

PHYLODEMOGRAPHY OF THE BLUE ROCKFISH (*SEBASTES MYSTINUS*) FROM
CALIFORNIA TO WASHINGTON

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Marine resource managers are often challenged with balancing use and sustainability of resources with limited data in dynamic marine environments. Though vagile life history stages are common in marine organisms, increasing evidence indicates intraspecific population substructuring exists in the marine realm. It is also recognized that life history characteristics driving demographic behavior of populations vary spatio-temporally. Spatial and temporal relationships of intraspecific populations must therefore be considered for proper management of these resources, though biological resolution on such levels is often limited. This thesis presents a method by which the combination of limited genetic and demographic information on evolutionary and ecological time scales can produce an historical and contemporary understanding of population dynamics useful for developing management decisions on resources in urgent need of swift management action. I call this approach “phylo demography” and illustrate the method by investigating the spatially distinct subpopulation dynamics of the blue rockfish (*Sebastes mystinus*) from California to Washington. Genetic samples ($N = 245$) of blue rockfish from eight sites throughout its range were taken to explore population substructuring. Sequencing of a 498 base pair portion of the mitochondrial DNA control region revealed two major subpopulations of blue rockfish, with the apparent genetic break occurring at Cape

Mendocino, CA. This is a relatively unexplored biogeographic break that may reveal a strong barrier for gene flow in other marine species. The northern group is a derivative of the southern group, with the last contact between the two regions occurring 2,000 to 6,000 years ago. With this information, structured subpopulations were then modeled using deterministic and stochastic five stage matrix population models and region specific life history information and vital rates. Demographic and environmental effects (due to intensity-varying El Niño events) were incorporated. Furthermore, genetic pairwise mismatch distributions were used to explore historical population dynamics of each region. The northern population was historically more stable and currently increasing compared to the unstable and most likely decreasing southern population. Age truncation, environmental variability, and fishing pressure are likely driving the southern subpopulation down. Using an introduced time-standardized elasticity method, a 13.5 to 14 inch size limit is recommended for the southern blue rockfish subpopulation to protect the “life history management unit” of the subadult stage and 8 reproductive year classes. The phylodemographic approach shows promise for developing sustainable management schemes for long-lived, slow growing, and late to mature marine organisms where other methods may be inappropriate. The method is also flexible enough to include new types of information on spatial structure and demographic parameters as data accumulate.

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TABLE OF CONTENTS

List of Tables.....	xi
List of Figures.....	xiii
CHAPTER 1: Phylodemography as it pertains to the integration and application of demography and genetics into studies of intraspecific population dynamics or, the relevance of a phylodemographic approach to population biology.....	1
Problems with metapopulation theory and PVA.....	4
So what about Phylodemography?.....	6
Does science really need another term?.....	8
LITERATURE CITED.....	8
CHAPTER 2: Population genetics and phylogeography of the blue rockfish (<i>Sebastes mystinus</i>) from Washington to California.....	15
ABSTRACT.....	16
INTRODUCTION.....	17
METHOD.....	22
Molecular marker.....	21
DNA collection, extraction, amplification, and sequencing.....	23
Genetic Diversity.....	23
Sample size.....	24
Population structure.....	24
Phylogeography.....	26
RESULTS.....	26
Sample Size.....	26
Genetic Diversity.....	27
Population structure and gene flow.....	28

Phylogeography.....	29
DISCUSSION.....	31
Population Structure.....	31
Gene flow in the nearshore system.....	33
Barriers to gene flow.....	35
Future Considerations.....	38
LITERATURE CITED.....	40
CHAPTER 3: Stochastic matrix modeling of genetically differentiated populations of the blue rockfish (<i>Sebastes mystinus</i>): An introduction to phylodemography.....	67
ABSTRACT.....	68
INTRODUCTION.....	69
METHODS.....	73
Matrix Population Model.....	73
Deterministic Model Parameter Estimation.....	77
Stochastic Model Parameter Estimation.....	80
Elasticities.....	83
Loop analyses.....	84
Historical Demography.....	85
RESULTS.....	86
Deterministic models.....	86
Stochastic models.....	86
Elasticities.....	87
Loop analyses.....	90
Historical Demography.....	91
DISCUSSION.....	91
Ecological population dynamics of blue rockfish subpopulations.....	91
Evolutionary population dynamics of blue rockfish subpopulations.....	101

Phyloendemography.....	102
LITERATURE CITED.....	105

LIST OF TABLES

TABLE	PAGE
CHAPTER 1	
1. Examples from primary scientific literature demonstrating different approaches to combining demographic and genetic in populations studies.....	14
CHAPTER 2	
1. Suspected population structure of some rockfishes off the Pacific coast of the United States.....	55
2. Per area genetic diversity and neutrality test statistics for a 498 bp region of the blue rockfish mtDNA control region.....	56
3. Sequence divergence (below diagonal; standard deviation above) among blue rockfish sample areas.....	57
4. Relative frequencies of nucleotide bases of the mtDNA control region in blue rockfish at each location.....	58
5. Pairwise comparisons of genetic differentiation (below diagonal) and gene flow (above diagonal) among 8 blue rockfish sample sites.....	59
6. Differentiation among blue rockfish sample sites according to the AMOVA framework of hierarchical analysis under three hypothesized levels of geographic structure.....	60
CHAPTER 3	
1. Blue rockfish life history parameters per area and matrix model.....	117
2. Monthly survivorship estimates per stage per model per area.....	118
3. Deterministic population parameters based on annual rates of increase for two blue	

rockfish subpopulations.....	119
4. Yearly population growth rates (r and λ) for blue rockfish subpopulations under increasingly stochastic conditions.....	120
5. Deterministic and standardized (to the projection interval) elasticity values for each stage of the blue rockfish matrix model.....	121

LIST OF FIGURES

FIGURE	PAGE
CHAPTER 2	
1. Site location and sample number of blue rockfish collections. Arrows indicate potential barriers to dispersal.....	61
2. Cumulative segregating site curves.....	62
3. Pairwise geographic vs. genetic distances within and among regions of blue rockfish populations.....	63
4. Neighbor-joining and minimum evolution trees based on Kimura 2-parameter model.....	64
5. A 50%-majority consensus tree based on maximum parsimony.....	65
6. Simplified Minimum Spanning Network of blue rockfish haplotypes.....	66
CHAPTER 3	
1. Summary map of genetic sampling sites, sample sizes, and hypothesized location of population break in blue rockfish.....	122
2. General 5-stage <i>Sebastes</i> life cycle used for each subpopulation of blue rockfish.....	123
3. Deterministic matrix population models for two subpopulations of the blue rockfish.....	124
4. Life cycle graph of the blue rockfish decomposed into two types of loops.....	125
5. Intrinsic rates of increase and 95% confidence intervals (error bars) for deterministically and stochastically derived growth rates from each blue rockfish subpopulation.....	126

6. Percent elasticities based on deterministic and stochastic elements for each of the five stages of the matrix models of two subpopulations of blue rockfish.....	127
7. Elasticity ratios standardized to survivorship within the adult stage (P_5).....	128
8. Loop elasticity values for four self loops ($E_{A,A}$; $E_{SA,SA}$; $E_{SJ,SJ}$; $E_{L,L}$) and 2 reproductive loops ($E_{L,A,L}$; $E_{L,SA,L}$).....	129
9. Mismatch distributions of northern and southern blue rockfish subpopulations.....	130
10. Pelagic Juvenile blue rockfish abundance off central California from 1986 to 2001.....	131
11. The phylodemographic approach to population modeling.....	132

CHAPTER 1

Phylo demography as it pertains to the integration and application of demography and genetics into studies of intraspecific population dynamics or, the relevance of a phylo demographic approach to population biology.

(Author's note: I have always loved the verbose titles endowed to many Victorian-era scientific monographs. Because I have no intention of publishing this overview, I thought it an appropriate place to indulge in such an ornamented appellation.)

Population biologists seek to understand the cause and effects associated with changes in population abundance and distribution over time (Kingsland 1995). As the human population swells and interacts with increasing frequency and strength to affect animal and plant populations in many negative and undetermined ways, much scientific effort has shifted towards the sustainability of biological resources. Often, scientists can gain a deeper understanding of population biology, and therefore offer more informed advice to managers, when information is integrated from traditionally separate scientific disciplines. Unfortunately, the influential disciplines of demography (evaluation of vital rates and population structure on population growth), and genetics have not often been combined, mired in arguments as to which set of information is more informative, and therefore more useful to resource managers (Lande 1988; Boyce 1992; Caro and Laurenson 1994; Caughley and Gunn 1996; Brooks 1997; Clarke and Young 2000). While demographers have traditionally measured population growth rates, breeding habits, and migrations, geneticists have focused on the changes in fitness, rates of inbreeding and gene flow, and loss of genetic diversity (Hedrick and Miller 1992; Clarke

and Young 2000; Thrall et al. 2000). Although these demographic and genetic measures are similar in perspective, and it is agreed that demography and genetics interact at the population level (Neigel 1997; Richards 2000), a persistent dialogue of genetic inferiority remains. Brooks (1997) typifies the vilification of including genetics in the diagnostic study of population biology by stating, “Conservation and genetics, like pop and politics, don’t mix. A swift divorce should leave both science and what’s left on Earth, in better shape.”

Despite such antagonistic proclamations, there have been several, if not disparate, studies that do successfully and usefully marry demographic and genetic information (Table 1). Most influential is the development of conservation biology (Gilpin and Soulé 1986), often represented in the burgeoning studies of metapopulation biology (Levins 1969; Hanski and Gilpin 1997) and population viability analysis (PVA; (Boyce 1992; Burgman and Possingham 2000; Morris and Doak 2002). Both approaches are not mutually exclusive, employing a variety of biological data to ultimately identify viable populations by describing population persistence over time. The metapopulation approach contains a diverse group of models (Hastings and Harrison 1994; Harrison and Taylor 1997; Holyoak and Ray 1999), derived from the simplified model of Levins (1969), having in common the assumptions that the metapopulation consists of a group of local populations connected by some degree of migration that have nonzero probabilities of extinction and subsequent colonization (Hanski and Simberloff 1997; Harrison and Taylor 1997; Thrall et al. 2000; Smedbol et al. 2002). And though the real strength of

metapopulation analyses is the emergent population dynamics at the metapopulation level, it has produced interesting studies combining demography and genetics (Hanski and Gilpin 1997; Young and Clarke 2000). PVA is a general modeling approach that estimates future population size and extinction risks by incorporating life history, genetics, habitat, disease and other species specific biological information interacting to affect persistence (Gilpin and Soulé 1986; Shaffer 1990; Mace and Lande 1991; Hansen et al. 1999; Livingston and Jurado-Molina 2000; Coulson et al. 2001). Because both metapopulation biology and PVA often focus on how habitat fragmentation affects the persistence of small populations, most studies have focused on the influences of environmental and demographic stochasticity, loss of genetic variation, and inbreeding depression (Hanski and Gilpin 1997; Young and Clarke 2000) on probabilities of population extinction and persistence. It is generally accepted that environmental stochasticity (i.e. random environmental variation) and demographic stochasticity will cause a population to become extinct well before genetic factors (low genetic variation and inbreeding depression) will (Lande 1988; Murphy et al. 1990; Caro and Laurenson 1994; Clarke 2000; Holsinger 2000; Oostermeijer 2000; Thrall et al. 2000; Feral 2002). Despite the acceptance that environmental and demographic factors are usually more important to population persistence in the short-term, genetic factors can not be ignored, and further integration of demographic and genetic analyses in conservation biology are deemed essential (Lande 1988; Pimm et al. 1989; Nunney and Campbell 1993; Milligan

et al. 1994; Nunney 1994; Avise 1995; Hedrick et al. 1996; Neigel 1997; Young and Clarke 2000).

Problems with metapopulation theory and PVA

Though resource managers have increasingly used metapopulation analyses and PVA to understand population dynamics, each approach has many shortcomings as applied to marine resources. For instance, the assumption of metapopulation theory that populations undergo extinction and colonization events may not be applicable to many populations being managed. The main objective of metapopulation theory is to understand emerging population behavior at the metapopulation level that drives population dynamics, and therefore persistence. Populations that do not exhibit regular extinction/colonization events rely more on local population dynamics than metapopulation dynamics (Harrison and Taylor 1997; Smedbol et al. 2002). The assumption of population extinction/colonization may be valid on evolutionary time scales-- considering all species and, therefore, populations will become extinct at some point (Eldridge 1994)— but not on ecological time scales that concern resource managers. This is particularly true for marine populations where very few instances of extinction/colonization events on ecological time scales are recognized (Smedbol et al. 2002); therefore, marine population dynamics are driven more by localized population dynamics and not emergent metapopulation properties. Regardless, Smedbol et al. (2002) revealed the word ‘metapopulation’ continues to be invoked in marine studies when there is no proof of a

metapopulation, and such unwarranted use is facilitated by blurred conceptual notions of what a metapopulation is. They urge that metapopulation theory not be used in marine systems unless it is strictly and consistently defined, and applicability is justified.

Secondly, while both metapopulation analyses and PVA attempt to provide predictions as to population persistence, the accuracy of the predictions depend on several factors (Shaffer 1990). The only way such predictions can hold up are if the data used are of unquestionable reliability and static in nature (Burgman and Possingham 2000; Coulson et al. 2001). Any deviations or stochastic events (and by definition, stochastic events are random and difficult to predict) not contained in the data set used may render any predictions at minimum useless and at the worst dangerous to resource management. The farther in the future the predictions are made, the less reliable they are. PVA also often requires extensive data sets on vital rates and habitat quality that are not available for most marine populations, limiting its usefulness in these systems.

Thirdly, most metapopulation and PVA theory has been devised under the conditions of small fragmented populations. What about populations that are not in danger of biological extinction, but are near commercial extinction? What about responsible management of resources before they are depressed or fragmented? Additionally, most metapopulation and PVA theory was developed in terrestrial plant and animal systems (Harrison and Taylor 1997; Richards 2000), which raises the question as to their applicability to marine systems (Neigel 1997).

So what about phylodemography?

Phylodemography is an integration of demographic, population genetic, and environmental information into a comprehensive tool specifically modeling the historical and current dynamics of spatially structured intraspecific populations. It is apparent that metapopulation analysis and PVA are not appropriate for studying the population dynamics of all species; I have therefore developed phylodemography as an alternative approach of combining genetic and demographic information to analyze population dynamics when either metapopulation analysis or PVA approaches are not appropriate for the species in question. The name is derived from John Avise's term "phylogeography", an increasingly popular way of describing the geographic distribution of genealogical lineages (Avise 2000). And while phylogeography melds information from several disciplines including demography and genetics, its aim is to connect population dynamics on ecological time scales with historical population structure on evolutionary time scales. Phylodemography uses the accumulating information from phylogeographic studies and incorporates it into population models to place evolutionary lineages in ecological contexts (I have chosen to use matrix population models in this thesis because they are a very powerful and flexible ecological tool (Caswell 2001)). A phylodemographic approach, therefore, avoids the pitfalls of equating genetic analysis solely with genetic variance or heterozygosity (Dodson et al. 1991; Milligan et al. 1994; Avise 1995) and demography strictly with population size and age structure. I have developed phylodemography particularly for marine resource managers to use when

biological data are limited, but management is needed. It is the combined population modeling of life history and genetic information, and not exclusive from either metapopulation biology or PVA, but emphasizing current population status and connectivity over population persistence predictions. Insights offered through a phylodemographic approach will offer resource managers information on spatially structured life history relationships currently needed to manage deterministic effects (i.e. harvest) on populations in light of the stochastic events that drive population dynamics.

The remainder of my thesis is as follows: Chapter 2 is a basic analysis of the population genetics and phylogeography of the blue rockfish (*Sebastes mystinus*), an important rockfish in the nearshore fisheries from California to Washington. The main objective is to determine substructuring of populations throughout this species range. IN chapter 3 I then take the information from Chapter 2 and, using the best information on survivorship, age and growth, fecundity, and environmental influences for each substructured area, construct a five stage matrix model to determine subpopulation growth rates and stage-based elasticity values. The population genetics of each region is then further explored to reveal area-specific historical demography. This combination of genetic and demographic information on evolutionary and ecological time scales to produce an historical and contemporary understanding of population dynamics is phylodemography.

Does science really need another term?

Probably not. The strict specialization of science into multiple subdisciplines can cause narrow-minded research goals, loss of big picture sense, factions, and inhibition of scientific progress (see above debate between demography and genetics). However, phylodemography is an integrative approach to the study of population dynamics that encourages invention in investigation, discouraging exclusionary specialization. I feel phylodemography offers something different from other approaches and therefore needs to be distinguished and set apart. Often new terms inspire growth and development of ideas, whether the term is accepted or rejected. I hope this thesis inspires ideas and offers a way in which progress will be made towards responsible management and stewardship over natural resources.

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Table 1. Examples from primary scientific literature demonstrating different approaches to combining demographic and genetic data in population studies.

Study	Approach
Clarke 2000	Estimates adult and juvenile survivorship from information obtained through genetic markers.
Dietz et al. 2000	Measures inbreeding depression in a population tracked for all births, deaths, immigrants, emigrants. Compares mortality measure between inbred and non-inbred populations
Gaggiotti and Vetter 1999	Examines the affects of life history strategies and environmental variability on genetic diveristy.
Goldstein et al. 1999	Use genetics markers to determine population realtionships and changes in historical population size.
Lande 1982	Life history evolution modeled using genetic correlations among life history characters.
Mills & Smouse 1994	Incorporation of inbreeding depression into matrix population models.
Olivieri & Gouyon 1997	Combines population matrix modeling and genetics to study the evolution of life histories.
Pease et al. 1989	Modeled changes in population growth and phenotypes in changing environements
Promislow et al. 1999	Genomic demography: using matrix population models to measure transposition and excision rates in genomes.
Promislow & Tatar 1998	Explores the demography/genetics realtionship by modeling mutation effects on mortality and longevity.
Tallmon et al. 2002	Abundance and genetic variation information combined give different and more insightful population information than either information alone.
Young et al. 2000	Stochastic matrix models used to model relationship between population persistence and high genetic diveristy and low correlated paternity.

CHAPTER 2

**Population genetics and phylogeography of the blue rockfish (*Sebastes mystinus*)
from Washington to California.**

ABSTRACT

Resolving stock structure for marine species with high degrees of potential dispersal is essential for developing appropriate fishery management plans. Blue rockfish (*Sebastes mystinus*) are one of the most important recreationally-caught fishes in California and Oregon, yet the degree of spatial structuring between localized populations is not understood. I took 245 samples of blue rockfish from eight locations throughout its range and used sequences from a 498 base pair portion of the mitochondrial DNA (mtDNA) control region to describe genetic diversity, population structure, and phylogeography. Haplotype diversity was high, but nucleotide diversity was low, indicating historical instability in blue rockfish population dynamics. Cumulative genetic diversity curves indicate that two sites (FAR and SNI) were likely undersampled and that generally 15 to 25 samples are needed to accurately assess mtDNA genetic diversity within a population. Significantly high levels of population differentiation were detected among sample sites (maximum pairwise $F_{st} = 0.246$, $P < 0.01$), with a distinct break ($\Phi_{CT} = 0.149$, $P \ll 0.0001$) between two subpopulations north and south of Cape Mendocino. When regional distinction is considered, there is no overall trend between geographic and genetic distances and thus the stepping-stone model is not sufficient to explain population differentiation. Cape Mendocino may prove to be an important biogeographic barrier to other marine organisms, but has not been extensively explored as such. The northern subpopulation was derived from the southern subpopulation by an asymmetrical flow of

genetic material northward; little contact has been made between the populations for potentially thousands of years. Therefore repopulation of a depleted southern subpopulation is unlikely to come from the northern subpopulation.

INTRODUCTION

The combination of complex hydrography, few apparent barriers to dispersal, and vagile life history stages of many marine species is thought to facilitate spatially extensive, yet ecologically relevant demes in the marine environment (A vise 1992; Gold et al. 1994; Palumbi 1994; Waples 1998; Shaw et al. 1999). But recent work in marine population biology has challenged the notion that intraspecific marine populations are often interconnected on ecological time scales (A vise 2000; Cowen et al. 2000). Though marine species tend to show higher levels of gene flow and lower levels of overall genetic variation compared to freshwater and anadromous species (Gyllensten 1985; Hedgecock 1994; Neigel 1994; Waples 1998), panmixia within a species is not always realized (Neigel 1997). Isolation-by-distance and stepping stone models can explain some levels of intraspecific differentiation among ecologically connected populations (Johnson and Black 1982; Palumbi et al. 1997; Palumbi 2000; Wilke and Davis 2000), but not all abrupt genetic discontinuities (Riginos and Nachman 2001).

Clarifying the relationship between spatially structured populations is essential for marine resource managers who attempt to identify stock relationships (stock defined here as reproductively isolated, and therefore demographically and genetically separate,

populations; Carvalho and Hauser 1995; Waples 1998) and recruitment sources that affect marine population dynamics (Ferris and Berg 1987; Lee et al. 1995; Shields and Gust 1995; Bagley et al. 1999; Roques et al. 2002). Whereas morphological and other phenotypic differences among populations may be inadequate to distinguish stocks (Ihssen et al. 1981; Carvalho and Hauser 1995), the use of molecular biological tools to determine genetic markers that elucidate intraspecific population structure has become increasingly important in the study of marine systems and may offer a way to identify practical management units (Ferris and Berg 1987; Pella and Milner 1987; Stepien 1995; Bowen 1999). Rockfishes (genus *Sebastes*) are an ecologically diverse and economically important group of fishes that are of particular concern to fisheries managers in the Northeast Pacific Ocean (Yoklavich 1998; Parker et al. 2000; Love et al. 2002).

