SPATIAL AND TEMPORAL VARIATION IN GROWTH RATE OF BLUE
ROCKFISH (*SEBASTES MYSTINUS*) IN NEARSHORE CENTRAL CALIFORNIA
DETERMINED USING A PHYSIOLOGICAL BIOMARKER

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TITLE:

Spatial and Temporal Variation in Growth
Rate of Blue Rockfish (S*ebastes mystinus*) in
Nearshore Central California Determined
using a Physiological Biomarker

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ABSTRACT

Spatial and Temporal Variation in Growth Rate of Blue Rockfish (S*ebastes mystinus*) in

Nearshore Central California Determined Using a Physiological Biomarker

Ellie Brauer

Identifying areas of high fish population productivity is crucial for protecting

habitats essential to fish growth and reproduction and, ultimately, for achieving

sustainable fisheries. Historically, evaluations of habitat quality have relied heavily on

linking spatial variation in fish abundance to environmental parameters such as substrate

category, depth, or bathymetry. That approach, however, assumes that areas of high fish

abundance best support growth and reproduction of a species and thus may fail to detect

spatial or temporal variation in population attributes, such as somatic growth rate, which

can be central to recruitment success and survival. In this study, we employed a novel

physiological approach using the hormone insulin-like growth factor-1 (Igf-1) as a blood-

based 'biomarker' for recent growth rate to determine patterns of spatial and temporal

variation in growth of Blue Rockfish (*Sebastes mystinus*) along nearshore central

California, USA. Blue Rockfish were sampled between 2016 and 2018 from two different

regions ~60 km apart on the central coast of California: the Piedras Blancas region and

the Point Buchon region. In each region, sampling was conducted in a Marine Protected

Area (MPA) and in an adjacent non-protected area. In all years, Blue Rockfish in the

Piedras Blancas region had consistently higher growth rates compared to the Point

Buchon region. Yearly differences in average Igf-1 values were similar for fish collected

from the Piedras Blancas and Point Buchon regions, suggesting that broad-scale, annual

variation in food availability affects Blue Rockfish growth rates similarly across this geographic extent of the central California coast. While no consistent differences in Igf-1 were observed for fish sampled at protected MPA and adjacent non-protected areas, spatial variation on the scale of 500 m was observed across some sites sampled on the same day, suggesting that Blue Rockfish growth can vary substantially across even relatively constricted habitat locations. Temporal variation in growth rates was also observed on the scale of < 1 month across some sampling sites. These findings illustrate how Igf-1 can provide a tool for identifying recent growth rate variation in wild Pacific rockfishes with the potential to improve management of economically and culturally important nearshore marine fishes.

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1. INTRODUCTION

Attaining sustainable fisheries in California is dependent on our ability to accurately assess the quality of habitat, fish population productivity, and the efficacy of fisheries management practices such as marine protected areas (MPAs) (Jennings and Kaiser, 1998). And yet, despite the general acceptance that habitat variation influences the productivity of marine fish stocks, identifying high quality and essential habitats remains a challenge for most marine species. Habitat quality has historically been assessed by relating an index of fish abundance to environmental characteristics such as temperature, depth, bathymetry, or substrate type (e.g., Meng et al., 2002; Rooper and Martin, 2009; Young and Carr, 2015; Carrasquilla-Henao et al., 2019). Efforts are then made to link observed variation in the density, composition, or richness of marine fishes either to substrate categories (i.e., rocky reef, sandy bottom) or multivariate indices to ascertain locations of high-quality habitat (Rubec et al., 1998; Diaz et al., 2004; Young et al., 2010). In these approaches, however, what constitutes a habitat category is often dictated by the resolution of habitat mapping efforts used, and conclusions are commonly based on the assumption that areas of high fish abundance best support growth and reproduction of those species. And yet, relationships between habitat conditions and fishery productivity are complex (Thorson et al., 2021), and habitats that are most productive may not always be the areas with the highest fish abundance. Bridging the gap between mapping physical habitat parameters and identifying essential fish habitat will thus require integrative approaches capable of linking habitat directly to processes that shape marine fish population productivity, such as growth and reproduction.

