LIFE HISTORY CHANGES IN FEMALE BLUE ROCKFISH, SEBASTES MYSTINUS, BEFORE AND AFTER OVERFISHING, IN CENTRAL CALIFORNIA

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Katherine Tyler Schmidt

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The Undersigned Faculty Committee Approves the

Thesis of Katherine Tyler Schmidt:

LIFE HISTORY CHANGES IN FEMALE BLUE ROCKFISH,

SEBASTES MYSTINUS, BEFORE AND AFTER OVERFISHING, IN

CENTRAL CALIFORNIA

Dr. Gregor M. Cailliet, Moss Landing Marine Laboratories Professor Emeritus

Dr. Scott L. Hamilton Moss Landing Marine Laboratories Professor of Ichthyology

Dr. Richard M. Starr Moss Landing Marine Laboratories Research Faculty

Marsha Moroh, Dean College of Science, Media Arts, and Technology

Approval Date

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DEDICATION

To all those fishes, who are so delicious, and whom I also love. Gotta go fishin'...

ABSTRACT

Life history changes in female Blue Rockfish, *Sebastes mystinus*, before and after overfishing, in central California by Katherine Tyler Schmidt

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Life history parameters are critical inputs for the stock assessments used to inform the management of fisheries. However, life history parameters of fishes vary due to external influences, such as environmental variability, density-dependent resource competition, and fishing removals causing evolutionary trait changes. Blue Rockfish, *Sebastes mystinus*, are important sport fish along the central California (CA) coast and were overfished by 1985. Because life history traits can change following heavy fishing removals, my thesis compares the current life history parameters of growth, length at maturity, age at maturity, and fecundity of females to parameters obtained before the stock declined to overfished levels.

Recent genetic analyses have revealed 'Blue Rockfish' to be a cryptic complex of two species, whereas managers continue to recognize only a single species. Without an official species description for the second fish, the 'Blue Rockfish' species are referred to as Type 1 and Type 2. I evaluated whether female life history traits differed between these two species, and as available for males. The lifetime maximum size (L_{max}) of Type 2 females was lower than Type 1 females, and the growth characteristics were significantly different between the species for females. Type 2 females matured at significantly smaller sizes than Type 1 females; at 50% length at maturity Type 2 females were 222 mm TL compared to 239 mm TL for Type 1 females, while at 100% maturity Type 2 females were 264 mm TL compared to Type 1 females at 282 mm TL. Male values were significantly different between species at only at the 50% length at maturity; Type 2 male 50% length at maturity was 212 mm TL while Type 1 was 251 mm TL. No differences were found between the age-at-maturity values of the species, for females or males. There was no evidence for species-level differences in the length-fecundity relationships.

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In testing for geographic differences in life history traits among central CA collection locations, few significant differences were found; females from Half Moon Bay, CA had significantly different 100% age at maturity and a different length-fecundity relationship. All other life history traits were similar among collection locations.

The contemporary population of female Blue Rockfish (data of species and areas combined) reached a smaller L_{max} and had significantly different growth characteristics from the 1980s population. Length at maturity has decreased significantly since the 1960s estimates. Length at 50% maturity declined from 272 to 232 mm TL, while the length at 100% maturity declined from 349 to 274 mm TL. Age at maturity also declined significantly since 1980s estimates; age at 50% maturity decreased from 6 to 4.6 yr, and age at 100% maturity decreased from 11 to 6.8 yr. However, the length-fecundity relationship remained the same between the 1960s and 2010s time periods.

These observed life history changes could be caused by environmental variation, density dependence, or fisheries-induced evolution. The directional changes seen in length- and age-at-maturity values did not occur as would be expected in a situation driven by energetic limitations (i.e. environmental variation, density dependence). Previous length-at-maturity value differences attributed to yearly fluctuations (± 10 mm TL) were much smaller than the differences seen in these comparisons over decades of dramatic changes in fishing pressure. The life history changes found here reflect those of a population responding to increased fishing mortality and are more similar to other observations of fisheries-induced evolution. It is recommended that these current female Blue Rockfish life history trait values be incorporated into stock assessments and any future management decisions for these species. It is also recommended that the life history of other overfished rockfishes be re-evaluated as changes may be occurring in their biological traits in response to increased fishing mortality.

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This thesis project could not have been completed if not for the generosity of many charter boat companies, owners, captains and deckhands who allowed me to ride along on their regular trips to sample Blue Rockfish. The central CA charter boats that I gratefully boarded were the F/Vs: Huli Cat, Queen of Hearts, Ankeny Street and Tigerfish from Half Moon Bay; Checkmate, Star of Monterey, Caroline and Chubasco from Monterey; and Fiesta, Princess, Admiral and Pathfinder from Morro Bay. Also, my appreciation goes to all the recreational anglers aboard those boats who let me sample their Blue Rockfish before fillet or even gave me whole fish for this study.

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INTRODUCTION

Many species of marine fish can exhibit variation in their life history traits due to external factors in the environment. The external factors of temperature, prey and habitat availability, and predation pressure can produce plasticity in life history characteristics (Brown 1995, Stearns 1992). If the expressed phenotypes of certain life history parameters are advantageous, those genotypes will become dominant within a population and can cause the evolution of life history traits, sometimes rapidly (Reznick & Ghalambor 2005).

Overfishing is another external factor that can cause the evolution of life history traits in wild fish stocks (Trippel 1995, Law 2000, Reznick & Ghalambor 2005, Conover 2007). In such cases, trait changes are called fisheries-induced evolution (FIE), and produce predictable, directional changes in growth rate, length and/or age at maturity, and fecundity of females in fished stocks. The selective harvest of fishing on a population increases the mortality rates of sub-adult and adult fish so that any life history genotypes that express early reproduction are advantageous and selected for (Gunderson 1997, Stockes & Law 2000, Conover 2007), with their life history traits changing in a pattern similar to what would be expected of any population subject to increased mortality rates (Stearns 1992).

Fisheries-induced evolution has been replicated in laboratory-controlled settings where a phenotypic trait, such as size, can be selected against, and reproductive trait changes then follow in subsequent generations (Conover & Munch 2002). In controlled settings, the strength of selective mortality is often known, the rapidity of the gene mutations can be calculated, and the persistence of the trait changes in the subsequent generations after the selective forces cease can be measured (Reznick et al. 1997). These effects have also been observed in several wild, fished populations (Rjinsdorp 1991, 1993, Trippel 1995, Horn et al. 1998, Kronlund & Yamanaka 2001, Yoneda & Wright 2004, Rjinsdorp et al. 2005, Jorgensen et al. 2009) and produced in manipulated field experiments (Edeline et al. 2007, Reznick 1997, Bryant & Reznick 2004, Reznick & Ghalambor 2005).

Often, life history trait changes that occur in response to fisheries exploitations are difficult to document in wild populations for simple reasons. First, accurate historical estimates of fish reproductive biology prior to the onset of fishing are rare, because fisheries research often follows, rather than precedes economic interests and stock declines. Second, converting life history values found in older reports can be tedious to impossible, because the accepted methodology used to establish past life history values has changed as science progressed. For example, using fish scales as an aging structure was a common technique in past studies, but is no longer recommended for many species (Chilton & Beamish 1982).

Commercial and recreational fisheries are a part the economies of many communities in central California and these fisheries depend on the sustainability of, and continued access to, groundfish stocks (Starr et al. 2002, PFMC 2003). Because these groundfish fisheries are so important to coastal livelihoods, the Magnuson-Stevens Fishery Conservation and Management Act (MFCMA 1976) and the U.S. Sustainable Fisheries Act of 1996 details that the Pacific Fishery Management Council (PFMC) plans, created by the National Marine Fisheries Service (NMFS), must rebuild stocks should they fall below the overfished threshold. The PFMC qualifies a stock as overfished if the existing stock biomass, or spawning stock biomass, is calculated at less than 25% of the unfished biomass, or $<0.25B_0$ (Punt & Ralston 2007). According to this definition, many rockfishes (Sebastes spp.) - important components of the west coast groundfishes – were overfished by the 1990s, if not earlier (Parker et al. 2000, Love et al. 2002, Hilborn & Hilborn 2012). Stock assessments conducted by NMFS for 62 east North Pacific rockfishes have shown that six currently classify as overfished (Dick et al. 2009, Hamel & Ono 2011, He et al. 2011, Taylor & Wetzel 2011, Field 2013, Gertseva & Thorson 2013, Wallace & Cope 2013), and are being managed for rebuilding targets, rather than maintaining harvest levels (Punt & Ralston 2007).

Groundfish stock assessments require many types of information, including the life history of the species under scrutiny, to complete a useful assessment (Wallace & Fletcher 2000). Only the 'best available estimates' of the life history characteristics are used in stock assessment models. This is because the traditional population models used in full stock assessments are sensitive to any life history value changes (Cooper 2006).

Many of the stocks that suffered the biggest fishing impacts in the east North Pacific are also some of the latest-to-mature rockfish species (e.g. *Sebastes pinniger, S. levis,* and *S. ruberrimus*; Love et al. 2002). Overfished rockfish species such as these are not in a position to be evaluated for FIE effects because, according to their long maturation schedules, insufficient generations have passed since overfishing occurred. Edeline et al. (2007) and Stearns (1992) hypothesize that a likely minimum number of 3-4 generations must pass for FIE changes to manifest. However, evaluating possible FIE effects is pertinent to fisheries scientists, because it would affect stock assessment accuracy by changing the life history values of the overfished population for an indeterminate amount of time.

A rockfish species that may demonstrate FIE effects is the Blue Rockfish, *Sebastes mystinus*. Though rarely recognized as an overfished rockfish species, the 2008 Blue Rockfish stock assessment indicated overfishing removals had begun by the mid-1970s. By 1985, the spawning biomass was reduced below the overfished threshold, and the population hit a low of 10% of virgin biomass in 1994 (Key et al. 2008, Figure 1). These removals were primarily attributed to hook-and-line recreational fishing, which targets larger fish, and may magnify any life history trait changes otherwise driven by increased mortality (Conover & Munch 2002).



Figure 1. 'Blue Rockfish' landings in metric tons from commercial (trawl, live-fish, and gillnet) and recreational (hook-and-line private and charter) fisheries, and the estimated percentage of the population remaining, 1960 — 2006 (from Key et al. 2008).

Past life history parameters exist for Blue Rockfish, estimated from collections that occurred before the stock was overfished, in the 1960s (Miller et al. 1967) and in the 1980s (Wyllie-Echeverria 1987). Miller et al. (1967) provided female length-at-maturity information, as well as the fecundity by length of 11 females. Wyllie Echeverria (1987) established length- and age-at-maturity parameters for many rockfish species, including Blue Rockfish. Both of these studies were conducted in central California and fish were taken from important recreational fishing ports. A recent age and growth study conducted by Laidig et al. (2003) indicated that 3 to 4 generations should have matured within the time between the population low and the time sampling occurred for the present research.

All past life history values estimated for Blue Rockfish of central California have been made from a mix of two recently identified cryptic species (instances that refer to an undefined mix of the cryptic species complex will hence be written: 'Blue Rockfish'). 'Blue Rockfish' were first described from syntypes taken off Monterey, CA by Jordan and Gilbert (1881). 'Blue Rockfish' were considered a single species and assessed as a single stock from Point Conception, CA to the California-Oregon border (Key et al. 2008). Buford et al. (2011*a*, *b*) typed two genetically distinct species of rockfish that appeared morphologically similar enough that they were both identified as *Sebastes mystinus* previously (Cope 2004, Burford & Larson 2007, Burford 2009).

Comparing Burford et al.'s (2011 *a*, *b*) results of geographic distribution and the collection location of the original museum specimens of 'Blue Rockfish' (Jordan & Gilbert 1881), it is highly likely that the original Blue Rockfish species description correlates with Burford's Type 2, while the cryptic species is Burford's Type 1 (henceforth written: Northern Blue Rockfish) (M. Burford Reiskind, *personal communication*). Catch composition from the California Collaborative Fisheries Research Program (CCFRP) collected from 2011 – 2013 shows that the abundance of each species varies among nearshore rocky reef sampling sites throughout central California (Table 1). Based on these observations, the Blue Rockfish (Burford's Type 2) is found more readily in the Monterey and Morro Bay fishing grounds; while the Northern Blue Rockfish (Burford's Type 1) is more common north of Monterey, CA. Geographic differences in these species contributions to the 'Blue Rockfish' populations

	Northern Blue		% types in
	RF/	Blue RF/	total catch
Harbor/ sample area	Type 1	Type 2	(T1/T2)
Princeton/ (HMB)	660	595	8.2/7.4
Monterey/ (MON)	269	941	6.3/21.9
Morro Bay/ (MOR)	172	733	4.4/18.8

Table 1. Composition of the two 'Blue Rockfish' species in nearshore research surveys of central CA, <120ft water depth, 2011 – 2013 (R. Starr, Moss Landing Marine Laboratories in Moss Landing, CA, unpublished CCFRP data/ *personal communication*, February 2014).

in past datasets may explain the slight differences in past 'Blue Rockfish' life history values reported by Miller et al. (1967) and Wyllie Echeverria (1987). Thus, an assessment of life history differences between these two cryptic species of 'Blue Rockfish' is warranted. Overall, it is unclear if the life history characteristics presented by Miller et al. (1967) and Wyllie Echeverria (1987) are influenced overtly by different compositions of these species in their samples.

If FIE has affected 'Blue Rockfish' populations and their life history values have changed, accounting for any value differences would be critical to stock assessment accuracy. Continued use of older, and possibly erroneous, life history estimates could lead to errors in the fisheries models used to advise stock managers. This stock could be at risk of either over- or under-exploitation, and overregulation, without the consideration of possible life history trait changes or how the trait values may differ between the species. As a member of the "slow growing, late to mature" genus that has adapted to the California Current environment (Love et al. 2002), this stock, with its fishing history and current life history traits, can serve as a representative to determine if, or how, FIE affects overfished rockfishes in general.

