copper rockfish on Arbutus Reef was not observed in the density estimates for either copper or quillback rockfish on the other two reefs.

The significant increase in density of copper rockfish on Arbutus Reef in the first fall following the removal of quillback rockfish initially suggested that copper rockfish were affected by the presence of quillback rockfish and that interspecific competition was occurring. This was also supported by the absence of an increase in the density of copper rockfish on Beach Reef during the same time period. The decrease in the density of copper rockfish back to pre-manipulation densities following the second year of post-manipulation (fall 1988), however, indicated that any competitive effect of quillback rockfish on copper rockfish was transitory.

Recruitment to Manipulated Reefs

Log Reef

The number of copper rockfish on Log Reef in February 1987, immediately prior to their removal, was estimated as approximately 109 fish. With the commencement of removal operations in March 1987, it became obvious that copper rockfish were moving on to Log Reef while the removal operations were taking place. Based on a population census of Log Reef in early April, it was estimated that approximately 70 copper rockfish had moved on to Log Reef during March (Fig. 40a). After this initial influx of copper rockfish to Log Reef, the number of copper rockfish

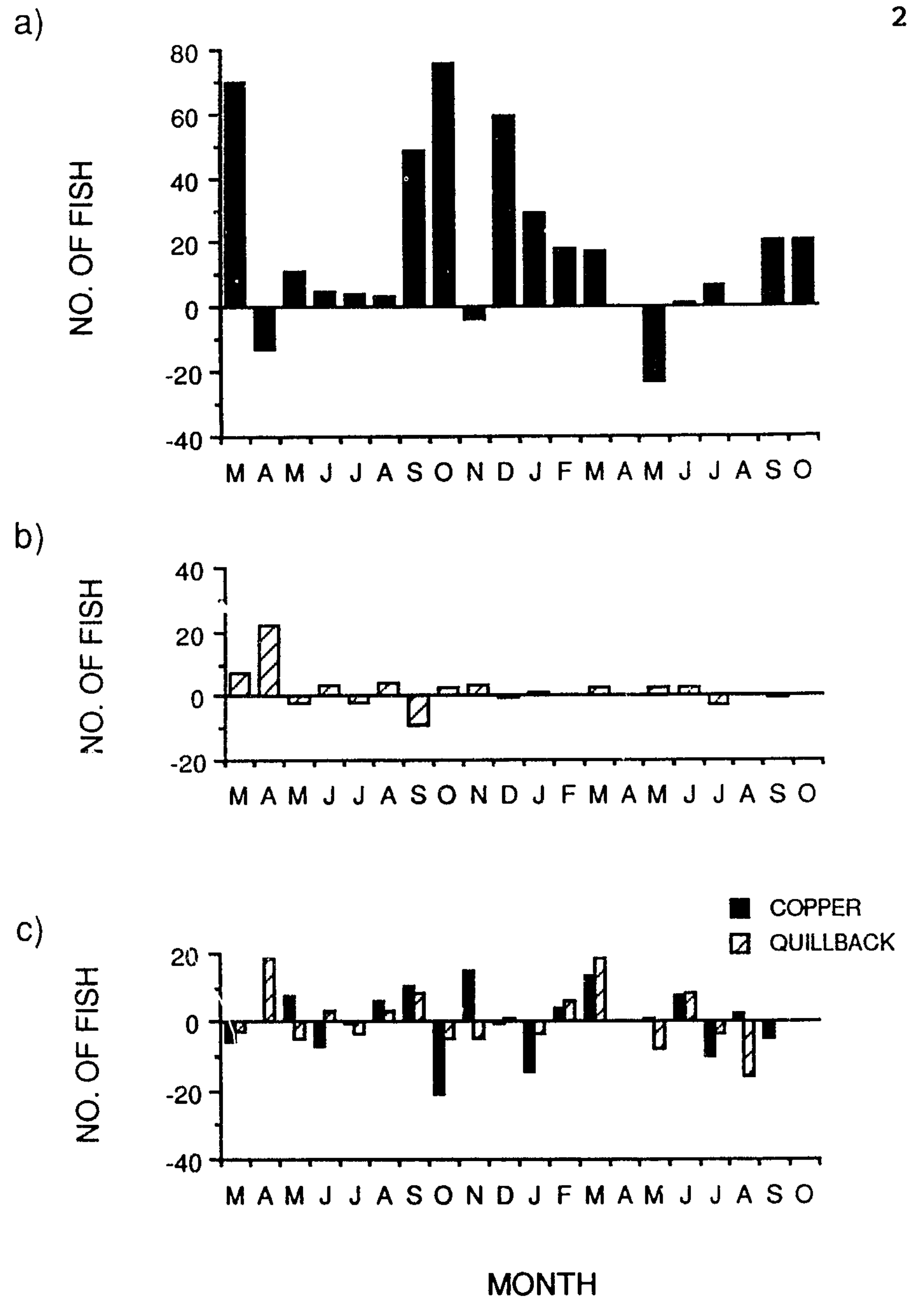

Fig. 40. Immigration and emigration by a) copper rockfish to Log Reef following removal of copper rockfish; b) quillback rockfish to Arbutus Reef following removal of quillback rockfish; and c) copper and quillback rockfish on Beach Reef following sham manipulation.

moving on to Log Reef lessened (Fig. 40a) and it was possible to reduce and maintain a relatively low density of copper rockfish on Log Reef during the spring and summer (April-August) of 1987 (Fig. 39b). From September 1987 to March 1988, however, copper rockfish again "flooded" on to Log Reef and 17-75 copper rockfish moved on to Log Reef each month (with the exception of November) (Fig. 40a). This made maintaining the removal of copper rockfish from Log Reef difficult and, although copper rockfish densities were reduced during this time period (fall 1987 and winter 1988), the overall densities were still relatively high (Fig. 39b). Again, in the spring and summer of 1988 the recruitment of copper rockfish to Log Reef slowed and, as in April 1987, it was estimated that some copper rockfish had actually moved off Log Reef (Fig. 40a). In September and October 1988, copper rockfish again moved on to Log Reef, although apparently not to the same extent as in the previous fall (Fig. 40a). In total, 441 copper rockfish were removed from Log Reef, approximately four times the initial population level.

The immigration of copper rockfish onto Log Reef during the fall coincided with decreasing temperatures, with the surface water becoming colder than the water temperature on the reefs at 21 m (Fig. 38b). Conversely, their emigration from, or a lack of immigration to, Log Reef coincided with the surface temperatures being higher than the water temperatures on the reefs. Although correlational, this indicated that the movement of copper rockfish on and off the reef may be cued, at least in part, by differential water temperatures between shallow water (as exemplified by surface temperatures) and deeper water (i.e., as on the reefs).

Arbutus Reef

The number of quillback rockfish on Arbutus Reef in February, prior to their removal, was estimated as 35 fish. After removal, there was an initial movement of quillback rockfish onto Arbutus Reef in March and April 1987 (Fig. 40b). After April 1987, however, very few quillback rockfish moved onto Arbutus Reef (Fig. 40b) and densities could be easily maintained near zero (Fig. 39c). In total, 60 quillback rockfish were removed from Arbutus Reef, almost two times their initial population level.