Measurements of somatic growth rate can be a valuable metric for assessing population productivity in marine fishes. Growth rate impacts survivorship and has been shown to be an important predictor of juvenile recruitment success and survival (Duffy and Beauchamp, 2011; Beamish and Neville, 2021). In some targeted species, individual growth rate has been shown to be the strongest indicator of a population's resiliency to exploitation since higher growth contributes directly to the available consumable biomass (Caselle et al., 2010; Denney et al., 2002). Growth rate can also be positively associated with reproductive output, as fecundity is often a function of size in marine fishes (Roff, 1983; Vallin and Nissling, 2000; Birkeland and Dayton, 2005; Mehault et al., 2010).

Despite somatic growth rate being a critical component in fish population dynamics, measuring growth rates in wild fish is often time consuming and expensive, and growth rate data is only rarely used when identifying habitat quality. One commonly used method for obtaining growth rate data is the capture-mark-recapture technique, which requires the tagging of large numbers of fish and then the subsequent recapture of those same individuals (Pradel, 1996); such recapture can be particularly challenging in marine systems where habitat areas are commonly unconstrained. An alternative method for measuring growth rate is the use of otolith ear bones; otoliths are extracted from a fish, and the age of the fish is then determined by counting the annuli on the otolith (Campana, 1990). However, otolith studies are time consuming and terminal for the fish. In addition, there can be a high degree of variability between otolith accretionary growth and somatic body growth under dissimilar environmental conditions, metabolic rates, or life stages, which may lead to inaccuracies in growth rate estimates (Ashworth et al., 2017; Hare and Cowen, 1995; Mosegaard et al., 1988; Wright et al., 2001).

A promising novel method for quantifying growth rate variation in wild fish is the use of blood-based physiological 'biomarkers' that reflect an individual's somatic growth rate. Such a 'biomarker' would need to be a readily quantifiable substance that reliably and quantitatively reflects variation in growth rate. In several marine and freshwater fishes, insulin-like growth factor-1 (Igf-1), a hormone involved in the endocrine regulation of bone and muscle growth (Duan, 1997; Reinecke et al., 2005; Laviola et al., 2007), has shown strong promise as a 'biomarker' indicative of individual variation in growth rate (Picha et al., 2008; Beckman, 2011). In fish, nutritional and reproductive status affect the concentration of Igf-1 in blood circulation (Beckman, 2011). The extraction of blood and the subsequent measurement of Igf-1 from fish can be nonlethal, fast and relatively inexpensive. Igf-1 has been validated as a physiological indicator for growth rate variation in economically important aquaculture species including salmonids (Beckman et al., 1998, 2004a,b; Shimizu et al., 2009; Kawaguchi et al., 2013), Atlantic cod (*Gadus morhua*; Davie et al., 2007), sea bream (*Sparus aurata*; Pérez-Sánchez et al., 1995; Mingarro et al., 2002), tilapia (*Oreochromis mossambicus*; Uchida et al., 2003), and several other fishes (e.g., Dyer et al., 2004; Picha et al., 2006), in which an individual's circulating concentration of Igf-1 correlates positively with an individual's rate of somatic growth. That positive relationship between Igf-1 and growth rate emerges from the physiological mechanism wherein Igf-1 regulates growth: individual fish ingesting more food produce more Igf-1 in the liver and release more of that Igf-1 into blood circulation to stimulate somatic growth (e.g., Beckman et al., 2004a,b; Norbeck et al., 2007; Pierce et al., 2007; Shimizu et al., 2009; Hack et al., 2019). Despite the tractability of using Igf-1 for obtaining growth data on wild fish populations of interest

for fisheries management and conservation, there have been relatively few studies to date employing this approach in wild fish populations (but see: Andrews et al., 2011; Ferris et al., 2014; Wechter et al., 2017; Duguid et al., 2018; Journey et al., 2018).