Most rockfishes (at least 65 species; Love et al. 2002) live within the dynamic California Current System (CSS), a system of currents from Alaska to Costa Rica that show a variety of spatially and temporally large and small scale events. The CCS is characterized by a general equatorward flow, but nested within it are shelf and nearshore circulatory events that change seasonally and spatially in strength and direction (Hobson and Chess 1988; Botsford et al. 1994; Morgan and Botsford 1998; Leet et al. 2001). Upwelling is an important, transient feature of a portion of the California Current system during spring and summer months (Strub et al. 1987; Bakun 1996). This phenomenon of offshore transported water replaced by deeper, colder, more nutrient rich water facilitates a highly productive nearshore environment, providing periods of abundant resources for

most life stages of macrofauna (Bakun 1996). Along with this generous provision of nutrients, this system of water transport may also provide means of connecting localized populations of generally residential subadult and adult fishes, such as many rockfish species (Rocha-Olivares and Vetter 1999).

Local populations of rockfishes may or may not be connected genetically within the CCS. Genetic connectedness is maintained by the mixing of individuals at some point in their life history, allowing reproductive interaction and the transfer of genetic material. For instance, adults spatially separated for most of their lives may migrate to a certain area to reproduce, or larvae may be transported to areas away from where they were spawned and remain there as adults (Yoklavich et al. 1996). High genetic relatedness of individuals in different areas may indicate that the areas exchange individuals. Intraspecific genetic connectedness can determine how subpopulations—usually defined simply by separate geographic areas—are related.

Rockfishes are characterized by internal fertilization and live birth, extruding hundreds of thousands of larvae that may remain in the water column for several months (Love et al. 1990; Haldorson and Love 1991; Moser 1996; Love et al. 2002). In many of the species, the adults are sedentary; therefore the planktonic larval and juvenile stages provide the only potential means of connecting distant populations. Though the larval stage is mostly passively planktonic, it is not well understood, but often assumed, that such an extended period of larval dispersement provides a sufficient mechanism to mix

populations. Many rockfish born in the early spring are believed advected offshore during the upwelling season, mixing with conspecific larvae from other areas, then transported inshore during periods of relaxation (Larson et al. 1994; Yoklavich et al. 1996).

Several studies have investigated population structure in rockfish along the Pacific coast (Table 1). Though methods vary (some potentially insufficient to detect structure) a general trend has emerged: nearshore species demonstrate more substructuring than offshore species, with the extent of structuring varying among species. The general trend of more population structuring on smaller geographic scales among nearshore and estuarine fishes compared to deep shelf, slope and pelagic species is also emerging among other marine fishes in the Northeast Pacific (Waples 1987; Waples and Rosenblatt 1987; Hedgecock et al. 1989; Stepien 1995; Jagielo et al. 1996; Stepien 1999; Bernardi 2000; Bernardi and Talley 2000; Stepien et al. 2000; Terry et al. 2000; Dawson et al. 2001; Riginos and Nachman 2001; Stepien et al. 2001; Dawson et al. 2002). Though mechanisms behind this pattern are not known, oceanographic conditions and habitat discontinuities may be of particular relevance (Riginos and Nachman 2001).

Blue rockfish (*Sebastes mystinus*) populations, which effectively range from southern California to Washington (Love et al. 2002), are the most important fish in the central and northern California recreational fishery and second only to the black rockfish (*Sebastes melanops*) in the Oregon recreational fishery (Leet et al. 2001; Love et al. 2002; Starr et al. 2002). This schooling fish is often found in large numbers around and

within kelp forest and rocky nearshore reefs (Love et al. 2002), and seasonally abundant juveniles provide food for many nearshore fish and bird species (Miller and Geibel 1973; Baltz 1976; Follett 1976; Roberts 1979; Ainley et al. 1981; Ainley et al. 1993; Hobson et al. 2001; Love et al. 2002). Despite its importance to nearshore ecology and commerce, blue rockfish stock structure remains unknown.

This study uses sequence data from the variable mitochondrial DNA (mtDNA) control region to: (1) describe sequence variation and genetic diversity, (2) population structure and gene flow and (3) phylogeography of the blue rockfish from eight locations throughout its range. The main goal is to test the null hypothesis of no population structure in blue rockfish, with a preliminary hypothesis of expected population structure in this nearshore fish at one or more of several potential biogeographic breaks (Fig. 1).

METHODS

Molecular marker

Mitochondrial DNA (mtDNA) has gained increasing acceptance as an appropriate genetic marker for population genetics and phylogeography for five main reasons (Avice 2000; Feral 2002): (1) mtDNA generally evolves ten times faster than nuclear DNA (Brown et al. 1979; Hedrick and Miller 1992), offering a large number of analytically useful genetic characters (Mitton 1994; Stepien 1995); (2) mtDNA generally does not recombine (Hayashi et al. 1985), allowing mutation to accumulate without intragenomic mixing; (3)

the millions of copies of mtDNA within an individual are generally homoplasmic and clonally inherited (Awise 1994; Park and Moran 1995; Stepien and Kocher 1997); (4) Different regions of mtDNA evolve at variable rates, allowing systematic, ecological, and evolutionary questions to be addressed (Saccone et al. 1987; Park and Moran 1995; Bowen 1999); and (5) mtDNA is usually maternally inherited, therefore any structuring implied through mtDNA divergence implies strong demographic autonomy of the matrilineage over ecological time (Awise 1995). These traits reduce the effective population size of mitochondrial genomes to one-fourth that of nuclear genomes (Nei and Tajima 1981), resulting in stronger genetic drift and greater ability to record differences among populations. The control region, a non-coding segment that contains both a highly conserved (“conserved sequence blocks”— good for primer development) and highly variable (left and right domains) portions (Brown et al. 1986; Saccone et al. 1987; Lee et al. 1995), has continued to prove useful for revealing intraspecific population differentiation in rockfishes (Julian 1996; Seeb 1998; Rocha-Olivares and Vetter 1999; Gilbert 2000) as well as other fishes (Ferris and Berg 1987; Neigel 1994; Stepien 1995; Stepien and Kocher 1997; Bernardi 2000; Bernardi and Talley 2000; Terry et al. 2000).

DNA collection, extraction, amplification, and sequencing

Archived and newly collected fin clips were collected from blue rockfish at eight different sites (Fig. 1) representing the effective range of the species (Love et al. 2002). DNA was extracted following a modified salt extraction protocol of Medrano et al. (1990) and

electrophoretic bands were detected on a 0.8% agarose gel. The following primers were used to amplify a 498 base pair section of mitochondrial DNA (mtDNA), including the highly variable L domain of the D-loop control region: AAGCACTTGAATGAGCTTG (L15926; Rocha-Olivares and Vetter 1999) and CCTGAAGTAGGAACCAGATG (H16498; Meyer et al. 1990). The following polymerase chain reaction (PCR; Mullis and Faloona 1987) protocol was used for amplification: 1 μ l of DNA and 0.1 μ l of Taq polymerase in a standard 25 μ l reaction thermal cycling at 1 min for 90° C plus 36 cycles of 1 min at 94° C, 1 min at 52-54° C, and 1 min at 72° C, plus 5 min at 72° C. All amplifications were visualized on a 1.5% agarose gel and purified products using QIAGEN's QIAquick PCR Purification kit, and sequenced in the laboratory of Northwoods DNA, Inc using dye terminator sequencing chemistry and ABI 377 sequencing technology. Sequencing of PCR product is considered to provide the fullest amount of genetic information per gene marker (Faber and Stepien 1997; Feral 2002). Sequences were edited in Chromas v. 2.21 and aligned in Clustal X v. 1.8 (Thompson et al. 1997); all alignments were evaluated and confirmed by myself.

Genetic data analysis

Genetic Diversity

Haplotype (h) and nucleotide (π ; average proportion of pairwise difference per sequence) diversity, number of segregating sites (S), and mean pairwise differences were used to describe genetic diversity in all areas. The transition to transversion ratio (tr:tv) and

nucleotide composition per area was also determined for descriptive value. Tajima's D statistic (Tajima 1989) was calculated to test for neutrality of mtDNA mutations. All calculations were made using the software programs DNAsp v. 3.98 (Rozas and Rozas 1999) and Arelquin v. 2.0 (Schneider et al. 2000).

Sample size

In an attempt to evaluate whether sufficient samples for each area were collected to characterize genetic diversity, nucleotide polymorphisms (θ , the proportion of nucleotide sites expected to be polymorphic per sequence; calculated in DNAsp v. 3.98) and S were plotted against number of sequences to generate a cumulative genetic diversity curve (adapted from cumulative species curves; see Elliot 1971). Whereas S may overestimate the amount of samples needed to adequately characterize population sequence diversity because of accumulating segregating sites without overall increased sequence diversity, using θ per sequence may potentially underestimate approximation of ample sample size because segregating sites are standardized to number of sequences (Hartl and Clark 1997). A general leveling of each curve is usually indicative of adequate sample size within each method (Elliot 1971; Ferry and Cailliet 1996); therefore, recommended sample size for blue rockfish populations was determined somewhere between the approximations of each method.

Population structure

Population structure among sites was investigated using pairwise comparisons of population genetic variation (based on Wright's (1951) fixation index, F_{st}) and an

Analysis of Molecular Variation (AMOVA;). Slatkin's (1995) linearized transformation of F_{st} was used, that linearizes genetic distances with increasing divergence times. Gene flow among sites was estimated using Wright's Nm (Hartl and Clark 1997) and calculated from F_{st} values. Because most populations violate the assumptions of indirectly measuring gene flow from F_{st} values (Waples 1998; Whitlock and McCauley 1999), estimated gene flow should not be interpreted as actual numbers of migrants per generation. The relative magnitudes of the estimates, though, are useful to compare among areas and was considered here.

The AMOVA framework estimates the variance component of hierarchical population subdivision and calculates Φ_{st} , a statistic analogous to F_{st} , based on pairwise differences among sequences (Excoffier et al. 1992). Three hypothesized subdivisions were tested: (1) No subdivision; (2) Two regions: North (containing Washington and Oregon) and South (containing all California sites); (3) Two regions: North (containing Washington, Oregon, and Farallon Is.) and South (all California sites excluding Farallon Is.). Non-parametric significance of fixation indices F_{st} and Φ_{st} was calculated non-parametrically using 110 and >20,000 psuedo-replicated permutations, respectively. All population structure calculations and significance tests were performed in Arlequin v. 2.0 (Schneider et al. 2000). A Mantel's and partial Mantel's (removing the affect of region) test using 10,000 permutations for significance was also used to explore the relationship between geographic and genetic distance using the MANTEL program from R Package v. 4.0 (Casgrain and Legendre 2001).

Phylogeography

Phylogeographic relationships were reconstructed using neighbor-joining and minimum evolution distance methods, the Kimura 2-parameter distance model, 500 bootstrapped replicates, and the olive rockfish (*Sebastes serranoides*) as an outgroup (based on the phylogeny of Rocha-Olivares et al. 1999). A 50%-majority consensus tree based on maximum parsimony (MP) was also recovered for a non-distance comparison. All trees were constructed in MEGA v. 2.1 (Kumar et al. 2001). Because of poor tree resolution, a minimum spanning network (MSN) based on the pairwise differences between operational taxonomic units (OTUs) was also constructed (using the MSN output in Arlequin v. 2.0) to represent the relationship between haplotypes.

RESULTS

Sample Size

The conservative cumulative segregating site curves show a moderate leveling off beyond 30 samples (Fig. 2A); however, in the more liberal nucleotide polymorphism curves (Fig. 2B), a rough leveling occurs around 10 to 15 samples (note: though standard errors are not plotted here for convenience, they do decrease as sample size increases). A third line of evidence for ample sample size per area is given by the standard error for the mean pairwise differences (Table 1). Standard error (SE) is very low for all areas except SNI with the lowest sample size (N=5). Elevated variances are also seen in the other two areas of lower sample size (FAR (N=17) and BC (N=24)) compared to the remaining

areas. Combining all three lines of evidence indicates the sample size for mtDNA control region sequences should be at least 15 to 25 samples to properly assess genetic diversity within the area. This number is well above samples sizes used in many mtDNA studies (Waples 1998). In this study, only SNI and possibly FAR seem undersampled.

Genetic Diversity

Haplotype diversity was high (all sites at or close to the maximum value of 1.00), but nucleotide diversity low (as defined by Bowen and Grant 1997 for the mtDNA control region) in all sample sites of blue rockfish (Table 2). These results are similar to the genetic diversity found in a similar portion of the mtDNA of the rosethorn rockfish (*Sebastes helvomaculatus*; Rocha-Olivares and Vetter 1999). Grant and Bowen (1998) suggest that high haplotype and low nucleotide diversity reveals distinct population instability, mainly population growth following a period of reduced effective population size. All sites conformed to tests of neutrality ($P > 0.1$) and therefore did not violate the assumption of neutral gene mutation within the mtDNA control region.

Sequence divergence within each site was low (Table 2) compared to the sequence divergence found in other intraspecific comparisons (Avice and Lansman 1983; Mitton 1994), but on average higher than that found in *S. helvomaculatus* for a similar mtDNA region (1.59%, SD = 1.18%; Rocha-Olivares and Vetter 1999).

Pairwise divergence among populations (Table 3) was higher between most populations than the total mean divergence (Table 2), except between the following

subpopulations: WA and OR; FB, BC, NR, & SM. All pairwise divergence comparisons among sites were greater than divergence within sites (Tables 2 & 3).

Nucleotide composition (Table 4) within each site was similar, with blue rockfish mtDNA control regions being richest in adenine and thymine and low in guanine and cytosine. While this pattern of nucleotide bases is consistent with the control region in other marine fishes, the relative contribution of guanine and cytosine is lower compared to other teleosts (Stepien 1995; Dawson et al. 2002), but higher than average nucleotide compositions of rockfishes within the subgenus *Sebastomus* (Rocha-Olivares et al. 1999). High transition to transversion ratios (tr:tv; Table 2) indicates that the degree of multiple substitutions is low in blue rockfish, indicative of relative young populations (Kocher and Carleton 1997). Washington, Oregon, and Farallon Is. populations exhibit the highest tr:tv ratios, and therefore the shallowest lineage times.

Population structure and gene flow

Significant genetic differentiation was evident among blue rockfish sample sites (Table 5). Pairwise F_{st} values indicate a significant regional genetic differentiation between WA/OR/FAR (referred hereafter as “North”) and FB/BC/SM/NR/SNI (referred hereafter as “South”) subpopulations. Higher levels of gene flow were also found within compared to between the hypothesized regional grouping of North and South subpopulations (Table 5).

Tested within the AMOVA framework, highly significant differentiation among the eight sites was found (Table 6A). When this analysis is extended to specific regional differentiation between North and South regions, highly significant differentiation among sites and between regions is demonstrated, while within group differentiation is low (Table 6B,C). Regional placement of the FAR subpopulation within the AMOVA framework had small effects on the overall significance of regional differentiation, though FAR was less differentiated from the North group (Table 6B,C).

Among all sites, a significant trend of increasing genetic distance with increasing geographic distance was demonstrated (Mantel $r = 0.486$, $P = 0.015$; Fig. 3, thick line), initially indicating genetic differentiation consistent with isolation by distance. Removing the effects of region (i.e. North and South groupings) though, reveals a non-significant relationship between genetic differentiation and geographic distance (partial Mantel $r = 0.18$, $P = 0.24$; Fig. 3). Plots of intra- and inter-regional comparisons (Fig. 3, thin and broken lines) illustrate the results of the partial Mantel test, signifying that isolation by distance is not a satisfactory explanation of the genetic differentiation among sites. The above evidence supports a North-South regional differentiation of blue rockfish subpopulations.

Phylogeography

Large numbers of haplotypes and small divergence times made for large and tightly branched trees; branches were collapsed in the following reconstructions to facilitate

analysis. A nonrandom grouping of “North” haplotypes emerges in the most derived ends of all trees (Figs. 4 & 5). Though there is very little support for the distance trees (bootstrapping values for nodes in Fig. 4 < 20%), due partially to the number of closely related haplotypes from a recent divergence, 90 haplotypes demonstrated relatively high bootstrapped values (defined here as > 50%). All high bootstrapped relationships supported a North (N=46 high bootstrapped values) and South (N= 44 high bootstrapped values) population distinction. Bootstrapped consensus trees (not shown) demonstrated a star phylogeny indicative of a recent population breaks. This general relationship indicated by the distance methods is also apparent in the MP reconstruction (Fig. 5): low numbers of cross-regional (i.e. northern and southern subpopulation) haplotype mixing, seen mostly in the North group, but overall strong regional alignment with the North and South groupings. Bootstrapped values were unresponsive of the MP consensus tree.

Another way to explore haplotype relationships is with a minimum spanning network (MSN). To interpret the MSN relationships, all haplotypes within 2 mutation steps from each other were collapsed into one group. Three large haplotype groupings (two “South”, one “North”) and four medium groupings (all “North”) were distinguished and exclusively contain members of each region (Fig. 6). These groupings represented 49% of North haplotypes and 46% of South haplotypes. All other haplotypes groupings were rare and radiated from one of these major groupings. The observation that major northern groupings all radiate from the biggest southern grouping is suggestive of a historically asymmetrical movement of southern haplotypes northward. The closer

association of some very rare southern haplotypes to northern rather than southern haplotypes is likely due to close divergence in evolutionary time of the two regions and the maintenance of more rare haplotypes in the younger northern lineage.

DISCUSSION

Population Structure

No previous work has investigated the population structure of the blue rockfish throughout its range. And although blue rockfish are livebearers with protracted larval and juvenile dispersal periods, biologically significant barriers to dispersal not consistent with isolation by distance occur. Multiple lines of evidence support the minimum separation of the blue rockfish population into two stocks: Washington/Oregon (northern) and California (southern). This finding is consistent with the suggestion by Laidig et al. (in press) that blue rockfish off central and northern California are one population and the accumulating evidence that significant population structuring exists among other nearshore rockfishes along the Pacific coast of the United States (Table 1). And while Fort Bragg and southern California sites show high genetic connectivity, the central Californian Big Creek subpopulation demonstrated low, but significant pairwise F_{st} values among all California sites. Whether the distinction of this subpopulation is biologically important, or just a factor of a high noise to signal ratio due to lower sample size (Waples 1998) at Big Creek is unclear and therefore does not warrant a separate central Californian stock distinction at this time.

The ambiguous relationship of the Farallon Islands' subpopulation is also difficult to currently explain. Those samples showed a statistically significant alignment with the northern stock, yet is well within the geographic range of the southern stock. While sampling error may exaggerate the true relationship between the Farallon Islands and other Californian subpopulations (sampling error ranges are 0.033 to 0.049 Waples (1998), excluding San Nicholas Islands subpopulation), this still does not explain the close relationship between the Farallon Is. and the Washington/Oregon complex. Increased samples size at the Farallon Islands and samples taken from the Cordell bank area—an offshore seamount 25 miles north of the Farallon Islands that also contains blue rockfish— would help resolve this ambiguous subpopulation relationship.

The northern stock of blue rockfish is younger and derived from the southern stock, a split which may have occurred 2,000 to 6,000 years ago (based on molecular clock calibrations for the mtDNA control region of 6% and 2% per million years (Rocha-Olivares et al. 1999 and Stepien 1999). High transition to transversion ratios, positioning within the phylogenetic trees, and branching relationships in the MSN fully support an asymmetrical and evolutionarily recent, but non-ecologically relevant, contribution of southern stock genetic material to the northern stock (Wares et al. 2001). This historical one-way flow of genetic material indicates the evolutionary importance of the southern stock—especially the highly abundant central and northern California populations—to the original establishment of blue rockfish in the northeast Pacific. Estimates of gene flow between populations are misleading in two ways: 1.) Estimates from F_{st} always

violate at least one of the numerous assumptions based on the island model of migration (Waples 1998; Whitlock and McCauley 1999) and therefore estimate only the relative number of migrants per generation; and 2.) Gene flow may be unidirectional. In the case of the blue rockfish, there is little evidence to indicate historical gene flow contribution from the northern stock to the southern stock, though gene flow estimates here indicate very low numbers of migrants per generation. It therefore seems the northern stock is incapable of providing sufficient recruits to repopulate the heavily targeted southern stock over ecological or evolutionary times under current hydrological and geological regimes. This is important to understand because of the increased fishing pressure on nearshore rockfish due to increased regulations on offshore species and specific indicators of population stress in the southern blue rockfish stock (Karpov et al. 1995; Mason 1998; Starr et al. 2002).

Gene flow in the nearshore system

The establishment and maintenance of separate blue rockfish stocks is attributable to the complex interaction of oceanographic, behavioral, ecological, and biogeographic factors on early life history stages (Ralston and Howard 1995; Riginos and Nachman 2001).

There is much evidence that the typical blue rockfish progeny— having approximately a four-month pelagic phase (Krigsman 2000; Tenera 2000)— are extruded during the late winter/early spring months (Wales 1953; Miller and Geibel 1973; Carr 1983; Moreno 1993; VenTresca et al. 1995; VenTresca et al. 1996) then advected offshore during the

spring upwelling season (Ainley et al. 1993; Larson et al. 1994; Yoklavich et al. 1996); juveniles then return to the nearshore in the spring/early summer, possibly during periods of relaxation and onshore transport (Larson et al. 1994; Yoklavich et al. 1996).