Beach Reef

Immediately prior to the sham manipulations on Beach Reef, the number of copper and quillback rockfish on the reef was estimated as 26 and 29 individuals respectively (Fig. 40c). During and after the month of sham manipulations (March 1987), the fluctuations in emigration and immigration observed for both copper and quillback rockfish indicated that some fish were moving on-and-off the reef, but there did not appear to be any consistent trend in the direction or timing of their movements.

Size of Fish on Reefs: Effects of Manipulations

Beach Reef

Quillback rockfish on Beach Reef censused prior to the sham manipulation (fall 1986 and winter 1987) were of similar size to those censused in the complementary post-manipulation period (fall 1987 and winter 1988) ($\chi^2_1 = 0.48$, $P = 0.49$). The majority of quillback rockfish censused on Beach Reef were of size category 3.70 ± 0.04 ($\overline{X} \pm 1SE$, $n = 754$) and size of quillback rockfish did not vary among seasons ($\chi^2_3 = 4.48$, $P = 0.21$).

Copper rockfish censused on Beach Reef in the pre-manipulation period, however, were significantly larger (4.09 ± 0.06, $n = 483$) than copper rockfish censused on the reef in the complementary post-manipulation period (3.55 ± 0.10, $n = 136$) ($\chi^2_1 = 20.88$, $P = 0.00$). Size of copper rockfish censused on Beach Reef were not different among seasons ($\chi^2_3 = 7.10$, $P = 0.07$), however, and averaged 3.90 ± 0.04 ($n = 920$).

Log Reef

Copper rockfish removed from Log Reef in the initial manipulation (March 1987) were on average 232 ± 4 mm (Size 4) (*n* = 119) in total length (Fig. 41a). There was no difference between the average size of male and female copper rockfish initially collected from Log Reef ($\chi^2_1 = 0.11$, $P = 0.74$). In addition, the ratio of female:male rockfish collected was not different from 50:50 ($\chi^2_c = 0.21$, $P > 0.50$).

Copper rockfish collected from Log Reef after the initial manipulation (after March 1987) were significantly smaller than copper rockfish collected in the initial removals ($\chi^2_1 = 87.17$, $P = 0.00$) and averaged 187 ± 3 mm total length (Size 3) (*n* = 322) (Fig. 41b). There was also no difference between the size of male and female copper rockfish moving onto Log Reef after the initial removals ($\chi^2_1 = 0.01$, $P = 0.95$). The ratio of females to males collected, however, was significantly different than 50:50, with more males collected than females ($\chi^2_c = 6.29$, $P < 0.02$).

The average size of quillback rockfish on Log Reef did not change between the pre-manipulation censuses (fall 1986 and winter 1987) and the complementary post-manipulation censuses (fall 1987 and winter 1988) ($\chi^2_1 = 1.91$, $P = 0.17$), and averaged 3.40 ± 0.02 (Size 3) (*n* = 2677). There was also no difference in the size of quillback rockfish censused on Log Reef among seasons ($\chi^2_3 = 3.33$, $P = 0.34$).

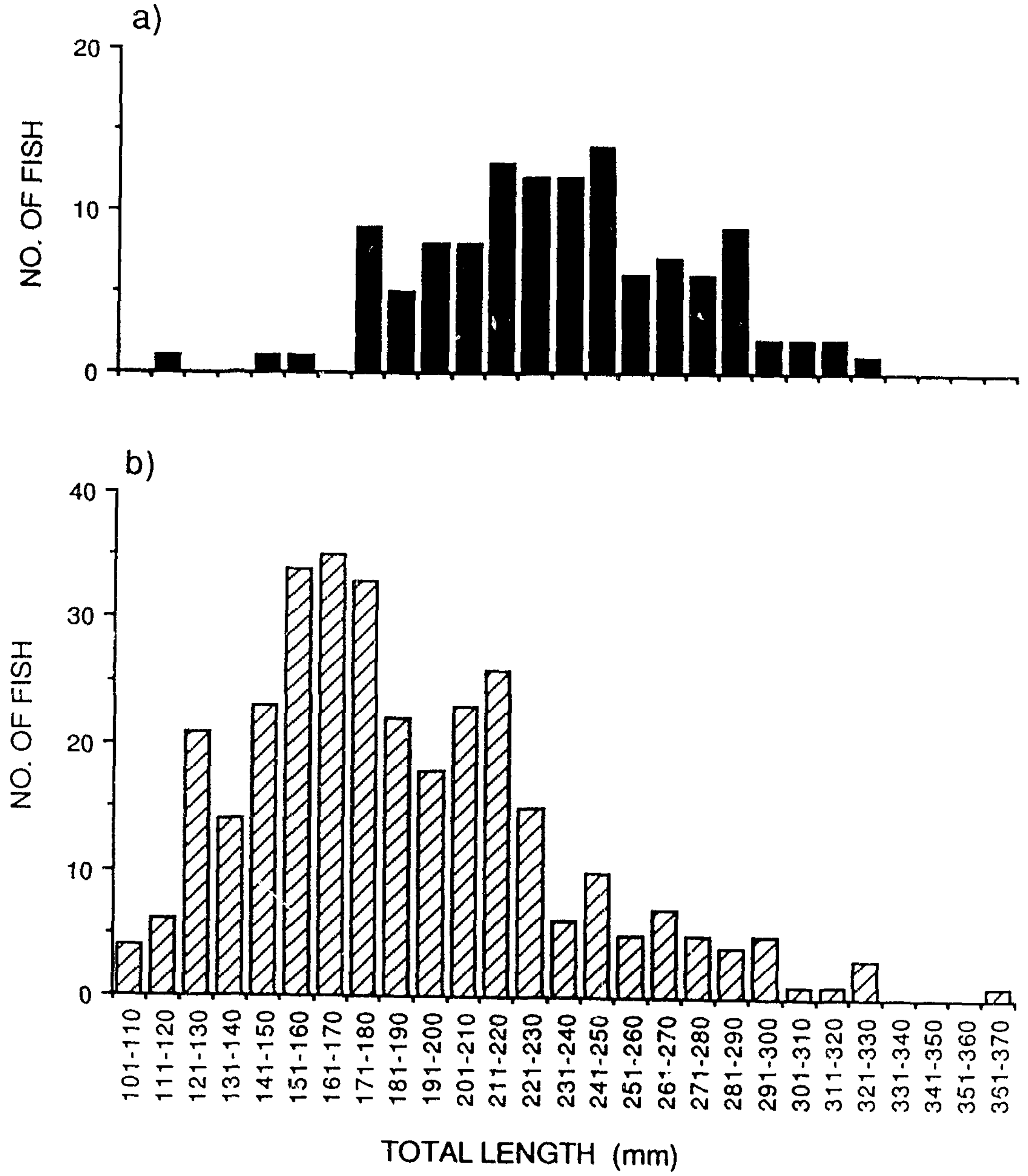

Fig. 41. Size of copper rockfish removed from Log Reef: a) fish collected in the initial removal in March 1987; and b) fish collected in removals after March 1987.