To evaluate if life history trait changes have occurred in the 'Blue Rockfish' stock of central California after the period of heavy fishing (Figure 1), following predictions of FIE theory (i.e. decreases in the growth, size and age a fish population becomes mature, and increases in fecundity), I collected mainly female 'Blue Rockfish' samples throughout central California, 2010–2012 (2010s). Most fish were sampled from the hook-and-line Commercial Passenger Fishing Vessel (CPFV) fishery. Females were targeted over males, as changes to their life history traits would be more pertinent to fisheries scientists (Key et al. 2008), though male values were also estimated as available. I compared the life history values of the two 'Blue Rockfish' species, by sex, to see if there were differences in the life history values between the species. I then examined the influence of the geography on the life history traits of female Blue Rockfish. Finally, I compared current life history values of female 'Blue Rockfish' (data of species combined) with pre-overfishing estimates, to see if directional trait changes had occurred after overfishing.

METHODS AND MATERIALS

PAST RESEARCH AND HISTORICAL DATA

Historic life history parameter values of 'Blue Rockfish' were available from three studies conducted off central California: Miller et al.'s (1967) report on the ecology and life history of 'Blue Rockfish;' Wyllie-Echeverria's (1987) synopsis of the maturity characteristics of 34 species of rockfish; and Laidig et al.'s (2003) article on the age and growth of 'Blue Rockfish.' I conducted personal interviews with at least one of the authors from each study to ensure I properly interpreted their results, confirmed their methods and techniques used, and opportunistically received raw historic datasets whenever available so I could use them in later statistical comparisons.

Miller et al.'s (1967) report provided life history information and reference for the historic fishing grounds that had substantial removals of 'Blue Rockfish.' The fish used to establish their life history values were all collected from Monterey, CA. Unfortunately, their information on growth and age at maturity was unusable because scales were their ageing structure (scales are now regarded as poor estimates of the total age of most rockfishes after maturity; Chilton & Beamish 1982). A frequency histogram of the total lengths (TL) of 645 female immature and mature 'Blue Rockfish' was digitized using program GetData Graph Digitizer 2.24, and the extracted data of TL and maturity were used to calculate a historic length-at-maturity curve for females collected from 1964 – 1965 (1960s). A scatter-plot of the total fecundity of 11 females by TL (cm) was also digitized to extract raw data and used as the historic length-fecundity values.

Wyllie-Echeverria (1987) summarized the life history of 34 species of rockfish off central CA, including 'Blue Rockfish.' Her work supplied a descriptive chart of macroscopic and microscopic gonad characteristics used to establish maturity status and the length- and age-at-maturity logistic equations for both sexes. Logistic maturity models created from the data of maturity status and length, or age, of individual fish provide generalized biological reference points for a population by estimating the percent of reproductively mature adults. Sometimes the 50% length at maturity will be used to set size limits within a fishery (Cooper 2006).

For her age-at-maturity estimates, Wyllie-Echeverria read the surface of whole otoliths submerged in ethanol to establish fish age. This technique is no longer considered best practice for fish older than 16 years because the width of the annuli decrease drastically in the growing edges of the otoliths in mature fish and can lead to the underestimation of the true maximum ages (Chilton & Beamish 1982). However, Wyllie-Echeverria assumed this was not an issue because maximum ages were not the main focus of her work.

From Wyllie-Echeverria (1982), the logistic equation variables reported for female length and age at maturity were used to calculate the 1st, 50% and 100% maturity values:

Female 'Blue Rockfish' maturity coefficients values (Wyllie Echeverria 1982):

$a_{\text{Length at maturity}} = -0.3368$	aAge at maturity= -0.8022
$b_{ m Length}$ at maturity= 9.5090	$b_{ m Age \ at \ maturity} = 5.0097$

The raw data used to estimate these variables could not be obtained, even after consultation (T. Wyllie-Echeverria, *personal interview*), therefore no estimates of variation around the past life history values could be available for use in statistical analyses.

Laidig et al.'s (2003) article on the age and growth of 'Blue Rockfish' of central CA provided estimates of growth parameters for 'Blue Rockfish' caught from 1978 – 2002. This study used the break-and-burn technique to estimate the ages of the fish, which performs well for this species (D. Pearson, *personal communication*). Laidig et al. (2003) also validated 'Blue Rockfish' annuli up to 24 years using marginal increment analyses and confirmed 2 bands (one opaque and one translucent) are deposited per year. Raw lengths and ages of 982 female fish collected from years 1980 – 1982 (1980s) were received from co-author D. Pearson (SWFSC, *personal communication*, October 2012). Don Pearson indicated this dataset represented the same 'Blue Rockfish' that Wyllie-Echeverria (1987) had sampled, so growth estimates for the same fish from T. Wyllie-Echeverria's study were made available. Because specimen collection occurred prior to the realization of the existence of the 'Blue Rockfish' cryptic species complex, these

datasets did not offer any additional species information. It was assumed that these data contained an unknown composition of 'Blue Rockfish' species comparable to collections that occurred for my thesis samples of the 2010s.

STUDY AREAS

Ports, and their associated fishing grounds, were selected as study areas to represent current 'Blue Rockfish' life history values of the contemporary central California population. Study areas were chosen based upon important sample sites in Miller et al. (1967) and Wyllie-Echeverria (1987). These ports historically supported a substantial recreational fleet presence (Miller et al. 1967, Karpov et al. 1995), and these areas continue to receive recreational fishing (Love et al. 2002, Starr et al. 2002, Key et al. 2008). The three harbors selected were Half Moon Bay (HMB), Monterey (MON), and Morro Bay (MOR), California (Figure 2). Given the geographical separation of these harbors, this sample design enables tests of small-scale regional variability in life histories; while the overall life history values estimated from these data represent the traits of typical 'Blue Rockfish' populations within central California.

COLLECTION AND PROCESSING

Similar collection methods to the past studies were adopted to ensure that comparisons between historic and current datasets, collected 30 – 50 years apart, were not biased. I collected fish primarily with hook-and-line fishing gear, both by independent sampling on personal craft and by salvaging samples from recreational angler bags aboard charter vessels. Fish collected on independent sampling trips were sometimes taken outside of recreational fishing seasons, but always within recreational depth restrictions. The most common terminal tackle employed consisted of two Super Fly shrimp flies or Sabiki rigs (5/0 gauge hook size or smaller), with and without squid bait, on a weighted line. The smaller hooks available on Sabiki rigs proved better gear to catch smaller (< 250 mm TL) 'Blue Rockfish' than shrimp flies. Relatively few fish were captured by use of spear guns, or salvaged from recreation spear divers' stringers. Additional fish were sampled from the freezer holdings of unassociated research



Figure 2. Map of the central CA study areas and their associated harbors: Half Moon Bay (HMB), Monterey (MON) and Morro Bay (MOR).

activities that collected 'Blue Rockfish' from similar sample areas with similar gear during the same time period (Davis et al. 2010). Sample collections followed stipulations in approved California Department of Fish & Wildlife scientific collecting permit #10664 (Project #1), and all fish handling and use was approved by the Institutional Animal Care & Use Committee of San Jose State University, protocol #953.

Fish were processed and samples were taken according to protocols outlined in Table 2. An attempt was made to sample at least ten female fish in each ten-millimeter TL size bin, from 150 - 350 mm. This sampling scheme was applied to the three study areas, and then again for each species, totaling 776 fish sampled for this thesis. Males were sampled opportunistically because they were underrepresented in the hook-and-line catches.

SPECIES ASSIGNMENT

The original 'Blue Rockfish' species description (Jordan & Gilbert 1881) appears to be an accurate representation of Type 2 fish, and so all Type 2 individuals in this thesis will be in reference to the original species, the Blue Rockfish (Figure 3b). The cryptic species, Type 1, will be referred to as the Northern Blue Rockfish (Figure 3a). Although an official common or scientific name is currently unavailable, I chose to use this name because of a latitudinal division of these two species along the east North Pacific coast (Burford et al. 2011*b*).

Collected fishes were assigned to species in the field based on morphological characteristics. When possible, a digital photograph was taken of each fish before dissection, as a record of the external characteristics at the time of species assignment. Specimens can lose coloration and body shape definition within minutes of death, so the optimal time to assign species was just after capture. Blue Rockfish follow the characters of the original species description, with usually a light to medium blue background under dark spotting or blotching spread evenly over the sides (Figure 3b). Blue Rockfish also tend to have a more oval body shape, especially as individuals increase in length. Blue Rockfish have a shorter maxilla; the back of the maxilla stops before the back of the eye pupil. They also have a reduced chin knob. If the specimen is a mature female in the vitellogenic stage of maturation, her ovaries will appear yellow to orange, due to the

Procedures	Technique/ Method	Purpose
1) Euthanized fish	If alive, fish were sedated in a MS-222 & seawater bath, then forcefully struck with fish club to induce cranial compression and brain death.	Reduced handling stress and pain, according to IACUC approved guidelines for fish euthanasia (AMVA 2007), before dissection and tissue sampling.
2) Recorded fish measurements	Total and fork lengths were measured to nearest millimeter on a flat measuring board.	Decided length grouping, the independent variable in growth, maturity, and fecundity relationships.
3) Assigned ID code to all samples	Codes represented sample area, species, sex, and total length bin.	Codes ensured that all information and tissues taken corresponded to an individual and insured permit sample numbers were not exceeded.
4) Photographed each fish	A digital photograph was taken immediately after death, before dissection.	Allows for future meristics/ measurements to be conducted, and serves as a record of the visual characteristics of each individual.
5) Weighed whole fish	Whole fish were weighed on a portable hanging Pesola scale (+/- 2 grams, no correction for stomach weight), whenever possible.	Allows for future analyses of maturity and fecundity in relation to fish weight.
6) Determined sex	Sex assignment was based on internal determination after dissection.	External sexing of rockfish is difficult and not advised; only internal assignment was used.
7) Assigned gonad maturity stage	Macro-morphology stage assignments were made in the field, and gonads were harvested.	Maturity assignment corresponded to descriptions by Wyllie-Echeverria (1987), required hand lens and tactile examination of gonads for proper assignment.

Table 2. Fish processing procedures and data collection steps employed during study.

Table 2 cont'd.

Procedures	Technique/ Method	Purpose
8) Weighed gonads	Wet weight of gonads was recorded to the nearest 0.01 of a gram, cleared of unassociated tissues, in lab.	Fecundity estimates created from the preserved samples could be converted to unpreserved wet weight after relationships length-fecundity relationships are created.
9) Preserved gonads	Excised gonads were placed in separate cotton bags with their ID codes and preserved in a $50 - 70\%$ methanol solution.	Preservation allowed for later dissection and microscope evaluation of gonads to ensure that the correct maturity stage was assigned, and enabled egg counts.
10) Microscopic review of maturity assignment	At least 10% of fish in each maturity stage were reviewed under a dissecting scope and/or microscope, for microscopic characteristics corresponding to specific maturity states.	Checked maturity assignment against cellular morphology described by Shaw et al. (2012).
11) Weighed liver	Weighed liver, clear of unassociated tissue, to nearest 0.1 g, in lab.	The weight of the liver relative to the weight of the fish, called the hepatosomatic index, can be used a proxy of condition (Giulio & Hinton 2008).
12) Removed otoliths	Both sagittal otoliths were removed from the head of all fish, cleaned of excess tissue in water, dried, and stored dry in paper envelopes with identification code.	Sagittal otoliths are used in age determination in rockfish, as they are the largest and most easily viewed pair of otoliths (Chilton & Beamish 1982).

Table 2 cont'd.		
Procedures	Technique/ Method	Purpose
13) Fin clips	Fin clips were taken, one off the left pectoral fin and	Some samples were used to check the accuracy of species assignments genetically. The careful record
	in 95% ethanol with ID code on the vial. Long-term storage of the samples was in a -10° C freezer.	of these fish could make these samples desirable to
14) Disposed of carcasses	Once sampling was complete, all remains were frozen and then taken to a rendering company for disposal.	future genetic studies on FIE life history changes. The rendering company used remains to make a usable product.

a) Type 1/ Northern Blue Rockfish



b) Type 2/ Blue Rockfish



Figure 3. Photos of a) Type 1/ Northern Blue Rockfish (this individual could easily be mistaken for a Black Rockfish, *Sebastes melanops*) and b) Type 2/ Blue Rockfish, *Sebastes mystinus*. These photos are of freshly captured fish, alive and with little evidence of barotrauma injuries.

coloration of the oil globules deposited in the eggs. This coloration persists to at least the fertilization stage.

Northern Blue Rockfish are the species most likely misidentified as a Black Rockfish, *Sebastes melanops*, (and were once suspected of being a hybrid between Black and Blue Rockfishes). They have a light to dark, grey/ steel blue background, under darker grey static-like or uneven blotching on their flanks (Figure 3a). In particular, Northern Blue Rockfish have a darkish band of localized mottling on their upper dorsal surface, similar to the dorsal markings of Black Rockfish. Their body shape is more elongate and has sharper edges, similar again to Black Rockfish, and could be described as bass-like body type. In larger individuals, Northern Blue Rockfish have relatively pronounced chin knobs. They also have longer maxillas that extend past the edge of the pupil to the back of the eye but not beyond (Black Rockfish will always have maxillas that extend past the eye, even in juveniles). Northern Blue Rockfish females in the vitellogenic stage of oocyte development have white to light pink ovaries.