Blue Rockfish and other nearshore rockfishes (genus *Sebastes*) support commercial and recreational fisheries of considerable economic and cultural value as part of the broader groundfish fishery in California and other areas of the Eastern North Pacific Ocean. These species are a common target for recreational fishers along with a suite of other rockfish species that characterize nearshore rocky reef communities (Cope, 2004; Wendt and Starr, 2009). Recently, the use of Igf-1 as a reliable physiological indicator of growth rate was validated in laboratory studies of Olive Rockfish (*Sebastes serranoides*, Hack et al., 2018) and Copper Rockfish (*S. carinus*; Hack et al., 2019) (**Fig. 1**). Those studies confirmed that circulating Igf-1 concentrations are lower in *Sebastes* rockfishes – as well as in Cabezon (*Scorpaenichthys marmoratus*), a related species also within Order Scorpaeniformes (Strobel et al., 2020) – when individuals are experiencing reduced growth due to food restriction and elevated in individuals showing higher growth when consuming greater amounts of food (Hack et al., 2018, 2019).

In this study, we used Igf-1 to assess variation in recent growth rate in Blue Rockfish (*Sebastes mystinus*) from central California, USA. Specifically, we examined spatial and temporal patterns of variability in Igf-1 as an indicator of growth rate variation in Blue Rockfish from 2016 to 2018. Blue Rockfish were collected from within and adjacent to two Marine Protected Areas (MPAs) in central California: the Piedras Blancas State Marine Reserve and the Point Buchon State Marine Reserve, both of which have been closed to fishing since 2007. Because of the variation in expression of Igf-1

between different reproductive life stages, we specifically analyzed Igf-1 in Blue Rockfish that were equal to or smaller than the length at which 50% of Blue Rockfish from the central coast are sexually mature (Schmidt, 2014). We predicted that, given the response of Igf-1 to variations in diet in laboratory kept rockfish (Hack et al., 2018, 2019), there would be significant and meaningful variation in Igf-1 and that it could be used to assess variation in short-term growth rate of wild populations of Blue Rockfish. We tested variation in Igf-1 levels on three spatial scales: between the Piedras Blancas and Point Buchon regions, between MPAs and adjacent reference locations within each region, and between different small scale (500 m^2) collection sites within each MPA or reference location. In order to explore temporal variation in Igf-1 and to assess the temporal consistency of spatial trends, we also examined interannual variation in Igf-1 levels across the three years from which samples were collected. Due to multiple factors that could impact food availability and quality, such as potential variation in abundance between MPAs and reference areas, we predicted that protection status would have a significant impact on Igf-1 levels and that the impact would be consistent across the two MPAs. We also predicted that, due to the potential for oceanographic conditions and habitat variation between and within regions to drive variation in food abundance and quality, there would be significant variation in Igf-1 levels interannually and on multiple spatial scales.

2. MATERIALS AND METHODS

2.1. Study Locations and Animal Collection

Blue Rockfish were studied at two sites approximately 60 km apart on the coast of central California, USA (**Fig. 2**). Rockfish collection occurred as part of sampling by the California Collaborative Fisheries Research Program (CCFRP), which is a long-term collaborative study between researchers and local fishers that aims to monitor the effects of MPAs on nearshore groundfish populations in California (Wendt and Starr, 2009). CCFRP has been conducting annual fish population surveys to assess the effects of MPAs on fishes, including Blue Rockfish in central California, since 2007 (Wendt and Starr, 2009; Yochum et al., 2011). The collection of blood samples from Blue Rockfish for the current study was conducted during CCFRP monitoring surveys in 2016-2018. Additional details on the sites and methods for those CCFRP surveys are provided in Starr et al. (2015). This research was approved by the California Department of Fish and Wildlife (Scientific Collection Permit SC-4793), and all animal collections were approved by the California Polytechnic State University Institution Animal Care and Use Committee (Protocol # 1504 and 2108).

Blue rockfish were collected from within the Point Buchon State Marine Reserve (17.4 km^2) and the Piedras Blancas State Marine Reserve (26.9 km^2), both of which have been completely closed to commercial and recreational fishing since September 2007. Rockfish were also collected from non-protected areas adjacent to the Point Buchon and the Piedras Blancas State Marine Reserves. These non-protected areas will hereon be referred to as 'reference' areas. These reference areas were selected on similarities in

rocky reef habitat composition, depth, and oceanographic conditions with the corresponding nearby marine reserve (Yochum et al., 2011).