Arbutus Reef

The size of quillback rockfish removed off Arbutus Reef during the initial manipulation (March 1987) averaged 218 ± 8 mm total length (Size 4) ($n = 37$), and there was no difference in the average size of males or females collected in the initial removals ($\chi^2_1 = 0.31$, $P = 0.58$). Males and females were also equally represented in the initial removal ($\chi^2_c = 1.73$, $P > 0.10$).

Quillback rockfish collected from Arbutus Reef after the initial removals (after March 1987) were the same size as quillback rockfish initially collected ($\chi^2_1 = 0.01$, $P = 0.93$). In addition, males and females collected after the initial removals were of similar size ($\chi^2_1 = 1.80$, $P = 0.18$) and the sex ratio was not different from 50:50 ($\chi^2_c = 0.70$, $P > 0.25$).

The average size of copper rockfish on Arbutus Reef was different between the pre-manipulation and post-manipulation censuses: copper rockfish censused in the pre-manipulation period (fall 1986 and winter 1987) (3.9 ± 0.02, $n = 2016$) were, on average, larger than copper rockfish censused in the complementary post-manipulation period (fall 1987 and winter 1988) (3.4 ± 0.04, $n = 762$) ($\chi^2_1 = 146.18$, $P = 0.00$). This indicated that the copper rockfish moving onto Arbutus Reef during the fall and winter (Fig. 39c) were smaller fish compared with copper rockfish present before the removal of quillback rockfish.

Activity of Fish

Beach Reef

Activities of copper rockfish censused on Beach Reef in the pre-manipulation period were not different from the activities of copper rockfish censused in the post-manipulation period ($\chi^2_1 = 0.08$, $P = 0.78$), and most fish were perched in the open (Activity = 3.11 ± 0.05, $n = 624$). Activities of copper rockfish did vary seasonally ($\chi^2_3 = 25.46$, $P = 0.00$), however, and copper rockfish censused in the spring, summer, and winter were more active in the water column (swimming or hovering) (3.42 ± 0.10, $n = 591$) than fish censused in the fall (2.98 ± 0.07, $n = 334$) (Dunn's Multiple Contrasts, $P < 0.05$).

Quillback rockfish censused on Beach Reef in the fall and winter before and after the manipulation also had similar activities ($\chi^2_1 = 1.75$, $P = 0.18$), and were primarily perched in the open (3.03 ± 0.04, $n = 760$). Activities of quillback rockfish on Beach Reef also varied seasonally ($\chi^2_3 = 56.25$, $P = 0.00$), with fish censused in the spring and summer using the water column (3.43 ± 0.07, $n = 466$) more than fish censused in the winter and fall (3.05 ± 0.05, $n = 760$) (Dunn's Multiple Contrasts, $P < 0.05$).

Differences in the activities of copper and quillback rockfish censused in the pre- and post- manipulation fall-winter periods were not significant ($\chi^2_1 = 0.34, 0.12$; $P =$

0.56, 0.73, for pre- and post- manipulation respectively). In addition, there were no significant differences between species in their activities in each of the four seasons (χ^2_1 = 1.62, 0.40, 1.12, 0.83; P = 0.20, 0.52, 0.29, 0.36, for winter, spring, summer, and fall respectively).

Overall, the activities of copper and quillback rockfish on Beach Reef were very similar with most fish observed perched in the open. In general, the activities of the two species were also similar with fish active in the water column in the spring and summer. Copper rockfish also were frequently observed hovering or swimming in the winter.

Log Reef

Copper and quillback rockfish censused on Log Reef in the pre-manipulation period had different activities (χ^2_1 = 170.74, P = 0.00). Copper rockfish were observed in shelter holes and crevices more than quillback rockfish, which were observed mainly perched in the open or hovering.

Activities of quillback rockfish censused on Log Reef in the pre-manipulation period, however, were not different from their activities in the post-manipulation period (χ^2_1 = 0.37, P = 0.54) and most fish were perched in the open or hovering, in both the pre- and post- manipulation periods (3.13 ± 0.02, n = 2683). In the absence of copper rockfish, therefore, quillback rockfish had not increased their use of crevices and shelter holes. A competitive effect of copper rockfish on quillback rockfish based on activities was therefore not supported.

Activities of quillback rockfish varied seasonally (χ^2_3 = 35.46, $P = 0.00$) and fish were more active in the water column in the summer and fall (3.28 ± 0.04, $n = 1963$) than in the winter (3.03 ± 0.03, $n = 1084$). Activity of fish in the spring was intermediate between summer/fall and winter (3.19 ± 0.05, $n = 566$) (Dunn's Multiple Contrasts, $P < 0.05$).

In addition, copper rockfish immigrating onto Log Reef in the fall and winter following the initial manipulation were more active in the water column than copper rockfish in the pre-manipulation period (3.38 ± 0.09, $n = 340$) (χ^2_1 = 60.52, $P = 0.00$). Copper rockfish in the post-manipulation period were also more active in the water column than quillback rockfish in the post-manipulation period (χ^2_1 = 7.00, $P = 0.01$).

Arbutus Reef

Activities between copper and quillback rockfish censused on Arbutus Reef during the pre-manipulation period were significantly different (χ^2_1 = 31.30, $P = 0.00$). Although both species were observed most frequently near the substrate perched in the open, copper rockfish were observed perched in crevices and shelter holes (2.63 ± 0.03, n = 2011) more often than quillback rockfish (2.88 ± 0.04, n =

775), similar to their pre-manipulation activities on Log Reef.

Activities of copper rockfish censused on Arbutus Reef before and after the removal of quillback rockfish, however, were not different ($\chi^2_1 = 2.98$, $P = 0.08$), and fish in both periods were primarily observed in close association with the substrate, perched in the open, in crevices, or in shelter holes (2.67 ± 0.03, $n = 2775$).

It was therefore apparent that copper rockfish had not significantly changed their activities (e.g., increased their use of the open perches and the water column) in the absence of quillback rockfish. A competitive effect of quillback rockfish on copper rockfish was therefore not supported based on the activity-habitat niche.

Copper rockfish censused on Arbutus Reef varied their activities on a seasonal basis ($\chi^2_3 = 101.90$, $P = 0.00$), however, and fish censused in the summer were observed swimming in the water column more frequently than fish censused in the spring and fall. In addition, copper rockfish censused in the winter were observed more often in shelter holes and crevices than fish in the spring and fall (Dunn's Multiple Contrasts, $P < 0.05$).

The activities of quillback rockfish censused on Arbutus Reef in the pre- and post- manipulation periods were not different ($\chi^2_1 = 0.01$, $P = 0.92$), although small sample size for quillback rockfish in the post-manipulation period restricted any interpretation. Most quillback rockfish censused on Arbutus Reef during the fall and winter, in both pre- and post- manipulation periods, were either perched in the open, in crevices, or in shelter holes (2.88 ± 0.04, *n* = 792).

