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Structure of Yelloweye Rockfish (*Sebastes ruberrimus*) Populations in British Columbia

Yamanaka, K.L.
Withler, R.E.
Miller, K.M.

Fisheries and Oceans Canada
Science Branch
Pacific Biological Station
Nanaimo, B.C. V9R 2K6

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ABSTRACT

Genetic analyses of 2520 yelloweye rockfish at 13 microsatellite loci were conducted in 1999-2000. Twenty-five samples were collected at nine sites from northwestern Vancouver Island (49.50 N 127.5 W) to southeast Alaska (57.18 N 136.07 W) and included Bowie Seamount (53.30 N and 135.60 W). Allelic diversity and observed heterozygosity levels at microsatellite loci were high, indicating that effective population size was large. Pairwise tests of allele frequencies between samples did not refute the hypothesis that all samples were drawn from a single panmictic population. Although the genetic data provides evidence of a single ‘unit stock’ among yelloweye rockfish in this study, the age composition data indicate that demographic factors vary on a much smaller spatial scale. Adult yelloweye rockfish are resident over specific rocky habitats and move little. The low level of genetic differentiation among yelloweye rockfish is likely the result of larval dispersal by ocean currents. Hence the combination of biological characteristics (longevity and sedentary behavior) and fishery harvests, have caused detectable changes in yelloweye rockfish population parameters. The general north to south cline of increasing total mortality estimates highlights the influence of fishing on local population structure. Heavily fished populations are characterized by a truncation of the age distribution as older individuals are removed by fishing and not replenished rapidly by adult immigration or population growth. The use of management units for yelloweye rockfish, which are geographically smaller than the single panmictic population detected, is recommended.

RÉSUMÉ

En 1999-2000, on a effectué de analyses génétiques de 2520 sébastes aux yeux jaunes à 13 locus de microsatellites. Vingt-cinq échantillons provenant de neuf sites ont été prélevés entre le nord-ouest de l'île de Vancouver (49,50° N 127,5° O) et le sud-est de l'Alaska (57,18° N 136,07° O), incluant le mont sous-marin Bowie (53,30 °N et 135,60° O). La diversité allélique et les niveaux d'hétérozygosité observés aux locus de microsatellites étaient élevés, révélant l'importance effective de la population. Les essais par paire de fréquences d'allèle entre les échantillons n'ont pas infirmé l'hypothèse selon laquelle tous les échantillons auraient été tirés d'une seule population panmictique. Bien que les données génétiques suggèrent que les sébastes aux yeux jaunes échantillonnés dans cette étude appartiennent au même « stock », les données sur la composition selon l'âge indiquent que les facteurs démographiques varient sur une échelle géographique beaucoup plus petite. La distribution des larves par les courants océaniques est probablement à l'origine du faible niveau de différenciation génétique parmi les sébastes aux yeux jaunes. Cependant, les adultes de cette espèce fréquentent des habitats rocheux bien délimités et se déplacent peu. Par conséquent, les caractéristiques biologiques (longévité et comportement sédentaire), combinées aux captures, ont occasionné des changements observables dans les paramètres de la population de sébastes aux yeux jaunes. Le gradient général nord-sud des estimations de mortalité totale à la hausse souligne l'influence de la pêche sur la structure de la population locale. La brisure observée dans la distribution selon l'âge caractérise les populations très exploitées étant donné que l'immigration d'adultes et la croissance de la population s'effectuent à un rythme plus lent que celui des captures de poissons âgés. Il semble prudent d'utiliser des unités de gestion pour le sébaste aux yeux jaunes, qui sont, géographiquement parlant, plus petites que la seule population panmictique détectée.

1 BACKGROUND

1.1 Natural history

Rockfishes are in the genus *Sebastes* and, along with the thornyheads, *Sebastolobus*, make up the Scorpaenidae family in British Columbia (B.C.). The rockfishes are a diverse group of fish, represented by over 35 species in B.C. (Hart 1973) and by at least 50 species between the Gulf of California and the Bering Sea (Eschmeyer and Harold 1983). A unique aspect of *Sebastes* in the NE Pacific is that they have recently undergone an explosive species radiation, relative to sister groups in the NW Pacific and Atlantic. The oldest species separations are estimated at 18 million years ago, with the rapid radiation of species estimated at 8.5 million years ago (Johns and Avise 1998). Rockfishes occupy a wide range of habitats and exhibit great diversity in behaviour and ecology. In California, near the centre of distribution for the genus, most of the rockfish species occur in general sympatry. Californian fossil records of the genus *Sebastes* date back to the Upper Pliocene, 5 million years ago (Barsukov 1991).

1.2 Life history

Yelloweye rockfish (*Sebastes ruberrimus*) is one of the largest of the rockfishes and are recognized by their bright yellow eyes and orange colour. They can be found in complex rocky habitats from the Aleutian Islands to northern Baja California and have been found in depths from 15 to 550 m. Yelloweye rockfish are sedentary, benthic dwellers that feed primarily on other rockfishes, herring, sand lance, shrimps and crabs.

Yelloweye rockfish are a slow growing, long-lived fish. Fish in excess of 40 years are common in the commercial catch and the maximum age recorded in B.C. is 117 years. The age of 50% maturity for these fish overall is around 19 years of age. Rockfishes are viviparous and supply nutrients to developing embryos (Boehlert and Yoklavich 1984). Females may produce between 2,000 and 3,000,000 eggs annually (Haldorson and Love 1991). In B.C., mating takes place in the fall. After insemination, females are able to store the sperm for several weeks before fertilizing the eggs (Wyllie Echeverria 1987). The embryos develop and hatch over a period of 4-5 weeks prior to parturition, or the release of the larvae, in the spring. Larvae and juveniles are found in the upper mixed zone of the ocean and are dispersed by physical transport processes (Loeb et al. 1995, Kokita and Omori 1999) before settlement to nearshore rocky habitats. Once settled, yelloweye rockfish tend to become resident over suitable rock habitats. Typically, rockfishes move bathymetrically with age, with the larger, older fish occupying deeper habitats (Yamanaka and Richards 1993, Lea et al. 1999).

1.3 Management

Yelloweye rockfish are primarily caught using hook and line gear and are targeted by commercial, recreational and Aboriginal fisheries. Up until 1986, the majority of the commercial landings of yelloweye rockfish were taken incidentally during the targeted salmon, halibut, dogfish or lingcod fisheries (Yamanaka and Richards 1992). In 1986, a hook and line rockfish licence category (ZN) was established to allow the regulation of a directed hook and line rockfish fishery. Gear types allowed under the ‘ZN’ licence are longline, handline, rod and reel and troll.

The ZN fishery is managed by total allowable catch (TAC) limits in five regions of the coast, not including the seamounts. The fishery is managed through fishing options, seasonal openings and fishing period limits (Yamanaka and Kronlund 1997b, Kronlund and Yamanaka 1997). The Seamount rockfish fishery is managed by "scientific" licence that requires collection of biological data and in some cases, the use of fishery observers (Yamanaka and Kronlund 1997a). The Groundfish Management Unit, Pacific Region, Fisheries and Oceans Canada (DFO) grants these licenses.

Yelloweye rockfish is targeted in the ZN Option B fishery. Fishing is conducted largely by longline gear and the fish marketed whole as a premium fresh product ($5.75 CDN per kg). Estimated coastwide commercial catches of yelloweye rockfish were 607 tonnes in the 1999 fishing season. This catch was split into 209 t from the directed ZN hook and line fishery, 260 t from the incidental catch in the halibut fishery, 32 t from the incidental catch in the dogfish and lingcod fisheries and 16 t from the Seamount fisheries. Incidental catch of inshore rockfish also occurs in the groundfish and shrimp trawl fisheries. There is no coastwide estimate of catch by species for rockfish in the recreational or Aboriginal fisheries.

A significant obstacle to the management of rockfish fisheries throughout the northeast Pacific has been the assessment of bycatch and the composition of the catch by species (Parker et. al. 2000). Rockfishes are incidentally caught in all other hook and line fisheries and because of their low survival rate after release must be considered as part of the catch. Largely due to regulation, this incidentally caught rockfish is under-reported. In B.C., the non-reporting of rockfish catch, which includes bycatch and discards is also complicated by the historic problem of not identifying rockfish to species. Landed rockfish catches were reported on fish slips between 1954 and 1995 by gear type in two rockfish categories, red rockfish and other rockfish (Yamanaka and Richards 1992). Individual species catch trends are impossible to reconstruct without other sampling methods to assess species compositions.