Rockfish were caught via hook-and-line fishing at designated sites at depths of < 40 m either within a reserve or adjacent reference area. That depth maximum for fish sampling sites was selected to reduce the incidence of barotrauma among collected fish (Starr et al., 2015). Fishing at both locations occurred from July to September within predesignated 500 m^2 cells (**Fig. 2**), with 22 cells at the Point Buchon MPA and reference area and 57 cells at the Piedras Blancas MPA and reference area. On a given sampling day, four cells were selected randomly and were then fished for three (3x) 15 min intervals for a total of 45 min of fishing time per cell. Fishing during those 15 min periods consisted of researchers and/or volunteer anglers using a mixture of barbless baited hooks, feathered lures, or metal jigs as part of a hook-and-line fishing effort while the fishing vessel drifted within the designated cell. Fishing was ceased if the vessel drifted outside of the cell until the boat could be repositioned back inside the cell. After fish were caught via hook-and-line, they were placed in a bucket of seawater that was periodically replaced. Blood samples were collected from all fish within 5 min of capture, after which fish were released. Respective marine reserve and non-protected reference cells were sampled on consecutive days with the exception of two occurrences where subsequent collection occurred two days after the initial collection date (**Table 1**). All cells were sampled with replacement for the next sampling date such that cells sampled during a given reserve-reference paired sampling date were immediately available again for random selection for all future sampling dates. For most cells, two water temperatures were collected using a Sea-Bird SBE19plus CTD (Sea-Bird Scientific, Bellevue, WA,

USA): one measurement was taken at ~1 m depth and another at variable depths up to 26 m depth, depending on bottom depth at that sampling location. Data on the species composition, catch per unit effort (CPUE), and body size distributions of fish collected as part of the CCFRP marine reserve monitoring efforts will not be addressed in the current study, but have been reported for years prior to 2016 elsewhere (e.g., Starr et al., 2015). Instead, the following data and analyses will focus solely on the Blue Rockfish sampled for Igf-1 and growth variation analyses.

Blood was collected from a total of 1,812 Blue Rockfish between 2016 through 2018 from the two MPAs and corresponding reference sites (**Table 2**). Some of the largest Blue Rockfish sampled were likely to be sexually mature based on previously reported sizes for sexual maturation in the species (Schmidt, 2014; Echeverria, 1987; Miller et al., 1967). Since our focus was to assess spatial and temporal variation in somatic growth rate in juvenile Blue Rockfish, we removed all fish > 22 cm from the analyses such that most individual fish used in the analyses were reproductively immature. This cutoff of 22 cm length was selected to reflect the average length of male and female Blue Rockfish at 50% maturity as reported by Schmidt (2014). Removing fish larger than 22 cm in length resulted in a total of 1,273 of the 1,812 total Blue Rockfish available for analysis. Sample sizes (*n*) of fish sampled per reserve location and date are provided in **Table 1**. For each fish sampled, a small volume (< 0.5 mL) of blood was collected from the caudal vasculature using a heparinized syringe. The collection of blood from caudal vasculature is a well-established, non-lethal method for sampling blood from fish (e.g., Lawrence et al., 2020), and all rockfish were released immediately following blood collection. Collected blood was placed into heparinized tubes and

immediately placed on ice for the duration of the fish survey trip (up to 8 h). Blood was

then centrifuged at 3000 x g for 10 min at 4°C, and the resulting plasma stored at -

80°C. The number of fish sampled per date and cell was influenced by the total number

of Blue Rockfish caught, the rapidity at which those fish were being caught and

processed for other data, and the availability of personnel to collect blood.