During the period of peak blue rockfish parturition (January and February throughout California), surface wind drift conditions are usually shoreward, promoting retention of larvae (Parrish et al. 1981). As spring upwelling conditions form, the larvae—approaching transformation size to the pelagic juvenile stage—are advected offshore, residing relatively deep in the water column (Lenarz et al. 1991; Larson et al. 1994); the deep residence and large sizes (Larson et al. 1994) are indicative of the ability to vertically migrate that may prohibit further advection offshore (Roques et al. 2002) while reducing mortality rates (Yoklavich et al. 1996). Most genetic mixing of localized nearshore populations is expected at this stage. As the juveniles grow they become more capable of horizontal migrations; at this time relaxation events and short periods of onshore transport may combine with the behavioral movement shoreward to provide new recruits of mixed genetic stock to the nearshore populations (Wyllie Echeverria 1987; Farrell et al. 1991; Morgan and Botsford 1998; Wing et al. 1998). Cyclonic eddies (Owen 1980), alongshore frontal zones (Richardson and Percy 1977; Wing et al. 1998), “upwelling shadows” (areas of warmer, fresher water inshore of upwelling zones; (Graham et al. 1992; Graham and Largier 1997; Botsford 2001), and other localized circulatory events create seasonally and spatially transient retention zones around certain geographic features that also promote the maintenance of nearshore rockfish recruits

(Morgan and Botsford 1998). Increasing the variance around these generalized recruitment events are oceanographic changes occurring on weekly (Wing et al. 1995; Wing et al. 1995; Wing et al. 1998; Wing et al. 1998), interannual (Ralston and Howard 1995; Lundquist et al. 2000), decadal (El Niño /La Niña; Yoklavich et al. 1996; Lundquist et al. 2000), and interdecadal (regime shifts; Steele 1996; Lluch-Belda et al. 2001) time periods. And though uncertainty in annual recruitment is large (VenTresca et al. 1995; MacCall 1996; Yoklavich et al. 1996), rocky reef and kelp habitat— and therefore blue rockfish populations— are patchily distributed along the northeast Pacific coast, and the extent of offshore mixing at these early life history stages has never been quantified, genetic mixing remains sufficient to homogenize the various locally isolated populations of blue rockfish along a large portion of the California coast. One very important factor maintaining genetically panmictic populations is the long-lived nature of blue rockfishes (Laidig et al. in press), wherein overlapping generations and deep age structuring increases the pool of genetic variation available each year (a phenomena termed the “storage effect”; Warner and Chesson 1985; Ellner and Hairston Jr. 1994; Caceres 1997). Why, then, is the blue rockfish not genetically homogenized along its whole range? Why is the stepping stone model inappropriate to fully describe genetic variation in blue rockfish populations when each population may be expected to coastally disperse 100 to 200 km (Botsford et al. 1998)? And where potentially is this genetic break located?

Barriers to gene flow

Several promontories or prominent geographic structures lie within the blue rockfish range, representing potential biogeographic breaks (Fig. 1). Sampling in this study is insufficient to positively determine which, if any, promontories may be important to the structuring of blue rockfish populations, but the results here do provide insight. The California Current System has traditionally been broken into four major regions based on different hydrologic patterns (Parrish et al. 1981; GLOBEC 1994): British Columbia south to Cape Blanco or Cape Mendocino (Region 1), Cape Mendocino to Point Conception (Region 2), Point Conception to Punta Baja, Mexico (Region 3), and Punta Baja to Cabo San Lucas, Mexico (Region 4; GLOBEC 1994). The most widely studied biogeographic break within the California Current is between Regions 2 and 3 at Point Conception (Burton 1998). Though this geographic area marks the boundary between the Oregonian and California biogeographic provinces, accumulating evidence indicates little relationship between intraspecific phylogeographic breaks and the Point Conception biogeographic boundary (Burton 1998; Gilbert 2000). Results from this study add to these previous findings and indicate no significant phylogeographic structuring of blue rockfish across Point Conception. In light of this study, only two of the remaining geographic structures from Figure 1 likely contribute to the blue rockfish phylogeographic break: Cape Mendocino and Cape Blanco, each of which delineate the boundaries of the Eel River Basin (California Department of Fish and Game 2002

Nearshore Fishery Management Plan) and the “Eureka” management area designated by the International North Pacific Fisheries Commission (Williams and Ralston 2002).

With regard to the blue rockfish stock structure, Cape Mendocino is the most compelling of the two promontories for several reasons. It is highly geologically dynamic, being one of the few places in the world where three major plates (Pacific, North American, and Juan de Fuca/Gorda; known as the “Mendocino Triple Junction”) collide nearshore (Henstock et al. 1997), potentially affecting the explosive speciation of rockfishes (Johns and Avise 1998) since the Miocene. But of more relevance to this discussion of contemporary barriers to gene flow is Cape Mendocino’s position as the area of maximum upwelling within the California Current System (Parrish et al. 1981; Largier et al. 1993; GLOBEC 1994; Bakun 1996). Gunderson and Sample (1980) noted that maximum abundances of rockfishes are found in central California and the Pacific Northwest, but the local minimum is near Cape Mendocino (Parrish et al. 1981). This area of converging currents and strong upwelling and weak relaxation events may prohibit the return of juvenile blue rockfish to nearshore areas (Magnell et al. 1990; Bakun 1996). This intense area of turbulent water mixing may also be too much to maintain fine-scale food patches fed upon by young blue rockfish. Both conditions create an inhospitable “dead zone” to local larval populations, decreasing survival and gene flow, thus creating different stocks over time (Iles and Sinclair 1982). The region between Cape Mendocino and Cape Blanco may effectively define this zone (Gunderson and Sample 1980), creating a shifting buffer (due to interannual environmental variation)

of almost 300 km between the two blue rockfish stocks. Gabriel (1982) demonstrated that low standing stocks and low diversities characterized demersal fish assemblages between Cape Blanco and Cape Mendocino, while also noting this area “incurs the largest annual variation in north-south surface wind stress of any area between Cape Flattery and Point Hueneme.” An additional feature to this area is the Mendocino Escarpment, a major submarine ridge that extends 2,500 km westward from Cape Mendocino that limits the amount of nearshore habitat available to nearshore fishes like blue rockfish, and appears to be a distributional barrier to other rockfishes (Williams and Ralston 2002). Cape Mendocino has previously been shown to be a phylogeographic break in other species (Rawson et al. 1999; Dawson et al. 2001), but this geographic break has not been explicitly tested. Blue rockfish genetic material taken at Cape Mendocino and within the area between Cape Mendocino and Cape Blanco would help resolve blue rockfish population substructuring in this area, while exploration of population breaks in other taxa may establish this area as a major biogeographic break for other nearshore fishes.

Future Considerations

I have suggested several ways to clarify stock structure in the blue rockfish, but several additional possibilities remain. The coastal oceanographic dynamics within the California Current System are characterized by high spatial and temporal variability. Such environmental stochasticity and seasonal dependence of rockfish on environmental conditions (Larson 1991; VenTresca et al. 1995) have created multiple mechanisms by

which populations may genetically vary. The “sweepstakes-chance hypothesis” (Hedgecock 1994; Hedgecock 1994) is one hypothesis offered to explain chaotic genetic heterogeneity in early life stages of marine organisms, although this does not seem to be the case in some nearshore rockfishes, possibly including blue rockfish (Gilbert 2000; Burford 2001). Despite those findings, multi-year sampling throughout the age structure of local populations will increase fine-scale resolution of intrapopulation phylogeographic relationships (Hedgecock 1994).

And although the mtDNA control region has proven useful in discerning intraspecific phylogeography, one marker is only a portion of the entire genome and cannot register all informative evolutionary events. The use of multiple genetic markers has increased the resolution and power of genetics studies, revealing genetic structure where lone markers do not (Burton 1994; Milligan et al. 1994; Ferguson and Danzmann 1998). Because statistically significant genetic structure was not found beyond the two blue rockfish stocks identified does not mean additional structure does not exist (Hedgecock 1994; Hedrick 2001). Highly variable microsatellite markers have successfully identified increasing genetic structure in other rockfishes (Buonaccorsi et al. 2002); the inclusion of these and other genetic markers combined with these current results and intensive multi-year population sampling will further resolve stock structure in the blue rockfish and provide marine resource managers with the information needed to make well-informed decisions regarding the sustainable management of this and other important nearshore resources.

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Table 1. Suspected population structure of some rockfishes off the Pacific coast of the United States.

Species	Common Name	Substructure	Method/Marker	Source
Nearshore				
<i>S. atrovirens</i>	Kelp rockfish	North/South of Pt. Conception none b/t S. CA and C. CA	headspine meristics mtDNA RFLP	Love & Larson 1978 Gilbert 2000
<i>S. auriculatus</i>	Brown rockfish	Washington; California	allozymes	Seeb 1998
<i>S. carinus</i>	Gopher rockfish	N. CA (Ft. Bragg); C. CA (Monterey to San Luis Obispo); S. CA (Ventura/ Pt. Loma)	microsatellites	Vetter <i>et al.</i> 2001
<i>S. caurinus</i>	Copper rockfish	Puget Sound; California California; Washington; Alaska S. CA (Sam Miguel I.); N. CA (Crescent City); Puget Sound	meristics allozymes/mtDNA RFLP microsatellites	Chen 1986 Seeb 1998 Buonaccorsi <i>et al.</i> 2002
<i>S. chrysomelas</i>	Black-and-yellow rockfish	N. CA (Ft. Bragg); C. CA (Monterey to San Luis Obispo); S. CA (Ventura/ Pt. Loma)	microsatellites	Vetter <i>et al.</i> 2001
<i>S. maliger</i>	Quillback rockfish	Puget Sound; Alaska to California	allozymes/mtDNA	Seeb 1998
<i>S. melanops</i>	Black rockfish	WA to mid-OR; mid-OR to CA WA to N. OR; N. OR to S. CA none b/t OR and WA	allozymes tag/recapture data allozymes	Barker 1996, unpublished Wallace <i>et al.</i> 1999 Barker 1999
<i>S. mystinus</i>	Blue rockfish	none b/t C. and N. CA	microsatellites	Burford 2001
<i>S. rastrelliger</i>	Grass rockfish	N. CA (north of SF); S CA	microsatellites	Vetter <i>et al.</i> 2001
Shelf/Slope				
<i>S. flavidus</i>	yellowtail rockfish	none from WA to CA none b/t Vancouver I., WA & CA	allozymes rDNA RFLP	Wishard <i>et al.</i> 1980 McGauley & Mulligan 1995
<i>S. goodei</i>	Chilipepper	none from WA to CA	allozymes	Wishard <i>et al.</i> 1980
<i>S. helvomaculatus</i>	Rosethorn rockfish	North/South of B.C. (Canada)	mtDNA sequences	Rocha-Olivares & Vetter 1999
<i>S. paucispinis</i>	Bocaccio	None from OR to CA None along CA coast	allozymes microsatellites	Wishard <i>et al.</i> 1980 Vetter pers. com.
<i>S. pinniger</i>	Canary rockfish	WA to s. OR; s. OR to CA single panmictic stock	allozymes	Wishard <i>et al.</i> 1980 STAT 1999

Table 2. Per area genetic diversity and neutrality test statistics for a 498 bp region of the blue rockfish mtDNA control region.

AREA	N	h (SD)*	(π) **	S^{\wedge}	Mean pairwise differences (S.D.)	Mean % sequence divergence (S.D.)	Tr:tv ratio (S.D.)	Tajima's D statistic (P-value)
Neah Bay, WA	42	0.998 \pm 0.006	0.0191	53	9.50 \pm 0.95	1.82 (0.10)%	7.7 (2.2)	-0.811 (P>0.1)
Charleston, OR	50	0.990 \pm 0.007	0.0183	60	9.08 \pm 0.73	1.79 (0.10)%	6.8 (2.1)	-1.123 (P>0.1)
Fort Bragg (FB), CA	32	1.000 \pm 0.008	0.0168	56	8.36 \pm 0.99	1.63 (0.17)%	4.3 (1.1)	-1.478 (P>0.1)
Farallon Is. (FAR), CA	17	1.000 \pm 0.020	0.0231	51	11.48 \pm 3.55	2.23 (0.25)%	6.6 (1.6)	-0.999 (P>0.1)
Big Creek (BC), CA	24	1.000 \pm 0.012	0.0199	57	9.88 \pm 1.84	1.91 (0.17)%	5.1 (1.2)	-1.375 (P>0.1)
Naples Reef (NR), CA	43	0.999 \pm 0.005	0.0177	67	8.78 \pm 0.80	1.73 (0.13)%	4.8 (1.3)	-1.548 (P>0.1)
San Miguel I. (SM), CA	32	0.992 \pm 0.011	0.0169	55	8.38 \pm 1.00	1.67 (0.13)%	4.8 (1.2)	-1.431 (P>0.1)
San Nicholas I. (SNI), CA	5	1.000 \pm 0.126	0.0233	24	11.60 \pm 15.54	1.86 (0.13)%	4.4 (2.7)	0.052 (P>0.1)
Total	245	0.998 \pm 0.007	0.0199	138	9.86 \pm 0.17	1.98 (0.04)%	5.6 (1.3)	-1.746 (0.1>P>0.05)

*gene diversity

**nucleotide diversity

^Number of segregating sites

Table 3. Sequence divergence (below diagonal; standard deviation above) among blue rockfish sample areas.

	WA	OR	FB	FAR	BC	NR	SM	SNI
WA		0.30%	0.30%	0.30%	0.40%	0.40%	0.30%	0.40%
OR	1.90%		0.40%	0.30%	0.40%	0.40%	0.40%	0.40%
FB	2.10%	2.10%		0.30%	0.30%	0.30%	0.30%	0.30%
FAR	2.10%	2.10%	2.20%		0.40%	0.30%	0.30%	0.40%
BC	2.40%	2.40%	2.00%	2.40%		0.30%	0.30%	0.40%
NR	2.20%	2.20%	1.70%	2.30%	2.00%		0.30%	0.40%
SM	2.10%	2.10%	1.70%	2.20%	1.90%	1.70%		0.30%
SNI	2.40%	2.40%	2.00%	2.60%	2.40%	2.20%	2.10%	

Table 4. Relative frequencies of nucleotide bases of the mtDNA control region in blue rockfish at each location.

C = cytosine; T = thymine; A= adenine; G = guanine.

Area	N	%C	%T	%A	%G
WA	42	18.29	31.84	36.10	13.77
OR	50	18.30	31.78	36.16	13.75
FAR	17	18.31	31.86	35.85	13.98
FB	32	18.40	31.88	35.93	13.79
BC	24	18.72	31.60	35.67	14.01
NR	43	18.50	31.78	35.91	13.80
SM	32	18.40	31.90	35.86	13.84
SNI	5	18.63	31.65	35.82	13.90

Table 5. Pairwise comparisons of genetic differentiation (below diagonal) and gene flow (above diagonal) among 8 blue rockfish sample sites.

Fst/Nm	WA	OR	FB	Far	BC	NR	SM	SNI
WA		inf	2.96	175.48	2.36	2.80	3.16	2.49
Oregon	0.0000		2.76	24.43	2.03	2.57	2.80	2.03
Fort Bragg	0.1689**	0.1813**		4.92	6.81	inf	inf	6.81
Farallon Is.	0.0029	0.0205	0.1017**		4.18	4.51	5.83	4.76
Big Creek	0.2119**	0.2464**	0.0734**	0.1195**		7.73	9.56	3.27
Naples Reef	0.1784**	0.1948**	0.0000	0.1109**	0.0647**		inf	3.27
San Miguel I.	0.1580**	0.1783**	0.0000	0.0857**	0.0523**	0.0000		5.85
San Nicholas I.	0.2004**	0.2124**	0.0608*	0.1050*	0.1528*	0.1058*	0.0855	

* $P < 0.05$

** $P < 0.01$

Table 6. Differentiation among blue rockfish sample sites according to the AMOVA framework of hierarchical analysis under three hypothesized levels of geographic structure.

A. Hypothesized structure: No geographic subdivision

Source of variation	d.f.	Variance components	% variation	Φ -statistic	<i>P</i> -values
Among sites	7	0.5096	9.90%	$\Phi_{ST} = 0.0990$	$\ll 0.00001$
Within sites	237	4.6359	90.10%		

B. Hypothesized structure: Two regions (North: WA OR; South: FB, FAR, BC, NR, SM, SNI)

Source of variation	d.f.	Variance components	% variation	F-statistic	<i>P</i> -values
Among groups	1	0.6282	11.58%	$\Phi_{CT} = 0.1158$	0.03516
Among sites, within groups	6	0.1627	3.00%	$\Phi_{SC} = 0.0339$	$\ll 0.00001$
Within sites	237	4.6359	85.43%	$\Phi_{ST} = 0.1457$	$\ll 0.00001$

C. Hypothesized structure: Two regions (North: WA OR, FAR; South: FB, BC, NR, SM, SNI)

Source of variation	d.f.	Variance components	% variation	F-statistic	<i>P</i> -values
Among groups	1	0.6282	13.32%	$\Phi_{CT} = 0.1332$	0.01683
Among sites, within groups	6	0.1627	1.60%	$\Phi_{SC} = 0.0185$	$\ll 0.00001$
Within sites	237	4.6359	85.07%	$\Phi_{ST} = 0.1493$	$\ll 0.00001$

P values calculated from >20,000 permutations



Figure 1. Site location and sample number of blue rockfish collections. Arrows indicate potential barriers to dispersal.

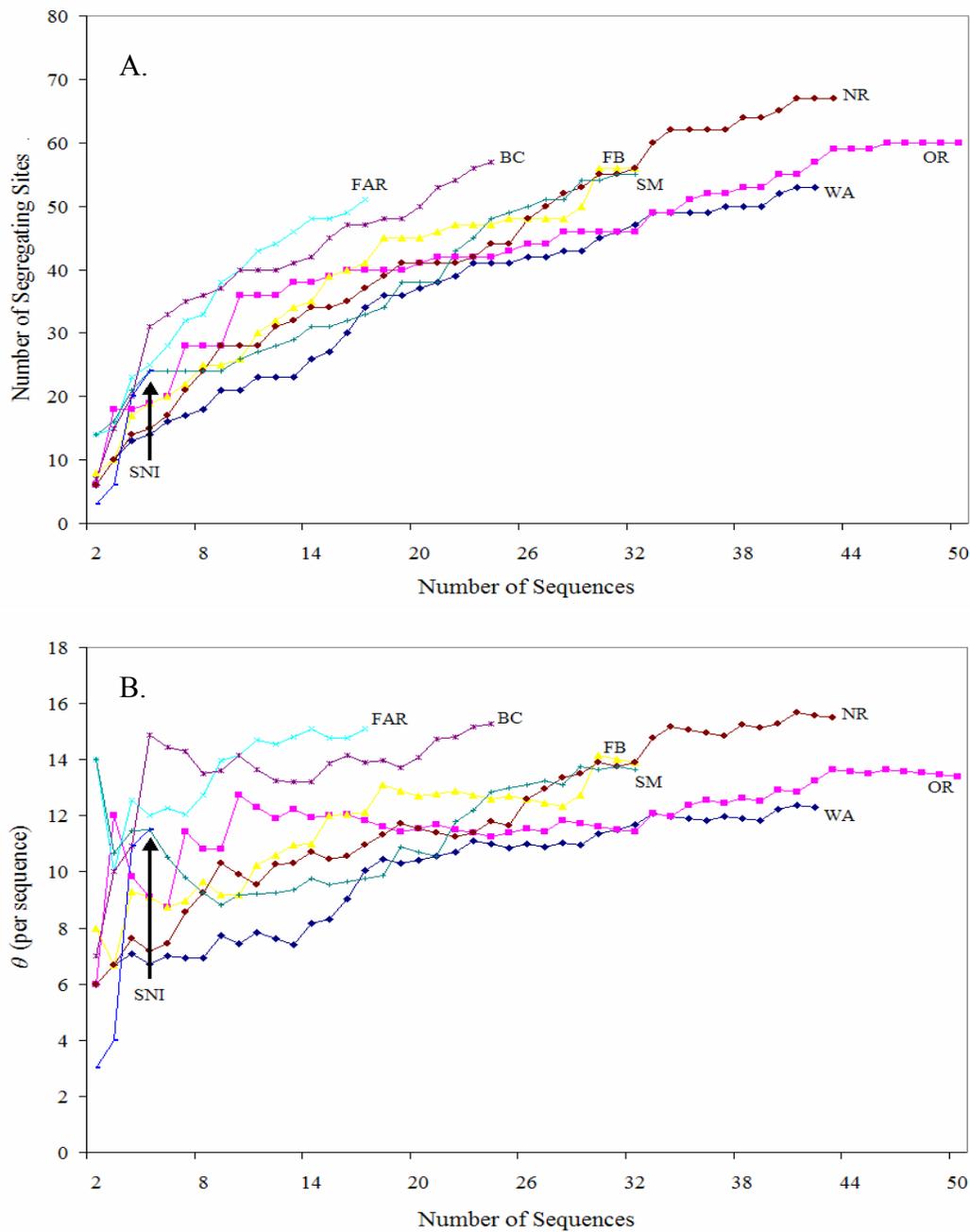


Figure 2. A.) Cumulative segregating site (S) curve and B.) Mean nucleotide polymorphisms (θ) per number of sequences for eight blue rockfish sample sites. Site abbreviations are as follows: WA = Washington; OR = Oregon; FB = Fort Bragg; FAR = Farallon Islands; BC = Big Creek; NR = Naples Reef; SM = San Miguel Island; SNI = San Nicholas Island.