The problem of spatial management arises from the biology of yelloweye rockfish. Yelloweye rockfish are slow growing, late maturing, long-lived, associate exclusively with specific rocky reef habitats and as adults are sedentary. These fish are easily targeted in specific habitats that are found and revisited using modern fishing aids. Catch rates are maintained as fishermen move from reef to reef, giving no indication from the overall catch or catch trend that the population is in decline. A dramatic decline in catch rate is experienced once all available fishing reefs are depleted. Once depleted, populations may take many decades to recover due to the inherently low productivity of rockfish stocks (Leaman 1991). Given these life history traits, rockfish are considered likely to benefit from using harvest refugia or 'no-take' marine protected areas as an additional spatial management tool. Harvest refugia have been used recently in B.C. as a precautionary measure to conserve rockfish stocks (DFO, Integrated Fishery Management Plan Rockfish Hook and Line Inside and Outside 1999).

1.4 Stock Assessment

A major impediment to yelloweye rockfish stock assessment and hence the determination of sustainable total allowable catches (TACs), is the lack of an abundance estimate or reliable abundance index. *In-situ* methods to estimate abundance are being developed using the submersible "DELTA". Submersible surveys are expensive and are limited in their spatial coverage, however, they are the only feasible method to directly assess yelloweye rockfish biomass. These fishery independent visual estimates of abundance may be used in conjunction with habitat indices and traditional fishery dependent abundance indices to estimate relative fish abundance over larger spatial scales where there are fishery data and no direct surveys. Using visual abundance estimates and habitat assessments, allowable biological catches (ABCs) have been estimated for the demersal shelf rockfish (DSR) fishery in southern, southeast Alaska (O'Connell et al. 1998, O'Connell and Carlile 1993).

Identification of a unit stock for yelloweye rockfish has also been problematic. Inshore rockfish adults are sedentary but their planktonic larvae are dispersed to an unknown extent by ocean currents. Adult populations are associated with and remain stationary over specific rocky reef habitats. The spatial scale of one of these populations may be as little as a square kilometer. For practical purposes, inshore rockfish stock delineation has been assumed directly from the geographic units used in fishery management; Strait of Georgia, West Coast of Vancouver Island, Central Coast, North Coast and the Queen Charlotte Islands.

The distribution of genetic diversity among individuals and populations within species reflects the extent to which different spawning groups are consistently isolated from each other in time and space. Because rockfishes have pelagic larvae that are dispersed in ocean currents, extensive gene flow may occur over large geographic regions. Some species may form closed populations, in which each local population produces its own larval recruits. Other species likely have one or multiple 'source' populations that provide larval recruits for 'sink' populations over wide geographic areas. Thus, a self-sustaining population, or stock, may be a single panmictic breeding population that is isolated from all other conspecifics. Conversely, a stock may be composed of many subpopulations among which larvae disperse to varying degrees.

1.5 Oceans Strategy

As a signatory of the Convention on Biological Diversity (Rio, 1992), Canada is committed to maintaining biodiversity at the genetic population, species, and ecosystem levels. The Canadian Biodiversity Strategy (1995) provided a framework for implementation of the Convention and a means of ensuring the conservation of biodiversity while allowing use of biological resources in a sustainable manner. The *Oceans Act* (1997) is a significant initiative aimed at promoting good stewardship of aquatic resources, including conserving biodiversity. While information from research surveys and fisheries have provided information on the distribution and abundance of many marine species and a general understanding of ecosystems, very little research has been done to quantify biodiversity. The development of specific criteria for measuring biodiversity is essential if Canada is to be able to document progress in conserving biodiversity.

1.6 ‘no-take’ Marine Protected Areas (MPAs)

The maintenance of genetic diversity is critical for the long-term survival of exploited marine organisms and for the fisheries they support. For marine groundfish, MPAs can provide areas for conservation of biodiversity, as well as a continuing source of larvae for recruitment into harvested populations outside the protected area. In order for an MPA to fulfill these goals, it must encompass an area that harbours one or more self-sustaining populations of the target species of sufficient size that it can withstand both the large fluctuations in reproductive success characteristic of these species, and current levels of environmental change. However, little is known of the population structure or stock delineation of most marine fish in British Columbia.

The type of population structure determines in part whether a single large MPA or several small MPAs will provide better protection for genetic diversity in a given species. The number of individuals required to prevent the net loss of genetic diversity depends not only on the stock structure, but also on the proportion of individuals that make more or less equal contributions to the next generation. To maintain biodiversity on an ecosystem level, an MPA must accommodate viable populations of numerous marine organisms with disparate population structures, habitat requirements, and harvest regimes, as well as maintain the prey and predator species associated with target species.

2 INTRODUCTION

For the purpose of conserving intraspecific biodiversity, both evolutionary significant units (ESUs) and management units (MUs) based on the genetic structure of a species need to be identified (Moritz 1994). Evolutionary significant units are important phylogeographic subdivisions within species (those based on historical separations or fluctuations in abundance that are still evident in the gene pool) whose maintenance might be recognized as critical for long-term conservation of biodiversity. MUs are individual metapopulations and/or local populations, whose preservation is critical for short-term maintenance of the species range and abundance. Delineation of the genetic structure of a species is dependent on the development of appropriate genetic markers to quantify the partitioning of genetic diversity among the local populations, metapopulations and ESUs.

In 1998, we developed molecular techniques (amplification of microsatellite loci) to enable surveys of genetic diversity in yelloweye rockfish (*Sebastes ruberrimus*), an exploited species for which there are stock delineation concerns. In the first year, we analyzed 800 yelloweye collected throughout B.C. (including the Bowie Seamount MPA) at three genetic loci.

The research conducted in 1999-2000 was the second phase of a two-year program to examine the temporal (on a seasonal and annual basis) and spatial (offshore and throughout coastal B.C. waters) distribution of genetic diversity in the yelloweye rockfish of British Columbia. In particular, sampling was designed to address the following questions:

1) Do multiple samples of yelloweye rockfish collected over space and time throughout British Columbia indicate the existence of two or more populations, which might be considered separate genetic entities in efforts to conserve intraspecific biodiversity?

2) Do samples of yelloweye rockfish collected during breeding and nonbreeding times indicate segregation into single populations during breeding and a mixture of fish from different populations in migratory or feeding aggregations during nonbreeding periods?
3) Does Bowie Seamount possess one or more groups of genetically distinct yelloweye rockfish that could be protected if the Seamount becomes a MPA?
4) Do the bright and dark yelloweye phenotypes on Bowie Seamount (and at Barber Point on the southwest coast of the Queen Charlotte Islands) constitute separate genetic groups at either or both sites?

We completed the genetic analysis of approximately 2500 yelloweye rockfish at 13 microsatellite loci, including the 800 samples analyzed at three loci in the first year of study. Samples were collected from northwestern Vancouver Island to southeast Alaska and included Bowie Seamount. The analysis of the distribution of genetic variation within and among these samples is provided in this report along with a summary of biological data collected in conjunction with the genetic samples.

3 METHODS

3.1 Sampling sites and samples

The areas selected for sampling along the coast correspond to yelloweye rockfish research survey areas established in 1997 (Kronlund and Yamanaka 2001). These areas represent contrasting levels of fishing pressure in the Queen Charlotte Islands and the upper West Coast of Vancouver Island. The St. James and TopKnot areas are considered heavily fished relative to the Tasu and Triangle Island areas, respectively (see Figure 1). Generally, the heavily fished areas are closer to home ports, considered more protected and hence easier to fish. In 1997 when the research surveys began, the Tasu area was considered by the fishing industry to be the most remote and therefore the least fished.

In 1999, concern over the rockfish stocks and the inability to set sustainable harvest levels for the inshore rockfish fishery, the St. James, Triangle and TopKnot areas, as well as, many other areas along the coast, were closed to the commercial rockfish fishery. These Rockfish Conservation Areas or rockfish protection areas were instituted as an additional management measure in concert with lowered total allowable catches, in 1999. In 2000, this closure was extended to the halibut and dogfish hook and line fisheries. Since 1999, the Tasu area is the only remaining research survey area that is open to commercial fishing.

Yelloweye rockfish samples were obtained from coastal areas through research surveys using commercial vessels in May 1998 with subsequent samples collected opportunistically from the commercial fishery along the coast and through special fishing permits. One hundred to two hundred yelloweye rockfish were randomly selected from the catch during fishing operations and either sampled onboard the vessel or stored fresh on ice for sampling at dockside. Together with the tissue sampling for biochemical analyses, biological characteristics of individual yelloweye rockfish were measured and otoliths extracted for ageing.