Movements of Tagged Fish

Beach Reef

With the start of censusing in October 1986, it was apparent that approximately 50% of the tagged copper and quillback fish had left or had been taken (by unknown causes) from Beach Reef in the intervening one to two months after their initial tagging (Fig. 42a,b). During the remainder of the pre-manipulation period (fall 1986 and winter 1987) the percentage of tagged quillback rockfish on Beach Reef remained relatively constant at around 40-50% (Fig. 42b). The percentage of tagged copper rockfish on Beach Reef during the pre-manipulation period decreased in November 1986 to approximately 35% and remained at 35-40% for the duration of the period (Fig. 42a).

Over a longer term, from October 1986 to October 1988, the percentage of tagged copper and quillback rockfish on Beach Reef steadily decreased (Fig. 43). After the first year of the study, approximately 80% of tagged copper and quillback fish were no longer on Beach Reef. Some of the movement off Beach Reef was due to the movement of fish

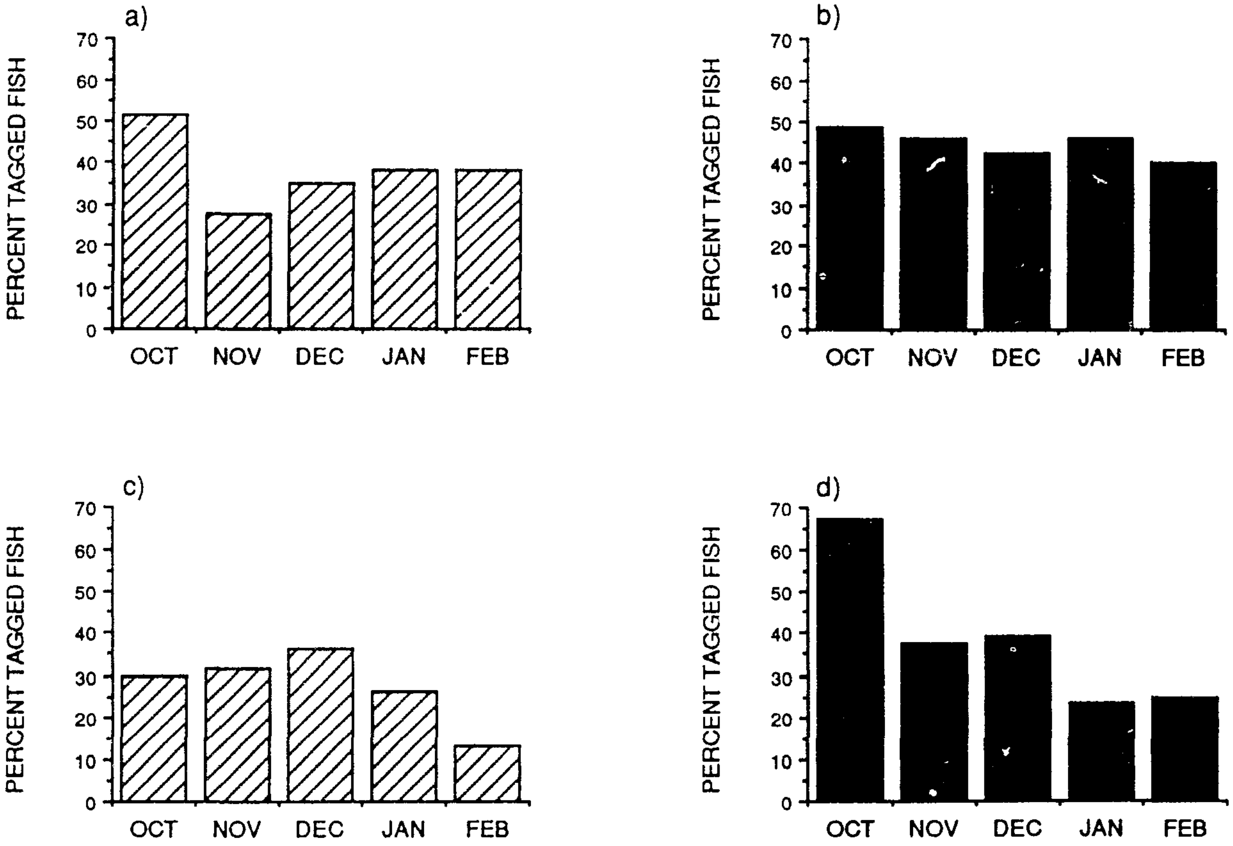

Fig. 42. Mean monthly percentages of tagged fish that were resighted during the premanipulation period: a) copper rockfish and b) quillback rockfish resighted on Beach Reef; c) copper rockfish resighted on Log Reef; and d) quillback rockfish resighted on Arbutus Reef.

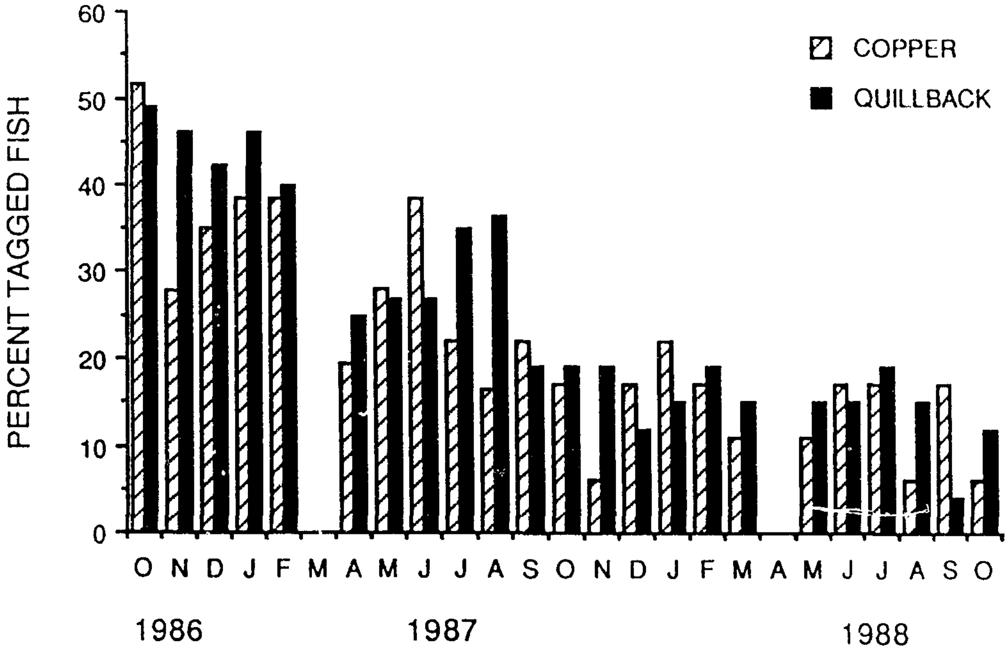

Fig. 43. Mean monthly percentage of tagged copper and quillback rockfish that were resighted on Beach Reef during October 1986-1988.

between reefs. Two female quillback rockfish tagged on Beach Reef were resighted 3 months later on Arbutus Reef. One of these females was subsequently resighted 4 months later, back on Beach Reef. As well, at least one female quillback rockfish was speared on Beach Reef by a SCUBA diver who reported the information as requested on the tag.