The accuracy of species assignments made during collection was verified with genetic techniques. Microsatellite loci were used in preference over the CO1 region (M. Burford, *personal communication*). Genomic DNA from fin clip samples of 60 fish were extracted at Moss Landing Marine Labs using a DNEasy Blood and Tissue Kit (Qiagen), following manufacturer's instructions. Nine microsatellite loci were amplified by conducting polymerase chain reaction on the extracted DNA at the Aguilar Lab, University of California Merced. Of the nine loci, six were used for the microsatellite analyses (*Sra.7-2, Sra.7-7, Sra.7-25, Sra.6-52, Sra.15-8, Sra.16-5*, GenBank Ass. No.: AF269054-57, 59, 61 respectively; Burford 2011*a*). Fragment amplification and scoring of the microsatellite loci followed the protocol of Burford and Larson (2007). The programs Genemapper (Applied Biosystems Inc.), Genetix (Belkhir et al. 2004), and Structure (Pritchard et al. 2000; Hubisz et al. 2009) scored the results based on allele types used in Burford (2011*a*), and assigned individuals into Type 1 or Type 2 groups.

MATURITY ASSIGNMENTS

Upon dissection, fish were assigned as either immature or mature based on maturity stage (Table 3). Maturity stage was based off external and cellular gonad

morphology as described by Wyllie-Echeverria (1987). An additional verification of maturity assignment was conducted with technicians of the early life history division at the Southwest Fisheries Science Center (N. Kashef and D. Stafford, *personal interview*), and by checking maturity stages against current NMFS accepted characteristics (Shaw et al. 2012).

I then ensured that my maturity assignments were consistent with T. Wyllie-Echeverria's assignments via an in-person interview. Select digital photographs of dissected female fish with exposed gonads and microscopic close-ups of developing oocytes were selected for review. These photographs represented the spectrum of difficulty associated with assigning maturity to rockfish throughout the developmental season. Tina Wyllie-Echeverria was asked to assign maturity blind to my maturity assignment. Out of the 27 evaluated fish, there was disagreement on the maturity status of four fish (85% agreement); however T. Wyllie-Echeverria tended to be less conservative when classifying fish to a reproductively mature status.

FECUNDITY ESTIMATES

After maturity status was established and the ovaries were removed, all vitellogenic ovaries were preserved in 50 – 70% methanol for at least 12 weeks. Preservation in methanol was described by Rijnsdorp (1991) as a successful alternative to more noxious preservation chemicals like formalin and Gilson's fluid. The minimum 12-week span allowed eggs to become rigid enough to survive separation before counts. Most ovaries were preserved while in the early to late vitellogenic stage (gonad stage 3, Table 3). During this stage, eggs are increasing in diameter from 0.2 mm to 0.9 mm at the time of fertilization. Methanol preservation method was ineffective on ovaries with fertilized eggs, because the prescribed concentration was not high enough to account for the increased amount of liquid present in fertilized eggs compared with vitellogenic eggs. Whole collection of ovaries during the fertilization and gestation stages at sea was impossible, as the ovarian wall was extremely thin and tore easily during those stages, and the eggs were loose within the ovary, so large quantities of eggs spilled out. Therefore, only ovaries with vitellogenic stage eggs were used in the fecundity counts.

Gonad stage	Cellular morphology	External morphology
1. Immature	Oogonial nests with oocytes <0.14mm. Ovarian wall 0.1mm thick.	Small and translucent to pink. Ovarian wall thin.
2. First year maturity	Oocytes <0.2mm. No evidence of resorption.	Pink with visible eggs. No black pigmentation. Ovarian wall thin.
3. Vitellogenesis	Mature oocytes 0.2-0.5mm in diameter within follicles. Ovarian wall 0.3-0.4 mm thick.	Yellow or white opaque eggs in grapelike clusters. Ovarian wall thickening.
4. Fertilization	Oocytes 0.9 mm. Yolk globule disintegration , ovulation, fertilization.	Large clear eggs free in ovarian cavity, but enveloped by a network of capillaries.
5. Eyed larvae (parturition)	Larvae developed within chorion with eyes pigmented black or yellow.	Large, soft, gray. Ovary breaks easily, and is filled with eggs and fluid.
6. Spawned	Oocytes 0.8-0.64 mm in diameter. Resorption of blood vessels, atretic oocytes, and residual larvae . Collapsed egg cases. Ovarian wall 0.5-1.0 mm thick.	Flaccid, reddish-purple, or grayish from residual larvae . Ovarian wall thick and tough.
7. Resting	Resorption and reorganization. Proliferation of oogonial nests. Ovarian wall 0.5-0.9 mm thick.	Firm, gray to pink. Tiny black dots indicate residual larvae, ovarian wall thick, tough, and loose from eggs.

Table 3. Macroscopic and cellular gonad characteristics used for maturity status assignment, as described by Wyllie-Echeverria (1987).*

*Bolded text indicates characteristics informative for this study.

The gravimetric method was used to estimate the total number of eggs from the total egg mass weight. To weigh the total egg mass inside of a female, the ovarian wall and supportive tissue were separated from the mass of eggs so that pure egg weight could be taken and used in the gravimetric calculations to estimate the total fecundity of the fish. At least three subsamples (≥ 0.01 grams) were taken from each egg mass. Subsamples were taken from various positions along the axial length of the ovary to reduce possible harvest location bias. The egg counts of a subsample were tallied under a Leica dissecting scope at a 10x - 32x magnification. For all vitellogenic ovaries (with oocytes ≥ 0.15 mm in diameter) total eggs per female were averaged using subsample counts made according to gravimetric method (Cailliet et al. 1986). The gravimetric method details creating a proportion out of the sum of tallied eggs and their weight, for a small subsample taken from the egg mass,

$$\frac{\sum Eggs_{SS1}}{Weight(g)_{SS1}} = \frac{x_{TotalFecunditySS1}}{Weight(g)_{TotalEggmass}}$$

*SS*1 = *Subsample*1

and solving that equation for x to estimate the total egg count, or fecundity, of the fish for a single subsample using the total weight of the egg mass present:

$$x_{TotalFecunditySS1} = \frac{\left(\sum Eggs_{SS1} \times Weight(g)_{TotalEggmass}\right)}{Weight(g)_{SS1}}$$

This calculation was repeated for at least three subsample counts to obtain three total fecundity estimates per female. The three total fecundity estimates were then averaged for a single, averaged, total fecundity per female. Eggs <0.15 mm and without oil globule investment (Shaw et al. 2012) were not included in the counts, as it was probable eggs of that size would not have developed into larvae that year.

The ovaries of immature fish were also preserved and checked for possible maturation but not were counted for fecundity, though oocytes (<0.10 mm) could be seen under the microscope. Not all fish recorded as mature could be used for fecundity estimates due to divergence between the fishing season and Blue Rockfish egg maturation schedule. While fish in the spent or resting stages, collected during the spring or summer months, were recorded as mature based on their ovarian size and

characteristics, those samples were unsuitable for fecundity counts as their oocytes were still very small, tightly packed, and difficult to separate to single eggs. Only in fall and winter did fish display optimal egg sizes, and these seasons coincided with open recreational fishing season, which operated May–December in central CA (Wyllie-Echeverria 1987, Key et al. 2008) during the years of collection in this study.

AGEING TECHNIQUES

The break-and-burn method was used to prepare all otoliths prior to reading (Chilton & Beamish 1982, Laidig et al. 2003). A single sagittal otolith was chosen from the pair of each fish, previously cleaned of extra tissue and dried. The chosen otolith was snapped in half laterally, across the nucleus, by securing the otolith between the index fingers and thumbs, and an increasing gentle pressure was applied until it broke. One of these halves was selected, and carefully heated over a sheltered flame until a browning of the halved face occurred.

The purpose of the controlled burn is to enhance the alternating patterns of translucent and opaque zones by darkening the translucent zones via charring. The desired degree of darkening is between a golden to dark brown, but heating the otolith half too long or holding it too close to the flame will cause black charring and smoking, which results in crumbling white ash edges unsuitable for accurate age estimation. This kind of charring was undesirable, as all bands were then obscured and the otolith became extremely fragile. If charring occurred on the first attempt, another attempt to properly burn the second half of the snapped otolith was made.

Darkened otoliths were positioned vertically, secured in modeling clay to hold the otolith half upright, for viewing. The broken and burnt surface was brushed with vegetable oil to enhance band contrast and minimize surfaces that would otherwise obscure bands, such as cracks and unevenness. Prepared otoliths were read at 20x - 60x magnification using a Leica dissecting scope under reflected light. A digital photograph was taken of the entire burned otolith cross-section face during the second reading, as well as a close-up photograph of the area read to establish the age of the fish, on the second read (Figure 4).



b)



Figure 4. Image of: a) an otolith prepared according to the break & burn method, brushed with vegetable oil, ready for counting; and b) the green dashes in Photo 2 indicate the nucleus/ birthmark, and the darkened bands representing 1 yr of growth. This fish was estimated to be nine years old.

Laidig et al. (2003) used edge analysis to validate that 'Blue Rockfish' otoliths deposit two growth bands each year; up to at least 23 yr of age for females and 25 yr of age for males. So in this study, each pair of burned (previously translucent) and opaque zones was assumed to represent one year of growth (Figure 4). Each otolith was read three times by the same reader, with at least 2 weeks between reads of the same individual. If there was not at least 60% agreement between any two of the three reads, a fourth read was conducted to replace the most aberrant value (Neer & Thompson 2005). Reads were conducted with knowledge of fish capture date and fish length because such information was helpful in estimating the birth date.

To determine the precision between reads of an individual, the coefficient of variation (CV) and index of average percent error (IAPE) were calculated. After the following calculations were made for all individuals, they were averaged to produce a mean CV and IAPE for a group (e.g. female Northern Blue Rockfish or male Blue Rockfish).

$$CV_{j} = 100\% \cdot \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_{j})^{2}}{R - 1}}}{X_{j}}$$

IAPE = 100%
$$\cdot \frac{1}{N} \sum_{j=1}^{N} \left(\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_i|}{X_j} \right)$$

N = total number of samples

R = number of age estimates or 'reads' for each otolith

 X_{ij} = the *i*th age estimate from the *j*th otolith

 X_j = the average estimated age from the *j*th otolith

To reveal any bias that may be correlated to increasing fish age; pair-wise age difference plots were constructed between age estimated in a single read on the independent axis and the mean the age estimates of another read for the same otoliths on the dependent axis. Plots of these points indicated no bias when following a one-to-one line.
DATA ANALYSES

To address questions about the current life history variation in 'Blue Rockfish' of central CA, I divided my samples by sex, species, and sample area. To compare the life history values over time, the historical datasets were treated in the same fashion statistically to maintain consistency in estimation methods, except in cases when raw historical data were unavailable.

Growth Characteristic

Lifetime growth curves were estimated using the Von Bertalanffy Growth Function (VBGF). Parameters from the VBGF were fit to the length-at-age data using a random effects model option, which incorporates uncertainty amongst the age estimations, in the modeling program IGOR+ created by Jason Cope (Cope & Punt 2007). The VBGF model was chosen for its comparability to other published growth functions.

3-parameter von Bertalanffy growth function:

$$L_t = L_{\max} \cdot \left(1 - e^{-k(t-t_0)}\right)$$

 $L_t = total length at age t$

 $L_{max} = asymptotic total length$

k =growth rate coefficient

to = theoretical age at zero length

Following published recommendations (Robertson et al. 2005; Jason Cope, *personal communication*) the length-at-birth coefficient, *to*, was fixed at zero in model runs as none of the available samples contained fish below two yr of age. The inclusion of one-year old fish in the model may have improved growth curve estimates, but because only sub-adult and adult fish were scrutinized with the purpose of comparing growth rates rather than exactly estimating them, and because true age-zero 'Blue Rockfish' are approximately 1.4 mm TL – or effectively size zero at age zero – the biological significance of the model was not affected by this decision. Estimates of *to* by sex can be found in Laidig et al. (2003), though that study did not separate 'Blue Rockfish' to species.

To examine differences in growth characteristics between groups, continuous 95% CI were calculated around the VBGF parameters L_{max} and k, following Kimura (1980) and Hamilton et al. (2011), using the R 3.0.0 GUI program, "Estimator of confidence intervals for von Bertalanffy Growth Function." These outer boundaries of 2-D 95% CI are called confidence ellipses. Visual comparison of the overlap of confidence ellipses between comparison groups was used to determine statistical significance. Overlap indicated homogeneity between comparison populations, while non-overlap indicated significant distinction.

Length- and Age at Maturity

Length- and age-at-maturity curves were estimated using the logistic regression function in JMP 10 (Intel) for the binomial data of maturity status (mature = 1, immature = 0) and the independent continuous variable of TL (mm) or age (yr). The length or age estimated for the 1^{st} , 50%, and 100% maturities, and their 95% confidence intervals (95% CI), were extracted from the predictive models, for later use in comparative parametric tests.

$$P_x = \frac{1}{1 + e^{ax+b}}, \qquad \qquad \ln\left(\frac{1}{P_x} - 1\right) = ax + b$$

 P_x = percent of the population that is mature

e = Euler's number, a mathematical constant that is the base of the natural logarithm (*ln*)

- a = slope
- b = y-axis intercept
- x = length or age at the maturity P_x

Maturity differences were evaluated with t-tests (two-sample or one-sample) for species and time period comparisons, and ANOVAs for geographical comparisons. The extracted lengths or ages of maturity for the 1st, 50%, and 100% levels were used in the statistical calculations instead of the means. For the lengths at maturity, the predicted length at maturity was subtracted from each total length within a group and between

groups to the length at maturity overall groups. The modified sums of squares (SS) equation used in this ANOVA is as follows:

$$SS_{Area} = \sum_{Areas} \left((Length @ Maturity_{Area} - Length @ Maturity_{OverallAreas})^2 \times n_{Areas} \right)$$
1.
$$SS_{Error} = \sum_{Areas} \left((TotalLengths_{Area} - Length @ Maturity_{Area})^2 \right)$$
2.
$$SS_{Total} = \sum_{Areas} \left((TotalLengths_{Area} - Length @ Maturity_{OverallAreas})^2 \right)$$
3.
$$df_{Areas} = \left(\# ofAreas - 1 \right), \quad df_{Error} = n \sum_{Areas} CountTotalLengths, \quad df_{Total} = df_{Error} - df_{Areas}$$
4.
$$MS_{Areas} = \frac{SS_{Areas}}{df_{Areas}}, \quad MS_{Error} = \frac{SS_{Error}}{df_{Total}}$$
5.
$$F = \frac{MS_{Areas}}{MS_{Error}}$$

This calculation was repeated for the lengths of 1^{st} , 50% and 100% maturities, and for the ages at maturity as well. The resulting p-values - determined from the F-values - and the degrees of freedom, established test group significance (significant p≤0.05).