3.2 Genetic Analyses

Approximately 2500 adult yelloweye rockfish (*Sebastes ruberrimus*) sampled from research and commercial fishery vessel catches between 1998 and 2000 were surveyed for genetic variation at thirteen microsatellite loci (Table 1). Twenty-five samples were analyzed to examine genetic variability within and between yelloweye rockfish from Sitka Alaska to Esperanza off the east coast of Vancouver Island (Figure 1). Samples were chosen to allow analysis of both spatial and temporal variation in allele frequencies, and to enable comparison of fish sampled from Bowie Seamount (180 km off the west coast of the Queen Charlotte Islands (QCI)) with those occurring in more nearshore coastal waters. In addition, two phenotypes of yelloweye rockfish (termed dark and bright, with respect to skin colour) were sampled at both Bowie Seamount and Barber Point, QCI to determine if the phenotypes represented different populations in either or both sites.

The 13 microsatellite loci were isolated from black rockfish (*Sebastes melanops*), Pacific ocean perch (*Sebastes alutus*) and yelloweye rockfish (Table 2). For each fish sampled, alleles were amplified for each locus using the polymerase chain reaction (PCR) and sized using standard electrophoretic techniques on an ABI 377 automated DNA sequencer (Olsen et al. 1996). Analysis of the allelic and genotypic frequency data was carried out using the Genetic Data Analysis (GDA) program of Lewis and Zaykin (2000) and GENEPOP version 3.1d (Raymond and Rousset 1985). Pairwise tests for genetic differentiation between samples were carried out on allelic frequencies with GENEPOP using χ^2 probability values in the Markov-Chain approach. The null hypothesis was that the allelic distribution at each locus was identical across samples. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice, 1989) for each locus. F_{ST} and Nei's (1972) genetic distance values were computed using GDA among all samples, and between dark and bright phenotypes sampled at Bowie Seamount and Barber Point, off the west coast of the QCI. F_{ST} (or the coancestry coefficient) is the correlation of genes of different individuals in the same population and can range from 0 to 1. The formula is:

$$F_{ST} = \delta_p^2/[p(1-p)]$$

where δ_p^2 is the variance over samples in the frequency of allele A, and p is the average sample frequency of allele A. In GDA, F_{ST} is calculated for multiple alleles and loci according to Weir and Cockerham (1984).

Non-zero estimates of F_{ST} values for a group of samples indicate that the individuals of each sample are more closely related to each other (i.e. have a more recent common ancestor) than they are to individuals of the other samples. Nei's (1972) genetic distance is a standard distance metric based on differences in allele frequencies between samples. The formula for the genetic distance is:

$$D = -\ln [G_{XY}/(G_X G_Y)^{1/2}]$$

where G_X, G_Y and G_{XY} are the means of $\sum p_i^2$, $\sum q_i^2$ and $\sum p_i q_i$ over all loci when p_i and q_i are the frequencies of the i^{th} allele in samples X and Y, respectively.

The genetic distance values were clustered with the neighbour-joining algorithm in a bootstrapped (1000 iterations) dendrogram to illustrate the genetic relationships among samples. GENEPOP was also used to estimate the pairwise average number of migrants between samples based on the private alleles method of Barton and Slatkin (1986). Very low numbers of migrants between spawning aggregates (i.e. less than 5) are sufficient to prevent differentiation in allele frequencies between locales for neutral genetic markers, such as microsatellite loci.

Hierarchial or analyses of allele frequency variation were carried out with nested ANOVA (random effects model) as described by Weir (1996). Hierarchical analysis of the variation between breeding (September to December) and nonbreeding (other months) fish nested within three regions (southern B.C., southern QCI, Bowie Seamount) was conducted. A hierarchial analysis of variation at the two sites (Bowie Seamount, Barber Point) at which both dark and bright phenotypes were sampled was conducted with phenotype nested within site. Finally, allele frequencies in fish from two relatively abundant ages (20-year-olds and 37-year-olds) at Bowie Seamount were compared in an effort to detect genetic differentiation among cohorts in yelloweye rockfish. Allele frequencies of the 37-year-old fish from Bowie were also compared with those of 20-year-old fish from other locations (Triangle Island, Topknot, Cape St. James and Barber Point).

4 RESULTS

4.1 Genetic variation within samples

All microsatellite loci examined were highly polymorphic in all 25 samples. The numbers of alleles observed at each locus and the observed and expected (under conditions of Hardy-Weinberg equilibrium) heterozygosities across all loci for each sample (Table 3) indicated a high level of intraspecific genetic variation. Allelic diversity (mean numbers of alleles observed over all loci) was high and relatively constant among samples (Table 3). Genotypes at all but three loci tended to be in Hardy-Weinberg equilibrium in most samples. For all three loci at which genotypes tended to be out of Hardy-Weinberg equilibrium (*Sme*6, *Sme*12 and *Sme*13), an excess of homozygotes was observed in almost all samples. Average observed heterozygosity by sample ranged from 66.6 – 73.7% (Table 3).

4.2 Genetic variation among samples

Differences in allele frequencies were compared on a pairwise basis among the 25 samples of yelloweye rockfish collected over a two-year period on a locus by locus basis. After applying the sequential Bonferroni adjustment to evaluation of significance, less than 5% of the comparisons (188/3900) were significant at the 5% level. Thus, the hypothesis that all 25 samples were drawn from a single panmictic yelloweye rockfish population could not be refuted. The analysis of gene diversity indicated that 99.9% of the observed genetic variation occurred within samples and only 0.1% was attributable to differentiation among samples (Table 2).

The overall coancestry coefficient (F_{ST}) value was 0.001, and values by locus ranged from 0 to 0.004 but tended not to differ significantly from 0 (Table 2). In a dendrogram in which samples were clustered by Nei’s (1972) genetic distance values, there was little spatial or temporal coherence in the cluster pattern (Figure 3). Multiple samples from the same site did not tend to cluster together, nor did samples cluster by season of collection. There was no obvious geographic pattern to the clustering, as samples from the south (Esperanza, Brooks Bay, Topknot) clustered with samples from the QCI (Tasu, Barber Point) as well as with some from Bowie Seamount (Figure 3). The Alaskan sample did not differ from those from British Columbia. In the dendrogram, the position of all nodes in a basal tree position (i.e. close to the tree trunk rather than the branch tips) indicated that individual samples showed no strong genetic affinity to each other, but instead tended to be equally differentiated. The bootstrap values for all branch nodes were less than 50%, indicating that no clustering in the dendrogram was supported in 50 or more of the bootstrapped trees. This, combined with the low values of genetic differentiation among samples, provided little evidence of structure among the samples. The apparently random pattern of clustering is in agreement with the analysis of genetic diversity which indicated that all samples were drawn from a single population. The average number of migrants per generation into the rockfish aggregations represented by each sample was 17.6, a number consistent with the observed lack of genetic differentiation among samples.

4.3 Bowie Seamount and Barber Point bright and dark phenotypes

Dark and bright yelloweye rockfish phenotypes were sampled at Bowie Seamount and Barber Point. The dark coloured fish are unusual and were first brought to our attention by fishermen who had caught these fish at Bowie Seamount but could not market them for a premium price (Figures 2a and 2b). Barber Point was also suggested as a coastal location where the dark coloured fish occurred. The dark phenotype is fished in the same general location as the bright phenotype but tended to be in shallower water, 40 – 120 M compared with 160 – 220 M for the bright phenotype.

Samples of the unusual dark yelloweye rockfish phenotype from Bowie Seamount and Barber Point were not differentiated genetically from samples of the bright phenotype from the same or other sites (Figure 3). Genetic distances were as great among temporally distinct samples of the same phenotype as between phenotypes. When analyzed independently, the 12 samples of bright and dark rockfish did not cluster by phenotype (bright vs. dark) or site (Bowie vs. Barber) (Figure 4). Again, the branch nodes of the dendrogram tended to be close to the trunk, rather than the branch tips, of the tree, indicating no strong affinities among the samples (Figure 4). At both sites, the combined samples of bright and dark yelloweye rockfish differed significantly from each other at only one locus out of thirteen, a difference that might be expected due to chance alone. In the hierarchial analysis of diversity, neither the effect of site ($F_{1,2}$=1.22, P>0.10) nor phenotype ($F_{2,8}$=0.93, P>0.10) was significant. Thus, there is no evidence that gene flow is restricted between the bright and dark phenotypes at either site.