Log Reef

In the three months intervening between when copper rockfish were tagged on Log Reef and the first month of censusing Log Reef, approximately 70% of the tagged copper rockfish had left Log Reef (Fig. 42c). For the next four months the percentage of tagged copper rockfish on Log Reef was approximately 25-35%, similar to that of copper rockfish observed on Beach Reef 3-6 months after their initial tagging (Fig. 42a). In contrast, of the four quillback rockfish tagged on Log Reef, three (75%) were still present at the onset of the censusing and for the duration of the pre-manipulation period.

Arbutus Reef

Approximately 70% of quillback rockfish tagged on Arbutus Reef in July and August were present during the October censuses (Fig. 42d). In the following two months this percentage decreased to around 40%, and in a further two months decreased to 25%. By the end of the pre-manipulation period, 7-8 months after tagging, approximately 75% of the tagged quillback rockfish had left or been removed from Arbutus Reef. This was similar to the percentage of quillback rockfish that had left Beach Reef 7-8 months after tagging (around April and May 1987) (Fig. 43).

As with Beach Reef, some of the movement of fish off Arbutus Reef was due to fish moving between reefs. Three quillback rockfish tagged on Arbutus Reef were resighted on Beach Reef 12 months (1 female, 1 male) and 15 months (1 female) later.

Therefore, regardless of the relatively constant density of copper and quillback rockfish observed during the pre-manipulation period (Table 27), individual rockfish were moving off, or on and off, the reef on which they were tagged. Movement of quillback rockfish off the reefs appeared to be slightly less than for copper rockfish (Fig. 42).

DISCUSSION

The lack of an increase in the density or activity niche of quillback rockfish in the absence of copper rockfish (Log Reef) demonstrated that copper rockfish did not have an interspecific competitive effect on quillback rockfish. Conversely, the transitory increase in the fall density of copper rockfish in the absence of quillback rockfish (Arbutus Reef) indicated that quillback rockfish did have a competitive effect on copper rockfish, but the effect was seasonal and at the most, transitory (not maintained).

The apparent asymmetrical, seasonal, and transitory interspecific competitive effect of quillback rockfish on copper rockfish may reflect a relatively common occurrence in natural populations. In the first instance, asymmetry of competitive interactions between species is common. Schoener (1983), in reviewing studies that specifically tested for symmetry in competitive intensity, found that there was a prevalence for asymmetrical competition between species (51/61 or 84%). Connell (1983) and Lawton and Hassell (1981) similarly showed that 61% (33/54) and 66% (23/35) of the species-pairs reviewed, respectively, were asymmetrical in their competitive interactions. In the majority of studies in which competition was shown to be operating, therefore, the competitive interactions between the species were asymmetrical.

Temporal variation in the occurrence of competition is not as well documented because many studies of competition are too short-term (i.e., less than one year) (Wiens 1977; Schoener 1982, 1983). Wiens (1977) suggested that competition occurs infrequently and only in times of an 'ecological crunch' when resources become severely limited, for example, as a result of environmental conditions such as drought. Dunham (1980), studying two sympatric iguanid lizard species in wet and dry years, supported Wiens' contention that competitive intensity varied year to year depending on environmental conditions. Connell (1983), reviewing temporal variability in competition, concluded that of all species showing competition, 59% showed annual variation. Temporal variation in the occurrence or intensity of competition was, therefore, as common an occurrence as a lack of variation.

The concept of the 'ecological crunch' contributing to the presence and intensity of competition can easily be reduced from Wiens' (1977) grander scale (i.e., years, decades, centuries) down to a smaller scale, such as seasons. This appeared to be a plausible explanation for the intermittent competitive effect of quillback rockfish on copper rockfish during the fall season. Overall, it was apparent that at least some copper rockfish undertook a seasonal movement: they moved onto the study reef areas in the fall and winter, and moved off the reefs in the spring and summer. Although not directly examined, the movement of copper rockfish on to the deeper reef areas during the fall may effectively create an 'ecological crunch' by causing the space or food associated with the reefs to become limiting to the population densities of sympatric copper and quillback rockfish During the fall, quillback rockfish are apparently competitively superior to copper rockfish and limit their population density. With the movement of some of the copper rockfish off the study reefs during the spring and summer, space or food limitations would be slackened and a competitive effect would either be lacking or too small to produce an observable effect on population densities.

The seasonal movement of copper rockfish was qualitatively supported by our personal observations (D. Murie, B. Clapp, G. Krause) which were made when we were positioned at our diving safety stops at 6 and 3 m (= 20 and 10 ft) during ascent from the study reefs. We noted that during the summer months there were relatively more copper rockfish in shallow water (<5 m) than in the fall and winter. However, it was not known whether these copper rockfish were moving horizontally along the coast, or were moving up from deeper waters. My study suggests that at least some copper rockfish in Saanich Inlet undertake a vertical seasonal movement. Seasonal movement of copper rockfish may also occur in other areas (e.g., Puget Sound, Washington) as Moulton (1977), Richards (1987), and Matthews (1990a) have all observed a greater density of copper rockfish on their study sites (<20 m water depth) during the spring and summer than during the fall and winter, the opposite of the population trends for copper rockfish on Log and Arbutus Reefs. Reefs used in my study in Saanich Inlet were considerably deeper (18-31 m), and hence my surveys recorded an increase in density of copper rockfish during the fall and winter rather than a decrease in their density as observed from reefs in shallower waters.

Consistent with my study, Moulton (1977) and Matthews (1990a) speculated that copper rockfish were moving into deeper water during the fall and winter. They presumed that this was due to the die-off of macrophytic algae (e.g., bull kelp, *Nereocystis leutkeana*; *Agarum fimbriatum*; *Pterygophora californica*) in shallow waters, which reduced protective cover and available prey for the fish. In my study area in Saanich Inlet, however, the only large alga that provides cover is *Agarum*, and it persists in Saanich Inlet throughout the year. Other possible reasons for the seasonal movement of copper rockfish could include: the decreasing temperature of shallow waters in the fall (Fig. 38b); or movement associated with reproductive activity, given that the majority of courting and mating activity occurs between October and March (Fig. 27, 28).

Richards (1987) suggested that observed decreases in copper rockfish densities in the fall and winter were more likely due to copper rockfish moving into crevices during the fall and winter and therefore becoming harder to detect during the survey dives. This was based on her observation that most copper rockfish were found in less than 20 m of water depth in the Strait of Georgia (Richards and Cass 1985). Copper rockfish on Log and Arbutus Reefs in Saanich

Inlet were also observed more frequently in close association with the substrate (e.g., perched in shelter holes, crevices, or in the open) during the fall and winter than in the spring and summer.