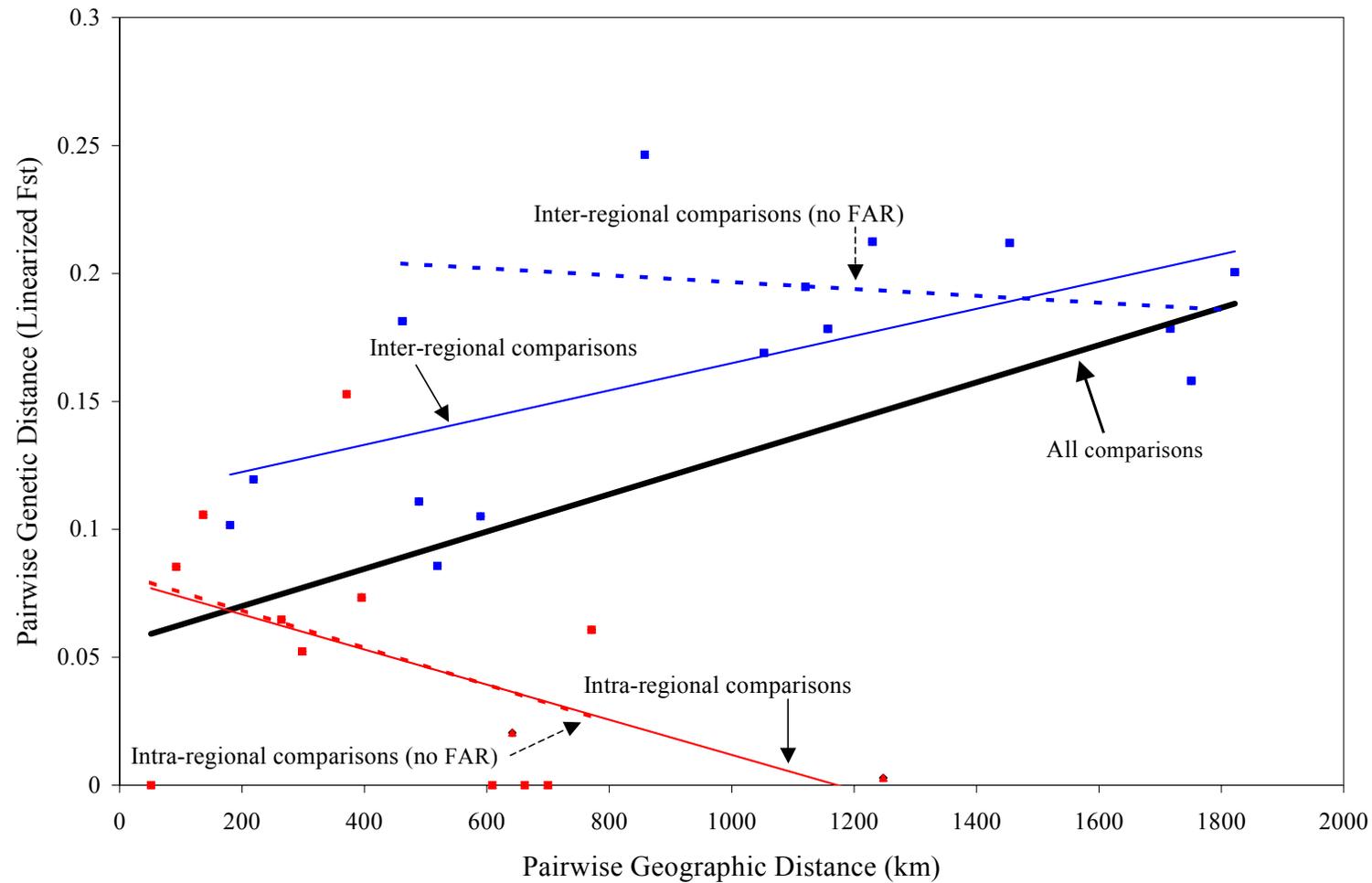


Figure 3. Pairwise geographic vs. genetic distances within and among regions of blue rockfish populations. Two regions are defined: 1.) Northern (WA/OR/FAR) and 2.) Southern (FB/BC/NR/SM/SNI). Broken lines relationships do not include FAR. Thicker solid line (all comparisons) indicates relationship when panmixia is assumed.

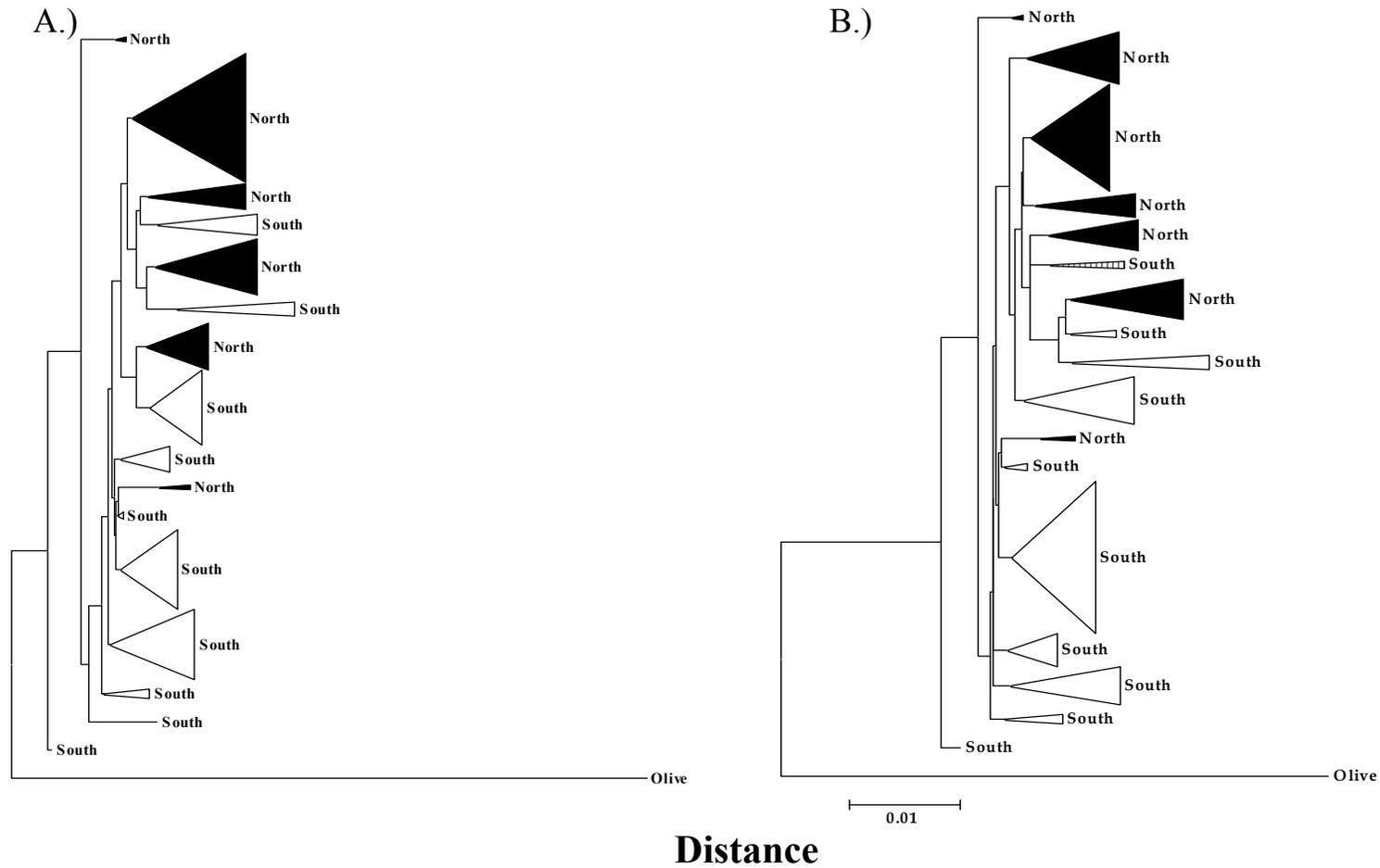


Figure 4. A.) Neighbor-joining and B.) Minimum evolution trees based on Kimura 2-parameter model. Blue indicated northern population (North = WA, OR & FAR) and red indicates southern populations (South = FB, BC, NR, SM, & SNI). Triangle size is indicative of the number of haplotype within grouping.

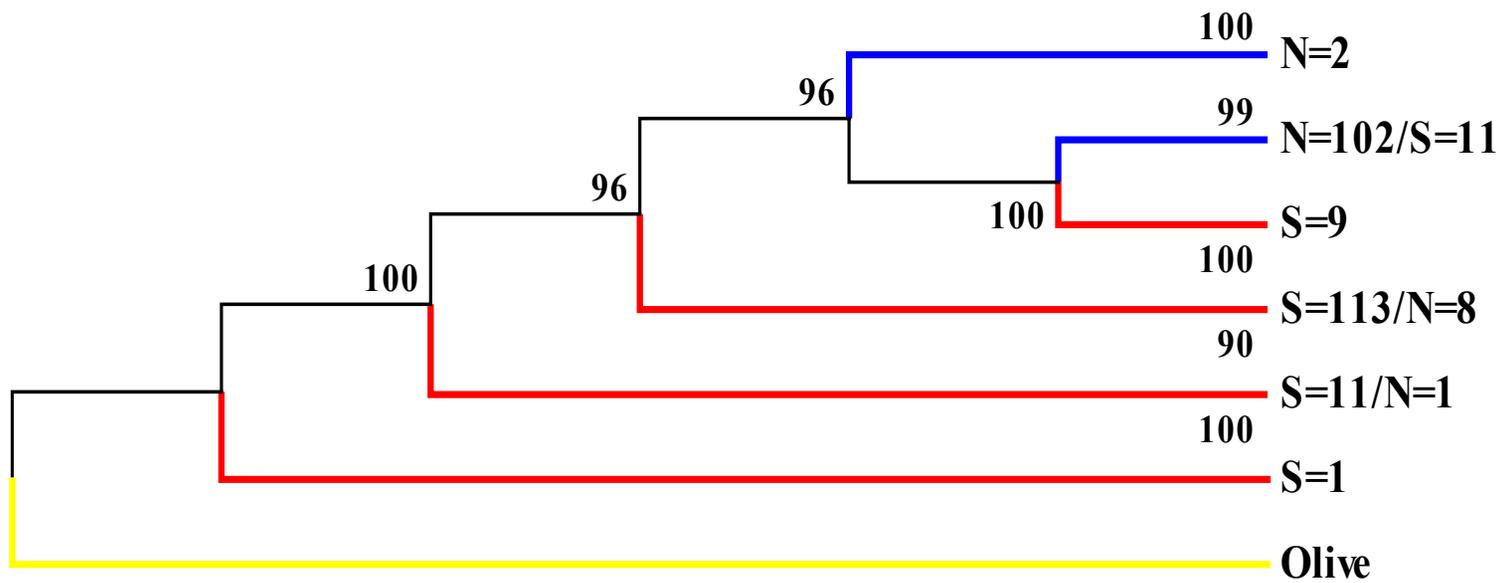


Fig 5. A 50%-majority consensus tree based on maximum parsimony. N= North (WA, OR, FAR); S = South (FB, BC, NR, SM, SNI); Olive= olive rockfish (outgroup). Branch labels are % consensus agreement among ~6700 trees.

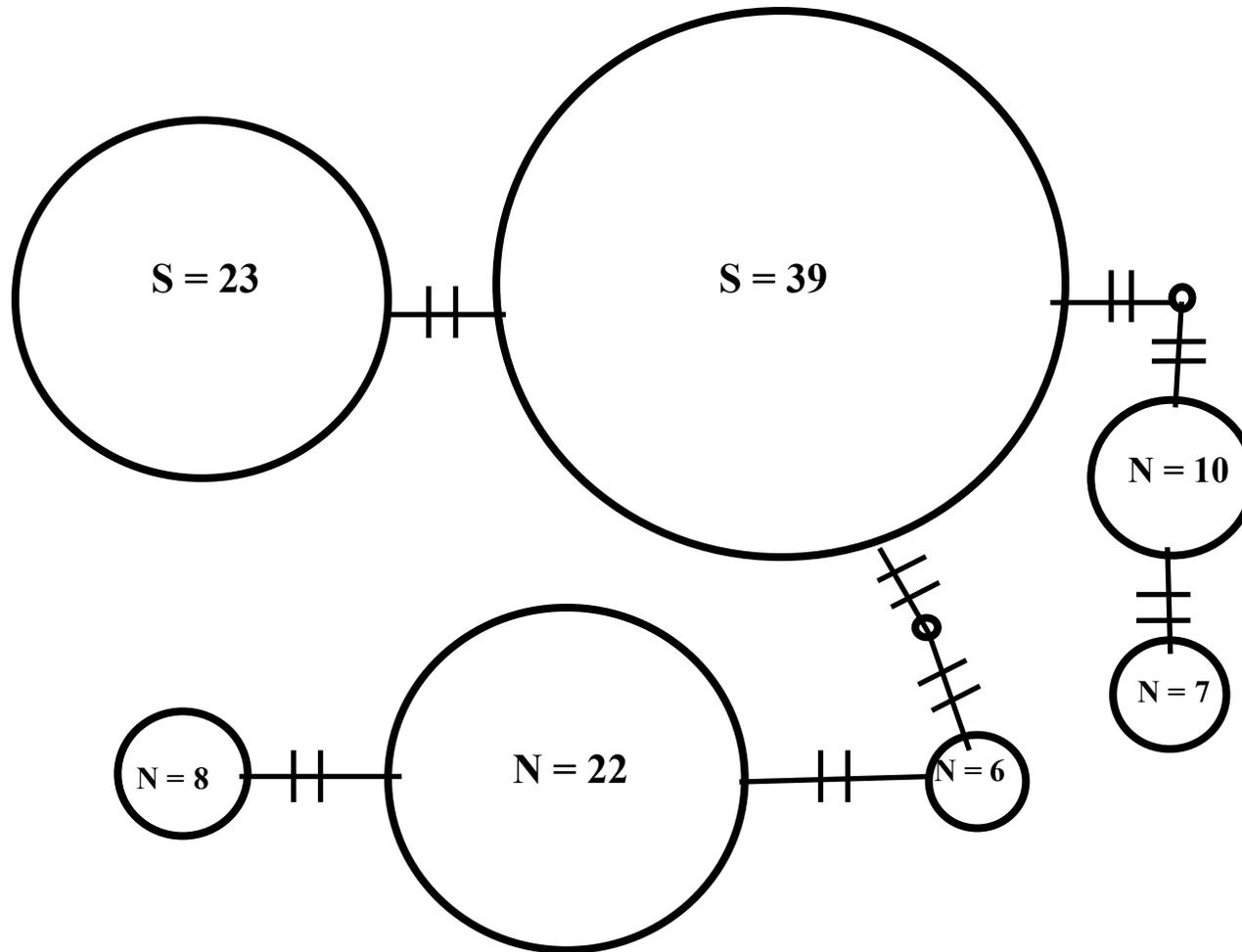


Figure 6. Simplified Minimum Spanning Network of blue rockfish haplotypes. To condense the widely spanning network, all haplotypes within two base pair changes were collapsed into the same group; therefore hash marks indicate number of base pairs in addition to two. The remaining haplotypes mostly radiated from the largest circles and are not included because they did not enhance the basic resolution or conclusion of the presented network. Number of haplotypes is given with circles and circles are in proportion to the number of haplotypes contained. Smallest circles represent 1 haplotype. N =North and S =South.

CHAPTER 3

Stochastic matrix modeling of genetically differentiated populations of the blue rockfish (*Sebastes mystinus*): An introduction to phylodemography.

ABSTRACT

This study introduces phylodemography as a method combining spatially explicit evolutionary and ecological information to evaluate the dynamics of reproductively distinct subpopulations for management purposes. It is specifically applicable to marine populations lacking resolution in basic biological parameters, but in need of swift management action. Five-stage matrix population models incorporating area-specific demographic and environmental stochasticity provided contemporary population growth rates and stage- and loop-based elasticity values, while genetic diversity and mismatch distributions provided historical population dynamics of two genetically distinct blue rockfish (*Sebastes mystinus*) subpopulations. Both subpopulations of blue rockfish are low productivity resources with varying periods of positive and negative growth. The southern population (below Cape Mendocino) is historically more dynamic and may currently be in decline because age truncation, vulnerability to strong El Nino conditions, and intense fishing pressure. Adult and subadult elasticities had the greatest affect on population growth and therefore should be targeted by management. A size limit of 13.5 to 14 inches is suggested because it protects an appropriate “life history management unit” of the blue rockfish defined as the full subadult stage and 7 to 8 reproductive year classes. Loop analyses indicate blue rockfish life histories favor somatic growth over reproduction and support the reliance of rockfish populations on extreme iteroparity to overcome repeated years of failed recruitment. Phylodemography emphasizes the importance of basic spatial representation of life history knowledge in population

modeling and this study is a first approximation to a fully realized phylodemographic approach.

INTRODUCTION

Resource managers are often challenged with the task of balancing use and sustainability of resources with limited data in complex and dynamic environments. This is certainly true for marine systems, with parameters such as temperature, salinity, currents, productivity, and biomass constantly changing at small and large spatio-temporal scales, creating multi-dimensional emergent properties (Strub et al. 1987; Bakun 1996; Wing et al. 1998; Field et al. 2001). Because marine systems are also difficult to sample, they are typically lacking in biological resolution compared to terrestrial systems (Neigel 1997). As a result, while effective management for many species is urgently needed now, the necessary information for this management has been slow to accumulate. The incorporation of basic biological information on different spatial and temporal scales is needed to enable marine resource managers to make educated decisions using the best possible science (1996 Magnuson-Stevens Fishery Conservation and Management Act).

Information on spatially explicit intraspecific population relationships in marine systems has accumulated rapidly over the past decade because advances in genetic technology have made the exploration of the phylogeography and population genetics of harvested marine populations more accessible (Awise 2000). Such spatial stock structure analyses provide the necessary resolution in biological information for fisheries managers

to develop proper management schemes that can protect the underlying genetic integrity and biocomplexity of a species (Carvalho and Pitcher 1995; Smedbol and Stephenson 2001; Hilborn et al. in review). Population connectivity can also determine potential effectiveness of a population at repopulating locally depleted populations; source, sink, and isolated populations all have different population dynamics (Hanski and Gilpin 1997). However, species are not usually managed at the subpopulation level because spatial and temporal dimensions are often deemed too complicated and therefore not considered.

Likewise, specific demographic information such as survivorship and reproduction— basic information needed to model population change over time— must be understood multi-dimensionally. Although marine resources are usually managed as single, panmictic stocks (Smedbol and Stephenson 2001), time/space changes in demographic parameters, due to environmental changes, random events, and/or spatial life history variation can significantly affect subpopulation growth rates (Zaitlin 1986; Winemiller and Rose 1992; Eldridge and Jarvis 1995; Longhurst 1998; Lowe et al. 1998; Smedbol and Stephenson 2001). Simple models that reflect intraspecific spatial relationships of life history characteristics would provide a useful tool by which marine resource managers could more effectively integrate accumulating species data and manage populations at higher resolutions.

I introduce the term “phyloendemography” to represent a link between the spatial and temporal changes that define historical (evolutionary) and present day (ecological)

structuring within populations. I develop phylodemography here as a method to apply accumulating phylogeographic and population genetic information with area-specific demographic measures to evaluate the dynamics of reproductively distinct subpopulations. This integrative and adaptive approach offers needed dimensionality to the evaluation of population change over time. In this study, I develop a phylodemographic model with particular application to rockfishes of the genus *Sebastes*.

Rockfishes are among the most important components of the west coast United States recreational and commercial fisheries, but are also some of the longest-lived and latest to mature fishes in those fisheries (Mason 1995; Parker et al. 2000; Love et al. 2002). Such life history traits limit the ability of rockfishes to recover quickly from heavy fishing and have contributed to severe declines in their abundances over the past twenty plus years (Gunderson 1984; Francis 1986; Love et al. 1998; Love et al. 1998; Mason 1998; Ralston 1998; Starr et al. 2002). Additionally, an emerging live-fish fishery has increased demand on nearshore species of rockfish (Leet et al. 2001; Starr et al. 2002), with stark population declines requiring tight fishing regulations and sustainable fishery management plans (as required by the 1996 Magnuson-Stevens Fishery Conservation and Management Act and the 1998 California Marine Life Management Act; (Weber and Heneman 2000)). The situation has become dire enough that the American Fisheries Society has recognized the urgent need for conservation and effective management of Pacific rockfishes (Musick et al. 2000; Parker et al. 2000).