4.4 Seasonal Variation

Twenty-two samples from three regions (Bowie Seamount, southern QCI [Cape St. James, Barber Point] and northern Vancouver Island [Brooks Bay, Esperanza, Topknot, Triangle]) were examined for differentiation between breeding and non-breeding samples. In the hierarchial analysis of variance, neither the effect of site ($F_{2,3}$=1.03, P>0.1) nor the effect of season ($F_{3,16}$=1.08, P>0.1) were significant. Samples collected during breeding season would be expected to be true ‘population’ samples (i.e. to consist of freely interbreeding individuals) whereas samples collected at other times might consist of more than one population (i.e. be mixtures of distinct breeding groups) that have aggregated for feeding or other activities but which will segregate before breeding. Samples collected during the non-breeding season did not display a greater heterozygote deficit than those collected at other times, providing no evidence that non-breeding samples consisted of mixtures of individuals from independent populations.

4.5 Cohort Variation

The comparison of allele frequencies between rockfish aged 20 and 37 years indicated no difference when it was restricted to samples from Bowie Seamount ($F_{1,5}$=0.73, P>0.1) or when 20-year-old fish from other sites (Cape St. James, Barber Point, Triangle Island, Topknot) were included ($F_{1,12}$=0.72, P>0.1). Thus there was no evidence of differing allele frequencies between the two year classes, with comparisons based on small sample sizes.

4.6 Age and Growth

Sagittal otoliths were extracted from otic cavities of the yelloweye rockfish collected. Over 2800 otoliths were aged by the break and burn technique (Chilton and Beamish 1982). Age statistics are shown by area in Table 5. Ages ranged from 6 to 109 and 7 to 99 years for males and females, respectively. Yelloweye rockfish are first vulnerable to longline gear from the age of 6 and 7 for males and females, respectively, and are assumed to remain vulnerable for the rest of their lives. Males tend to recruit to and leave the fishery at younger ages than the females.

Dark and bright yelloweye rockfish age histograms are shown in Figure 5 by sex for each phenotype and area sampled. The dark phenotype appears to have truncated ages compared with the bright phenotype from both the Bowie Seamount and the Barber Point sample locations. The shallower depths fished for the dark phenotype may explain this to some extent. Since most rockfish move bathymetrically with age, deeper rockfish tend to be older than the shallower ones (Yamanaka and Richards 1993, Lea et al. 1999). The commercial fishery commonly operates in the deeper water, at depths identical to those fished for the bright phenotype. Hence, for comparison to the coastal populations, only the bright phenotype at Bowie was used.

Figure 6 shows the Bowie age frequencies compared with those from the coastal areas. The high proportion of older fish (both males and females) at Bowie Seamount is noteworthy. Mean and median ages of the Bowie yelloweye rockfish are greater than those from the coastal areas (Table 5). The truncation of older individuals becomes more severe with decreasing latitude and is related to the relative fishing rates these areas have experienced (Kronlund and Yamanaka *in press*). The age of full recruitment appears to be 16 years at Bowie and increases with latitude to 18 years at Tasu, St. James and Triangle and 20 years at TopKnot. This change in age of full recruitment is most likely related to differences in fish growth and size at age (Figure 7). As shown from the size of fish at age 18 (Table 5), yelloweye rockfish size at age increases with increasing latitude. Therefore, fish in the south are smaller at age 18 than those in the north.

4.7 Mortality Estimates

Estimates of total mortality from catch curves (Ricker 1975) are shown in Figure 8. Recruitment is episodic in rockfish with exceptional years occurring with a frequency of every 15 to 20 years. Variable recruitment is problematic for catch curve analysis, however, for yelloweye rockfish the catch curve spans up to100 years and covers many cycles of good and bad recruitment years. Hence, catch curves may provide an estimate of Z based on average recruitment over the last century. The effect of good incoming recruitment of yelloweye rockfish (upper end of the catch curve) will cause a steeper slope and bias estimates higher. This effect is indistinguishable from harvests (F>M) resulting in the removal of the older age groups in the population.

Total mortality rates (Z) estimated from catch curves (Ricker 1975) and from maximum ages (Hoenig 1983) are shown in Table 5. A recently aged female from Bowie (not in this study) was discovered to be 112 years old. Using this older age in Hoenig's equation results in an estimate of M=0.041. The Bowie Seamount yelloweye rockfish population is as close to "unfished" as we can get in B.C. and provides a valuable reference population or bench mark for comparison with the coastal yelloweye rockfish populations that have all experienced fishing.

5 DISCUSSION

This study provided strong evidence that yelloweye rockfish in British Columbia from northern Vancouver Island to the Queen Charlotte Islands and Bowie Seamount form a genetically homogeneous population or metapopulation that could be considered a single ESU. Allelic diversity and observed heterozygosity levels at microsatellite loci were high, indicating that effective population size(s) was large. Pairwise tests of allele frequencies between samples did not refute the hypothesis that all 25 samples were drawn from a single panmictic population. Over 99% of the genetic variability detected at 13 microsatellite loci was contained within samples, and less than 1% was partitioned among samples. Genetic similarities among samples did not reveal a geographic basis for differentiation, and multiple samples collected from the same site were not more similar to each other than to samples from other locations.

The failure to detect population structure in a species does not preclude the existence of population subdivision that has gone unrecognized because of inadequate sampling over time and/or space, small sample sizes or the use of too few or too slowly-evolving genetic markers. Waples (1998) outlined considerations for detecting population subdivision in species with potentially high gene flow due to extensive adult or larval dispersal in the marine environment (i.e. accurately estimating small but real F_{ST} values). He indicated that the ability to detect genetic structure can be improved by surveying a large number of loci, random sampling of large numbers of adult individuals, and testing the stability of observed genetic differences over time. Stability in the geographic pattern of genetic differentiation over time increases confidence that a biologically meaningful population structure has been detected even when levels of differentiation are low. In contrast, a high level of temporal variation in allele frequencies indicates that true population structure has not been elucidated even when differentiation among geographic samples is great (Waples 1998).

This survey was based on an adequate number of microsatellite loci, which are sensitive indicators of population structure and adult sample sizes that were sufficiently large to enable accurate determination of allele frequencies at the highly polymorphic loci. Sampling over time, both within and among years, was conducted. As a result of the repeated sampling, the preliminary indications of geographic structure (the differentiation of Vancouver Island, Queen Charlotte Island and Bowie Seamount yelloweye) and of differentiation of the dark phenotype of yelloweye at Bowie Seamount (Withler et al. 1998) can be refuted. The extended sampling conducted in this study revealed a complete absence of stable differentiation among samples on either a spatial or temporal scale. Even the sample from Sitka, Alaska was undifferentiated from samples collected in southern British Columbia.

For all samples, the observed heterozygosities tended to be lower than those expected under conditions of Hardy-Weinberg equilibrium (random mating among individuals). The shortage of heterozygotes was primarily due to nonequilibrium values at three loci. This indicated that the three loci, all developed from black rockfish, may possess non-amplifying alleles in yelloweye rockfish. In contrast, a shortage of heterozygotes in particular samples may indicate the 'Wahlund effect', a heterozygote deficit that occurs as the result of the inclusion of individuals from two populations with different allele frequencies in a single sample. Under these conditions, the heterozygote deficit should be apparent in the sample at all loci at which allele frequencies differ between the two populations. Samples collected during nonbreeding season might be most likely to contain individuals from two or more populations for species in which feeding or migratory aggregations consist of individuals which segregate into multiple isolated spawning groups during breeding. No sample of yelloweye rockfish in this study exhibited a significant heterozygote deficit across loci that would indicate the presence of rockfish from two or more genetically distinct populations.