Length-Fecundity Relationships

The relationship between averaged total fecundity (dependent variable) by TL (mm) (independent variable) was evaluated using the curve estimation option in statistical program SPSStatistics 20 (IBM) for power regressions:

Fecundity =
$$a \cdot TL^b$$

Fecundity = total number of vitellogenic eggs estimated for a give size

a = scaling parameter

b = power exponent

TL = total length (mm) of a female

Error bars (standard error) of averaged fecundity were plotted to represent the precision of the fecundity estimates, but this information was only used as a means to discard fecundity estimates with very high uncertainty (i.e. error bars that extended over the total range of the data points). Average fecundity estimates that were beyond the maximum total fecundity of 'Blue Rockfish' (Wales 1952) were also considered erroneous and were removed prior to analyses.

To test for statistical differences in the fecundity-length relationship between the species, sample areas, and time periods, an analysis of covariance (ANCOVA) was utilized in SPSStatistics 20 (IBM), with the independent variable of TL (mm) and the dependent variable of log₁₀ transformed averaged total fecundity, to compare the interactions of variables. A Levene's test was used to test the assumption of equal variance before each test run. Interactions between the grouping factor and TL were examined for significance, before the main effects of the variables could be examined independently for significance, but left in the model for the most conservative results.

RESULTS

GENERAL COLLECTION

I collected a total of 776 Blue and Northern Blue Rockfish during the years 2010 – 2012, from the HMB, MON and MOR study areas of central CA. Approximately 374 fish were salvaged or donated from recreational anglers, 321 were caught aboard charter fishing vessels, 52 were collected on independent research fishing trips, and 29 were salvaged from the freezer holdings of Davis et al. (2010).

More females were collected than males, more Blue Rockfish were collected than Northern Blue Rockfish, more fish were caught in MON, and more samples were taken in 2011 than any other year (Table 4). Different study areas produced different compositions of species in their catches (Table 4, Figure 5 – 7, Pearson's X^2 =119.14, pvalue<0.0001). Half Moon Bay was dominated by Northern Blue Rockfish, while MON and MOR samples contained many more Blue Rockfish than Northern Blue Rockfish.

Blue Rockfish females mean TL was 281.6 mm (± 2.7 SE) and male TL was 221.7 mm (± 7.4 SE, Figure 8). Northern Blue Rockfish females mean TL was 256.5 mm (± 3.2 SE) and male TL was 222.4 mm (± 3.9 SE, Figure 9). As expected of hook-and-line collection methods, fewer smaller fish were collected than larger fish for either sex or species, however females were larger on average than males for both species.

		Blue Rockfish		Northern Blu		
Year	Sample area	Female	Male	Female	Male	Totals
2010	HMB	56	8	36	15	150
	MON	123	16	6	5	115
	MOR	79	6	3	1	89
2011	HMB	44	3	123	53	127
	MON	46	4	57	20	223
	MOR	29	1	22	10	62
2012	HMB			4		4
	MON	4	2			6
	Totals	381	40	251	104	776

Table 4. Tallies of fish collected for this study by species, sex, area, and year collected.

Note: Collection sites have been abbreviated; Half Moon Bay (HMB), Monterey (MON) and Morro Bay (MOR), California.



Figure 5. Blue and Northern Blue Rockfish collection locations for the Half Moon Bay study area, with total catch composition by species and sex in the pie diagram.



Figure 6. Blue and Northern Blue Rockfish collection locations for the Monterey study area, with total catch composition by species and sex in the pie diagram.



Figure 7. Blue and Northern Blue Rockfish collection locations for the Morro Bay study area, with total catch composition by species and sex in the pie diagram.



a)

Figure 8. Size frequency histograms of a) female and b) male Blue Rockfish total lengths (mm), collection years 2010 – 2012 combined, from central CA study areas.



a)

Figure 9. Size frequency histograms of a) female and b) male Northern Blue Rockfish total lengths (mm), collection years 2010 – 2012 combined, from central CA study areas.

SPECIES ASSIGNMENT

Of 45 individuals that were assigned to species in the field with confidence, 44 assignments agreed with the genetic results, for an overall accuracy of 97% (Table 5). Of fish assigned to species with some uncertainty, the genetic results showed that six out of nine assignments were correct. Of the three incorrect species assignments, Blue Rockfish were misidentified as a Northern Blue Rockfish, but there was not an example in which a Northern Blue Rockfish was mistaken as a Blue Rockfish. Fish earmarked as possible Blue Rockfish x Northern Blue Rockfish hybrids (3 individuals), ultimately typed as Northern Blue Rockfish. Hybrids may still exist within my samples because only a subset of the total collection was reviewed genetically; Burford et al. (2011*a*) found a 2% hybridization rate of the two 'Blue Rockfish' species within her samples.

Genetically Field ID as Genetically typed as Number Northern assignment ID as Northern typed as correctly Percent Blue RF Blue RF confidence Blue RF Blue RF assigned correct 24 23 25 47/48 97.9% Certain 24 Uncertain 4 5 1 8 6/9 66.7% 2 0 3 'Hybrid' 1 2/366.7%

Table 5. Genetic confirmation of species assignment of the two 'Blue Rockfish' species, by certainty of the scientist on the species assignment.

AGE PRECISION AND BIAS

The CV and the IAPE estimates for the all specie and sex groups fell below 20% (Table 6), which are considered normal performance levels for these species (D. Pearson, *personal communication*). Female Blue Rockfish had the highest amount of group variability around their ages (15.4%), while male Blue Rockfish had the lowest (1.6%). In contrast, the Northern Blue Rockfish species had similar amounts of disagreement between the sexes, and these values were lower than those calculated for Blue Rockfish females. Laidig et al. (2003) reported a better APE for 'Blue Rockfish' of only 5.6% between readers, but did not report an estimate of the amount of disagreement within the reads of a single reader.

The pair-wise age difference plots produced lines that strayed from the one-to-one slope (Figure 10 & 11). A single read of Northern Blue Rockfish otoliths performed relatively well when compared to the mean age that the other two reads produced, however a single read of individual female Blue Rockfish otoliths most often underestimated the mean of the other two reads. Fish older than 20 yr were the source of disagreement. This bias was considered acceptable because the disagreement of ages was systematically consistent between read comparisons and therefore easily corrected. The three reads were averaged over the all reads (Campana et al. 1995) when a single age estimate was required (e.g. age and growth plots and age at maturity). When age estimations were needed to estimate growth characteristics, all three reads were input into the VBGF estimator using a random effects model to incorporate the ageing error into the function (Cope & Punt 2007).

Table 6. The measures of age precision: IAPE, CV, and D for the 'Blue Rockfish' species, by sex, from 2nd and 3rd otolith reads.

Species	Sex	IAPE	CV	D
Blue Rockfish	Female	15.41%	12.48%	7.21%
	Male	1.58%	12.68%	7.32%
Northern Blue Rockfish	Female	10.73%	9.06%	5.21%
	Male	11.55%	9.76%	5.63%



Figure 10. Blue Rockfish pair-wise age difference plots by read number and sex (F=females, M=males).



Figure 11. Northern Blue Rockfish pair-wise age difference plots by read number and sex (F=females, M=males).

LIFE HISTORY DIFFERENCES BETWEEN BLUE AND NORTHERN BLUE ROCKFISH

Age and Growth

I estimated ages of 381 Blue Rockfish and 250 Northern Blue Rockfish females, and 39 Blue Rockfish and 104 Northern Blue Rockfish males. The TL of the largest Blue Rockfish female was 385 mm, but the oldest Blue Rockfish was 34.5 yr and 367 mm TL. The largest Northern Blue Rockfish female TL was 380 mm, and also provided the oldest Northern Blue Rockfish age estimate, 23.5 yr. The TL of the largest Blue Rockfish male was 325 mm, and it was the oldest male aged at 13.7 yr. The TL of the largest Northern Blue Rockfish male was 310 mm, but the oldest Northern Blue Rockfish male was estimated at 12 yr and 279 mm TL.

Growth characteristics were similar between the species for females. The von Bertalanffy Growth Functions (VBGF) of the females produced growth curves that were very close between species, with the Northern Blue Rockfish VBGF having a slightly higher L_{max} but otherwise similar growth coefficient, or curvature parameter, *k* (Table 7, Figure 12a). The 95% confidence ellipses of L_{max} and *k* of the females did not overlap and thus the lifetime growth curves of these species are significantly different (Figure 12b).

The growth trends were also similar between the species in comparisons of male data (Table 7, Figure 13a). The 95% confidence ellipses overlapped between species (Figure 13b), and so their growth characteristics were not significantly different. However, the shift in L_{max} and k between species was in the same direction as it was for females. The inability to detect species differences in growth may be due to the lower number of samples available for males, relative to the number available for females.

Sex	Species	n	k (±SD)	Lmax (±SD)	to	CV _{age}
Female	Blue RF	381	0.250 (0.006)	325.6 (2.49)	0	0.08
	Northern Blue RF	250	0.255 (0.007)	338.3 (4.219)	0	0.07
Male	Blue RF	39	0.405 (0.037)	261.4 (8.727)	0	0.12
	Northern Blue RF	104	0.345 (0.021)	285.6 (7.448)	0	0.09

Table 7. Blue and Northern Blue Rockfish von Bertalanffy growth function parameters L_{max} (TL in mm) and k, with standard deviations (SD), by sex.

Note A random effects model that incorporated all three age estimates was used; t₀ was set to zero.



Figure 12. Female Blue and Northern Blue Rockfish: a) individual estimated ages and total lengths (mm), with von Bertalanffy growth function (VBGF) curves overlaid; and b) the 95% confidence interval for growth parameters L_{max} and k, or confidence ellipses.



Figure 13. Male Blue and Northern Blue Rockfish: a) individual estimated ages and total lengths (mm), with von Bertalanffy growth function (VBGF) curves overlaid; and b) the 95% confidence interval for growth parameters L_{max} and k, or confidence ellipses.

Length at Maturity

The length of the smallest mature female was 217 mm TL, for both Blue and Northern Blue Rockfishes. The largest immature female Blue Rockfish was 257 mm TL and the largest immature Northern Blue Rockfish female was 266 mm TL. The smallest mature Blue Rockfish male was 196 mm TL and the smallest mature Northern Blue Rockfish male was 231 mm TL. The largest immature male Blue Rockfish was 249 mm TL and 303 mm TL for Northern Blue Rockfish.

Logistic regressions best described the relationship between maturity and TL for all species and sexes (Table 8, all p-values ≤ 0.001). For females, the length-at-maturity curves of the species had similar curve steepness to their asymptotes (Figure 14a). However, the overall maturity curve of female Blue Rockfish is to the left of the maturity curve of Northern Blue Rockfish females, indicating that Blue Rockfish females mature at smaller sizes than Northern Blue Rockfish females. The 95% CIs calculated for the length at 50% maturity of each species do not overlap, indicating that the maturity curves are significant difference between the species. Male Blue Rockfish also mature at smaller sizes than their Northern Blue Rockfish counterparts (Figure 14b).

On average, Blue Rockfish females are 16.7 mm TL smaller at 50% maturity, and 19.4 mm TL smaller at 100% maturity, than Northern Blue Rockfish females (Table 9). When I compared the lengths of 1^{st} , 50%, and 100% maturity with t-tests between species in females, there were significant differences between species for the 50% (p=0.015) and 100% (p<0.001) maturity lengths, but not for the length at 1^{st} maturity (Table 9). These results agree with Figure 14a, where the length-at-maturity curves of the species are closer to each other at 1^{st} maturity but gain separation during the rise to the 100% maturity length. For males, the 1^{st} (p=0.004) and 50% (p<0.001), but not the 100% lengths at maturity were significantly different between species (Table 9).

			а	b		
Sex	Species	n	(±SE)	(±SE)	r^2	p-value
Female	Blue RF	381	-0.117	26.077	0.902	< 0.001
			(0.021)	(4.921)		
	Northern Blue RF	250	-0.107	25.430	0.857	< 0.001
			(0.016)	(3.950)		
Male	Blue RF	40	-0.056	11.825	0.648	0.001
			(0.016)	(3.617)		
	Northern Blue RF	104	-0.060	14.968	0.589	< 0.001
			(0.012)	(2.940)		

Table 8. Blue and Northern Blue Rockfish length-at-maturity curve parameters a and b, with standard error (SE), by sex.

Note: All r^2 values are Nagelkerke r^2 .



Figure 14. Blue and Northern Blue Rockfish: a) female; and b) male length-at-maturity curves. Error bars around the 50% length at maturity represent the 95% CIs.

		Blue R	ockfish		Norther	n Blue Roc	kfish			
				Lower			_	Length at		
		TL	Upper	95%	TL	Upper	Lower	Maturity		
Sex	Maturity %	(mm)	95% CI	CI	(mm)	95% CI	95% CI	Diff. (mm)	t	p-value
Female	1^{st}	183.75	156.48	197.32	195.52	174.53	207.25	-11.77	-1.3588	0.1750
	50%	222.06	214.26	229.73	238.64	232.64	243.96	-16.58	-2.5712	0.0105
	100%	262.37	252.11	282.06	281.76	271.46	299.97	-19.39	-3.9983	< 0.0001
Male	1^{st}	129.67	-4.03	165.51	174.10	125.18	196.26	-44.43	-3.0432	0.0042
	50%	212.09	186.45	231.19	251.22	241.07	263.14	-39.13	-4.2582	0.0001
	100%	294.51	262.66	411.13	328.34	303.65	383.33	-33.83	-1.6767	0.1016

Table 9. Blue and Northern Blue Rockfish estimated length-at-maturity values for the 1st, 50%, and 100% maturities, and two sample t-tests results between the species for each percentage, by sex.