Blue rockfish are ecologically important components of coastal kelp forest and rocky reef assemblages (Hallacher and Roberts 1985) from California to Washington (Miller and Lea 1972; Love et al. 2002). They are also the most important fish in the central and northern California recreational fishery and are second only to the black rockfish (*Sebastes melanops*) in the Oregon recreational fishery (Karpov et al. 1995; Love et al. 2002; Starr et al. 2002). However, the population dynamics of blue rockfish are poorly understood. There are currently no species-specific regulations on blue rockfish catches. Because the blue rockfish is named as one of the 19 species of concern in the California Department of Fish and Game's Nearshore Fishery Management Plan (2002) and populations have shown signs of stress (Karpov et al. 1995; Love et al. 1998; Love et al. 2002), it is necessary to understand how current population conditions and future change may affect their population persistence. Increasing regulations that limit the fishing effort in deeper waters off the U.S. Pacific Coast promise to shift more pressure to nearshore environments (Starr et al. 2002), making evaluations of population viability for species in these areas, like the blue rockfish, particularly pertinent.

I propose a phylodemographic approach to the study of blue rockfish population dynamics (as a model for other rockfishes) by combining genetically derived phylogeographic and historical demographic information with outputs from matrix population models to more comprehensively model and provide greater understanding of the dynamics of blue rockfish populations throughout its range. Previous work (see Chapter 2) using a 498 base pair portion of the mitochondrial DNA (mtDNA) control

region detected a strong genetic break in blue rockfish populations in the vicinity of the Cape Mendocino region (Fig. 1), thus distinguishing two effective blue rockfish subpopulations north and south of that cape. The following study compares the contemporary and historical demography of blue rockfish between these two regions to gain insight into the evolutionary and ecological relationships of these subpopulations. Because blue rockfish subpopulations may be differentially affected by variance in certain demographic parameters and the dynamic conditions of the California Current System in which they live (VenTresca et al. 1995), comparisons are also made between deterministically and stochastically derived measures of population growth for each area.

METHODS

Matrix Population Model

Matrix population models were chosen as a tool to explore the demography of each blue rockfish subpopulation for three main reasons. First, the application of matrix models is increasing among ecologists and resource managers because they provide simple means of calculating basic population parameters (i.e. population growth rate (r, λ), generation time (T, μ_1), stable age/stage distributions (w), and reproductive value (v)) and modeling population dynamics and growth (Caswell 2001). Stage-based approaches are particularly useful when dealing with species lacking age-specific life history resolution, such as rockfishes (Caswell 2001), and have proven practical for modeling turtles, sharks, marine mammals, and other long-lived, slow growing species (Crouse et al. 1987; Brault and

Caswell 1993; Crowder et al. 1994; Heppell et al. 1996; Caswell et al. 1998; Heppell 1998; Cortes 1999; Brewster-Geisz and Miller 2000; Mollet and Cailliet 2002). Second, many demographic models are based only on the female portion of the population because females are the theoretical limiting factor in population growth. The genetic information from mitochondrial DNA used in this study to determine population substructure is maternally inherited and only represents genetic differentiation among mothers; models incorporating this genetic structure are therefore only germane to female-only models. Third, elasticity analyses are an important analytical extension of matrix models that decompose asymptotic population growth rate (λ) into proportional contributions of each demographic transition (or matrix element; de Kroon et al. 1986; de Kroon et al. 2000; Heppell et al. 2000; van Tienderen 2000).

In this study, a 5-stage (Fig. 2), birth pulse population model using a pre-breeding census (Caswell 2001) and fixed stage duration (appropriate when “stages” represent age classes (Caswell 2001)) was used to estimate the intrinsic growth rate (r) and finite population growth rate (λ) for the north and south blue rockfish subpopulations (as defined in Chapter 2). Each stage was based on one of two categorical state variables: environmental (pelagic juvenile, settled juvenile) or biological (larval, subadult, and adult stages). Each of these stages is a well-recognized and conspicuous stage in the life history of rockfishes (Love et al. 2002). The models were phrased in terms of size (because fecundity and survivorship are size-dependent), but ages defined each stage transition. A

projection interval of 1 month was used, based on shortest stage duration (pelagic juvenile stage).

The basic form of the population matrix equation is:

$$N_{t+1} = A * N_t \quad (1)$$

where N_{t+1} = Resultant population stage vector at time t+1

N_t = Population stage vector at time t

A = Transition matrix:

$$\begin{pmatrix} P_1 & 0 & 0 & F_4 & F_5 \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix} \quad (2)$$

As time increases, all resultant eigenvalues from the matrix (2) converge on the dominant eigenvalue, which is equivalent to λ (Caswell 2001). The transition matrix then behaves as the dominant eigenvalue ($A = \lambda$) and equation (1) becomes

$$N_{t+1} = \lambda * N_t \quad (3)$$

Because λ is a finite growth value, subsequent conversion to r is simply $\ln \lambda = r$ (Brewster-Geisz and Miller 2000). Stable stage distributions (w) and reproductive stage values (v) are the corresponding right and left eigenvalues of the transition matrix, respectively, when λ is reached (Caswell 2001).

Transition matrix elements of growth to the next stage i (G_i), survival within a stage i (P_i), and fertility of stage i (F_i) were estimated from stage-based probabilities of survivorship (σ_i), probability of growth from stage i to $i + 1$ given survival through stage i (γ_i), and mean reproductive output of mature females (m_i) respectively as

$$G_i = \sigma_i \gamma_i \quad (4)$$

$$P_i = \sigma_i (1 - \gamma_i) \quad (5)$$

$$F_i = \sigma_i m_i \quad (6)$$

with

$$\sigma_i = e^{-Z_i} \quad (7)$$

where Z_i = total instantaneous mortality rate ($Z = M + F$) and

$$\gamma_i = \frac{(\sigma_i/\lambda)^{T_i} - (\sigma_i/\lambda)^{T_i-1}}{(\sigma_i/\lambda)^{T_i} - 1} \quad (8)$$

where T = duration of stage i ; and

λ = the finite rate of increase (as defined above) approximated as 1 and reiterated until a converged value is reached (Caswell 2001).

Alternatively, G_i and P_i , can be approximated when λ is assumed to equal 1 as follows (Crouse et al. 1987; Cortes 1999):

$$G_i = \frac{\sigma_i^{T_i} (1 - \sigma_i)}{1 - \sigma_i^{T_i}} \quad (9)$$

$$P_i = \left(\frac{(1 - \sigma_i^{T_i - 1})}{1 - \sigma_i^{T_i}} \right) \sigma_i. \quad (10)$$

Deterministic Model Parameter Estimation

Three types of information are needed to construct the elements of the transition matrix:

1) Age and growth; 2) Survivorship; and 3) Reproductive information (maturity and fecundity; Tables 1 and 2). Age and growth parameters (average maximum size (L_∞) and average growth rate (K)) from the von Bertalanffy Growth function (VBGF; (von Bertalanffy 1938) for the southern blue rockfish population were obtained from Laidig et al. (in press). A VBGF was fit to female age at length data (N= 280; provided by the Washington Department of Fish and Game) using the program *IGOR* (Cope 2000). The age and growth parameters are used to estimate survivorship for the subadult and adult stages and estimate fecundity at size (described below). Longevity (ω) was established as the oldest aged female in each area ($\omega_{\text{North}} = 47$; $\omega_{\text{South}} = 41$) and defines the duration of the adult stage (P_5) and total internal size of the five-stage matrix.

Natural mortality rates (M) were estimated for each stage and, if possible, each area separately. A mean monthly larval mortality rate was estimated for both areas by

using an averaged estimate of daily natural larval mortalities for several fish larval stages summarized in McGurk (1986). Both area matrices also used a settled juvenile natural mortality rate based on the average mortality rate determined from Adams and Howard (1996), who directly measured settled juvenile blue rockfish mortality in northern California. Subadult and adult mortality rates per area were calculated using the age-based approach of mortality estimation from Chen and Watanabe (1989), which incorporates individual growth rates (K) and age at maturity (α) into an estimation of age-specific mortality rates. Age-specific estimates were weighted with an *a priori* age distribution (with slope = -1) and then averaged; these values are the weighted average per stage mortality estimates. These estimates were then checked against mortality estimates calculated using methods presented in Jensen (1996) and mortality rates for black rockfish (a rockfish species of similar life history as the blue rockfish) based mostly on tag/recapture data and catch curve estimates (Barker 1979; Gowan 1983; Wallace and Tagart 1994; STAR 1999; Dorn 2000). Survivorship estimates per stage (σ_i) were calculated using equation (7). No prior survivorship estimates were available for the pelagic juvenile stage; therefore, pelagic juvenile stage survivorship was estimated as the month 4 survivorship value from logistic curves fit to scatter plots of survivorship over time for each area, using the previously estimated survivorships of the larval, settled juvenile, subadult, and adult stages.

Fertility values (F_i) were determined using equation (6); m_i values were estimated from halved monthly fecundity estimates (to obtain number of females born per female

per month, assuming an equal sex-ratio of offspring at birth) based on a blue rockfish size-specific fecundity equation (blue rockfish are believed to be yearly pulse breeders, but to fit the projection interval of this model, fecundity was broken into monthly batches). Because no previous size-specific fecundity equation was available for blue rockfish populations, a relationship was constructed using fecundity at size measurements for blue rockfish culled from various publications (Wales 1953; DeLacy et al. 1964; Miller et al. 1967; Miller and Geibel 1973; Matarese et al. 1989). This resultant exponential size-specific fecundity equation was

$$f = 0.0031(TL)^{5.1812} \quad (11)$$

where f = number of larvae per year

TL = total length in cm

therefore

$$m_5 = \frac{\sum_{x=\alpha+1}^{\omega} f_x}{(2 * 12)} \quad (12)$$

One will notice matrix F_4 corresponds to a fertility estimate within the subadult stage. Because this model uses a pre-breeding census, individuals become mature before they are counted as adults; this is represented by matrix element F_4 (Brault and Caswell 1993). By definition, matrix element F_4 then incorporates $m_\alpha = f_\alpha/2$, where f_α is 67,023 (North) and 48,441 (South). Complete deterministic matrices for both areas are given in Fig. 3.

Matrix population model calculations were carried out using the PopTools (Greg Hood <http://www.cse.csiro.au/poptools/>) add-in for Excel and checked using MATLAB®. The basic matrix analysis output of PopTools also provides two measures of generation time that were included in the results: 1) T : the time required for a population to increase by R_o (net reproductive rate); and 2) μ_1 , or the mean age of the parents of the offspring produced by a cohort over the cohort's lifetime (Caswell 2001).

Stochastic Model Parameter Estimation

In addition to the parameters used for the deterministic model, it was recognized that vital rates can change over time because of plasticity in life history traits and dynamic conditions in temperate environments; therefore demographic and environmental stochastic affects on r and λ were explored. Two levels of demographic stochasticity (settled juvenile survivorship and age at maturity) and 1 level of environmental stochasticity (El Niño events) were incorporated singularly and in sequential combination to increase the complexity of each model and to illustrate the successive increase of complexity on population growth.

The two levels of demographic stochasticity were modeled as follows: mean (0.006, with a range of 0.001 to 0.008) daily settled blue rockfish juvenile instantaneous mortality rates were provided in Adams and Howard (1996). These values were converted to monthly rates and modeled as a normal distribution around the monthly mean mortality value (Table 2). Therefore, mortality rates were used in the distribution,

then converted to survivorship estimates for the matrix model. This is important to point out because variance in instantaneous mortality and finite survivorship measures are not proportional (Hunter et al. 2000). A normal distribution was also used to approximate the distribution of age-at-maturity values (Hunter et al. 2000); average age-at-first-maturity per area was based on the deterministic model value, with a standard deviation of 1 year assumed for both areas, established from literature values (Table 1). Monte Carlo simulations of 1,000 iterations were used to recalculate r and λ and construct upper and lower 95% confidence intervals around the mean population growth estimates.

Environmental stochasticity was incorporated into population growth estimation by modeling the affects of El Niño events on the fertility matrix elements. El Niño events occur roughly every 2 to 7 years, but vary in intensity. Quinn et al. (1978) used a 250-year time period to reconstruct the frequency and magnitude of El Niño events. These data, combined with El Niño occurrences and strengths post-1978 to present, led to an average of about 25 El Niño events per century, of which 9 can be considered strong in magnitude. There are regional differences in the way different magnitude El Niños are manifested. While weak to strong El Niño events are general manifested in California, only strong El Niños register off Oregon and Washington (Cannon et al. 1985; Huyer and Smith 1985). Biological effects of El Niño events, therefore, also are manifested differently in each area. Generally, delayed phytoplankton blooms can instigate recruitment failure, while loss in body weight and fat reserves may cause reproductive failure in some rockfishes (Guillemot et al. 1985; Lenarz and Wyllie Echeverria 1986;

Larson 1991; Lenarz et al. 1995). Reproductive failure during El Niño events is well documented in blue rockfish (VenTresca et al. 1995) with gonadal index values dropping 50 to 75% during strong El Niños.

Using the above information, environmental stochasticity was modeled as followed: A binomial distribution of yearly El Niño occurrence was established for each area, with a 9% possibility of El Niño conditions (corresponding to only strong El Niños) occurring in the northern subpopulation and a 25% possibility (corresponding to any possibility of any magnitude El Niño) in the southern subpopulation. A second binomial distribution determining the magnitude of the El Niño in the southern subpopulation was set with probabilities of 36% (i.e 9 of 25) for strong El Niños and 64% for moderate/weak El Niños. A positive conditional statement of El Niño occurrence augmented the fertility element in the north by a factor of 0.75 for strong El Niños and in the South by factors of 0.75 and 0.25 for moderate/weak and strong El Niños respectively. Monte Carlo simulations of 1,000 iterations were used to again recalculate r and λ and construct upper and lower 95% confidence intervals around the mean population growth estimates. PopTools was used to run all Monte Carlo simulations and stochastic matrix calculations.

Though not modeled as a stochastic affect in this study, estimates of current fishing mortality (F) were also included in the analysis. Fishing mortalities based on other recreationally caught rockfishes ($F=0.1$; (Gowan 1983) were assigned to the South subpopulation, which sustains the most heavy and consistent fishing pressure, whereas a

lower value ($F = 0.035$) was assigned to the less-fished northern subpopulation. Both these values were added to the subadult and adult stages because blue rockfish in both areas are believed first recruited to the fishery at 1 to 2 years (Miller et al. 1967; McClure 1982; Laidig et al. in press).

Elasticities

One very powerful way of determining how changes in vital rates affect population growth is the use of sensitivity and elasticity analyses (de Kroon et al. 1986; Heppell et al. 1999; Caswell 2000). These approaches allow one to compare changes in parameters— such as fertility and survivorship— that are not measured in the same units. Elasticity analysis allows one to determine which matrix parameters most influence population growth rate relative to all other matrix elements. The elemental elasticity equation is given as

$$e_{ij} = \frac{a_{i,j}}{\lambda} \frac{v_i * w_i}{\langle w, v \rangle} \quad (13)$$

where $a_{i,j}$ = transition matrix element

$\langle w, v \rangle$ = the scalar product of vectors w and v ,

with summed elemental elasticities equaling 1.

Elasticity calculations were performed using PopTools on all deterministic and stochastic models, with Monte Carlo simulations (1,000 iterations) adding 95%

confidence intervals to average matrix element elasticities calculated from stochastic models. A concomitant analysis summarizing stage-specific elasticity values (after Heppell et al. 1999) allows one to determine and compare relative contribution of stages to population growth across stages and between regions. Elasticity ratios (Heppell et al. 1999) were also calculated and compared across separate matrix elements. Additionally, because stages are of different durations, time standardized elasticity values (to 1 month) were calculated to allow for additional inter-stage and time-specific comparisons. This representation of elasticities is also useful because some stages may contain many year classes, making it difficult to manage the full range of that stage's influence (i.e. elasticity) on population growth. The time-standardized stage elasticity can therefore be used as an efficient management tool by evaluating appropriate size limits in the following manner: a life history management unit (LHMU) is defined by a portion of the manageable life history of an organism that comprises 50% of the total elasticity (therefore minimizing the elasticity ratio of managed and non-managed elasticities to 1:1). This management unit may overlap stages in the matrix. In this case, standardized elasticity values are incrementally added up across stages to obtain the 50% elasticity LHMU requirement.

One can also calculate a less conservative estimate for the southern subpopulation by correcting the time standardized stage elasticity to represent the non-linear relationship of time-specific adult stage elasticities. The previous method assumes all within stage adult elasticities are equivalent, but in fact, adult elasticities usually decay

exponentially over time. Three other general relationships are also expressed: 1) average time standardized elasticity is usually 0.2 to 0.3 of the maximum (first) adult stage standardized time elasticity; 2) time stage elasticity equivalent to the average time standardized elasticity value is roughly 0.3 to 0.4 of the last adult time stage (Cope, unpublished data); and 3) adult elasticities approach zero as individuals approach maximum longevity (because there is only a small chance an individual will make it that far). With these general rules and assuming values of 0.25, 0.35, and 0.00001 for the above three relationships respectively, an alternative size limit was calculated (detailed in the Results section).

Loop analyses

Loop analyses (Groenendael et al. 1994; de Kroon et al. 2000), traditionally used to compare the elasticities of life history traits, were employed here to explicitly compare the elasticities of two types of loops: 1.) self-loops (representing survival within stages) and reproductive loops (representing reproductive pathways; Fig.4). Elasticities for self-loops are simply defined by the P_i matrix element, whereas the reproductive loops are based on the summed characteristic elasticity value for each step in the loop. The characteristic elasticity in turn, is equal to the F_i matrix element of that loop. One characteristic of loop analyses is all individual loop elasticities sum to one. As an example, say there is a 3-stage matrix with one reproductive loop and an F_3 elasticity value of 0.1 and one self-loop (P_3) with an elasticity value of 0.7. The self-loop elasticity

is 0.7, whereas the reproductive loop is three steps long (G1->G2->F3->G1) times the characteristic elasticity (0.1), which equals 0.3. Both loops (0.7 and 0.3) thus sum to 1.

Historical Demography

The theory of Rogers and Harpending (1992) that episodic population growth, decline, and stability are distinguishable in the distribution of pairwise nucleotide differences between haplotypes was used to explore the historical demography of each blue rockfish subpopulation. Mismatch distributions of pairwise differences and sudden expansion model parameters were estimated using mtDNA sequence data from Chapter 2 and a non-linear least squares technique (Rocha-Olivares and Vetter 1999; Schneider and Excoffier 1999; Schneider et al. 2000). Unimodal distributions usually indicate dynamic populations. The mismatch distribution theory assumes weak recombination and is adequate for this analysis because mtDNA does not recombine. Goodness-of-fit to models of sudden expansion was tested using a bootstrapped sum of square deviations (SSD) method (Schneider and Excoffier 1999; Schneider et al. 2000). Harpending's raggedness index (Harpending 1994) was also calculated, with larger index values indicating multimodal distributions and thus more stable populations. All computations were performed using Arlequin v. 2.0 (Schneider et al. 2000). Haplotype and nucleotide diversities from Chapter 2 were also used as indicators of historical population dynamics following the interpretation of Grant and Bowen (1998).

RESULTS

Deterministic models

The northern subpopulation of blue rockfish has a calculated annual rate of increase (15.8%) that is greater than the southern population (6.3%; Table 3). Generation times were lower in the northern subpopulation versus the southern population. The adult stage reproductive value was greater in the south than in the north, whereas subadult reproductive values were greater in the north than in the south.

Stochastic models

Stochastically derived mean values of population growth deviated from the deterministically derived values (Table 4). Variation associated with juvenile survivorship increased the mean growth rate compared to deterministic values, whereas all other levels of stochastic complexity had lower population growth rates than the deterministic results. Stochasticity associated with age at maturity had the greatest affect on subpopulation growth rates in both areas. Environmental stochasticity had a greater affect on southern than northern subpopulation growth rates. Overall, the combined two levels of demographic stochasticity affected subpopulation growth rates greater than environmental stochasticity associated with El Niños.

Wide confidence intervals were associated with most of the stochastically derived mean growth rates (Figure 5). All levels of stochasticity in the southern subpopulation included some level of negative population growth when confidence intervals were

considered. Fishing mortality and total combined stochasticity with fishing mortality were the only conditions under which mean population growth was negative in the southern population, though the mean population growth rate derived from combined demographic and environmental stochasticity events was only just above replacement. Growth rates remained positive in all scenarios for the northern subpopulation.

Elasticities

Elasticity values were greatest for the adult (North = 0.459; South = 0.491) and subadult (North = 0.393; South = 0.385) life stages for both areas, based on deterministic values. Over 85% (northern subpopulation) and 87% (southern subpopulation) of potential change in growth rates were thus attributed to these two stages alone. Mean stochastic elasticity values did not differ greatly from the deterministic elasticity estimates (Figure 6; (Benton and Grant 1996; Benton and Grant 1999), thus making deterministic-based elasticities a good approximation of stochastic elasticities. Fluctuations in elasticities, as defined by the 95% confidence intervals, were highest in the southern population, with the high end of the southern adult stage elasticity distribution approaching 80% of total elasticity; adult stage elasticity values for the northern subpopulation reached approximately 60%. These high values were attributable to stochastic changes in the age at maturity, which increased the duration of the adult stage.

Elasticity ratios standardized to the highest matrix element elasticity value (P_5 , survival within the adult stage) revealed that large changes in most matrix elements are

required to recover a loss in population growth (λ) due to a small change in adult survivorship (Fig. 7). For instance, to maintain a particular growth rate after a 10% decrease in the P_5 element would take concomitant increase of about 300% (for the North) and 500% (for the South) in the adult fertility element F_5 (based on stochastically determined ratios). Only the P_4 element (survivorship within the subadult stage) for both areas (with a ratio close to 1:1) produced a proportional change in λ that was similar to the effect of P_5 . Deterministically and stochastically determined mean elasticity ratios did not differ substantially from one another.