Overall, the interspecific competitive effect that quillback rockfish had on copper rockfish during the fall was also transitory, and resulted in a weak effect on the density of copper rockfish over time. In the first instance, the removal of quillback rockfish from Arbutus Reef and copper rockfish from Log Reef effectively opened up habitat that was potentially suitable for rockfish of either species. It was obvious, however, that copper rockfish were much more effective at recolonizing or recruiting into this space than quillback rockfish (Fig. 40). Patten (1973) also noted rapid re-colonization by copper rockfish in Puget Sound, Washington, with the original number of copper rockfish completely restored after a one month cessation of removals.

The recruitment effectiveness of copper rockfish may be a function of the available pool of recruits. Unlike coral reef fish communities, in which recruitment is almost always undertaken through settlement of dispersive pelagic larvae (Sale 1980; Roberts 1991), the recruitment of fishes to temperate rocky reefs is accomplished mainly by subadults and adults (Gascon and Miller 1981; Matthews 1985; Solonsky 1985). This was consistent with the pattern of recruitment of copper rockfish to Arbutus and Log Reefs in which fish were, on average, smaller than copper rockfish prior to the removals but none were young-of-the-year (YOY) and most were >100 mm total length (Fig. 41b). Barker (1979) also found that copper rockfish recolonizing a reef where the dominant fish species had been heavily exploited (removed) were, on average, smaller than copper rockfish observed prior to the removals. Larson (1980a), studying interspecific competition between gopher rockfish and black-and-yellow rockfish in California, also noted that fish invading areas where he had removed fish were relatively small compared with fish observed prior to the removals. Knowing that both species defend territories from conspecifics as well as heterospecifics (Larson 1980b), he speculated that these smaller fish were individuals that were not able to hold territories, or possessed suboptimal home ranges, prior to their occupying space on the experimental areas after the removal of larger fish.

Recruitment of rockfish to a rocky reef therefore depends on pelagic juveniles settling, for the first few years of life, in a suitable area near, but not on, a reef inhabited by larger rockfish. Copper rockfish recruiting on to Log Reef during the fall were between 121 and 220 mm total length (Fig. 41b) and therefore were around 2-5 yrs old (Fig. 21a). Small copper rockfish were evidently abundant in the study area because hundreds of them were able to recruit onto either Log Reef or Arbutus Reef in the absence of larger copper or quillback rockfish, respectively. In contrast, small quillback rockfish were noticeably scarce in the area, and were difficult to find for feeding and age analyses (Chapter III and V). In addition, in contrast to copper rockfish, quillback rockfish initially recruiting onto Arbutus Reef were the same size as the quillback rockfish initially removed from that reef. Barker (1979) also found that recruiting quillback rockfish were not significantly smaller than the size of quillback rockfish observed in his pre-removal period.

The large difference in recruitment between copper and quillback rockfish suggests that quillback rockfish juveniles may have a greater mortality rate than copper rockfish juveniles in this area. All the quillback rockfish I have seen in Saanich Inlet were always in depths greater than 15 m, regardless of size or season, and it may therefore be that their juveniles, once settled near the substrate, are prone to relatively greater predation than juvenile copper rockfish in shallow water because: 1) there is virtually no protective cover afforded by *Agarum* at greater depths in Saanich Inlet; and 2) in many fish, increasing size is correlated with increasing depth and very small quillback rockfish would therefore be susceptible to predation from relatively larger fish at depth

Juvenile quillback rockfish may also occur in specific nursery areas and, over a period of years, move out from these areas onto rocky reefs. There was no evidence to suggest that this was the case, however, because there were no nursery areas detected at depth using the *Pisces* submersible (Chapter II) and all post-settlement quillback rockfish juveniles (<50 mm in length) observed while SCUBA diving in Saanich Inlet were in small aggregations (1-2 individuals$\cdot$ m^{-2}) and encountered at depths >20 m over small cobble fields (pers. obs.).

In contrast, post-settlement copper rockfish juveniles were observed in Saanich Inlet in schools of approximately 75-100 individuals (pers. obs.). These schools were observed in August-September in depths <20 m and in close proximity to (<2 m) the sand/shell substrate that occurs between rocky areas in Saanich Inlet. In October and November these schools were noticeably smaller (5-30 individuals) and were observed over areas of rock substrate covered with *Agarum*. Qualitatively, therefore, post-settlement juveniles and subadult copper rockfish were observed in much higher densities than juvenile quillback rockfish in Saanich Inlet.

The poor recruitment of subadult and adult quillback rockfish onto Arbutus Reef also indicated that the available recruitment pool of relatively large quillback rockfish in Saanich Inlet was limited. This may have been a result of mortality due to fishing pressure: the rockfish fishery in the 1950s and 1960s was centred around southern Vancouver Island, including Saanich Inlet, and quillback rockfish typically comprise ~85% of the catch (Hand and Richards 1991). Commercial fisheries on rockfish in the Strait of Georgia, including Saanich Inlet and adjacent areas, has persisted since the 1950s and increased substantially in the late 1970s and again in the mid-1980s (Hand and Richards 1991). Fishing pressure has effectively decreased stock abundances of rockfish in the Strait of Georgia and has recently resulted in reduced limits and actual closure of the fishery in some areas (Richards and Cass 1987; Hand and Richards 1991).

The transitory nature of the observable, but weak, interspecific competitive effect of quillback rockfish on copper rockfish indicated that the effect may have been mediated by intraspecific competition within the copper rockfish population. The initially large increase in copper rockfish density on Arbutus Reef (Fig. 39c), in the first fall after the removal of quillback rockfish, was followed not only by a decrease in their density to pre-manipulation levels, but also by increased variability in their population estimates. As the activities of copper rockfish were not different between the pre- and post- manipulation periods, it must be assumed that the variability in the population estimates was due to a substantial number of copper rockfish moving off and on Arbutus Reef. The instability of the copper rockfish population density following their initial recruitment to Arbutus Reef in the fall may be due to strong intraspecific competition, which could reduce the interspecific competitive effect to a level that was no longer detectable (Connell 1983). Interspecific competition, in general, may go undetected if intraspecific competition is stronger (Connell 1983). Assessing the presence of intraspecific competition within copper or quillback rockfish populations was not part of the design of my study. It would nevertheless be worthwhile to consider intraspecific competition in future studies because of the large recruitment potential of copper rockfish.

Experimental manipulation of population densities is regarded as an effective way of testing, directly, the presence or absence of interspecific competition (Dunham 1980; Pianka 1981; Schoener 1983). In manipulating the populations, however, it is assumed that "all other factors" (other than the density reductions/enhancements) are equal (Dunham 1980). Including a control or non-manipulated population in the experimental design presumably allows one to judge how 'equal' these 'other factors' are among the experimental populations. If the experimental design is to remove species 'A' and see if its potential competitor (species 'B') can increase in its absence, and vice versa, it must be assumed that both species at least have the physical potential to increase (recruit). The control, however, cannot provide a basis for examining this assumption because it gives only information on the persistence of copper and quillback rockfish populations (the constancy of their relative abundance), not their stability (ability to return to pre-perturbation abundances) (Connell 1978; Sale 1980). Most obvious from the population manipulations of copper and quillback rockfish, however, was the large difference between the species in their apparent recruitment abilities. Copper rockfish may be able to stabilize manipulated populations (on an annual basis at least) relatively quickly following perturbation. Quillback rockfish obviously cannot stabilize a perturbed population if their pool of recruits is inadequate.