2.2. Quantification of Igf-1 concentrations

Plasma Igf-1 concentrations were quantified using a time-resolved

fluoroimmunoassay (TR-FIA) method (Small and Peterson, 2005), which was developed

from an RIA method as described by Shimizu and colleagues (2000). This TR-FIA

method has been described in detail elsewhere (Ferris et al., 2014), and had been

previously validated for use in *Sebastes* rockfishes (Hack et al., 2018, 2019), as well as

other related fish within Order Scorpaeniformes (Strobel et al., 2020). The TR-FIA assay

utilized dissociation enhanced lanthanide fluorescence immunoassay (DELFIA®)

reagents (Perkin-Elmer, Waltham, MA, USA) and anti-Igf-1 antiserum to Barramundi

(*Lates calcarifer*) (GroPep BioReagents, Ltd., Thebarton, SA, Australia). Recombinant

salmon Igf-1 was used as the standard. Europium (Eu)-labeled tracer was made through

custom labeling of recombinant tuna Igf-1. Note that this tracer differed from that used in

previous descriptions of this TR-FIA method (e.g., Ferriss et al., 2014; Hack et al., 2018,

2019), which used Eu-labeled recombinant salmon Igf-1 as tracer.

All plasma samples were assayed using DELFIA® Assay buffer and goat anti-

rabbit IGG-coated 96-well plates (Perkin Elmer). Plasma samples (25 μL) were extracted

prior to assay. Samples and standards were incubated with anti-Igf-1 antibody for 24 h at

4°C prior to the addition and subsequent incubation with Eu-Igf-1 solution for another 20 h at 4°C. A 200 µl volume of enhancement solution (Perkin Elmer) was then added to each well and the plate was incubated for 10 min at room temperature on an orbital shaker. The plate was then washed using DELFIA® wash buffer, and read on a Victor3 1420 Multilabel plate reader (Perkin Elmer). Samples from each year (2016 to 2018) were assayed separately such that individual plates only included fish from a single year, and samples were allocated within a plate via stratified spatial arrangement such that each plate contained balanced variation in habitat location, protection status site, and date within the year of sampling. Each assay plate also included four wells, which included neither tracer nor sample in order to account for background levels of fluorescence and three wells that included only tracer which represents the maximum level of binding. Each measurement was corrected for background fluorescence by subtracting the mean background level of fluorescence from each concentration. All samples were assayed in duplicate. To account for potential variation between assay plates, three inter-assay pools (IPs) of plasma from the same source were quantified in every plate. The concentration of Igf-1 in those IPs translated to 60%, 50%, and 35% of maximum tracer binding. A linear regression of IP percent bindings and Igf-1 concentrations was used to standardize sample concentrations in order to reduce the effect of random inter-assay variation. All data were analyzed using WorkOut2™ software (Perkin Elmer), and a four parameter logistic equation was used to generate the standard curve. In cases when the duplicated plasma samples from the same fish gave Igf-1 concentration values with a % coefficient of variation (CV) > 7% and there was more than a 10 ng·mL^{-1} difference between the duplicates, the fish was either re-assayed or excluded from analysis. Fish samples that

resulted in Igf-1 concentrations outside of an acceptable % binding range of 80 to 20% were also rerun using a modified extraction volume. The resulting mean intra-assay % CV was 7.5% and mean inter-assay variation was 16.1%. Outlier Igf-1 values that were three standard deviations away from the overall mean were removed from analysis.

2.3. Statistical Analyses

All statistics were two-tailed and conducted using JMP v.14 software (SAS Institute Inc., Cary, NC, USA), and $\alpha = 0.05$ was used for all statistical comparisons. An ANOVA model was used to examine how Blue Rockfish Igf-1 concentrations varied in relation to geographic sampling region (Point Buchon or Piedras Blancas), habitat protection status (protected marine reserve or non-protected reference area), year, and all associated interactions. To account for temporal variation in the marine environment and because MPA and associated unprotected reference areas in the same region were sampled on consecutive days, a nested 'pair' variable was included in the ANOVA model to link paired sampling dates. Sampling date (day and month) was not included in the model due to limited and uneven representation of dates across the main variables of interest (year, location, and protection status), and lack of evidence of consistent seasonal differences between July and September in Igf-1 levels in each year of sampling. Tukey HSD tests were used for *post hoc* pairwise comparisons. For each sampling year, Brown-Forsythe tests were used to test for differences in the variability of individual fish Igf-1 values between MPA and non-MPA reference regions in the Piedras Blancas and Point Buchon geographic regions.