It is possible that the large number of age classes included in the samples of yelloweye rockfish analyzed in this study obscured genetic variation among cohorts that could arise from "sweepstakes-style" recruitment success. According to this hypothesis, even in populations of high abundance only a small fraction of mature adults effectively contribute to reproduction in each generation because of a limited window of oceanographic conditions compatible with successful spawning and/or recruitment (Hedgecock 1994). Spatial and temporal variability in recruitment success may lead to detectable genetic drift among cohorts and to 'chaotic genetic patchiness', in which samples in very close proximity are as genetically differentiated as ones very far apart (Larson and Julian 1999). Although proximal samples of yelloweye in this study were sometimes as different as distal ones, there was little genetic variation among any samples in excess of that expected due to sampling error alone. There was no difference in allele frequencies between yelloweye rockfish ages 20 and 37 sampled at Bowie Seamount in 1999, or between the Bowie 37-year-old fish and 20-year-old fish from Triangle Island, Topknot, Cape St. James and Barber Point. Thus, there was no indication that this species experiences 'sweepstakes-style' recruitment although the small samples of fish in each age class available for comparison (37 20-year-old fish and 24 37-year-old fish at Bowie, and 121 20-year-old fish from other sites) may have decreased the power of the age comparisons. However, the lack of spatial or temporal variability in allele frequencies among samples in this study, even in areas in which the older age classes were virtually absent, provides a stronger indication that spawning success is not variable enough to induce genetic drift. In addition, dominant year classes in yelloweye, indicative of highly successful spawning and recruitment, appear to be synchronous coastwide, providing no evidence of recruitment variability over limited spatial scales.

Long-lived species may maintain genetic variation even in the face of fluctuating environments and recruitment because of the "storage capacity' that results from the large cohort of adults produced from each strong recruitment (Warner and Chesson 1985, Ellner and Hairston 1994, Ellner 1996, Gaggiotti and Vetter 1999). These fish effectively 'store' a large number of genotypes within the reproductive population over many reproductive periods and are capable of contributing to both population size and genetic diversity when favourable spawning and recruitment conditions return. Interestingly, Gaggiotti and Vetter (1999) also suggest that even when marine fisheries collapse, fish species may be close to extinction as the result of demographic or environmental stochasticity before a marked reduction in genetic variation occurs.

Genetic homogeneity at mitochondrial, allozyme and microsatellite loci over geographic scales similar to one covered in this study has been observed for some *Sebastes* and *Sebastolus* species (Stepien 1995, Buonaccorsi et al. 1999) but other species exhibit significant heterogeneity over large and smaller scales (Seeb and Gunderson 1988, Rocha-Olivares and Vetter 1999, Hawkins et al. 1999). Life history differences (adult migratory behavior, passive larval drift, larval behaviour) and different population histories likely contribute to the different patterns of genetic variation (Gaggiotti and Vetter 1999, Buonaccorsi et al. 1999).

Yelloweye rockfish at Bowie Seamount were not genetically distinct from those in coastal locations, and there was no evidence that the dark and bright phenotypes at Bowie Seamount were members of independent populations. Bowie Seamount likely represents a 'sink' for yelloweye larvae transported offshore from coastal locations. The recently described Haida Eddy (Crawford and Whitney 1999) is generated by along shore currents, entraining larvae and then drifting offshore. This eddy was stationary over Bowie Seamount in August 2000 and may provide a mechanism for the dispersal of coastally derived yelloweye rockfish to the offshore region. However, reproduction on the Seamount also occurs and it is not clear to what degree, if any, the Seamount aggregation is dependent on immigration. As with all other sites included in this study, the amount of immigration (gene flow) is sufficiently great and/or constant to prevent genetic differentiation.

The bright and dark phenotypes may result from a genetic polymorphism that is selected for at Bowie Seamount because of the distinctly different colouration of habitat at these locations. At Bowie Seamount, the shallow-water habitat is very dark, with the substrate consisting of volcanic basalts, whereas coral production at greater depths provides a very light habitat. Thus, the two phenotypes may represent genetic morphs with different levels of pigment deposition that select the appropriate habitat. Alternately, the different colouration may not have a genetic basis, with the rockfish able to generate cryptic colouration to blend into their habitat. Yelloweye tend to occupy greater depths as they age, and the dark phenotype samples captured at shallower depths are composed of a disproportionate number of younger fish. It is possible that the descent of the fish from the dark to the light habitat at Bowie as they age is accompanied by modification of their skin coloration. The presence of intermediate types as documented in this study (Figure 2b), could occur whether the two phenotypes are genetically controlled or simply represent phenotypic plasticity. These results contrast with those reported for light and dark forms of dusky rockfish (*Sebastes ciliatus*) in the Gulf of Alaska, which apparently form two distinct groups between which genetic exchange is limited (Seeb 1999).

Although the genetic data provides evidence of a single 'unit stock' or phylogenetic lineage among yelloweye rockfish in this study (and perhaps over a larger geographic area), the age composition data indicate that demographic factors vary on a much smaller spatial scale. Yelloweye rockfish are aggregated over suitable rocky habitats that are distributed in a patchy fashion along the coast. The low level of genetic differentiation among yelloweye rockfish aggregations is likely the result of larval dispersal by ocean current transport. However, adult yelloweye rockfish are resident over these habitats and move little. Hence, the combination of biological characteristics (longevity and sedentary behavior) and fishery harvests, have caused detectable changes in yelloweye rockfish population parameters. The general north to south cline of increasing total mortality estimates highlights the influence of fishing on local population structure. Heavily fished populations are characterized by a truncation of the age distribution as older individuals are removed by fishing and not replenished rapidly by adult immigration or population growth.

The apparent contradiction between low genetic differentiation coastwide in yelloweye rockfish and spatially discrete local subpopulations may simply reflect the level of exchange of individuals among aggregations. Genetic homogenization may result from an average exchange of only one or a few individuals per generation whereas hundreds or thousands of immigrants over the history of the fishery may be required to mitigate the influence of fishing on population parameters. The number of migrants among the samples used in the genetic analysis of this study was estimated from the genetic data as 17.6. This is a high value, consistent with the observed lack of genetic differentiation among samples. Thus, although yelloweye aggregations occupying adjacent sites in a discontinuous habitat are genetically linked, their population dynamics are likely independent. Genetic similarity among aggregations cannot be interpreted to mean that, once harvest is curtailed, aggregations depleted by fishing will be replenished from nearby aggregations in a time frame of interest to resource managers.

The use of management units (MUs) for yelloweye rockfish, which are geographically smaller than the single ESU detected, seems prudent. For a long-lived species that recruits to the fishery at a relatively great age, an extended period of poor recruitments due to overexploitation and/or environmental adversity may go undetected for many years. Multiple MUs afford the possibility of restricting harvest in areas where fishing mortality is high and the effects of harvest on abundance and age structure have been most severe. The designation within each MU of harvest refugia or ‘no-take’ protected areas encompassing several aggregations in which older age classes are maintained may provide some buffering capacity for spawning biomass during periods of poor recruitment to the fishery. Little is known about the parameters of larval dispersal for yelloweye rockfish, and the genetic data of this study indicated that this species may constitute a ‘multiple source’ species (Carr and Reed 1993) that is well described by the island model of genetic differentiation (equal gene flow among all semi-isolated spawning aggregates). However, it is reasonable to assume that the magnitude of dispersal between pairs of subpopulations is negatively correlated with distance, at least in portions of the species range. Thus, a ‘stepping stone’ arrangement of several protected areas in a coastal corridor may facilitate genetic continuity among aggregations and the overall maintenance of high levels of genetic diversity within the species.

The limited fishing pressure on yelloweye rockfish at Bowie Seamount is evident from the older ages present in the population. Estimates of total mortality (Z) were determined to be equal to natural mortality rates (M) at Bowie Seamount. These are important reference points and may provide the basis for the development of limit reference points to achieve precautionary fishery management advice for yelloweye rockfish populations. Other important features of the Bowie Seamount population are the relatively undisturbed conditions in which they exist. This area of high rockfish abundance and shallow oceanic habitat is unique in B.C. and noteworthy for their significance to marine science.

6 SUMMARY

Yelloweye rockfish from northern Vancouver Island, southwest Queen Charlotte Islands, southeast Alaska and Bowie Seamount form a genetically homogeneous population or metapopulation that could be considered a single evolutionary significant unit (ESU). Although yelloweye rockfish adults are sedentary, dispersal of larvae through ocean transport most likely provides enough exchange of individuals to genetically homogenize populations.

Past harvests are detectable in spatially discrete yelloweye rockfish populations. Local populations of yelloweye rockfish will declined under fishing pressure when total mortality Z (F+M) is not balanced by recruitment. Bowie Seamount has proved invaluable for scientific study of yelloweye rockfish as these populations have seen little fishing pressure. Population parameters determined from Bowie Seamount provide an important unfished reference point.

The yelloweye rockfish population at Bowie Seamount provides a relatively unfished reference population for stock assessment and research and may possibly provide a ‘control’ for fishery and environmental effects on the coastal populations.