The large differences in recruitment abilities of the two species in relation to population manipulations also has important consequences for the management of copper and quillback rockfish. Quillback rockfish, in particular, would be susceptible to over-exploitation in localized areas in a relatively short time. Copper rockfish may be able to sustain over-fishing in localized areas for a relatively long time by drawing from a relatively large, mobile pool of recruits from adjoining areas. Ultimately, however, neither copper nor quillback rockfish can withstand sustained perturbations (e.g., fishing pressure) in localized areas without significant decreases in abundances. Rehabilitation of a localized area depopulated of quillback rockfish in Saanich Inlet, in particular, would take years (much greater than 3.5 yrs, based on Arbutus Reef).

Given the problems associated with differential recruitment of copper and quillback rockfish, experimental manipulations designed to test for competition may be best restricted to designs that attempt to force a decrease, rather than an increase, in the population density. It probably would not be profitable to try to artificially increase the population density of one rockfish species in order to observe whether the other species' density decreases or stays the same. As stated previously, rockfish are known to home to some degree, and transplanted individuals would probably not remain on the reef onto which they were moved. Manipulation of prey densities in the field would also be cumbersome, if not totally impractical, because much of the prey of copper and quillback rockfish is ephemeral (comprised of pelagic fishes and crustaceans, Chapter III). The avenue that appears to be the most advantageous to pursue would be to manipulate their habitat. Specifically, by reducing the availability of suitable shelter holes, crevices, and perching areas it would be possible to create a limited resource. It would then be possible to test for both the direction and strength of interspecific competition by controlling the degree of habitat reduction and observing the direction and strength of any decreases in population densities. To my knowledge, habitat reduction has never been attempted as a means of clarifying interspecific competition between fishes in marine ecosystems.

SUMMARY

Interspecific competition between copper and quillback rockfish was asymmetrical, seasonal, and transitory. Copper rockfish showed no interspecific competitive effect on the density of quillback rockfish. Quillback rockfish, however, appeared to have a competitive effect on copper rockfish during the fall. This effect was not sustained, however, possibly due to intraspecific competition within the copper rockfish population.

Copper rockfish appeared to move onto the study reefs in 18-31 m water depth, from shallower water (<20 m), during the fall and winter. Copper rockfish recruiting to reefs where the densities of quillback or copper rockfish had been reduced were smaller than fish observed on the reefs prior to the density reductions. Populations of copper and quillback rockfish on Beach Reef, the non-manipulated reef, were persistent on an annual basis. Individual copper and quillback rockfish, however, moved on and off the reef on which they were tagged, and some moved between reefs. Based on tag resightings, copper rockfish appeared to move slightly more than quillback rockfish.

CHAPTER VIII

GENERAL CONCLUSIONS

Sympatric populations of copper and quillback rockfish in Saanich Inlet, B.C., have similar habitat use, activities, feeding ecology, gut allometry, growth, and reproductive traits (Table 28).

Based on observations using the *Pisces IV* submersible, copper rockfish were sympatric with quillback rockfish in depths between 21 m and 65 m. Densities of both species were greatest in areas of complex habitat consisting of broken rock and boulder fields. Copper and quillback rockfish were observed most frequently perched in the open or hovering in the water column close to the substrate; copper rockfish were observed swimming more often than quillback rockfish.

Both copper and quillback rockfish relied on demersal crustaceans throughout the year and, in contrast, ate relatively few demersal fishes. Copper rockfish consumed a greater proportion of pelagic fishes than quillback rockfish, whereas quillback rockfish had a greater proportion of pelagic crustaceans in their diet than copper rockfish. Niche overlap in feeding habits based on mass of food resources consumed by copper and quillback rockfish was relatively high (>0.55) throughout the year, and in

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII.

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER II: DISTRIBUTION		
Depth Range (m)	0-65	21-115
Habitat	Complex substrate	Complex substrate
Activities	Hovering or perched in the open, swims more than QBR	Perched in the open or hovering, swims less than CR
Species Associations	QBR, CR, Tiger Rockfish	QBR, CR, Tiger Rockfish
CHAPTER III: FEEDING HABITS		
Composition of Diet (% occurrence)	Demersal crustaceans and pelagic fish	Demersal and pelagic crustaceans
Seasonal occurrence in the presence of food	Independent of season in spring and summer	Higher proportion
Size of Food Items Consumed	Same size of fish and pelagic crustaceans as QBR	Same size of fish and pelagic crustaceans as CR
	Larger demersal crustaceans than QBR	Smaller demersal crustaceans than CR

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII. (Cont'd).

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER III: FEEDING HABITS		
Diel Variation in Feeding	Crepuscular, secondarily day-time	Day-time
Seasonal Quantity of Food Consumed	Maximum in winter and greater than QBR	Maximum in winter and less than CR
Feeding Niche Breadth (Based on Mass)	Minimum in winter and narrow (0.023)	Minimum in winter and narrow (0.019)
Feeding Niche Overlap (Based on Mass)	Maximum in winter and high (0.996)	Maximum in winter and high (0.996)
CHAPTER IV: GUT ALLOMETRY		
Mass of Caeca Relative to Body Size	Similar to QBR	Similar to CR
Mass of Intestine Relative to Body Size	CR < QBR	QBR > CR
Length of Intestine Relative to Body Size	CR < QBR	QBR > CR
Mass of Stomach Relative to Body Size	CR > QBR	QBR < CR

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII. (Cont'd).

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER V: GROWTH		
Growth Coefficients	CR = QBR	QBR = CR
Asymptotic Lengths	Females: CR = QBR Males: CR = QBR	Females: QBR = CR Males: QBR = CR
Length-Mass Relationship	Less mass per unit length	Greater mass per unit length
CHAPTER VI: REPRODUCTION		
Size at 50% Maturity	Females: CR = QBR Males: CR = QBR	Females: QBR = CR Males: QBR = CR
Fecundity	CR = QBR	QBR = CR
Insemination	January-February	January
Fertilization	April	March
Parturition	June	May
Relative Gonadal Index		
Females	CR > QBR for maturity stages 1 and 6	QBR < CR for maturity stages 1 and 6

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII. (Cont'd).

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER VI: REPRODUCTION		
Relative Gonadal Index		
Females (Cont'd)	CR = QBR for maturity stages 3, 4, 5, and 7	QBR = CR for maturity stages 3, 4, 5, and 7
Males	CR > QBR for maturity stages 1, 5, 6, and 7	QBR < CR for maturity stages 1, 5, 6, and 7
	CR = QBR for maturity stages 3 and 4	QBR = CR for maturity stages 3 and 4
Relative Fat Index		
Mature Females	CR > QBR in winter CR = QBR in spring and summer CR < QBR in fall	QBR < CR in winter QBR = CR in spring and summer QBR > CR in fall
Mature Males	CR = QBR in winter and summer CR < QBR in spring CR < QBR in fall	QBR = CR in winter and summer QBR > CR in spring QBR > CR in fall
Immature Females	CR > QBR in winter CR = QBR in spring and fall	QBR < CR in winter QBR = CR in spring and fall

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII. (Cont'd).