Age at Maturity

The youngest mature female Blue Rockfish was 3 yr old and the youngest mature female Northern Blue Rockfish was 4 yr old. The oldest immature female Blue Rockfish was 6 yr old and oldest immature female Northern Blue Rockfish was 5 yr old. The youngest mature male Blue Rockfish was 4 yr old and the youngest mature male Northern Blue Rockfish was 3+ yr old. The oldest immature male Blue Rockfish was 9 yr old and the oldest immature male Northern Blue Rockfish was 10 yr old.

Logistic regressions best described the relationships between maturity status and increasing age (all p-values ≤ 0.001) for both females and males of each species (Table 10). The shapes of the female maturation curves of Blue and Northern Blue Rockfish are slightly different, because the steepness of rise to asymptote at 100% maturity is different, but the 95% CIs overlap around the age at 50% maturity (Figure 15a).

Similar trends are also seen between the species in the male age-at-maturity curves (Figure 15b). The shapes of the male maturation curves are very different from each other between species but their 95% CI bars also overlap. There was not a clear trend of one species maturing younger than the other, probably because a large amount of uncertainty in the estimates for the Blue Rockfish males because of low sample size.

The t-test results show less than 1 yr of difference between the ages at maturity of the species, for both females and males (Table 11), and none of the ages of maturity were significantly different between the species. This indicates that age-at-maturity data should not be separated to the species, neither for females nor males.

Sov	Spacias	n	$a(\mathbf{I}\mathbf{SE})$	$h(\mathbf{SE})$	n ²	n voluo
Sex	species	11	$u(\pm SE)$	$D(\pm SE)$	I	p-value
Female	Blue RF	381	-1.717 (0.310)	7.902 (1.424)	0.858	< 0.001
	Northern Blue	249	-2.508 (0.380)	11.511 (1.736)	0.764	< 0.001
	RF					
Male	Blue RF	39	-0.680 (0.193)	3.804 (1.156)	0.638	0.001
	Northern Blue	103	-0.868 (0.166)	5.378 (0.910)	0.555	< 0.001
	RF					

Table 10. Blue and Northern Blue Rockfish age-at-maturity curve parameters a and b, with standard error (SE), by sex.

Note: All r^2 *values are Nagelkerke* r^2 .



Figure 15. Blue and Northern Blue Rockfish: a) female; and b) male age-at-maturity curves. Error bars around the 50% age at maturity represent the 95% CIs.

		Blue F	Rockfish		Northe	rn Blue R	ockfish			
Sex	Maturity %	Age (yr)	Upper 95% CI	Lower 95% CI	Age (yr)	Upper 95% CI	Lower 95% CI	Age at Maturity Diff. (yr)	t	p-value
Female	1 st	1.92	0.45	2.66	2.76	1.97	3.19	-0.84	-1.149	0.2513
	50%	4.60	4.22	5.02	4.59	4.41	4.78	+0.01	0.0172	0.9864
	100%	7.27	6.48	8.89	6.42	5.96	7.25	+0.85	0.4341	0.6645
Male	1 st	-1.16	-10.37	1.51	0.90	-1.85	2.22	0.26	0.2628	0.7941
	50%	5.59	3.91	7.42	6.20	5.51	7.23	-0.61	-1.0805	0.2869
	100%	12.35	9.57	21.94	11.49	9.67	15.43	0.86	0.6576	0.5151

Table 11. Blue and Northern Blue Rockfish estimated age-at-maturity values for the 1^{st} , 50%, and 100% maturities, and two sample t-tests results between the species for each percentage, by sex.

Note: A two sample t-test was conducted.

Fecundity

The total fecundity estimates of Blue Rockfish ranged from approximately 12,000 eggs produced by a 5 yr old, 239 mm TL female, to 521,000 eggs from a 35 yr old, 355 mm total length female. The total fecundity estimates for Northern Blue Rockfish ranged from about 10,000 eggs produced by a 5 yr old, 253 mm TL female, to 444,000 eggs produced by an 8 yr old, 326 mm TL female.

Regressions of average total fecundity and female TL of Blue and Northern Blue Rockfishes produced significant power relationships (Table 12). The majority of the fecundity curve of Blue Rockfish was above that of Northern Blue Rockfish (Figure 16) though the curves cross at larger female sizes. This crossing is probably due to the influence of two larger Blue Rockfish females that produced lower than expected fecundity estimates, which suppressed the upper range of the Blue Rockfish lengthfecundity relationship. These two estimates were examined for possible estimation errors, but none could be found and the estimates were kept in the regression.

When I compared fecundity relationships of the species using an ANCOVA, the interaction term between the species group and total length was not significant (p = 0.225). The main effect of TL was significant while species was not (p=0.135, Table 13). These results indicate that these fecundity relationships are not different between the species, and support treating fecundity data of Blue Rockfish and Northern Blue Rockfish the same.

Table 12. Blue and Northern Blue Rockfish fecundity by total length (mm) of the female parameters, *a* and *b*, with standard errors (SE).

Species	n	a (\pm SE)	b (±SE)	p-value	\mathbf{r}^2
Blue RF	106	4.370e-08 (<0.001)	5.081 (0.243)	< 0.0001	0.808
Northern Blue RF	53	3.774e-010 (<0.001)	5.881 (0.601)	< 0.0001	0.653



Figure 16. Blue and Northern Blue Rockfish averaged total fecundity (in thousands of eggs) by total length (mm), by species.

Table13. ANCOVA test results of Blue and Northern Blue Rockfish fecundity per length of the female (TL in mm) between species.

Source	df	F	p-value
ANCOVA			
Total length	1, 157	344.505	< 0.001
Species	1, 157	2.257	0.135
Interaction term	1, 157	1.483	0.225

Note: Fecundity was log10 transformed before tested.

FEMALE BLUE ROCKFISH LIFE HISTORY DIFFERENCES AMONG AREAS

Total length frequency data were compared between the female Blue Rockfish from the geographic regions of HMB (n=100, mean TL= 281 mm), MON (n=173, mean TL= 273 mm) and MOR (n=108, mean TL= 295 mm), before life history trait analyses. The length frequencies of larger fish (>260 mm TL) were visually similar among areas, while the smaller size classes of fish were more variable (Figure 17). Monterey was the area with the largest presence of small fish (<230 mm TL). The Kolmogorov-Smirnov (K-S) tests between area-pairs, corrected for multiple groups, showed that only MON and MOR length frequencies distributions differed significantly from each other (Table 14).

In the age frequency histograms, similar trends were observed in the distributions among areas. Throughout all areas, 8 - 11 yr old fish had the strongest overall presence, and the frequency of fish of older ages (>15 yr) decreased with increasing age (Figure 18). However, MON (n= 173, mean age= 10.6 yr) had the highest frequency of very young fish (2-3 yr) and HMB (n=100, mean age= 9.9 yr) had a larger number of 4-5 yr olds, when compared to the other areas. Older ages in persisted MOR (n=108, mean age= 12.3 yr), with the exception of one fish in MON. The K-S test of age frequencies between area-pairs showed MOR to be different from HMB (Table 15).

Further statistical analyses of the mean lengths or ages were not conducted, because sample collection was not random and therefore such tests would not be valid. These length and age frequency data should not be interpreted as natural trends among these populations or in the fishery.



Figure 17. Female Blue Rockfish length frequency histograms of total lengths (mm), for the study areas of Half Moon Bay (HMB), Monterey (MON), and Morro Bay (MOR).

Table 14. Female Blue Rockfish Kolmogorov-Smirnov (K-S test) of the length frequency distributions, between study area-pairs.

Length frequencies	HMB x MON	MON x MOR	HMB x MOR
K-S test p-values	0.722	0.003	0.159



Figure 18. Female Blue Rockfish age frequency histograms of average ages (yr), for the study areas of a) Half Moon Bay (HMB), b) Monterey (MON), and c) Morro Bay (MOR).

Table 15. Female Blue Rockfish Kolmogorov-Smirnov (K-S test) of the age frequency distributions, between study area-pairs.

Age frequencies	HMB x MON	MON x MOR	HMB x MOR
K-S test p-values	0.132	0.132	< 0.001

Age and Growth

Blue Rockfish from HMB had the highest L_{max} , while fish from MON had the lowest (Table 16, Figure 19a). Because L_{max} is intrinsically linked to the growth coefficient *k*, the trend reversed when *k* values were compared. A higher number of smaller to medium fish collected in MON relative to the other sites may have driven its L_{max} lower. Even though MOR is the site furthest south, its VBGF was between of that of HMB and MON, so no latitudinal trends were obvious.

The confidence ellipse around the VBGF parameters of fish from MOR had more uncertainty in its estimate of k, and overlapped the confidence ellipses of the other areas (Figure 19b). However the confidence ellipses of HMB and MON did not overlap, indicating the growth characteristics of these areas were significantly different from each other, likely because fish from HMB have the largest L_{max}. Generally, all of the L_{max} and k parameters values are fairly close to each other, so geographic differences may not be biologically important.

Area	n	k (±SD)	L _{max} (±SD)	to	CV _{age}
HMB	100	0.218 (0.007)	344.5 (3.851)	0	0.13
MON	173	0.270 (0.011)	312.7 (3.607)	0	0.17
MOR	108	0.253 (0.013)	331.4 (4.165)	0	0.15

Table 16. Female Blue Rockfish von Bertalanffy growth function parameters L_{max} (TL in mm) and k, with standard deviations (SD), by area.

Note: A random effects model that incorporated all three age estimates was used; to was set to zero.



Figure 19. Female Blue Rockfish: a) individual estimated ages and total lengths (mm), with von Bertalanffy growth function (VBGF) curves overlaid; and b) the 95% confidence interval for growth parameters L_{max} and k, or confidence ellipses, for the study areas of Half Moon Bay (HMB), Monterey (MON), and Morro Bay (MOR).

Length at Maturity

The smallest mature female Blue Rockfish lengths collected were 217 mm TL from HMB and MON, and 231 mm TL from MOR. The largest immature female Blue Rockfish was 257 mm TL from HMB, 256 mm TL from MON and 266 mm TL from MOR. The regressions for all areas supported strong logistic relationships between maturity status and total length (Table 17).

Fish from MON matured at smaller sizes and reached the length of 100% maturity before females of the other two areas (Figure 20). The length-at-maturity curve from HMB had the most gradual slope to 100% maturity and HMB fish also had the largest length of 100% maturity. The 95% CIs around the 50% length at maturity overlapped for all areas, which indicates similarity.

The ANOVAs of the lengths of 1st, 50% and 100% maturity revealed no significant differences among the areas (Table 18). This agrees with the previous evidence of overlapping 95% CIs in Figure 20. There is no support for separating length-at-maturity data for female Blue Rockfish among study areas.

		а	b		
Area	n	(±SE)	(±SE)	\mathbf{r}^2	p-value
HMB	100	-0.070	16.566	0.742	< 0.001
		(0.018)	(4.635)		
MON	173	-0.125	27.832	0.906	< 0.001
		(0.030)	(6.780)		
MOR	108	-0.126	30.638	0.867	0.009
		(0.048)	(12.357)		
	2		2		

Table 17. Female Blue Rockfish length-at-maturity parameters a and b, with standard error (SE), by area.

Note: All r^2 *values are generalized* r^2 .



Figure 20. Female Blue Rockfish length-at-maturity curves by study areas, Half Moon Bay (HMB), Monterey (MON), and Morro Bay (MOR). Error bars around the 50% length at maturity represent the 95% CIs.

	HMB			MON			MOR					
Maturity %	TL (mm)	Upper 95% CI	Lower 95% CI	TL (mm)	Upper 95% CI	Lower 95% CI	TL (mm)	Upper 95% CI	Lower 95% CI	df (groups, total)	F	p-values
1^{st}	171.07	200.11	82.34	199.56	210.90	172.57	207.37	229.83	51.59	(2, 378)	1.828	0.162
50%	236.73	248.85	214.14	223.17	231.94	212.24	243.96	255.43	201.31		0.887	0.413
100%	302.39	361.48	282.05	260.01	291.68	247.24	280.55	365.80	266.27		1.673	0.189

Table 18. Female Blue Rockfish estimated length-at-maturity values for the 1st, 50%, and 100% maturities, and modified ANOVA results between the areas.

Age at Maturity

The youngest mature female Blue Rockfish in each area was a 4 yr old from HMB and MON and a 3 yr old from MOR. The oldest immature fish was a 5 yr old from HMB and MOR and a 6 yr old from MON. The logistic regressions indicated significant relationships between average age and maturity status (Table 19).

Female Blue Rockfish from MOR matured at younger ages compared to the other two areas; however there was substantial overlap between the 95% CIs, suggesting little difference (Figure 21). In ANOVA tests, only the age of 100% maturity proved significantly different among areas (Table 20). This single difference may be primarily due to the different shapes of the age-at-maturity curves of the areas. Overall, the age-atmaturity information among the study areas should not be considered different from each other.

Table 19. Female Blue Rockfish age-at-maturity curve parameters a and b, with standard errors (SE), by area.

Area	n	<i>a</i> (SE)	<i>b</i> (SE)	r^2	p-value
HMB	100	-0.986 (0.232)	5.153 (1.351)	0.657	< 0.001
MON	173	-1.608 (0.393)	8.518 (2.017)	0.918	< 0.001
MOR	108	-1.136 (0.358)	5.191 (1.762)	0.827	0.002

Note: All r^2 are generalized r^2 .