Bowie Seamount most likely receives coastally derived yelloweye rockfish larvae through ocean transport mechanisms such as the Haida Eddy. The relative importance of larval immigration and local reproduction and recruitment to yelloweye population biomass on Bowie is not known, but sufficient larval immigration occurs to prevent genetic differentiation between the yelloweye at Bowie Seamount and coastal regions.

7 RECOMMENDATIONS

Genetic population analyses of yelloweye rockfish indicate a single panmictic population throughout the entire spatial scale sampled which includes the offshore area from Southeast Alaska, Bowie Seamount, Southwest Queen Charlotte Islands, and Northwest Vancouver Island.

The management of this sedentary rockfish species should focus on mitigating harvest impacts on a local population scale as a precautionary strategy since the mechanisms of larval dispersal are unknown.

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Table 1. Sampling dates, locations and sample sizes for genetic analysis of yelloweye rockfish analyzed at 13 microsatellite loci.

Sample number and name	Date	Latitude decimal degrees	Longitude Decimal degrees	N
Bowie Seamount (D)	July 1998	53.28	135.74	90
Bowie Seamount (D)	July 1999	53.30	135.64	170
Bowie Seamount (D)	Aug 1999	53.32	135.63	90
Bowie Seamount (D)	Sept 1999	53.29	135.65	90
Bowie Seamount (B)	July 1998	53.28	135.74	95
Bowie Seamount (B)	July 1999	53.31	135.62	110
Bowie Seamount (B)	Aug 1999	53.30	135.64	90
Bowie Seamount (B)	Sept 1999	53.31	135.62	110
Barber Point (D)	May 1999	51.99	131.12	100
Barber Point (D)	Sept 1999	52.00	130.63	65
Barber Point (B)	May 1999	51.98	130.63	175
Barber Point (B)	Sept 1999	52.00	131.16	65
Sitka, Alaska	Dec 1999	57.18	136.07	90
Tasu	May 1998	52.72	132.14	80
Tasu	Jan 2000	52.77	132.19	180
Cape St. James	May 1998	52.15	131.35	85
Cape St. James	Jan 1999	52.03	131.13	80
Cape St. James	Oct 1999	52.00	130.66	130
Cape St. James	Feb 2000	52.07	132.25	65
Triangle Island	May 1998	50.78	129.31	80
Triangle Island	Jan 2000	50.72	129.12	145
Topknot	May 1998	50.49	128.25	85
Topknot	Mar 2000	50.48	128.27	135
Brooks Bay	Oct 1998	50.16	128.00	70
Esperanza	Sep 1999	49.50	127.50	45
Total				2520

Table 2. Microsatellite loci examined in yelloweye rockfish samples from British Columbia and Alaska. The number of alleles, F_{ST} value and percentage of variation that occurred within samples are shown for each locus. The source of primer sequences for each locus is also given.

Locus	Number of alleles	F_{ST}	(SD)	Intrasample diversity	Source
Sal1	28	0.004	(.003)	99.7	Miller et al. 2000
Sal3	10	0.0	(.001)	100	“
Sme1	12	0.001	(.001)	99.9	Seeb et al. GenBank
Sme3	39	0.002	(.001)	99.8	“
Sme4	37	0.001	(.001)	99.9	“
Sme5	10	0.001	(.001)	99.9	“
Sme6	9	0.002	(.002)	99.8	“
Sme8	17	0.001	(.001)	99.9	“
Sme11	16	0.002	(.001)	99.8	“
Sme12	16	0.0	(.001)	100	“
Sme13	16	0.002	(.001)	99.8	“
Sru9	14	0.004	(.002)	99.6	Miller et al. unpub.
Sru 20	18	0.0	(.001)	100	“
Overall	13	.001		99.9	

Table 3. Genetic diversity in yelloweye rockfish samples from Alaska and British Columbia. Expected heterozygosity based on observed allele frequencies (H_E), observed heterozygosity (H_O), and allelic diversity (mean number of alleles observed per locus) are given for each sample.

Sample	Date	H_E	H_O	Allelic diversity
Bowie Seamount (D)	July 1998	73.9	69.5	12.5
Bowie Seamount (D)	July 1999	73.0	71.5	14.2
Bowie Seamount (D)	Aug 1999	71.1	69.4	12.5
Bowie Seamount (D)	Sept 1999	74.2	71.2	13.3
Bowie Seamount (B)	July 1998	73.2	68.7	13.4
Bowie Seamount (B)	July 1999	73.3	71.4	13.4
Bowie Seamount (B)	Aug 1999	72.4	70.8	12.2
Bowie Seamount (B)	Sept 1999	72.5	69.9	13.5
Barber Point (D)	May 1999	73.8	71.2	13.5
Barber Point (D)	Sept 1999	72.1	68.4	11.8
Barber Point (B)	May 1999	72.7	70.9	13.8
Barber Point (B)	Sept 1999	72.5	69.9	11.8
Sitka, Alaska	Dec 1999	72.1	70.4	12.5
Tasu	May 1998	74.0	71.6	12.6
Tasu	Jan 2000	73.8	73.7	14.5
Cape St. James	May 1998	73.2	69.1	11.9
Cape St. James	Jan 1999	71.1	66.6	11.3
Cape St. James	Oct 1999	72.3	69.9	13.3
Cape St. James	Feb 2000	73.6	73.2	11.7
Triangle Island	May 1998	72.0	68.4	12.5
Triangle Island	Jan 2000	73.8	68.3	13.9
Topknot	May 1998	73.5	70.9	12.1
Topknot	Mar 2000	72.1	71.2	13.4
Brooks Bay	Oct 1998	73.6	72.0	11.8
Esperanza	Sep 1999	73.0	72.1	11.1
Mean		72.9	70.4	12.7

Table 4. Formulas used for estimation of life history parameters

1) von Bertalanffy growth function (von Bertalanffy 1938):

$$L_t = L_\infty \cdot (1 - \exp(-k \cdot (t - t_0)))$$

2) Estimate of Z (Ricker 1975)

$$Z_r = -(\log N_{t+1} - \log N_t)$$

3) Estimate of Z (Hoenig 1983):

$$\ln(Z_h) = 1.44 - 0.982(\ln(t_{\max}))$$

Table 5. Age analyses and population parameters.

Ages	male			female		
	$t_{\min}$	t_{median}	$t_{\bar{x}}$	$t_{\min}$	t_{median}	$t_{\bar{x}}$
Bowie - bright	6	22	29.4	7	34	36.0
Tasu	10	19	22.4	8	20	25.9
St James	9	20	23.9	11	19	24.9
Triangle	9	20	22.8	10	22.5	29.0
TopKnot	9	19	19	10	20	20.9

von B growth	male				female			
	L_∞	k	t_0	$L_{t=18}$	L_∞	k	t_0	$L_{t=18}$
Bowie - bright	80.3	0.045	6.2	53.1	82.8	0.037	7.6	50.5
Tasu	75.0	0.039	9.9	49.5	66.5	0.054	5.5	47.9
St. James	68.1	0.055	4.9	48.8	71.5	0.036	13.0	47.6
Triangle	64.4	0.075	-0.6	46.8	64.9	0.058	2.6	45.1
TopKnot	70.6	0.046	5.2	46.4	67.2	0.044	7.0	44.9

Mortality	male			female		
	Z_r	$t_{\max}$	Z_h	Z_r	$t_{\max}$	Z_h
Bowie - bright	0.0861	92	0.049	0.0431	99	0.046
Tasu	0.186	67	0.067	0.129	86	0.053
St. James	0.164	95	0.048	0.121	89	0.051
Triangle	0.213	59	0.076	0.136	88	0.051
TopKnot	0.454	44	0.102	0.332	66	0.068

Figure 1. Sampling locations and area names.