Standardized elasticity values reveal the pelagic juvenile stage as the most influential stage per unit time in affecting the population growth of both subpopulations of the blue rockfish; the adult stage had the least affect on λ per time unit (Table 5). The influence of the subadult stage on λ remains substantial despite standardization.

The LHMU was defined for the southern blue rockfish subpopulation by starting with the subadult stage— which showed high overall and standardized elasticities— because it is the first manageable portion of the blue rockfish life history that is recruited into the fishery. The overall stage deterministic elasticity value was 0.39; this was 0.11 below the target value 0.5. This implies that additional portions of manageable life history stages, mainly the adult stage, need to be added to the LHMU. Therefore, the adult stage standardized elasticity (0.0011; Table 5) was divided into the additionally needed elasticity value (0.11). This assumes that time standardized elasticities do not change within the stage over time. The value obtained (100) was the number of adult

months to be added to the end of the subadult stage to increase the LHMU to 0.5.

Converting this value to years (8.3), the LHMU became ~13 years. The size limit was then obtained by using the VBGF average length at 13 years, which is 35.3 cm or 13.9 inches. Rounding up, the very conservative size limit for the southern blue rockfish subpopulation should be 14 inches.

Using the non-linear relationship of time-specific adult stage elasticities, the maximum adult stage monthly elasticity was $0.0011/0.25$ or 0.0044 . Determination of the month the adult time-averaged elasticity (0.0011) is reached in the decay series was made by multiplying the maximum number of months in the adult stage (372 in the southern subpopulation) by 0.35 , which gives 130.2 months. Now having three values of time-standardized elasticity per time period, an exponential decay curve was determined ($y = 0.0095e^{-0.0159x}$). This curve was then used to estimate per month elasticity values for all months in the adult stage. From this point, determination of the size limit follows the first example, and the size limit was estimated to about 13.5 inches (342 mm), which includes about 7 reproductive year classes.

Loop Analyses

The elasticities of adult and subadult self-loops (representing survivorship within those stages) are greater than elasticities associated with either of the reproductive loops (Fig. 8). Survivorship thus has greater influence on population growth rates than the reproductive life history pathways.

Historical Demography

Mismatch distributions for both subpopulations are unimodal (Fig. 9) and do not reject the model of sudden population expansion following a recent bottleneck (North: SSD = 0.002, P= 0.47); South SSD = 0.0001, P= 0.98). Although statistically true, the fit of the model to the northern subpopulation is weaker than to south and slight bimodality is apparent, indicative of greater relative population stability. Harpending's raggedness index, although not statistically significantly different from the expansion model in either population, is higher in the northern population (HRI = 0.007, P = 0.45) compared to the southern population (HRI = 0.003, P = 0.82), also indicative of a relatively more stable northern population.

DISCUSSION

Ecological population dynamics of blue rockfish subpopulations

This phylodemographic study supports the previous notion of rockfishes as very low productivity resources in an unpredictable and unsteady environment (Francis 1986; Myers et al. 1999; Parker et al. 2000). According to criteria for defining population productivity based on population growth rate (r) set by Musick et al. (2000), both subpopulations of the blue rockfish are considered of low productivity when the deterministically derived population growth rates are considered. But when the stochastic influences of demography (settled juvenile survivorship and age at maturity) and

environmental change (El Niños) are incorporated, mean population growth rates for the southern subpopulation are only slightly above replacement, indicative of a very low producing resource; northern subpopulation growth rates decrease, but remain in the low productivity category (Table 4; Fig. 5). Although mean stochastic growth rate is positive in both subpopulations, there are substantial periods of negative population growth within both areas (though more so in the southern populations), illustrating how periods of large population growth are often followed by periods of decline. When fishing mortality is incorporated, the southern population is unsustainable (mean negative population growth) and the northern population productivity is very low (Table 4; Fig. 5).

Blue rockfish subpopulations in California are likely in current decline. Because blue rockfish are the major recreational fish in central and northern California and recreational fishing pressure in California is very high (Mason 1995), fishing mortality used in this study may be an underestimate of mortality attributable to fishing in this area; therefore average negative population growth rates may be even higher than presented here. Documented decreases in blue rockfish weight and length over time (Karpov et al. 1995; Mason 1998) and sequential population depletion on localized reefs (Mason 1995) are indicative of stressed or declining southern blue rockfish subpopulations.

Recreational blue rockfish catches from commercial passenger fishing vessels in southern California dropped 95.2% from 1980 to 1996 (Love et al. 1998). In comparison, recreational bocaccio (*Sebastes paucispinis*) catches dropped 98.7% in the same time period (bocaccio were being considered for inclusion on the United States Endangered

Species list (Musick et al. 2000)). Blue rockfish, once an abundant and important component of nearshore reefs in the southern California Bight have almost completely disappeared in that area (Love et al. 1998); localized power plant impingement data demonstrate major declines in blue rockfish recruitment to the southern California Bight (no impingement since 1984; (Love et al. 1998)). Currently blue rockfish are only abundant off the Channel Islands in southern California (Love et al. 2002).

This is the first model to capture the combined stochastic affects of demography and environment on a rockfish population. Lenarz et al. (1995) included the affects of El Niños on the productivity of chilipepper (*Sebastes goodie*), but assumed complete reproductive failure during El Niño, and did not factor in the varying strengths of El Niños. This study incorporates both spatial and temporal diagnostics of El Niño strength, as it influences reproductive effort, into each subpopulation model. Such models provide realistic complexity that simulates the dynamic nature of temperate marine populations. This study also demonstrates that environmental conditions indeed greatly affect population growth rates, but that the inclusion of heavy fishing rates tend to push these populations into declines (Hutchings 1999). It is hoped that the level of environmental stochasticity expressed in these models will provide a useful construct for other species living in the California Current System.

Population growth rates and ability to absorb demographic and environmental stochasticity are directly related to age structure. Two points regarding age structure were expressed by Longhurst (1998) that are relevant to rockfishes: 1) “the variability of the

age structure of natural populations is viable only within limits and if pushed beyond these limits, environmental stress may prevent recovery”; and 2) “any fishery is sustainable only if the age structure of the stock is not so truncated that reproductive potential cannot be maintained across appropriate periods of recruitment failure.” Fishing often reduces the age composition of populations by removing the larger, older individuals (Berkeley and Markle 1999). And because temperate environments are often temporally and spatially inconstant, more extensive age structures are required of populations to withstand long periods of failed recruitment (also known as “the storage effect”; Warner and Chesson 1985).

Both blue rockfish subpopulations are relatively long-lived, but age truncation is apparent in the southern subpopulations, as reflected by reduced longevity, decreased duration of the adult stage, and decreased size. Lower generation times, higher number of reproductive age classes, larger size at age (and therefore greater fecundity), and larger average catch at size (based on RecFIN data from 1980 to 2002) all contribute to a healthy growing stock in the north capable of withstanding moderate and infrequent El Niño conditions and moderate fishing pressure. Biomass and reproductive loss from intense fishing pressure plus stronger and more frequent El Niño conditions have maintained a truncated age structure in the southern subpopulation. Because fecundity is directly related to size, decreased age structure also decreases available biomass for reproduction, lowering the reproductive potential of the southern subpopulation. And though current southern blue rockfish subpopulations may on average be close to

replacement (Table 4), additional truncation of age structure may render the population incapable of weathering future environmental changes (MacCall 1996; Hutchings 1999; Hutchings 2001). The last major blue rockfish recruitment event in central California was in 1988 (Fig. 11). Simply put, since 1988, individuals born after 1983 have thus far had low probabilities of ever contributing to the sustainability or growth of the population, thus demonstrating the general need for iterated reproduction in rockfishes over many years.

The adult and subadult stages of both blue rockfish subpopulations influence population growth rate the most (i.e. highest stage elasticities) and are therefore useful targets of management (Caswell 2000); fortunately, they are also the most accessible to management. Miller and Geibel (1973) suggested a 10 inch (254 mm) size limit to help alleviate what they recognized as an “overutilized” fishery in central California, but no size limit was or has been implemented. This study, using the introduced method of time standardized stage elasticities, recommends a size limit of 13.5 (342 mm; based on time-corrected elasticities) to 14 inches (356 mm; based on averaged time standardized elasticities) to protect the appropriate LHMU specifically defined for the southern subpopulation as the full subadult stage and a minimum 7 to 8 reproductive year classes. This is greater than the average size of sampled caught blue rockfish from southern (276 mm) and northern California (285 mm) (RecFIN data).

Generally, an appropriate LHMU for any rockfish will need to include several reproductive year classes (Leaman 1991). Berkeley and Markle (1999) have

demonstrated, how in addition to greater fecundity, older, larger black rockfish females release larvae earlier in the reproductive season and have faster growing, more robust offspring. General increases in larval growth rate have been found to also increase larval survivorship in bluefish (Hare and Cowen 1997), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*) (Ottersen and Loeng 1999). Offspring from larger female rockfishes are therefore, believed to have increased chances of surviving harsh environments. Typically, rockfish fisheries— like the one for blue rockfish— start harvesting pre-mature individuals and fully recruit individuals into the fishery when only 1 or 2 reproductive years have past. A more recent live-fish fishery developed off southern California in the late 1980s and subsequently spreading northward into Oregon (Leet et al. 2001; Starr et al. 2002) specifically targets “plate-sized” and therefore smaller and usually immature individuals. For rockfish populations, these are unsustainable practices. Even when fishing pressure is removed, resilience is low (Leaman 1991) and it may take a depleted population over 15 years to show any indication of recovery (Adams 1980; Hutchings 2001).

Several issues need to be address when suggesting a size limit for rockfishes. The first is barotraumas. Because blue rockfish are mostly shallow dwelling, barotrauma should not affect releases of undersized individuals. Blue rockfish caught at deeper depths that may experience barotraumas obtain larger sizes (Laidig et al. in press) and therefore would theoretically be closer to the proposed size limit. Secondly, male blue rockfish obtain smaller sizes than females, with L_{∞} less than the proposed size limit

(Laidig et al. in press). Sex-based size limits are usually not tenable for rockfishes because externally sexing individuals can be difficult; this size limit, therefore, could potentially cause the fishery to extract almost exclusively the more demographically valuable females. But despite this danger, the proposed size limit would do more for the population than a lower size limit that includes both sexes more equally because the LHMU (by definition) is specifically designed for the female portion of the population and includes 50% of the overall elasticity, thus providing managers with the majority influence over population growth. Thirdly, size-selective harvests of larger fish may reduce the mean size and age of the population and have detrimental evolutionary effects on populations (Ratner and Lande 2001; Conover and Munch 2002). I argue that indiscriminant fishing on populations with extensive age structures may produce greater, more sustained effects on evolutionary and ecological population dynamics (as demonstrated by the southern blue rockfish populations). Indiscriminant fishing not only includes the potential evolutionary effects size-selective fisheries exert, but additionally offers no limit to the degree of age truncation and thus the extent of evolutionary effects that could occur. Setting aside a portion of an organism's life history (i.e. an LHMU) as an effective means to avoid such ecological and evolutionary effects can be viewed somewhat like a marine protected area; although effort would shift to older and larger individuals, more individuals will be reaching that size.

Some researchers have suggested that targeting the juvenile/subadult instead of the adult stage of marine species may be a better management practice. For instance,

Leaman (1991) pointed out the importance of incorporating reproductive value into *Sebastes* management plans. Because reproductive value curve usually peaks somewhere in the adult stage (with the final adult age class reproductive values decreasing) the adult stage should be protected (Leaman 1991; Caddy and Seijo 2002). Elasticities incorporate reproductive value, and therefore the suggested use of LHMUs does consider reproductive value and the importance of the adult stage as it affects population growth. The inclusion of reproductive classes in the rockfish LHMU is critical to its successive implementation.

Furthermore, Conover and Munch (2002) questioned the use of size limits that protect younger age classes because evolutionary sustainability may ultimately be jeopardized. Though their point is well taken, their study is applicable only to short-lived species (Adams 1980); harvest objectives based on shorter-lived species have proved inadequate for managing rockfishes (Leaman 1991).

Finally, Simpfendorfer (1999) demonstrated how targeting just the juvenile stage— under very low fishing pressure ($F = 0.021$; (Simpfendorfer 1999)— can produce sustainable harvests in a slow growing, long-lived, late-to-mature species. Though this may be true for species with low fecundity and large offspring, but consistent recruitment, it will almost certainly be unsuitable for species that experience long periods of failed recruitment, such as rockfishes (Leaman 1991). Note that the definition of an LHMU for each species does not require protecting the subadult stage— as it should for

rockfishes— and can therefore be adjusted to protect the most appropriate life history stages based on the biology of the resource in question.

In addition to defining stage-based LHMUs, time-standardized elasticity measures can reveal other biologically relevant population traits that may be missed with traditional age-based models. Ralston and Howard (1995) suggested that blue rockfish year-class strength is determined by the late pelagic juvenile stage and governed mostly by survivorship through the larval stage. The results of these stage-based models supports Ralston and Howard's (1995) findings by demonstrating that though it takes very large changes in larval survivorship (on the order of 500 to 1000% increases) to effect appreciable changes in λ , extraordinarily good environmental conditions could bring about such increases in survivorship because survivorship is generally extremely low. In this study, the pelagic juvenile stage was found to have the highest time-standardized elasticity, indicating the pelagic juvenile stage has the most influence on population growth rate per time interval. Survival through the pelagic juvenile stage may, therefore, also be very important in determining year-class strength (the models presented here incorporate environmental effects only through a reduction in fecundity; more comprehensive models will also include survivorship changes in the pelagic stages due to environmental conditions so as to demonstrate such potential affects of these stages on λ). Although Mollet and Cailliet (2002) point out very relevant advantages of using age-based over stage-based models, matrix models based on age rather than biological or environmental states can obscure life history interactions occurring within the age

construct. One year instead of one month projection intervals would not have revealed the importance of the larval and pelagic juvenile stage to the life history of the blue rockfish (though one month projection intervals do present their own problems, such as unrealistic fertility schedules). Biological reasoning and not just convenience in using particular age classes or stages should drive population modeling. The most useful approach is to include both age- and stage-based models for the same species to provide the advantageous perspectives of both methods.

The greater importance of survivorship elements and self-loops over reproductive elements and pathways is usually associated with low growth rates or declining populations (de Kroon et al. 2000), and is also consistent with the belief that temperate, long-lived species like rockfishes put more effort into sustaining somatic growth than into reproduction (Longhurst 1998; Love et al. 2002). Unpredictable environmental conditions on large and small time scales (Botsford et al. 1994; Francis et al. 1998) make sustained successful recruitment untenable, driving population growth rates lower. Temperate species therefore often buffer against dynamic environmental conditions with later maturity, higher fecundity, longer lives, and greater lifetime reproductive output (Adams 1980; Winemiller and Rose 1992; Landa 1997; Jennings et al. 1998; Hutchings 1999; Parker et al. 2000; Rochet 2000; Fagan et al. 2001). It is therefore more important for these fish to live another year than to reproduce (Leaman 1991). Often, compensation for increased subadult and adult mortality comes in the form of earlier ages of maturity and increased fecundity (Leaman 1991; Rochet 2000). But, as demonstrated by the

elasticity ratios and loop analyses for the blue rockfish, the concomitant changes required are often much too high for a population to realize; such life history compensatory constraints are illustrated by Clupeiformes populations as detailed in Rochet (2001).

Evolutionary population dynamics of blue rockfish subpopulations

Historical demographic analyses indicate that while both blue rockfish subpopulations are dynamic, the northern subpopulation is evolutionarily younger and has been more stable than the southern population (see also Chapter 2). This view of historical subpopulation dynamics is supported by both the mismatch distributions (Fig. 9) and the interpretations of haplotype and nucleotide diversities (Grant and Bowen 1998; Chapter 2) and indicates that rockfish populations in general, and blue rockfish populations in particular, undergo considerable natural fluctuations in population size over time. Such results are sensible, considering the present ecological model for the southern blue rockfish subpopulation demonstrates large effects of environmental changes (i.e. El Niños) on population growth. Long-term natural fluctuations of other fishes from the North Pacific are well documented (Soutar and Isaacs 1969; Soutar and Isaacs 1974; Baumgartner et al. 1992; Finney et al. 2000). Though, rockfishes have been components of Northeast Pacific coastal fisheries for thousands of years (Love et al. 2002), populations were probably inconstant and fluctuating coincident with temporally long and short changes in environmental conditions long before their inclusion in any fishery.

Phylo demography

Phylo demography is a method that places intraspecific evolutionary lineages in ecological contexts. The burgeoning fields of demography— especially life history theory (Stearns 1992; Landa 1997; Roff 2002)— and genetics— particularly phylogeography (Avisé 2000)— provide independent means by which pertinent information on generally data poor species are accumulating for resources in need of swift and efficient management. Phylo demography is offered as a method that combines these informative disciplines into a comprehensive tool of modeling the historical and contemporary dynamics of substructured populations lacking extensive life history information.

There are other approaches that have incorporated genetics and demography into studying spatially-explicit population dynamics— mainly metapopulation analysis and population viability analysis (PVA)— but they are of limited use in marine systems for two reasons. First, most have been developed mainly for plants, invertebrates, and amphibians in terrestrial systems (Harrison and Taylor 1997; Richards 2000) and the assumptions (e.g. metapopulation biology assumes that extinction/colonization events are ecologically relevant) may not be appropriate for marine systems (Neigel 1997; Smedbol et al. 2002). Second, both metapopulation analyses and PVA attempt to provide predictions as to population persistence, the accuracy of which depends on several factors (Shaffer 1990). The only way such predictions can hold are if the data are of unquestionable reliability and static in nature (Burgman and Possingham 2000; Coulson

et al. 2001). Any deviations or stochastic events not contained in the data set used may render any predictions at minimum useless and at the worst dangerous to resource management. The farther in the future the predictions are made, the less reliable they are. PVA also often requires extensive data sets on vital rates and habitat quality that are not available for most marine populations, limiting its usefulness in these systems (Coulson et al. 2001). Phylodemography does not emphasize predictions of population persistence, but instead presents a robust means of elucidating appropriate management strategies based on perturbation analyses (Caswell 2000) and general knowledge of current and historical population dynamics.

The phylodemographic approach illustrates how current management tools that do not incorporate population spatial structuring may be detrimental to the resources they are targeted to manage (Bailey et al. 1999; Smedbol and Stephenson 2001). In the case of the blue rockfish, an approach lumping the two subpopulations into one panmictic stock might have missed age truncation within the southern stock. Subsequent analyses would reflect a marginally growing stock, much like that seen in the northern population. It also would not allow for the differential effects of environmental change on different portions of the population. And, very importantly, it would ignore the fact that the blue rockfish is discontinuous throughout its range and therefore not a self-sustaining entity (see Chapter 2).

Furthermore, the phylodemographic approach allows one to compare past population dynamic behavior with current population trends for a deeper understanding

of what is needed for population management over time. Blue rockfish populations are temporally variable; this variance, though exacerbated by intense fishing pressure, is greatly due to the dynamic system in which they live. Life history characteristics of blue rockfish evolved for slow, but sustained growth over long periods of time in an unpredictable environment. This signal of negative and positive yearly population growth rates is clear in both the historical and contemporary demographic information. Management decisions can better evaluate the inclusion of further perturbations into each population by knowing the natural tendencies and potential capabilities of a population to react to the system in which it lives,

The results presented in this paper are a first approximation to a complete phylodemographic analysis (Fig. 11). Though informed and valuable decisions can be made with this information, the real strength of the phylodemographic approach is the adaptability of the models to progressive and varied data acquisition. The models are intuitive and flexible, offering the modeler the advantage of creating more complicated models as the information base increases. Models can also be made sufficiently general to be applied to several taxa (for instance, the model developed for the blue rockfish could easily be applied to any rockfish species or other organism with similar life history stages). The incorporation of advanced model analyses (Bayesian and Information-theoretic methods; Hilborn and Mangel 1997; Burnham and Anderson 2002) will allow for further informative construction of spatial structure and parameter probabilities (Punt and Hilborn 1997; Nielsen 2000; Pella and Masuda 2001; Cui et al. 2002). But first and

foremost, phylodemography emphasizes the importance of basic spatial representation of life history knowledge in population modeling. Without this essential information, intraspecific biocomplexity will suffer (Hilborn et al. in review), and management decisions will likely overestimate the ability of marine populations to compensate for imposed harvest regimes.

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Table 1. Blue rockfish life history parameters per area and matrix model. L_{∞} - average maximum size; K- average growth rate; t_{ω} - maximum age; t_{α} - age at first maturity

	L_{∞}	K	t_{ω}	t_{α}	Average Fecundity (females per female)**
Deterministic					
North	40.43*	0.178*	47 years*	4 years ¹	22907*
South	40.02 ²	0.149 ²	41 years ²	5 years ²	19552*
Stochastic					
North	40.43*	0.178*	47 years*	2 to 6 ¹	22907*
South	40.02 ²	0.149 ²	41 years ²	3 to 7 ^{2,3}	19552*

Note: the time step for the fecundities is one month.

* present study

1- McClure 1982

2- Laidig et al. *in press*

3 Wales 1953; Miller et al. 1967; Miller & Geibel 1973; Wyllie-Echeverria 1987

**Fecundity for F₅ stage only. See text for F₄ value.

Table 2. Monthly survivorship estimates per stage per model per area. L = larval; PJ = pelagic juvenile; SJ = settled juvenile; SA = subadult; A = adult.