Figure 21. Female Blue Rockfish age-at-maturity curves by study areas, Half Moon Bay (HMB), Monterey (MON), and Morro Bay (MOR). Error bars around the 50% age at maturity represent the 95% CIs .
	HMB			MON			MOR					
Maturity %	Age (yr)	Upper 95% CI	Lower 95% CI	Age (yr)	Upper 95% CI	Lower 95% CI	Age (yr)	Upper 95% CI	Lower 95% CI	df (groups, total)	F	p-values
1^{st}	0.57	2.28	-3.97	2.44	3.44	-0.07	0.52	2.32	-6.49	(2, 378)	1.733	0.178
50%	5.23	5.99	4.25	5.29	6.26	4.57	4.57	5.93	3.16		0.708	0.493
100%	9.89	13.79	8.39	8.16	11.33	6.95	8.61	15.51	6.84		5.23	0.005

Table 20. Female Blue Rockfish estimated age-at-maturity values for the 1st, 50%, and 100% maturities, and modified ANOVA test results between areas.

Fecundity

Power regressions indicated significant relationships between female TL and average total fecundity (Table 21), estimated from data of average total fecundity per female Blue Rockfish for 15 females from HMB, 45 females from MON, and 46 females from MOR. The fecundity curve calculated from MOR had the lowest r²-values, and could be due to anchoring within the function caused by data from two larger females that had lower fecundity estimates than would be expected for fish of their size (Figure 22).

The ANCOVA of the fecundity relationships among areas showed an interaction between geographic area and female TL such that the slope of the length-fecundity relationship differed by area (Table 22). However, the low sample numbers available for HMB could be influencing the significant interaction term and causing its slope of the length-fecundity relationship to appear the most different compared to the other locations. Whether the fecundity of Blue Rockfish should be separated by area is inconclusive at this time, but perhaps if more samples were available to represent HMB fecundity, its slope would be similar to that from MON and MOR.

Area	n	<i>a</i> (SE)	<i>b</i> (SE)	p-value	r^2
HMB	15	1.008e-13 (<0.001)	8.201 (0.892)	< 0.001	0.867
MON	45	5.626e-07 (<0.001)	4.627 (0.355)	< 0.001	0.798
MOR	46	3.278e-07 (<0.001)	4.730 (0.377)	< 0.001	0.782

Table 21. Blue Rockfish fecundity by total length (mm) of female parameters, a and b, with standard error (SE), by area.



Figure 22. Blue Rockfish averaged total fecundity (in thousands of eggs) by total length (mm), by study areas Half Moon Bay (HMB), Monterey (MON) and Morro Bay (MOR).

Table 22. ANCOVA test results of Blue Rockfish fecundity per length of the female (TL in mm) among areas.

Source	df	F	p-value
ANCOVA			
Total Length (TL)	1, 103	336.190	< 0.0001
Area	2, 103	8.255	0.0005
Interaction Term	2, 103	8.539	0.0004

Note: Fecundity was log10 transformed before tested.

LIFE HISTORY DIFFERENCES BETWEEN 'BLUE ROCKFISH' POPULATIONS OVER TIME

Age and Growth

The largest female TL from the 1980s period was 462 mm (after conversion from fork length; Echeverria & Lenarz 1984), and the largest female TL from the 2010s was 385 mm. The oldest fish from the 1980s was estimated to be 43 yr old, while the oldest from the 2010s was estimated at 35+ yr old. I calculated VBGFs from 982 female 'Blue Rockfish' from the 1980s dataset and 631 female 'Blue Rockfish' from the 2010s dataset (Table 23). The random effects model could not be used because the 1980s dataset only had one age estimate per individual available. The 1980s VBGF has a higher L_{max} but lower *k* values than the 2010s VBGF, indicating that 'Blue Rockfish' in the 1980s attained larger maximum sizes than fish from the 2010s (Figure 23a). The 95% confidence ellipses limits of the VBGF of the historic and current collections did not overlap (Figure 23b), indicating the growth characteristics of these two populations changed significantly between the time periods.

Table 23. Female 'Blue Rockfish' von Bertalanffy growth function parameters L_{max} and k, with standard deviations (SD), by time period.

Time period	n	k (±SD)	$L_{max}(\pm SD)$	to
1980-1982	952	0.217 (0.004)	381.5 (1.991)	0
2010-2012	631	0.271 (0.005)	323.3 (2.264)	0

Note: Both VBGFs were estimated with a standard, non-linear fit using one age read; to was set to zero.



Figure 23. Female 'Blue Rockfish' a) individual estimated ages and total lengths (mm), with von Bertalanffy growth function (VBGFs) curves overlaid, and b) 95% confidence interval for growth parameters L_{max} and k, or confidence ellipses, for time periods of the 1980 – 1982 (1980s) and 2010 – 2012 (2010s).

Length at Maturity

The smallest mature females from the 1960s and 1980s studies were 220 mm TL (Miller et al. 1967, Wyllie-Echeverria 1987). The largest immature female from the 1960s dataset was 340 mm TL, and 350 mm TL from the 1980s. The logistic regressions support significant relationships between TL and maturity status of the 1960s and 2010s time periods (Table 24, p-values) and the r^2 values ranged from 0.456 – 0.871. The length-at-maturity curve parameters of the 1980s were taken as presented by from Wyllie-Echeverria (1987) because the raw dataset was not available for analyses.

'Blue Rockfish' of the 2010s mature smaller than fish from either the 1960s or 1980s (Figure 24), while the historic maturity curves from the 1960s and 1980s overlapped. The limits of 95% CIs at the 50% maturity length of the 2010s were several centimeters away from overlap with the nearest curve, the 1960s. Because the 2010s length-at-maturity curve was closer to those from the 1960s than those from 1980s, the current 2010s lengths at maturity were tested against 1960s values.

In all cases, the values of 1st, 50%, and 100% lengths of maturity from the 2010s were smaller than the 1960s lengths at maturity however, only the 50% and 100% lengths at maturity were significantly different in a two-tailed t-test (p<0.0001, Table 25). The 50% length at maturity was 41 mm TL smaller for 2010s fish than 1960s fish and the 100% length at maturity was 75 mm TL smaller. All examined information indicates that length-at-maturity data of female 'Blue Rockfish' populations of the 2010s were fundamentally different from the historic populations (1960s, 1980s) and that female 'Blue Rockfish' matured at smaller sizes than previously estimated.

Table 24. Female 'Blue Rockfish' length-at-maturity parameters, *a* and *b*, with standard errors (SE) as available, by time period (Miller et al. 1967, Wyllie Echeverria 1987).

			$D(\pm SE)$	1	p-value
1964-1965 6	545	-0.060 (0.005)	16.333 (1.336)	0.456	< 0.001
1980-1982 1	70	-0.337 (na)	9.509 (na)	0.849	na
2010-2012 6	531	-0.108 (0.012)	25.020 (2.883)	0.871	< 0.001

Note: All r^2 values are Nagelkerke r^2 .



Figure 24. Female 'Blue Rockfish' length-at maturity curves, by time period. Error bars around the 50% length at maturity represent the 95% CIs, as available.

	1960s			2010s					
Maturity %	TL (mm)	Upper 95% CI	Lower 95% CI	TL (mm)	Upper 95% CI	Lower 95% CI	Length at Maturity Diff. (mm)	t	p-value
1^{st}	195.96	207.43	180.40	189.12	174.94	198.79	-6.84	-1.197	0.2318
50%	272.68	276.46	268.75	231.66	227.32	235.95	-41.02	-12.262	<0.0001
100%	349.40	363.82	338.75	274.21	266.95	285.84	-75.19	-20.068	<0.0001

Table 25. Female 'Blue Rockfish' estimated length-at-maturity values for the 1^{st} , 50%, and 100% maturities, and t-test results between each percentage for the time periods 1964 – 1965 (1960s, Miller et al. 1967) and 2010 – 2012 (2010s).

Note: A two sample t-test was conducted.

Age at Maturity

The youngest mature female reported in the 1980s dataset was estimated at 5 yr old and the oldest immature female was 11 yr old (Wyllie Echeverria 1987). A logistic regression between estimated age and maturity status of the 2010s confirmed the fit of the equation (Table 26).

'Blue Rockfish' collected in the 2010s matured at younger ages than fish from the 1980s (Figure 25). The upper limit of the 95% CIs around the age at 50% maturity of 2010s fish was >1 yr younger than the age at 50% maturity estimate from the 1980s. The predicted ages of 1^{st} , 50%, and 100% maturity differed significantly between the 2010s and 1980s (Table 27). The biggest difference in age at maturity between the time periods was found at the 100% age at maturity, with the 2010s population maturing 4.2 yr younger than the 1980s population. The smallest difference was at the age at 50% maturity, with the 2010s population maturing only 1.4 yr earlier than the 1980s. These data indicate not only are the datasets significantly different but, that half of the females of 2010s will be mature 1 - 2 years earlier than they would have matured in the 1980s, and all of the females will be mature 4 - 5 years earlier.

Table 26.	Female	'Blue R	ockfish	' age-at-	maturity	parameter	s a and b ,	with	standard
errors (SE	E) as avai	lable, by	y time p	eriod (W	/yllie Ec	heverria 19	987).		

		а	b		
Time period	n	(±SE)	(±SE)	r^2	p-value
1980-1982	90	-0.802	5.0097	0.937	na
		(na)	(na)		
2010-2012	630	-2.122	9.749	0.820	< 0.001
		(0.258)	(1.179)		

Note: 2010s estimate of r^2 is Nagelkerke r^2 .



Figure 25. Female 'Blue Rockfish' age-at-maturity curves, by time period. The error bar around the 2010s 50% age at maturity represent the 95% CIs.

19	980s		201	0s					
	Age	Upper	Lower 95%	Age	Upper 95%	Lower 95%	Age at maturity		
Maturity %	(yr)	95% CI	CI	(yr)	CI	CI	diff. (yr)	t	p-value
1 st	5	na	na	2.43	1.75	2.85	-2.57	-7.405	<0.0001
50%	6	na	na	4.59	4.42	4.77	-1.41	-4.947	<0.0001
100%	11	na	na	6.76	6.30	7.49	-4.21	-17.665	<0.0001

Table 27. Female 'Blue Rockfish' estimated age-at-maturity values for the 1^{st} , 50%, and 100% maturities, and t-tests results between each percentage for the time periods 1980 – 1982 (1980s, Wyllie Echeverria 1987) and 2010 – 2012 (2010s).

Note: A one sample t-test was conducted.

Fecundity

Only 11 fecundity estimates were available from the 1960s dataset (Miller et al. 1967). The fecundity estimates from the 1960s period ranged from a 255 mm TL female that produced 53,000 eggs, to a 330 mm TL female that produced 234,000 eggs. Both linear and power regressions supported relationships between 'Blue Rockfish' TL and total fecundity; the r^2 -values indicated that a linear relationship best described the 1960s data, while the 2010s data are adequately described with either model (Table 28). The 1960s dataset lacked larger females, which may explain why the linear relationship had a higher r^2 -value than the power equation. The 1960s fecundities plotted well inside the spread of the 2010s estimates (Figure 26). The ANCOVA between the 1960s and 2010s fecundity relationships indicated that there was no significant difference between the time periods (Table 29), despite the large difference in the time of collection.

Table 28. 'Blue Rockfish' fecundity by total length (mm) of the female parameters, a and b, with standard error (SE), by time period.

Time					
period	n	$a (\pm SE)$	<i>b</i> (± SE)	p-value	r^2
1960s	11	9.561e-09 (<0.0001)	5.324 (0.841)	< 0.001	0.817
2010s	159	1.689e-08 (<0.0001)	5.237 (0.245)	< 0.001	0.744

Note: Only the power length-fecundity parameters are presented.



Figure 26. Female 'Blue Rockfish' averaged total fecundity (in thousands of eggs) by total length (mm), by time period.

Table 29. ANCOVA test results of 'Blue Rockfish' fecundity per length of the female (TL in mm) between time periods.

Source	df	F	p-value
ANCOVA			
Total length	1, 168	44.497	< 0.0001
Time period	1, 168	0.036	0.850
Interaction term	1, 168	0.023	0.880

Note: Fecundity was log10 transformed before tested.

DISCUSSION

LIFE HISTORY DIFFERENCES BETWEEN THE BLUE AND NORTHERN BLUE ROCKFISH

The overabundance of one 'Blue Rockfish' species in a dataset could affect the outcome of life history parameter comparisons over time, if the composition of species in the datasets changed across the time periods. The catch composition of the 2010s samples was skewed to Northern Blue Rockfish in HMB and Blue Rockfish in MON, while 'Blue Rockfish' of either species were scarce in MOR and required focused sampling effort to bring up the catch numbers. These generalities about the species composition in these areas agree somewhat with other data from research fishing surveys that also reliably separate the two 'Blue Rockfish' species (Table 1).

Burford et al. (2011*b*) also found that the proportion of Northern Blue Rockfish increased with latitude, but this trend was not true for young-of-the-year 'Blue Rockfish,' which had high variability of occurrence in both species, indicating highly variable recruitment success along the central coast (Burford et al. 2011*a*). The different compositions of the two 'Blue Rockfish' species among the study areas in the 2010s could be related to variable recruitment success and habitat availability among the sample areas. The differing amounts of Blue and Northern Blue Rockfish found in the study areas is not of much concern for the time period comparisons, because this composition represents natural variation. Natural variation in the 'Blue Rockfish' species composition throughout central CA was probably present in the past datasets as well and it is unlikely that one 'Blue Rockfish' species has ever dominated over the other because they occupy similar ecological niches yet co-occur frequently (Starr et al. 2010, Burford et al. 2011*b*).