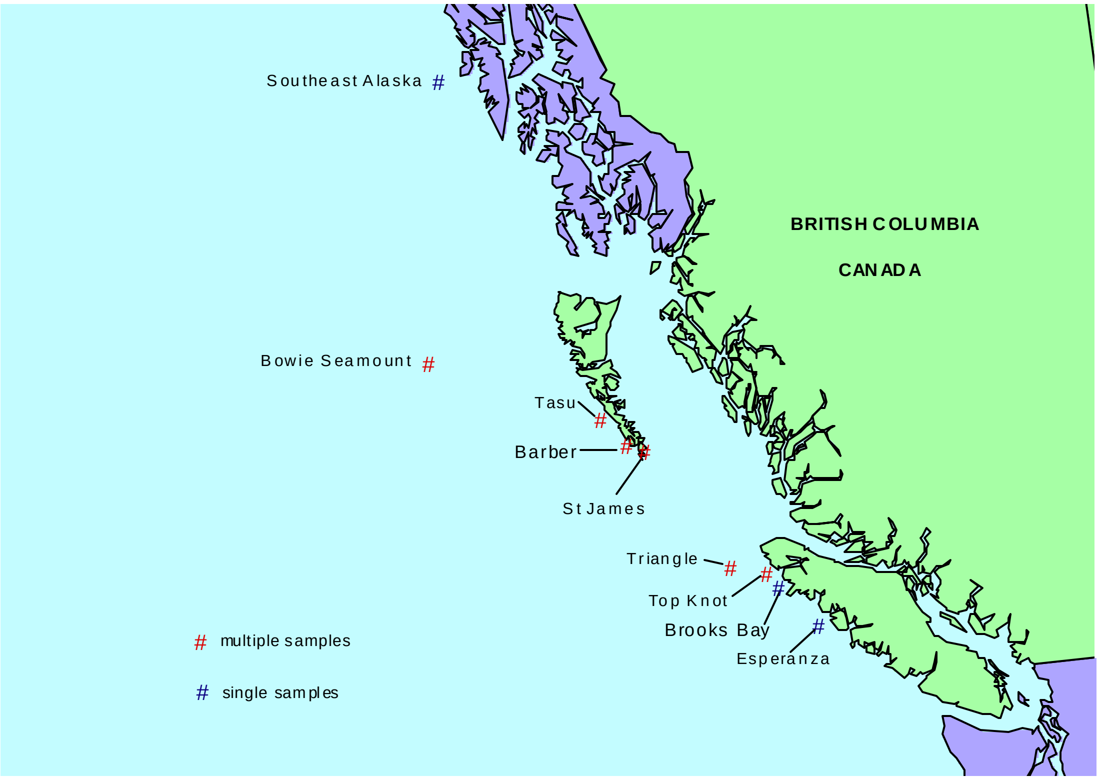


Figure 2a. Dark and bright yelloweye rockfish phenotypes from Bowie Seamount.

Figure 2b. Colour gradation in yelloweye rockfish from Bowie Seamount.

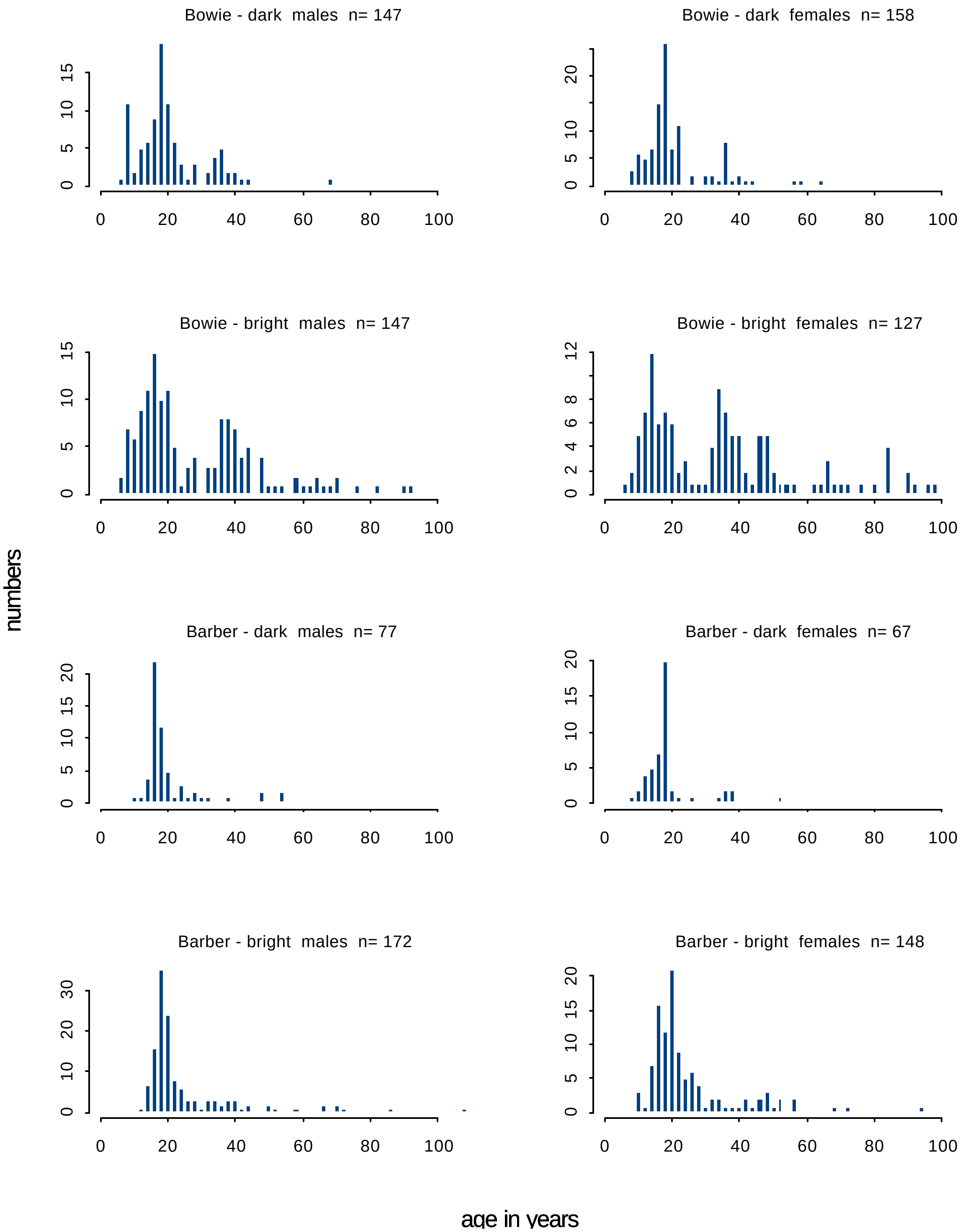
Figure 3. Genetic Distance Nei (1972)

```
               +------------------------------------------------Brooks Bay Oct98
         +-----|
         |     +-----------------------------------------Bowie D Sep99
       +-|
       | |    +--------------------------------------------Esperanza Sep99
       | +----|
    +--|      +---------------------Bowie B Sep99
    |  |
    |  |        +-----------------------Bowie D Aug99
   +|  +--------|
   ||           +--------------------------------------Triangle May98
   ||
   +|--------------CapeStJames Oct99
   |
   |    +--------------------------------Bowie D Jul98
   | +--|
   |-|  +-------------------Triangle Jan00
   | |
   | +-----------------------------Bowie B Jul99
   |
   |               +------------------Bowie B Jul98
   |           +---|
   |         +-|  +-------------------------Barber D May99
+--|         | |
|  |  +------| +-----------------------------------------------------Tasu May98
|  |  |      |
|  |  |      +-----------------------------------Topknot May98
|  |  |
|  | +|    +------------------------------------------------CapeStJames Jan99
|  | || +--|
|  | || |  | +---------------------------------------------------Barber B Sep99
|  | || |  +-|
|  | |+-|    +---------------------------------------CapeStJames Feb00
|  | |  |
|  +-|  |      +---------------------------Bowie D Jul99
|    |  +------|
|    |         +----------------Tasu Jan00
|    |
|    |   +------------------Topknot Mar00
|    |+--|
|    +|  +------------------------Bowie B Aug99
|     |
|     +---------------Barber B May99
|
|  +----------------------------CapeStJames May98
+--|
   |    +------------------------------------Barber D Sep99
   +----|
        +-------------------Alaska

|----------------|----------------|----------------|----------------|
0.017            0.012            0.008            0.004            0.000
```

Figure 4. Neighbour-joining tree

```
      +--------------------------------------Bowie D Jul98
+-----|
|     +--------------------------------Bowie B Jul99
|
|                +-------------------Bowie B Jul98
|     +----------|
|  +--|          +----------------------------Barber D May99
|  |  |
|--|  +---------------Barber B May99
|  |
|  +------------------------------Bowie B Aug99
|
| +--------------------------------------------------Barber D Sep99
|-|
| +------------------------------------Bowie D Aug99
|
|          +--------------------------------------------------------Barber B Sep99
|   +-------|
|   |       +---------------------------------Bowie D Jul99
+---|
    |     +-------------------------------------------------Bowie D Sep99
    +-----|
          +-----------------------Bowie B Sep99

|----------------|----------------|----------------|----------------|
0.015            0.011            0.007            0.004            0.000
```

Figure 5. Yelloweye rockfish age frequency histograms by area, phenotype and sex with samples sizes (n).