		L	PJ	Stage SJ	SA	A
Deterministic						
	North	0.0432	0.2480	0.8461	0.9692	0.9744
	South	0.0432	0.2465	0.8461	0.9698	0.9785
Stochastic						
	North	0.0432	0.2480	0.8461 ($\pm e^{-0.075}$)	0.9692	0.9744
	South	0.0432	0.2465	0.8461 ($\pm e^{-0.075}$)	0.9698	0.9785

Table 3. Deterministic population parameters based on annual rates of increase for two blue rockfish subpopulations. See METHODS section for meaning of symbols.

	NORTH			SOUTH	
r	0.142		r	0.061	
λ	1.158		λ	1.063	
T	4.21 years		T	5.14 years	
μ_1	4.97 years		μ_1	5.62 years	
Stage	Stable Age Distribution (w)	Reproductive value (v)	Stage	Stable Age Distribution (w)	Reproductive value (v)
Larval	99.4%	0.0%	Larval	99.3%	0.0%
Pelagic Juvenile	0.2%	1.4%	Pelagic Juvenile	0.2%	1.2%
Settled Juvenile	0.2%	5.8%	Settled Juvenile	0.2%	5.1%
Subadult	0.2%	23.4%	Subadult	0.3%	19.7%
Adult	0.1%	69.4%	Adult	0.1%	74.0%

Table 4. Yearly population growth rates (r and λ) for blue rockfish subpopulations under increasingly stochastic conditions. Upper and lower limits are based on 95% confidence intervals. Bolded values are values associated with the sequential combination of complexity levels. Red values indicate negative growth rates.

Complexity Level	Lower limit	r	Upper limit	Lower limit	λ	Upper limit
NORTH						
Deterministic		0.142			1.158	
Demographic stochasticity						
SJ Survivorship	-0.095	0.163 (0.026)	0.532	0.909	1.193 (0.042)	1.702
Age at Maturity	0.008	0.078 (0.001)	0.178	1.008	1.082 (0.002)	1.195
COMBINED	-0.149	0.094 (0.023)	0.458	0.862	1.112 (0.033)	1.581
Environmental Stochasticity						
El Niño	0.074	0.139 (0.001)	0.146	1.077	1.149 (0.001)	1.158
COMBINED	-0.139	0.0945 (0.022)	0.420	0.870	1.111 (0.03)	1.522
Fishing Mortality		0.104			1.110	
COMBINED	-0.181	0.0478 (0.024)	0.418	0.834	1.062 (0.03)	1.519
SOUTH						
Deterministic		0.057			1.059	
Demographic stochasticity						
SJ Survivorship	-0.115	0.080 (0.016)	0.377	0.891	1.093 (0.022)	1.458
Age at Maturity	-0.063	0.015 (0.002)	0.117	0.939	1.016 (0.002)	1.124
COMBINED	-0.155	0.032 (0.016)	0.341	0.857	1.041 (0.020)	1.406
Environmental Stochasticity						
El Niño	-0.138	0.037 (0.003)	0.061	0.871	1.04 (0.003)	1.063
COMBINED	-0.202	0.005 (0.016)	0.290	0.817	1.014 (0.018)	1.336
Fishing Mortality		-0.058			0.944	
COMBINED	-0.305	-0.107 (0.018)	0.209	0.737	0.907 (0.018)	1.232

Table 5. Deterministic and standardized (to the projection interval) elasticity values for each stage of the blue rockfish matrix model. Months indicate stage duration.

Stage	North			South		
	Months	Elasticity	Standardized	Months	Elasticity	Standardized
Larval	3	0.0232	0.0077	3	0.0177	0.0059
Pelagic Juvenile	1	0.0223	0.0223	1	0.0170	0.0170
Settled Juvenile	8	0.1021	0.0128	8	0.0798	0.0100
Subadult	36	0.3924	0.0109	48	0.3879	0.0081
Adult	516	0.4600	0.0009	432	0.4976	0.0012

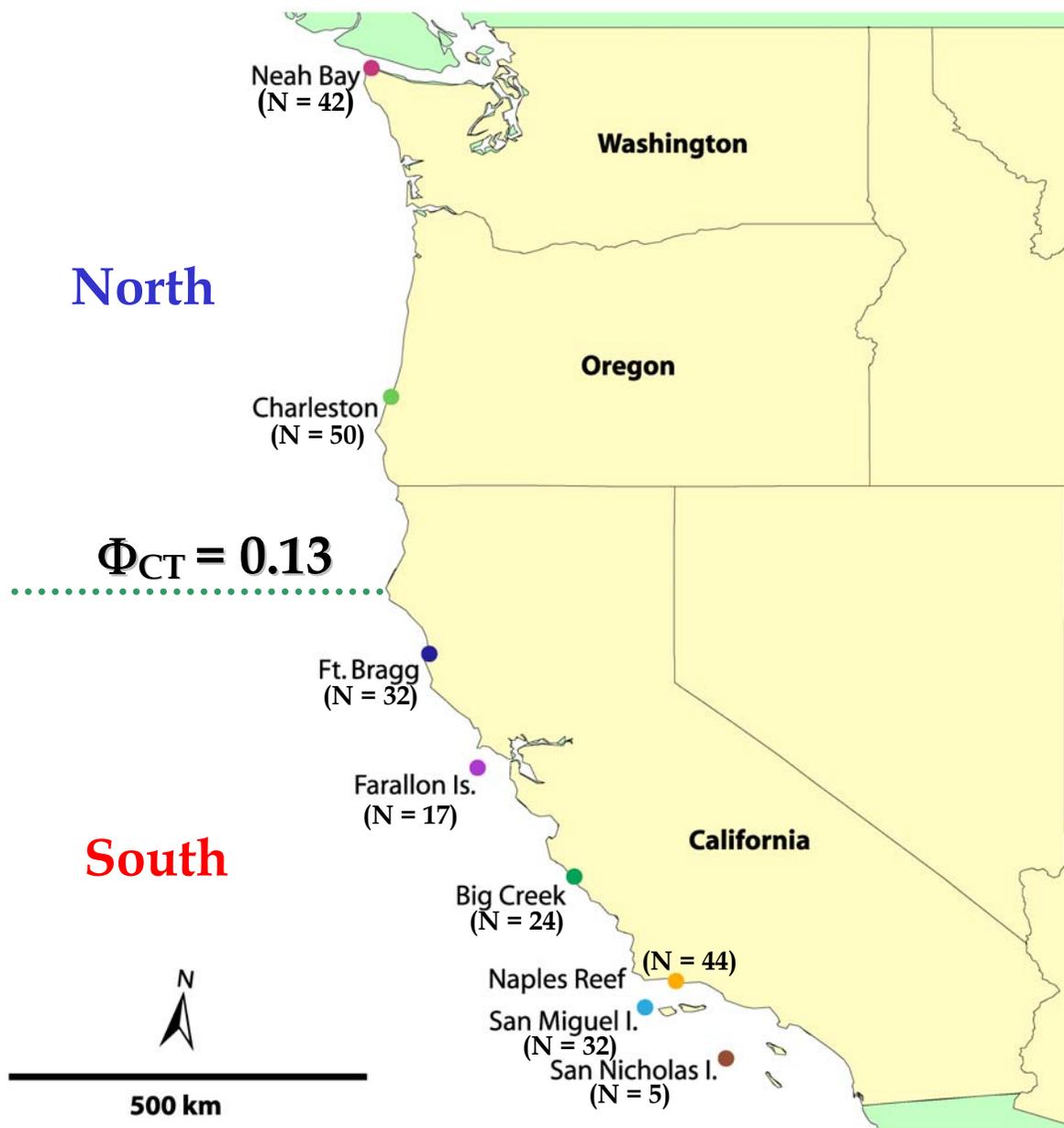


Figure 1. Summary map of genetic sampling sites, sample sizes, and hypothesized location of population break in blue rockfish. Note that the Farallon Is. site was more closely aligned with the North population. See Chapter 2 for details.

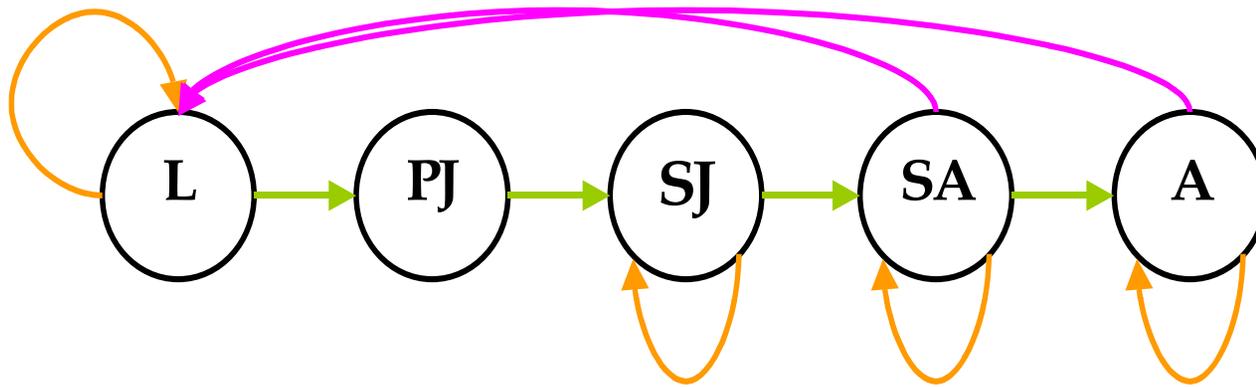


Figure 2. General 5-stage *Sebastes* life cycle used for each subpopulation of blue rockfish. L= Larval Stage; PJ = Pelagic Juvenile Stage; SJ = Settled Juvenile Stage; SA = Subadult Stage; A = Adult Stage.

A.) NORTH

$$\begin{pmatrix} 0.0414 & 0 & 0 & \mathbf{120.62} & \mathbf{989.39} \\ 0.0018 & 0 & 0 & 0 & 0 \\ 0 & 0.2480 & \mathbf{0.7913} & 0 & 0 \\ 0 & 0 & \mathbf{0.0548} & \mathbf{0.9545} & 0 \\ 0 & 0 & 0 & \mathbf{0.0148} & \mathbf{0.9744} \end{pmatrix}$$

B.) SOUTH

$$\begin{pmatrix} 0.0414 & 0 & 0 & \mathbf{87.18} & \mathbf{844.48} \\ 0.0018 & 0 & 0 & 0 & 0 \\ 0 & 0.2465 & \mathbf{0.7913} & 0 & 0 \\ 0 & 0 & \mathbf{0.0548} & \mathbf{0.9608} & 0 \\ 0 & 0 & 0 & \mathbf{0.0090} & \mathbf{0.9785} \end{pmatrix}$$

Figure 3. Deterministic matrix population models for two subpopulations of the blue rockfish: A.) North and B.) South. Bolded matrix elements indicate elements that change in the stochastic matrix models.

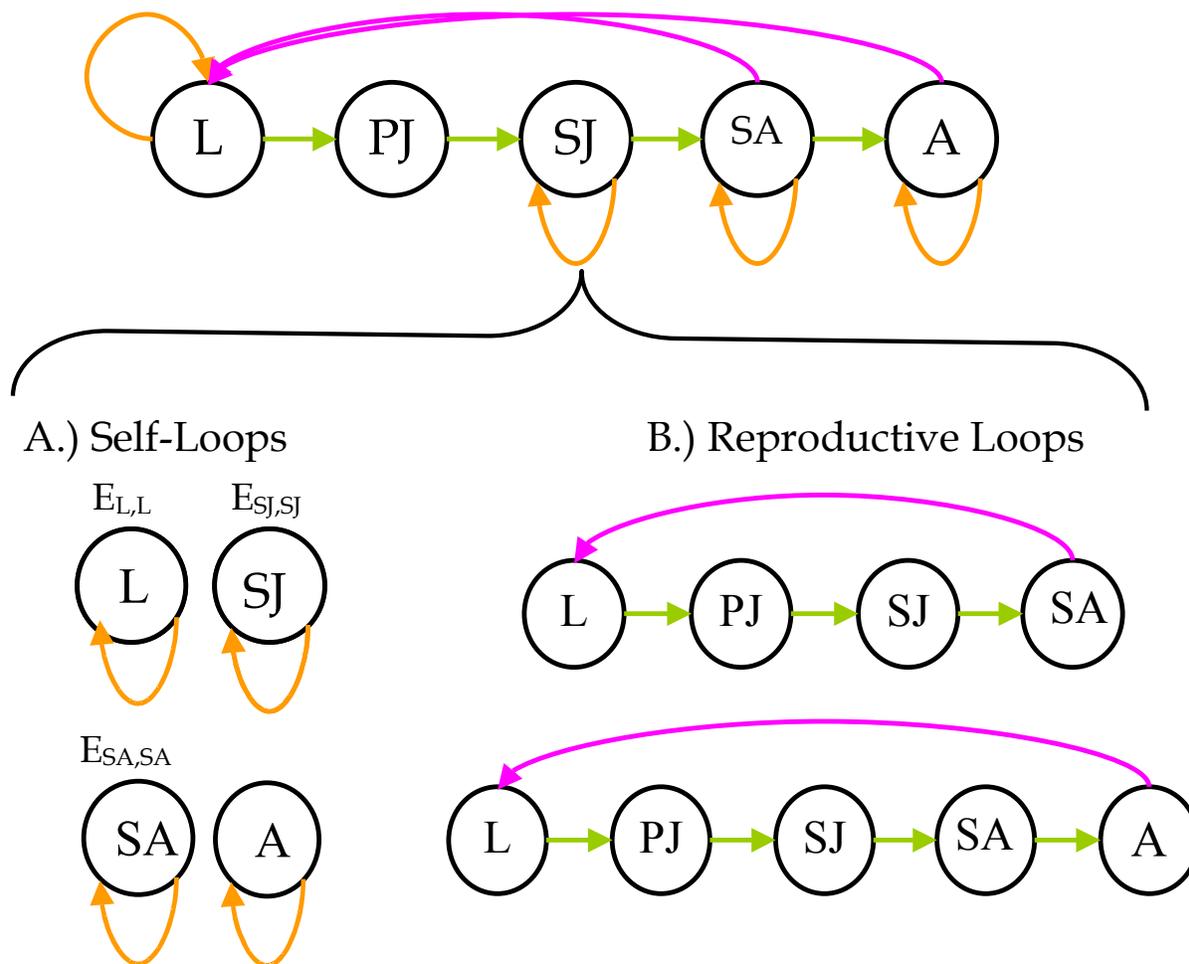


Figure 4. Life cycle graph of the blue rockfish decomposed into two types of loops: A.) Self-loops and B.) Reproductive loops or pathways.

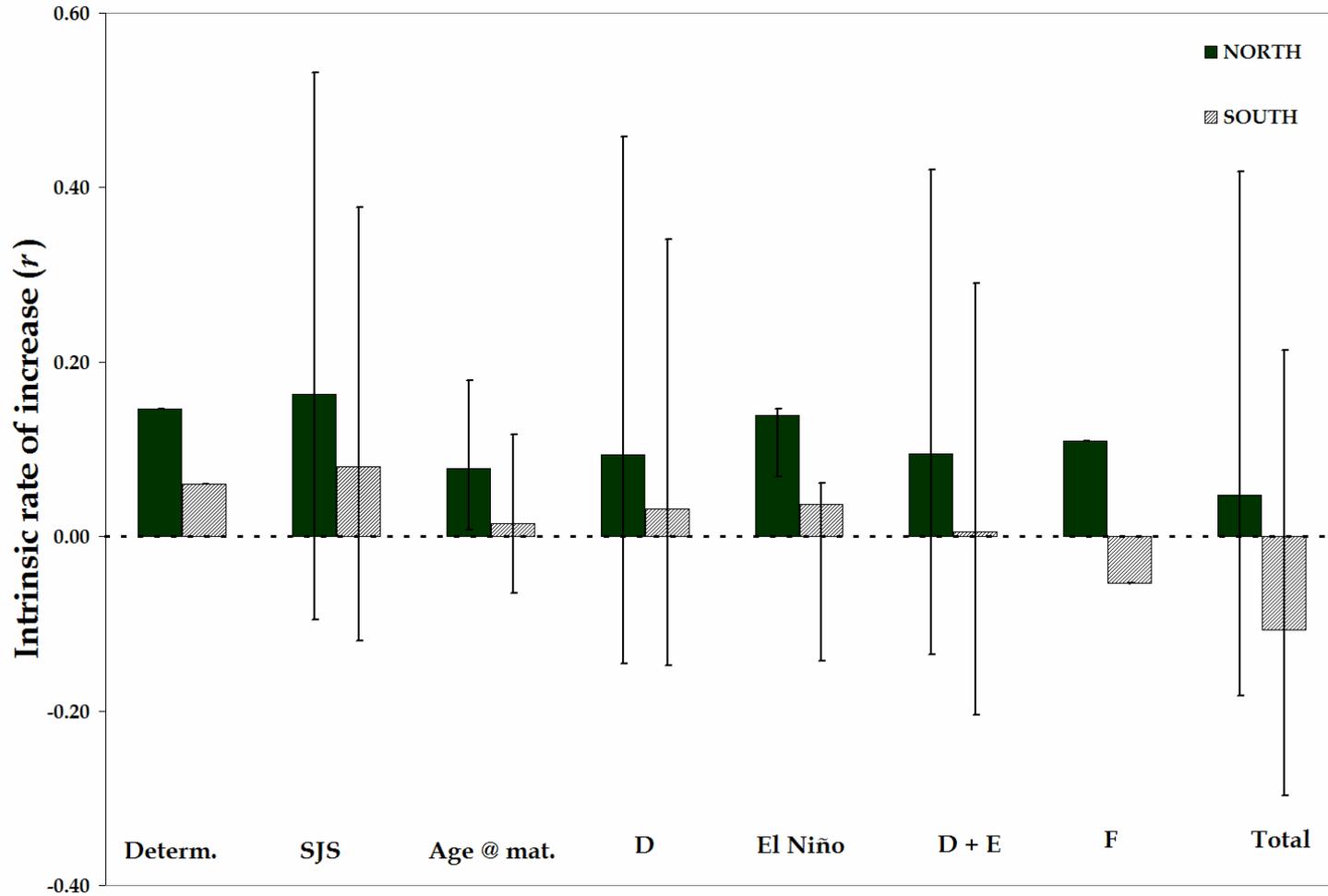


Figure 5. Intrinsic rates of increase and 95% confidence intervals (error bars) for deterministically and stochastically derived growth rates from each blue rockfish subpopulation. SJS = Settled Juvenile Survivorship; D = Total Demographic Stochasticity; E = Environmental Stochasticity (El Niño); F = Fishing mortality; Total= all factors combined.

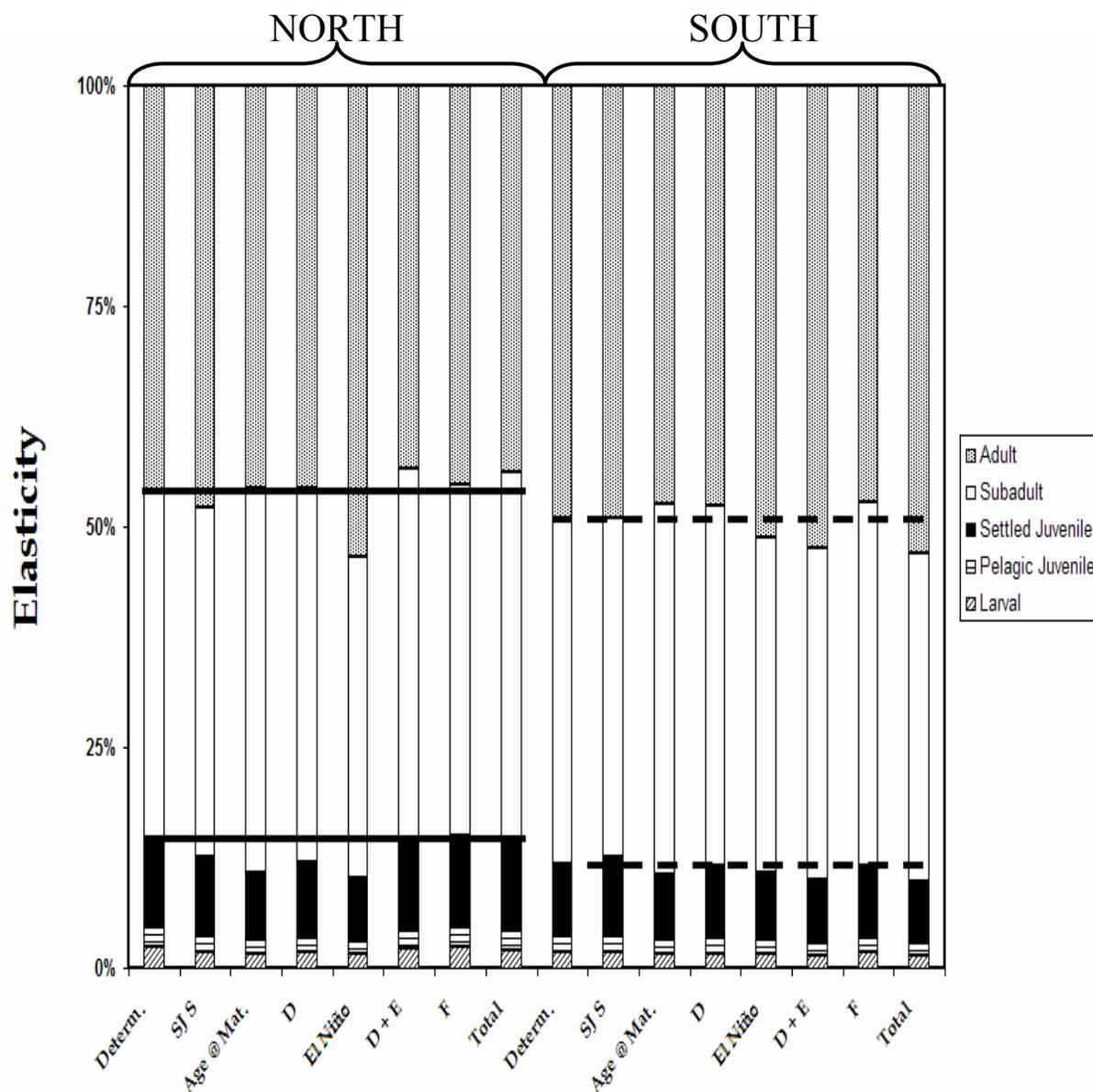


Figure 6. Percent elasticities based on deterministic and stochastic elements for each of the five stages of the matrix models of two subpopulations of blue rockfish. Lines are relative to deterministic values: Solid line- North; Broken line- South. SJS = Settled Juvenile Survivorship; D = Total Demographic Stochasticity; E = Environmental Stochasticity (El Niño); F = Fishing mortality; Total= all factors combined.