Certain studies enable comparisons of the life histories of other closely-related rockfish species, such as the Gopher and Black-and-Yellow Rockfishes (*S. carnatus* and *S. chrysomelas*; Wyllie-Echeverria 1987, Lea et al. 1999), and life histories were similar between such species. However, comparisons of the life history characteristics of *all* rockfish species within a recently separated cryptic species complex are not always possible. A number of eastern North Pacific rockfishes recently identified as cryptic species occur together, including the Vermilion and Sunset Rockfishes (*S. miniatus* and *S. crocotulus*; Hyde et al. 2008), two genetically distinct Rougheye Rockfishes (Gharrett

et al. 2011), two Dusky Rockfishes (*S. ciliatus* and *S. variabilis*; Orr and Blackburn 2004) and of course, the two 'Blue Rockfish' types (Burford et al. 2011*a*, *b*).

Knowing the differences between the life history parameters of all species within a cryptic species complex is important to managers. Differential harvest impacts to one species in a cryptic complex would be difficult to remedy if those species were managed together and targeted equally by the fishery. Species difficult to identify in the field and that readily co-occur could lead to the overfishing of species with the more harvestsensitive life history characteristics (Gharrett et al. 2011). In such situations, a rockfish cryptic species complex should be managed based on the slowest-growing, latestmaturing member with the lowest reproductive output. The initial use of conservative life history values when managing a cryptic species complex would mitigate problems associated with cryptic complexes and long-term harvest yield losses resultant from the strict moratoria that follow declaring a stock overfished. This study shows how similar the life history parameters within the 'Blue Rockfish' cryptic species complex can be, and that the differences seen here in the life history parameters would not be worrisome, but offers management the choice of species-specific or species-combined values.

Growth among rockfish species is highly variable, as the adult maximum sizes vary widely between species, from tiny Shortbelly Rockfish, *Sebastes jordani*, to massive Shortraker Rockfish, *S. borealis* (Love et al. 2002). However, growth parameters between some closely related rockfish species that are of similar adult sizes are very similar to each other (Johns and Avise 1998), such as between Gopher and Black-and-yellow Rockfishes, (*S. carnatus* and *S. chrysomelas*; Lea et al. 1999), Black and Yellowtail Rockfishes, (*S. melanops* and *S. flavidus*; Tagart et al. 2000, Wallace et al. 1989), or 'Blue' and Widow Rockfishes, *S. entomelas* south of 43⁰ Latitude (Laidig et al. 2003, Williams et al. 2000). The growth characteristics of the female Blue and Northern Blue Rockfishes were significantly different, and Northern Blue Rockfish females obtain larger sizes for a give age. Males showed trends similar to the females, but fewer samples precluded the ability to detect a difference in growth between the two species. My comparisons of the VBGF of Blue and Northern Blue Rockfishes agree with other growth studies of closely related, similarly sized rockfishes.

Northern Blue Rockfish and Blue Rockfish matured at the same ages (4.60 - 4.59)yr for females, 5.59 - 6.20 yr for males), but at significantly different sizes because Northern Blue Rockfish attain larger sizes for a given age. This may indicate that an energy allocation trade-off is occurring between the growth and reproductive output of these closely related species. These trade-offs between investment of energy resources in somatic growth or reproductive output can manifest in an increase in the number of offspring in smaller-bodied species of fish (Gunderson 1997, Reznick & Ghalambor 2005). While this trade-off is more often seen when smaller-bodied populations of the same species produce more offspring per female than larger-bodied populations, it could be possible that differences in egg production of these two closely related rockfish species occur as a result of such an energy trade-off. Female Blue and Northern Blue Rockfish mature at the same age. However, because of their growth characteristics, female Northern Blue Rockfish are slightly bigger than female Blue Rockfish at this age, and this translates into their larger length at maturity. Despite being larger bodied, female Northern Blue Rockfish produce slightly *fewer* eggs than Blue Rockfish females at the same body size. This agrees with the growth-reproduction trade-off theory and also with Sogard et al. (2005), showing that rockfish of older ages produce more eggs than younger fish of the same species, because Blue Rockfish will be slightly older than a Northern Blue Rockfish of a give size. The growth vs. reproduction trade-off theory may be applied to this situation because these species are so closely related genetically.

FEMALE BLUE ROCKFISH LIFE HISTORY DIFFERENCES AMONG AREAS

Many studies of Californian nearshore recreational species have shown that adjacent areas can exhibit variation in the 'Blue Rockfish' length compositions (Miller & Geibel 1973, Mason 1998, Stephens et al. 2006, Starr et al. 2010). The length and age frequencies of female Blue Rockfish from MOR differed significantly from the other areas. This probably reflects the lack of smaller and younger fish (170-220 mm TL) in the MOR samples, which were present in the HMB and MON compositions. Different length and age frequencies may reflect consistent recruitment success in the HMB and MON areas that was not realized in MOR (Laidig 2010). My samples were gathered over

a period of two years and from multiple locations within each study area and so should represent natural size composition differences among populations. Knowing small-scale differences in size and age demographics among local areas such as these would be very beneficial for stock assessment purposes (Key et al. 2008).

Growth characteristics can vary over small geographic scales, and these differences have been attributed to variable prey availability, temperatures and fishing pressures (Parrish et al. 1985, VenTresca et al. 1995, Kronlund & Yamanaka 2001, Yoneda & Wright 2004, Hamilton et al. 2011). Blue Rockfish that settled into the MON area have the opportunity to produce the highest growth parameters within the central CA region, because the nearshore habitat in the MON area is near an epicenter of nearshore upwelling and primary production that could easily support increased growth rates (Ryan et al. 2005). Instead, Blue Rockfish females from MON had the lowest L_{max} of all the regions examined.

Kronlund & Yamanaka (2001) and Yoneda & Wright (2004) found decreasing growth parameters in populations from areas adjacent to fleet harbors as the fishery developed and continued harvesting from those areas more often than grounds further from the established harbors. Monterey supports one of the oldest harbors in central CA and the highest number of CPFV recreational fishing days in comparison to other areas of this study (Karpov et al. 1995). This constant fishing pressure could be driving the larger changes in the growth characteristic seen here, in comparison to the other areas. Overall, these geographic comparisons of growth were over a fairly small scale when compared to the distribution considered for Blue Rockfish stock (Key et al. 2008) and should be pooled to estimate population-wide values.

Other studies reporting length-at-maturity differences within a marine fish species usually show an increase in length at maturity with increases to the latitude of collection site along the east North Pacific coast (Abookire & Macewicz 2003, Allen et al. 2006). This pattern of fish maturing at larger sizes at higher latitudes is also seen in 'Blue Rockfish' life history values over large geographic scales. Length-at-maturity values estimated from Oregon (F50%: 309 mm fork length; McClure 1982) were larger than those recorded from California (F50%: 272 mm TL, Miller et al 1967; F50%: 282 mm TL, Wyllie-Echeverria 1987). However, no significant differences were observed in the

length of maturity among adjacent areas for this study; in fact the most southerly site had the largest lengths at maturity. The expected latitudinal trend was probably not seen due to the relatively small increases in latitude, compared with the large geographic differences between the McClure (1982) and Wyllie-Echeverria (1987) studies.

Age-at-maturity differences are rarely observed over small spatial scales in rockfishes (Wyllie-Echeverria 1987), except in cases where large differences in fishing pressure also occur among those areas (Kronlund & Yamanaka 2001, Yoneda & Wright 2004). I found no difference in the age-at-maturity values among geographic regions, though the amount of uncertainty around the age at 50% maturity varied widely with region. As described by Trippel (1995), minor variations in age-at-maturity are typically natural so their comparatively slight magnitudes may be considered reflective of stable conditions.

Without a well-known co-varying environmental factor such as temperature or food availability, fecundity would not be expected to vary spatially among adjacent geographic areas. Eldridge & Jarvis (1995) found some spatial variation in Yellowtail Rockfish, Sebastes flavidus, fecundities when comparing the fecundities of younger fish but, these differences were not seen in older fish. A significant interaction between length of the female and collection region prevented examination of the main factors. The significant interaction indicates the relationship between the total length of the female and the number of eggs she can produce varies depending on her collection location. However, the fecundity to length relationship that was the most distinct from the others was from HMB, the area with the lowest sample number. It is likely that the low sample numbers prevented the fecundity relationship from HMB from being accurately described, which could mean this difference was not real. However, if the interaction was ignored and removed from the model, the factor of area was shown to be insignificant (p=0.700), as suggested by the similarity of the fecundity relationships from MON and MOR females. Though the fecundity relationship of HMB was statistically different from the other areas, I recommend that the fecundity estimates of the areas be pooled so that other trends may be examined. When the data is pooled and the sample numbers increase, the relationship is robust and could be used to represent Blue Rockfish, at least for the study region within central CA.

'BLUE ROCKFISH' LIFE HISTORY DIFFERENCES BETWEEN POPULATIONS OVER TIME

I identified changes in the life history characteristics of female 'Blue Rockfish' between two time periods. Before other drivers of these changes are discussed, it is worth examining how changes in fishery regulations over time may have affected the pool of available samples. Any sport regulations not in place during past collections may have caused bias in my sampling design, which could lead to the false-positive interpretation that my life history estimates are significantly different from the past estimates. Compared to the sport harvest regulations enforced during the historical studies, regulations applicable to 'Blue Rockfish' have become more restrictive concerning fishing gear, allowable fishing depths, open areas, and other particulars, such as angler daily bag limits and seasonal closures (Key et al. 2008).

Historically, sport anglers collect temperate, reef-associating rockfishes either by hook-and-line or spear fishing. Most of the 'Blue Rockfish' sampled in the past studies came from the CPFV or skiff fisheries that operated throughout central CA from the 1960s – 1980s (Miller et al. 1967, Karpov et al. 1995). Replicating the collection tools used in the past was relativity easy, as terminal fishing tackle and capture methods have not changed much since the researchers of the past studies collected fish. The fishing gear restrictions for the nearshore rockfish recreational fishery included a reduction in the number of hooks on the terminal fishing tackle down to two hooks in 2001 (Key et al. 2008). The reduction in hook number should not have a selective effect the pool of 'Blue Rockfish' available to be captured, so effects of gear restrictions on my sample pool compared to the past studies should be negligible.

Recent recreational harvest depth restrictions could bias a sample pool of rockfishes available for collection because many rockfish species experience ontogenetic shifts in habitat use when juveniles move to deeper waters as they reach maturation (Love et al. 2002). In rockfish species that move to depths deeper than the current recreational depth limit, fish taken from recreational catches would be more likely to include smaller, younger, and immature individuals due to restricted access from the entire population. Most areas sampled in the 2010s via recreational anglers were limited to 54.9 - 73.2 m bottom depth (180 to 240 ft). However, because 'Blue Rockfish' are a nearshore, shallow reef-associated group, adults are most often found in \leq 55m of water (Love et al.

2002). Therefore, the reduction in water depths open to recreational fish to \leq 73.2 m in 2001 (Key et al. 2008) is not likely to affect the comparisons of temporal shifts in life history values of 'Blue Rockfish.'

Area closures, adopted in part to halt the multi-species decline in west coast rockfish stocks, may have introduced sampling error to the 2010s sample pool by effectively denying access to a portion of 'Blue Rockfish' population. The majority of the central California Marine Protected Areas (MPAs) was established in 2007. However the coverage of these areas is small compared to the amount of nearshore areas open to recreational fishing (Gleason et al. 2006, Starr et al. 2010). Therefore, any sampling error or bias introduced into my sampling pool because of these area closures were considered negligible, especially since the 'Blue Rockfish' they protect make up only a small portion of the larger population, and because 'Blue Rockfish' are relatively a mobile, schooling species capable of moving beyond MPA boundaries on a daily basis (Miller & Geibel 1973, Hartmann 1987, Jorgensen et al. 2006). Overall, it does not appear that recent increases to the sport regulations have greatly affected the collections of fish used in the contemporary estimations of life history and that differences seen in the life history parameters thorough time come from other sources.

Dramatic shifts in 'Blue Rockfish' growth characteristics, and length- and age at maturity were observed between the historic and current populations. However the major question remains: Are these shifts due to fisheries-induced evolution (FIE) or other possible drivers, such as natural plasticity due to environmental influences (Kraak 2007), or increased energy allocations per individual in response to density-dependent preyreleases (Rose & Cowan 2000)? When considering the possible causes, the direction and magnitude of the traits shifts are key to interpreting the mechanism of change. The drivers behind plastic trait changes in fish are all associated with the amount of resources available per individual, regardless of the reason behind food variability. An increase to the amount of food per individual would lead to faster-growing fish expected to be larger at maturation, and whose larger bodies would support earlier reproduction. Conversely, if there was somehow less food per individual, growth and lengths at maturation would be expected to decrease, and ages at maturity would increase because additional years would be required for those fish to meet the energetic demands of reproduction. Because

the maximum size, length- and age at maturity have all decreased in 'Blue Rockfish,' their trait change directions disagree with the trait change outcomes expected of plasticity, driven by either environmental variability or density-dependence.

Assuming that this system is more complex than the previous simplistic explanation, plasticity could explain the trait changes seen in this thesis, if the oceanic environment fluctuated concurrently. Plasticity in life history traits occurs when a single genotype can express as more than one phenotype in a population, serving as a way for a population of organisms to cope with environmental variation. While these phenotypic differences may or may not be permanent throughout an individual's life and are not heritable, they would certainly influence the life history parameters estimated for a population at any given time point (Price et al. 2003). Values estimated from populations that experienced similar oceanic regimes should have the most similar life history parameters.

Marine fishes of the nearshore environment off central CA experience fluctuating ocean temperature and productivity on seasonal, annual, and decadal cycles (Wolter & Timlin 1998, Chavez et al. 2003, Wolter & Timlin 2011). The 'Blue Rockfish' life history data of the 1980s were estimated from fish that experienced a shift to an increasingly warmer Pacific Decadal Oscillation (PDO) phase and a strongly warm phase of the El Niño – Southern Oscillation (ENSO). However, the 'Blue Rockfish' populations of the 1960s and 2010s experienced the cooler phase of the ENSO cycle (e.g. La Niñas) and cooling PDO phases. VenTresca et al. (1995) illustrated a negative somatic and reproductive response in 'Blue Rockfish' to warm ENSO phases, which indicate that changing ocean conditions can illicit rapid changes to 'Blue Rockfish' life history traits, and likely reflect responses to reduced prey abundances.