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER VI: REPRODUCTION		
Relative Fat Index		
Immature Females (Cont'd)	CR < QBR in summer	QBR > CR in summer
Immature Males	CR > QBR in winter CR = QBR in spring, summer, and fall	QBR < CR in winter QBR = CR in spring, summer, and fall
Fat Cycle in Relation to Reproductive Cycle		
Mature Females	Complementary	Complementary
Mature Males	Coincident, secondarily complementary to reproduction	Coincident, secondarily complementary to reproduction
Immatures	Coincident	Coincident
CHAPTER VII: INTERSPECIFIC COMPETITION		
Population Density	CR do not affect QBR	QBR do effect CR, but affect is seasonal (fall) and transitory (not sustained)

Table 28. Ecological profiles of copper and quillback rockfish based on summary of results of Chapters II-VII. (Cont'd).

Ecological Parameter	Copper Rockfish (CR)	Quillback Rockfish (QBR)
CHAPTER VII: INTERSPECIFIC COMPETITION		
Activity Niche	CR do not affect QBR	QBR do not affect CR
Recruitment		
Number of Individuals	CR > QBR	QBR < CR
Size of Individuals	Pre > Post	Pre = Post
Movements based on Tagging	Similar to QBR	Similar to CR

particular during the winter (0.99). The greatest overlap in the use of food resources, however, occurred when niche widths for their diets were the narrowest (0.02 for both species) due to the predominance of juvenile herring in their diets. This was also coincident with the availability of large schools of juvenile herring in the environment, however, and herring were therefore probably not a limited resource in the winter. Extensive niche overlap between copper and quillback rockfish may therefore indicate an abundance of a shared resource rather than indicate competition for the resource.

The quantity of food consumed by copper and quillback rockfish was different among seasons. Copper rockfish consumed the greatest mass of food relative to their body mass during the winter when feeding on juvenile herring. Quillback rockfish also consumed the greatest quantity of food during the winter, but their consumption was significantly less than food consumption by copper rockfish during the same period. A greater proportion of quillback rockfish were found with food in their stomachs during the spring and summer, however, when the numerically dominant food items were pelagic crustaceans. The importance of fish prey in the diets of both copper and quillback rockfish increased as their body size increased.

Gut allometry of copper and quillback rockfish was similar in that it was consistent with both species being carnivores with relatively short intestines and large stomachs. Species-specific differences were evident, however, and copper rockfish had a shorter intestine and larger stomach relative to similar-sized quillback rockfish. This indicated that the gastrointestinal tract of copper rockfish was more typical of a fish that consumes fish prey and larger crustaceans, relative to quillback rockfish.

In general, copper and quillback rockfish had similar growth patterns with both sexes of both species attaining asymptotic lengths at 30-31 cm total length. In addition, growth coefficients of males and females of both species were similar ($K = 0.141-0.187$). Copper rockfish exhibited a slightly smaller increase in body mass per unit of increase in body length compared with quillback rockfish. This was indicative of copper rockfish having a more pelagic lifestyle compared with quillback rockfish.

Estimated lengths at first and 100% maturity for female and male copper and quillback rockfish were similar, with the possible exception of some male copper rockfish that reached sexual maturity at a relatively smaller size. Male copper rockfish were ripe, and potentially inseminated females, in January and February. Female copper rockfish carried fertilized eggs in April and May, and gave birth to their young primarily in June. The reproductive cycle of male and female quillback rockfish preceded that of copper rockfish by approximately one month, and parturition of quillback rockfish was mainly in May. The fecundity of copper and quillback rockfish was similar and relatively great for a viviparous fish, with fish of 300 mm TL giving birth to approximately 90,000 young.

Visceral fat cycles of female copper and quillback rockfish were complementary to their cycle of gonad maturation and gonad mass increase, and indicated that female rockfish used visceral fat stores as a source of energy for maturation of their eggs and nourishment of their developing young. Visceral fat cycles in male copper and quillback rockfish, however, were mainly coincident with the maturation and increase in the mass of their gonads. This indicated that male rockfish did not use visceral fat reserves in the maturation of their gonads (spermatogenesis). They may have used some fat reserves as an energy source during the period when they were ripe, however, perhaps for mating activities. The pattern of visceral fat accumulation and dissipation in immature male and female copper and quillback rockfish appeared to be primarily related to periods of feeding.

In general, the comparative ecological profiles of copper and quillback rockfish exhibited a large degree of overlap. Differences that did exist, however, consistently indicated that copper rockfish were suited to a more pelagic lifestyle than quillback rockfish. Despite the high degree of similarity between the two species, however, observed interspecific competition was asymmetrical, seasonal, and transitory, thus indicating that in these particular populations, contemporary interspecific competition is a weak process.

The asymmetry in the competitive effect was indicated by copper rockfish not having an effect on the density of quillback rockfish, but quillback rockfish having a competitive effect on copper rockfish. The competitive effect that quillback rockfish had on copper rockfish was seasonal because density of copper rockfish increased only in the absence of quillback rockfish in the fall season. This coincided with copper rockfish moving onto the study reefs from shallower waters (<20 m) during the fall and winter. These were relatively small fish, and copper rockfish moving onto reefs where quillback rockfish were removed (Arbutus Reef), or where copper rockfish densities were reduced (Log Reef), were of smaller sizes than the copper rockfish observed on the reefs prior to the density manipulations. This seasonal movement of copper rockfish appeared to be related to the decreasing temperature of relatively shallow water in relation to the water on the deeper reefs of the study, or to the reproductive activities (courting and mating) which take place during the fall and winter. The competitive effect was also transitory because it was strongest during the fall immediately following the initial density manipulation on Arbutu Reef, and appeared to weaken in the subsequent fall season. The initial movement of copper rockfish onto the deeper reefs in the fall and winter may create a short-term 'ecological crunch' for limited space or food resources, and hence an observable interspecific competitive effect. In the subsequent fall period when the effect was weak, however, interspecific competition was probably mediated by other factors, such as intraspecific competition within the copper rockfish population. A strong intraspecific competitive effect could have possibly worked to decrease the density of copper rockfish to a level where interspecific competition between the species would be undetectable.

Ecological theory purporting a major role for interspecific competition in structuring fish communities was therefore not supported by experimental manipulations of population densities of deep-subtidal, temperate rockfishes. The asymmetrical, seasonal, and transitory occurrence of weak interspecific competition demonstrated that competition between these rockfish species is dynamic, and cannot account for the pattern of species association. Alternative hypotheses based on the importance of intraspecific competition, predation, or environmental variability must therefore be considered in future research.

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