Bowie - dark males n= 147

Bowie - dark females n= 158

Bowie - bright males n= 147

Bowie - bright females n= 127

Barber - dark males n= 77

Barber - dark females n= 67

Barber - bright males n= 172

Barber - bright females n= 148

Figure 6. Yelloweye rockfish age frequency histograms by area and sex with samples sizes (n).

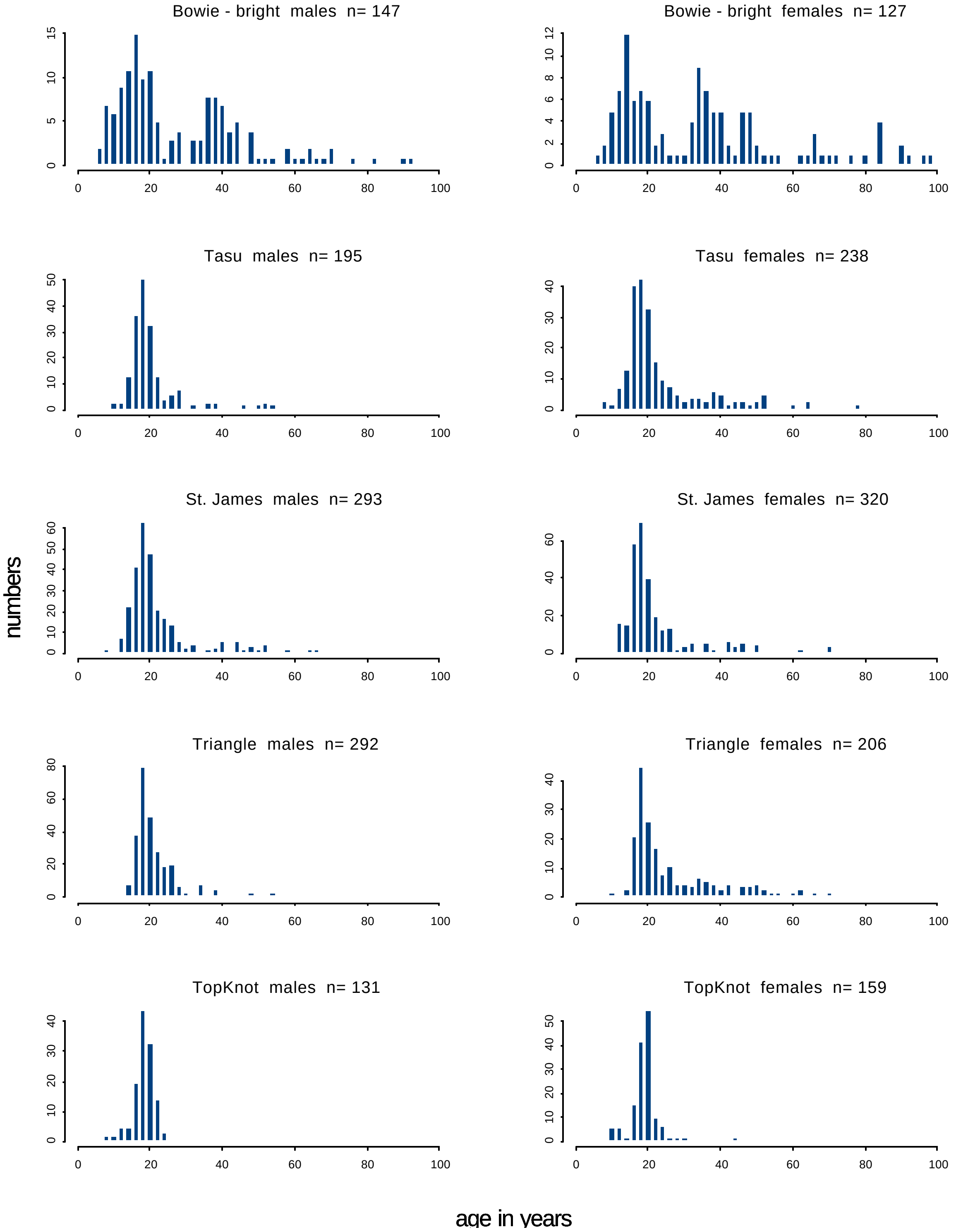


Figure 7. Yelloweye rockfish age at length in centimeters by area and sex with sample sizes (n) and von Bertalanffy growth function parameters.

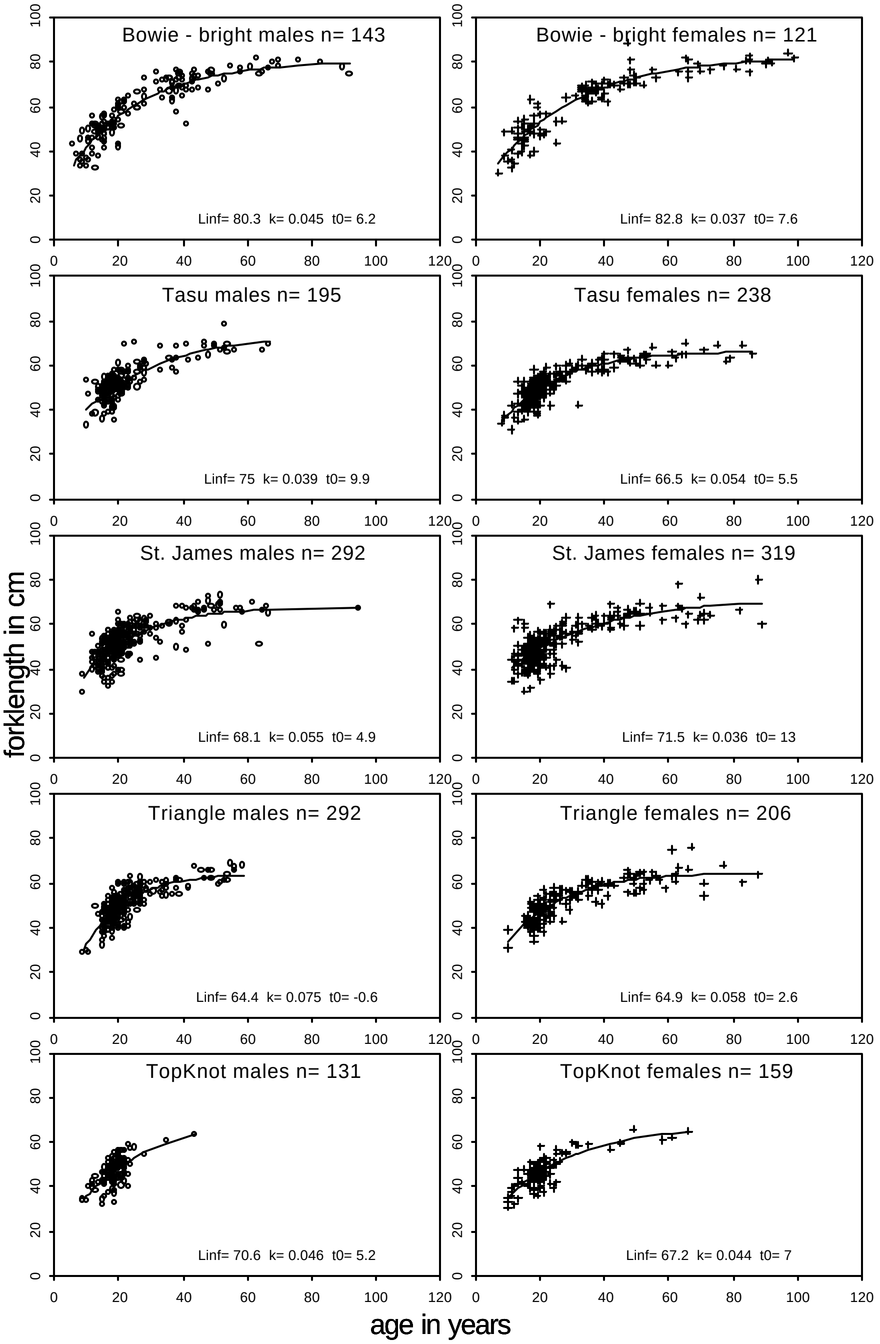


Figure 8. Catch curves (Ricker 1975) for yelloweye rockfish by area and sex with sample sizes (n) and total mortality estimates (Z).