The greatest evidence that these changes to the life history parameters of 'Blue Rockfish' are driven by something other than environmental variability can be found by comparing the two historic estimates (1960s vs. 1980s), and the oceanic regimes those fish experienced, to each other. Estimates from Miller et al. (1967) should have described fish that matured at a larger size than the fish of Wyllie-Echeverria's (1987) study because of increased food per individual available in the 1960s during the cool PDO and ENSO phases experienced. Instead, Miller et al. (1967) reported fish that

matured <20 mm TL smaller than the 1980s fish at the 50% length at maturity. This <20 mm difference at the 50% maturity length should represent the variation attributable to environmental influences, though in the wrong direction.

Life history trait values of growth and maturity of 2010s fish would be expected to be higher in comparison to 1980s values, due to increased food per individual fish as a result of the increased primary productivity associated with cooler ocean regimes during the most recent decade. Instead, few of the fish of the current population ever reached the L_{max} estimated for 'Blue Rockfish' of the 1980s, and growth and maturation were significantly lower than estimates from both historical time periods. There was a >40 mm difference in TL between estimates of the 50% length at maturity for the 2010s and the 1960s samples, which was time period that experienced the most similar environmental conditions to the current population. At 100% maturity, this difference was even greater, 75 mm TL. This change is more drastic than differences previously attributed to yearly or decadal environmental influences (i.e. natural plasticity).

Wyllie-Echeverria (1987) observed slight deviations in other rockfish species ageat-maturity values across years. She reported +/- 1 yr difference in the age at 50% maturity of female Yellowtail Rockfish and male Chilipepper Rockfish, *S. goodei*, among sampling years, however these ages returned to the overall 50% age-at-maturity estimation in the last year-to-year comparison. Wyllie Echeverria (1987) attributed these age-at-maturity variations to trait plasticity forced by environmental variability, because the values fluctuated in the same direction for both species during the same years. In comparison to 2010s values, the 50% age-at-maturity decline by -1.41 yr from the 1980s indicates that cohorts now mature 1 - 2 years earlier than previously estimated, with 50% of the population mature by 4 - 5 yr of age in the 2010s, compared to the 6 - 7 yr of age in the 1980s. These differences increase when the age at 100% maturity is examined, which is currently >4 yr earlier than observed for the 1980s population. The magnitude of this shift in the age at maturity is much larger than any previous changes attributed to environmental plasticity; therefore this variation comes from another source.

Density-dependent competition for food resources could be an alternate explanation to the life history changes seen here. When the density of conspecifics affects the amount of resources available per individual of that group (i.e. competition for

the same limited food resources), the population's life history traits adjust following fluctuations in the population's abundance, and often decrease as population abundance increases (Brown 1995, Rose & Cowan 2000). 'Blue Rockfish' feed on mostly pelagic and planktonic prey resources supplied by favorable oceanic conditions (VenTresca et al. 1995, Love et al. 2002). The amount of energy required by the 'Blue Rockfish' population is dwarfed by amount of energy available to them, and changes in prey availability are not likely to be influenced by 'Blue Rockfish' abundance (Chavez et al. 2003). However, even if the number of planktivorous predators limited the amount of prey per fish, density-dependence is still unlikely to explain the trait changes observed in this study. The 'Blue Rockfish' are recovering from being overfished (Key et al. 2008) and are currently at ~30% of their unfished abundance. The life history values estimated before overfishing occurred should have represented fish that grew and matured smaller and younger compared to the population of today, because of higher 'Blue Rockfish' abundance and higher intraspecific competition for resources. Instead, my data showed the opposite, with fish from the 2010s being smaller, growing slower, and maturing earlier during a time of low population abundance. Therefore, density-dependent effects were eliminated as a contributor to the observed life history changes, and thus FIE is the most parsimonious explanation.

'Blue Rockfish' mean lengths have declined since the 1970s (Karpov et al. 1995, Mason 1998, Lea et al. 1999, Starr et al. 2010) and have not recovered despite increasing recreational restrictions (Key et al. 2008). Increased fishing mortality can cause changes to growth characteristics of a stock by removing the benefit of escaping predation by growing large, because humans are the predators that target adults (Reznick et al. 1997, Conover & Munch 2002, Conover 2007, Edeline et al. 2007, Jørgensen et al. 2009). Changes in growth characteristics found here are more similar to those found in FIE studies where increased harvest mortalities cause individuals of fished stocks to grow slowly and remain small. The shift in the selection gradient from low adult mortality in natural environments to high adult mortality in harvested stocks demands conformity to the new mortality patterns, and fish whose predecessors have traded growth for earlier reproduction have increased evolutionary fitness over those that mature later. Additionally, the shapes of the 1960s and 2010s length-at-maturity curves were somewhat different. The curve of the 2010s dataset had a steeper slope from lengths at 1st to 100% maturity, though the size at 1st maturity remains the same. The smallest mature female 'Blue Rockfish' reported in either previous study was 219-220 mm TL (Miller et al. 1967, Wyllie-Echeverria 1987) and this range held true for this study as well. The consistency in observed length at 1st maturity indicates that there may be a minimize size before reproduction is possible in 'Blue Rockfish.' The 2010s population has the lowest length at 100% maturity of the three time periods and the steepest slope, which indicates that the range of lengths over which 'Blue Rockfish' mature is decreasing. This population may be squeezed between the physiological limit of minimum reproductive size and the size at which fishing increases adult mortality. If this trend of decreasing length at maturity persists in future generations, 'Blue Rockfish' length at maturity could be so forced by fishing mortality that 100% of fish that reach 220 mm TL become mature.

A decrease in the age at maturity in a stock indicates a population stressed by overfishing (Trippel 1995). Earlier maturation would enable a population to replace themselves at a rate closer to fisheries removal rates. However, this trend of decreasing age at maturity contrasts with rockfish life history strategy in natural settings, which favors building up body condition before reproduction so future reproductive success is assured. Younger and smaller females shouldering a greater portion of the larval production may suit a harvest-driven environment briefly but may not be the best strategy in the long term. Early maturation could lead to poorer body conditions in mothers and/or poor quality larvae. This would be risky for both generations' survival and evolutionary fitness, especially in a rockfish that should display increased maternal investment in larvae survival as maternal age increases (Trippel 1995, Law 2000, Berkeley et al. 2005).

The fecundity-length relationship of the 2010s is indistinguishable from that of the 1960s. An organism's evolutionary fitness is increased if the number of offspring that survive after its death is increased through adaptations (Stearns 1992). Even though fish from these time periods experienced similar ocean conditions, it is surprising that the relationship was so conserved across such a large time period (+45 yr), and these results

are contrary to FIE theory predictions. Fecundity per length of a female would be expected to increase after fishing impacts, with either more offspring per reproductive cycle or an increase of reproductive cycles per year (Rjinsdorp 1991, 1993, Reznick et al. 1997). Because neither trait plasticity nor FIE explains the uniform fecundity relationship, I believe the reason may lie in their high natural larval mortality rate.

Mortality drives the evolution of life history traits (Stearns 1992). Individual rockfish larvae face low odds of survival from parturition to successful settlement in the nearshore as young-of-the-year. Until settlement, rockfish larvae are almost completely dependent on favorable ocean conditions for survival, after the energy reserves bequeathed from the mother run out. Therefore, rockfish species experience many years with extremely low recruitment success and the occasional year of high success every decade or so (Love et al. 2002). To have an evolutionary advantage in this challenging system, the rockfish lineage must have found an optimum between the minimum size of successful larvae and maximum number of larvae per mother. The physical amount of volume within a mother rockfish of a certain size constrains maximum number of successful larvae she can house at that size. By adapting their life history traits, rockfish have buffered against complete recruitment failure most years and yet, are still able to capitalize in years with benevolent conditions. If these constraints of rockfish fecundity are taken into consideration, it is possible the length-fecundity relationship was already highly adapted against high mortality events and is more conserved in its value, while the other life history trait changes in female 'Blue Rockfish' are examples of FIE theory.

A conundrum persists in studies that view 'fisheries as a large-scale experiment on life-history evolution' (Rijnsdorp 1993). FIE studies of wild stocks can only imply causation to fishing, not eliminate all other possible drivers, because they are observations of nature, not manipulated experiments. There are elegant laboratory and *in-situ* manipulative experiments that have demonstrated that harvested fish populations evolve life history traits rapidly, in directions counter to the selective mortality forces (Reznick et al. 1990, Conover & Munch 2002, Reznick & Ghalambor 2005, Edeline et al. 2007). These studies execute their purpose exactly, to isolate and describe a process and its signals that might otherwise have been dampened or unseen in natural settings due to confounding influences. However these manipulative examples are not used as

undeniable evidence that fishing can influence fish life histories, because it is difficult to advocate the use of extrapolated results from controlled, isolated experiments onto wild stocks that exist in large and complex environments. The next step in FIE research will be examining the genetic drift in gene regions that influence maturity and life history trait expression. Until all the associated mortality pressures, environmental variables, and genetic heritability of life history traits are known, it is unlikely that a scientific consensus will be reached regarding whether phenotypic plasticity or genetic changes are the most important mechanism to FIE life history changes (Browman et al. 2008, Kuparinen & Merilä 2008, Jørgensen et al. 2008).

Many researchers have promoted buffering fish stocks against undesirable genetic drift because FIE trait changes may persist even after the cessation of overfishing due to a lack of genetic diversity, which may remove the population's ability to return to previous trait values (Law 2000, Conover & Munch 2002, Coltman et al. 2003, Reznick & Ghalambor 2005). If managers of living resources are concerned with the trend of wild populations 'changing' their biological characteristics to 'keep up' with human fishing selection, then the only course of action is to preserve the genetic of the larger-growing individuals by ensuring their survival and contribution to the future genetic pool. For 'Blue Rockfish,' and rockfishes in general, which may not survive capture without knowledgeable handling and release techniques (Jarvis & Lowe 2008), one0 way to preserve the genetics of big fish is to put MPAs in place before overfishing occurs. This would preserve the genetic variation naturally present in an unfished population, like a genetic bank that can buffer against genetic drift. Both designated MPAs and de facto areas that are lightly fished due to their isolation should contain increased genetic/ life history trait diversity when compared to areas that display directional trait changes.

Human impacts on wild populations are pervasive and undeniable, as more study cases are being recognized in various forms and via different mechanisms (Palumbi 2001). Without acknowledging the impacts our selective harvesting leaves on a wild population, we set up ourselves for future disappointment and the results can lead to a persistent decrease in available yield for future generations. Only by realizing the power our choices hold for wild populations can we effectively mitigate and possibly reverse these trends, if we so desire.

MANAGEMENT RECOMMENDATIONS

I recommend the use of species-combined reproductive life history characteristics of Blue and Northern Blue Rockfishes for the purposes of stock assessment models and management efforts, because the sizes of any differences found between life history values of the species were small. The species-combined traits presented here could be used to represent updated estimates of 'Blue Rockfish' for the early 2010s time period. The historical values for all 'Blue Rockfish' life history studies prior to 2005 are an unknown composition of the two species that will not be resolved to species, unless those studies also collected some type of genetic material from each individual and follow through with post hoc genetic typing of each sample. Any future species-specific fisheries research conducted on 'Blue Rockfish' would either have to consider substantial training for project personnel to ensure proper field identification or include genetic identification via tissue samples as part of the collection. Thus, I recommend against efforts to separate the 'Blue Rockfish' data to species unless a specific need is present. Using species-combined life history values allows the use of all 'Blue Rockfish' data, past, present or future, regardless of the attention paid to correct species identification at the price of only a slight loss in accuracy.

I would also recommend that the 2010s species-combined values of length at maturity, age at maturity, and growth characteristics presented here replace the past values for future fisheries science work with these species. Many important management decisions are based on stock assessment model projections and so current models should use values that most accurately describe the current condition of the stock. By using my values, the replacement and growth capacities of the models will be closer to the true, recent population values and the population can be more effectively managed. Because the length at maturity and age at maturity are smaller and younger than previously thought, the actual spawning biomass of the population should be larger than estimated. Most 'Blue Rockfish' enter the fishery after they reach 240 mm TL, and this new length-at-maturity estimate would indicate most of these fish should be mature and have produced at least once before fishery-based mortality occurred. Thus, the 'Blue

Rockfish' stock health should be better than previously thought. The maximum 'Blue Rockfish' harvest yield cannot be realized unless these life history values are used to project acceptable biological catches in upcoming stock assessments. However, it should be cautioned that the life history values presented here most accurately represent the 'Blue Rockfish' populations of central California at present, and may differ from other 'Blue Rockfish' populations of different latitudes and/or populations that have experienced differing levels of past fishing pressures.

Finally, the life histories of other *Sebastes* spp. should be investigated for changes following fishing impacts. Key signals can be checked before a life history comparison study is undertaken. Obviously, a rockfish stock should show evidence of decline due to fishing removals and have available information of their life history available prior to the height of the fishing impacts. Also, the methods used to gather that past life history information must be clear, reliable and reproducible (which discounts any age-at-maturity or growth information from scale-based ages). An indicator of a stressed population useful in tracking changes to population size are declines of mean lengths over time from a defined fishing area. For 'Blue Rockfish,' a persistent decline of mean lengths was observed in sport caught fish over a long time period (Mason 1998), and the same population of 'Blue Rockfish' never recovered the larger mean lengths, though their population abundance has rebounded (Key et al. 2008). A continued depression of mean lengths concurrent with population recovery is a helpful indicator that a population may be responding to overfishing with trait changes. Another indicator of a stressed population is a change to the age at maturity (Trippel 1995) but establishing age at maturity is quite an investment of resources and time. Therefore, an examination of available mean length information is a much quicker and more cost effective preliminary check of possible FIE influences before a full-fledged study is initiated.

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