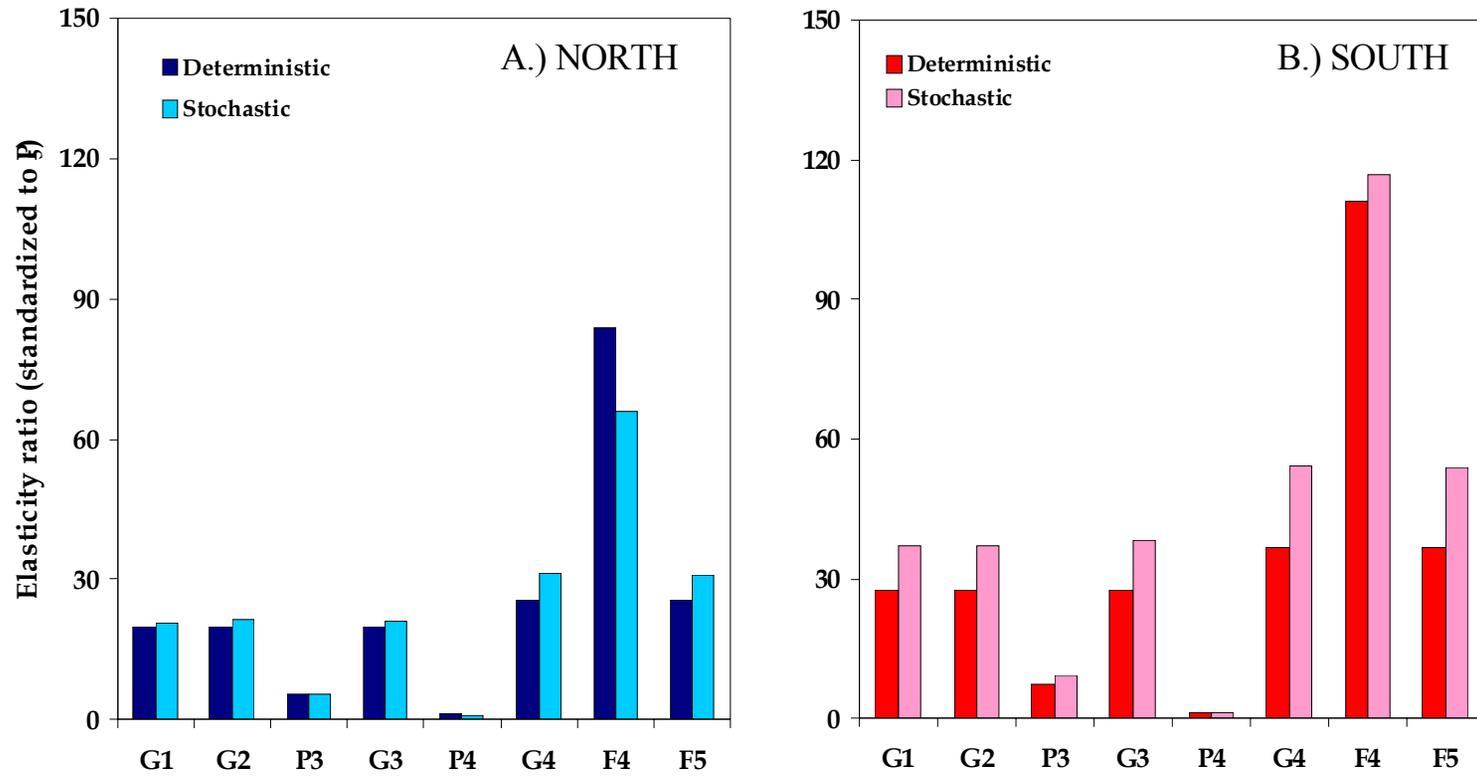


Figure 7. Elasticity ratios standardized to survivorship within the adult stage (P_5). The stochastic values represented are those calculated from the combination of demographic and environmental stochasticity parameters. The extremely high elasticity ratio values (460 to 860) for the matrix element P_1 are not included because they obscured all other matrix element relationships.

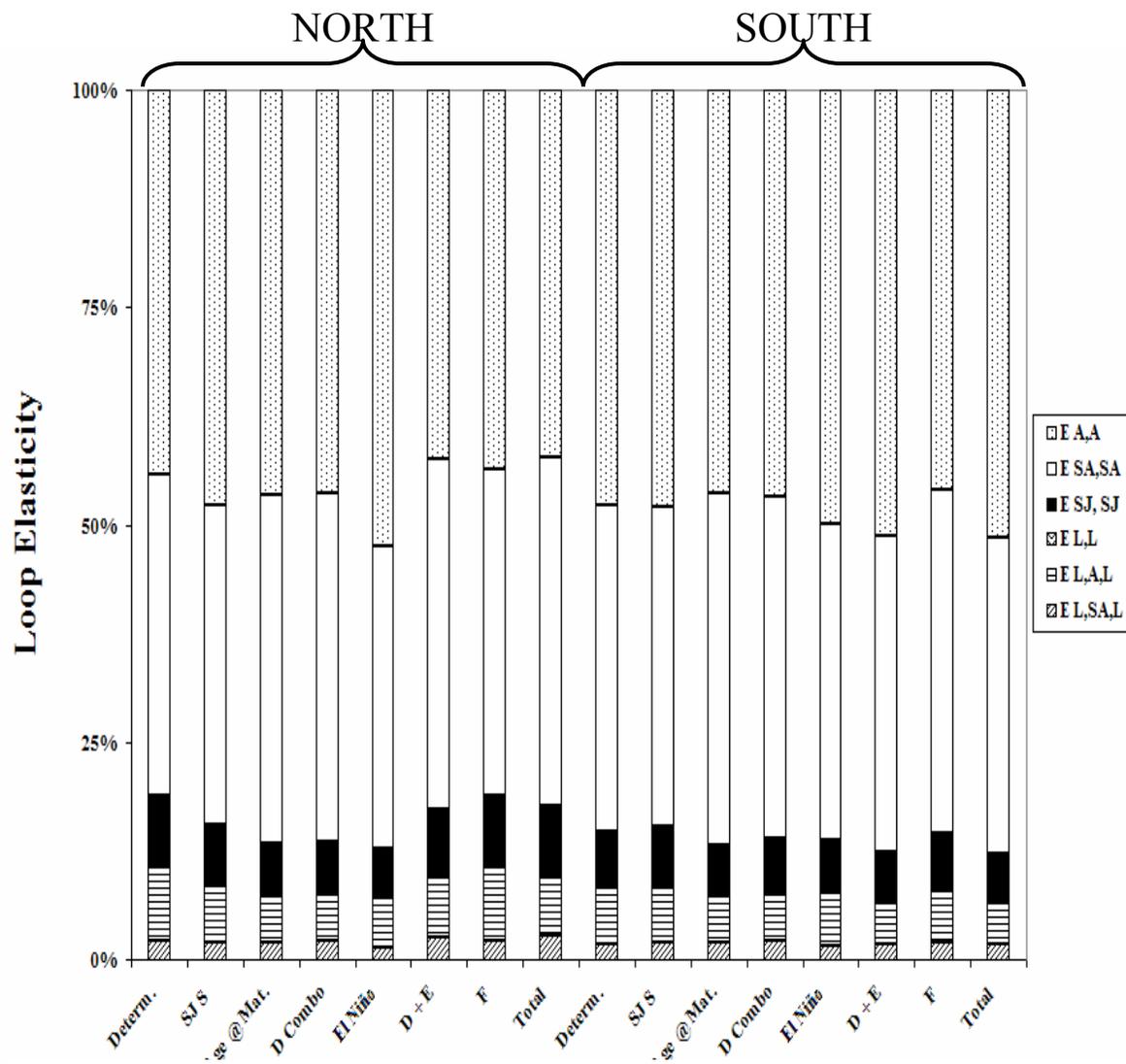


Figure 8. Loop elasticity values for four self loops ($E_{A,A}$; $E_{SA,SA}$; $E_{SJ,SJ}$; $E_{L,L}$) and 2 reproductive loops ($E_{L,A,L}$; $E_{L,SA,L}$). The self loop $E_{L,L}$ is undetectable on this chart because the elasticity values are so small.

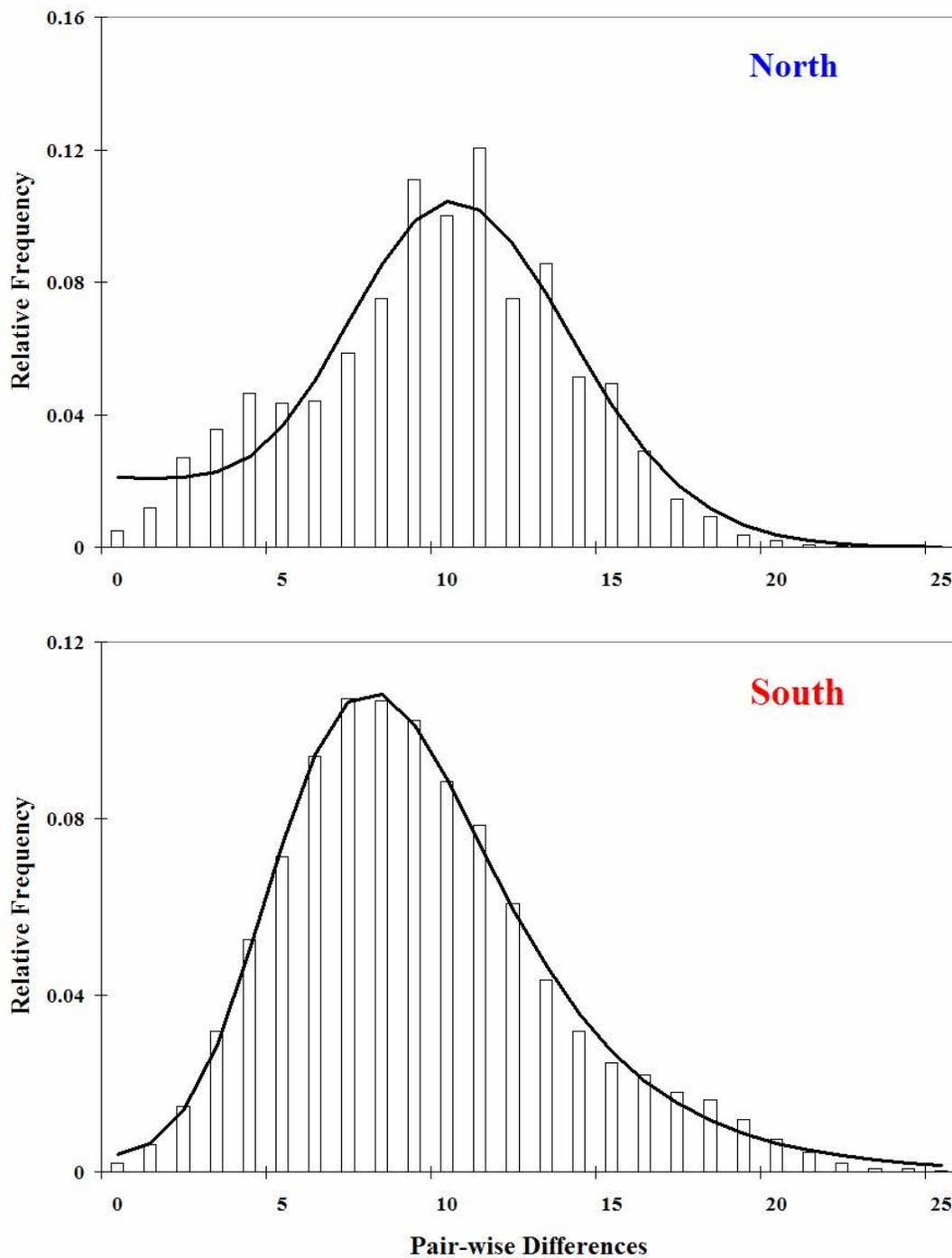


Figure 9. Mismatch distributions of northern and southern blue rockfish subpopulations. Observed values (bars) are compared to the model of sudden population expansion (line).

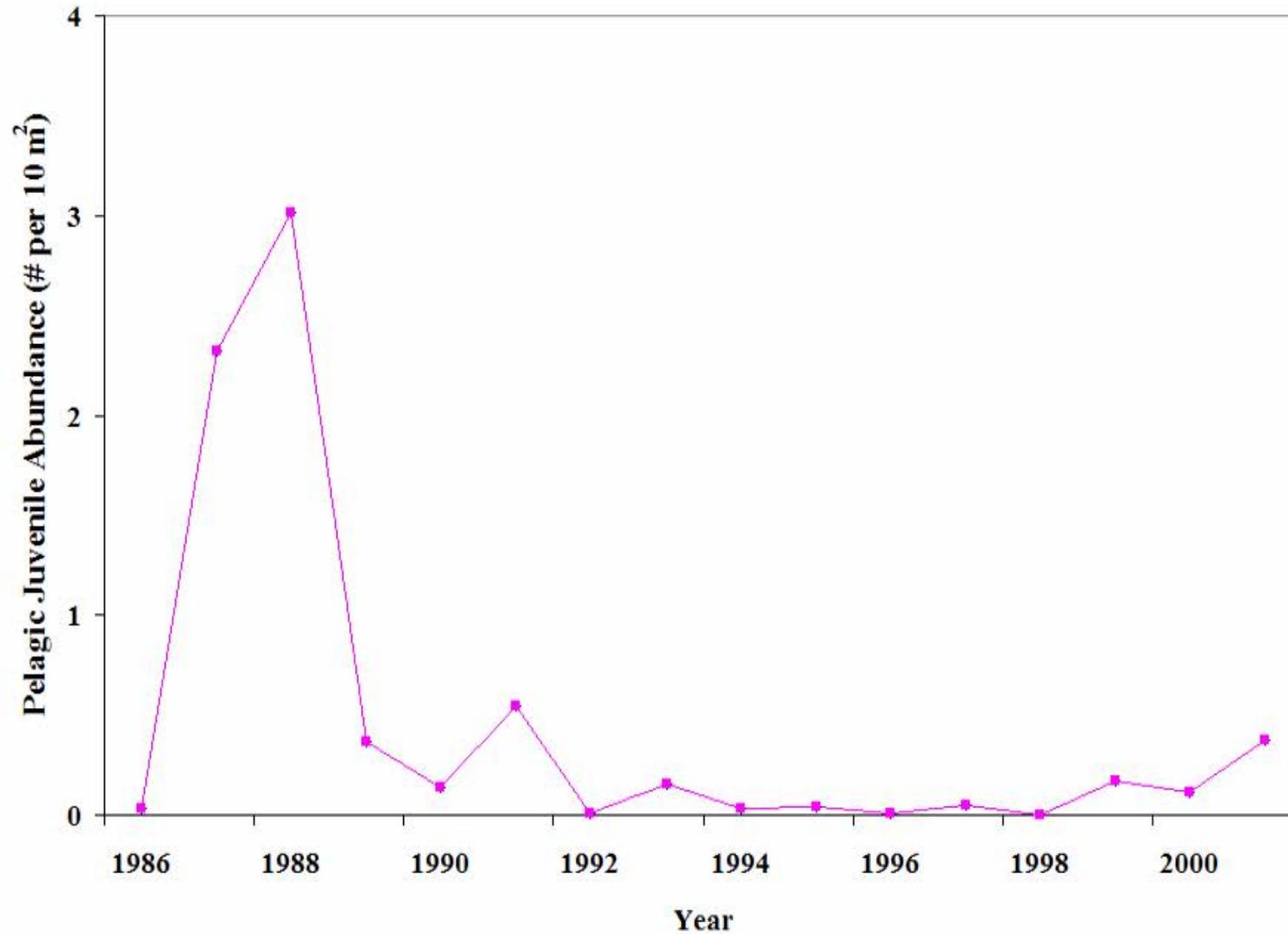


Figure 10. Pelagic juvenile blue rockfish abundance off central California from 1986 to 2001. Standard abundance index is based 10 m² MOCNESS tows (data provided by Steve Ralston, NMFS).

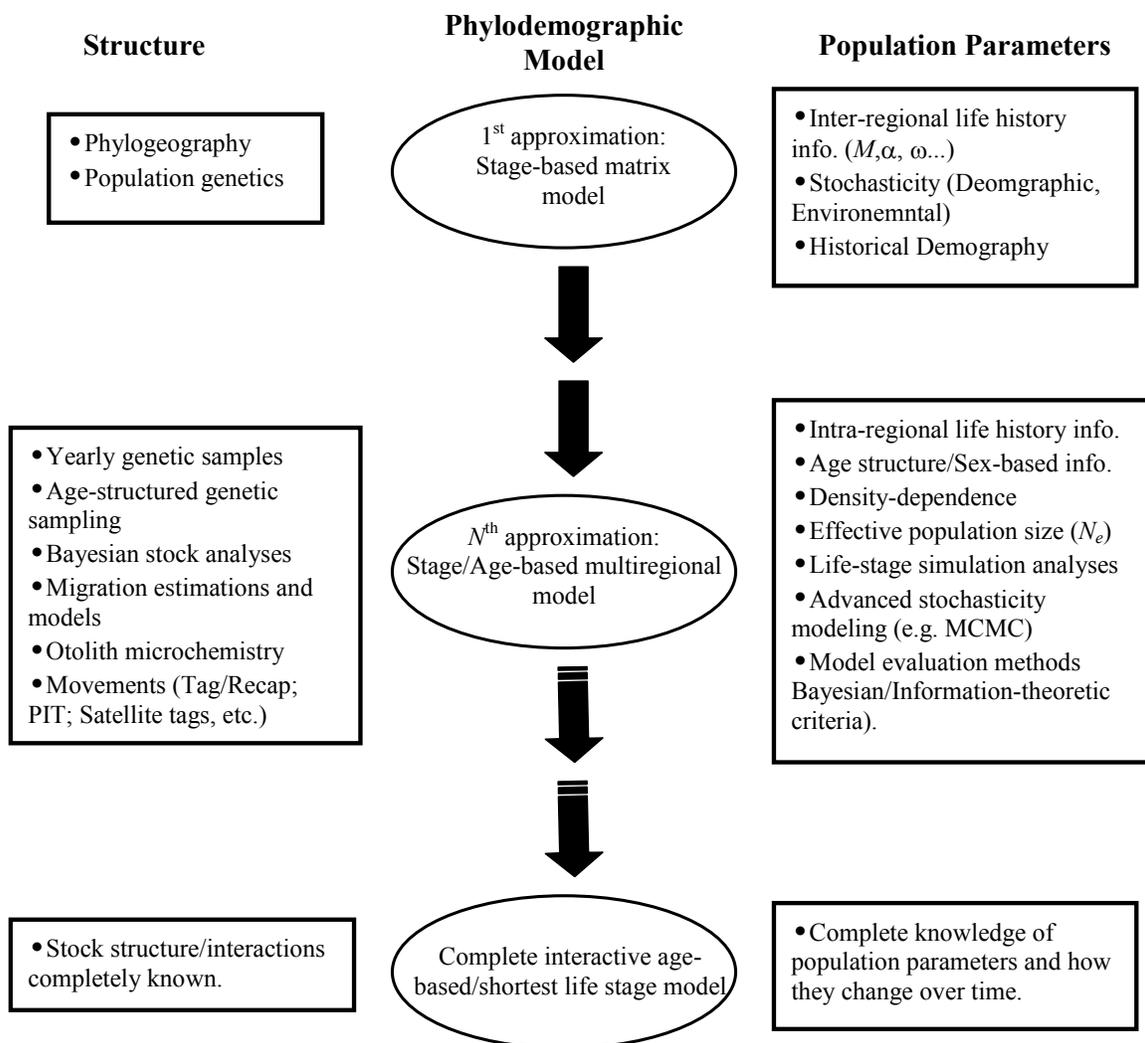


Figure 11. The phylogenetic approach to population modeling. Accumulating information on population structure and demography is added to each successive model as one approaches a model that includes all possible interactions and ranges of population parameters.