There is evidence that length, in addition to nutritional status, can relate positively to plasma Igf-1 concentrations in fish (Shimizu et al., 2009; Ferriss et al., 2014). However, due to the lack of independence between length and growth rate and the fact that there is evidence that nutrition status has a much greater impact on Igf-1 levels than body size, the results we present here do not include length as a covariate (Beckman, 2011). Parallel analyses using ANCOVA model that includes length as a covariate are provided in **Appendix 2**. In addition, variation in body size (total length [TL], ± 1 cm) of all Blue Rockfish caught and sampled for blood was examined using an ANOVA model with geographic sampling location ('Point Buchon MPA' or 'Piedra Blancas MPA'), habitat protection status (protected marine reserve or non-protected reference site), year, and all interactions between those factors. While analyses reported are for the N = 1,288 fish that were < 23 cm in length, we also tested whether any statistical conclusions held using all Blue Rockfish collected. Those additional statistical analyses using all fish collected are provided as **Appendix 1**; note that statistical conclusions were similar when using only fish < 22 cm total length and when using all Blue Rockfish sampled. As with Igf-1 values, Brown-Forsythe tests were used to test for differences in variances of individual fish lengths between MPA and non-MPA reference regions in each year of sampling.

In order to examine finer-scale spatial variation in Igf-1 levels between predesignated 500 m^2 cells, we selected the subset of dates for which the minimum sample size of Igf-1 levels was at least 12 per cell and used ANOVA models to test for variation in Igf-1 between cells. The lower sample size limit of $n = 12$ fish per cell was selected based on the relationship between standard deviation of average Igf-1 values per

cell on a given date. This resulted in three available dates to assess fine-scale spatial variation: July 24th 2017, August 7th 2017, and July 23rd 2018. While the random sampling of 500 m^2 fishing cells led to few cells being sampled more than once in a given year, repeated sampling of the same cell in the same year did occur for a small subset of the cells. Analysis of Igf-1 values in those cells sampled repeatedly in the same year was used to test for short-term (within the July to September sampling period within the same year) variation in Blue Rockfish growth. Only cells repeatedly sampled within the same year and with a sample size of $n \geq 5$ for both dates of sampling were analyzed. Mean Igf-1 values within the same cell were analyzed using Student's t tests, as preliminary covariate analyses revealed that using body length as a covariate had no effect on any statistical conclusions regarding short-term changes in Blue Rockfish Igf-1 concentrations for fish collected within a given 500 m^2 sampling cell in the same year.

3. RESULTS

3.1. Regional, annual, and MPA-associated variation in Igf-1

Significant variation in Blue Rockfish Igf-1 concentrations was detected between the Piedras Blancas and Point Buchon regions. Blue Rockfish from the Piedras Blancas region had higher mean Igf-1 than conspecifics from the Point Buchon region (**Fig. 3a**) ($F_{1,1246} = 61.1162$, $p < 0.0001$). That regional difference in mean Igf-1 was consistently observed in each of the 2016, 2017, and 2018 sampling years, even though average Igf-1 values also varied across years ($F_{2,1246} = 12.2158$, $p < 0.0001$), with Igf-1 values in both regions higher in 2016 compared to 2017 and 2018 (**Fig. 3b**).

While MPA protection did not have consistent effects on Blue Rockfish Igf-1 concentrations across the Piedras Blancas and Point Buchon regions (**Fig. 4a**), mean Igf-1 levels differed between MPA and non-MPA reference locations in 2018, but not in 2016 or 2017 (**Fig. 4b**) (year·protection status interaction: $F_{2,1246} = 3.6537$ $p = 0.0262$). At both Piedras Blancas and Point Buchon, Blue Rockfish caught in 2018 had higher mean Igf-1 concentrations within the unprotected reference locations compared to the adjacent protected MPAs (**Fig. 5a**). In 2016 and 2017, however, Igf-1 was similar between the MPAs and adjoining reference locations in both regions. In each sampling year, Blue Rockfish caught in the MPA or reference locations of the Piedras Blancas region were larger in body length, on average, than conspecifics captured in the Point Buchon region (**Fig. 5b**) (year * region * protection interaction: $F_{2,1253} = 4.4980$, $p = 0.0113$).

3.2. Length association with Igf-1

As in other fishes (e.g., Coho Salmon, Shimizu et al., 2009; Lingcod, Ferriss et al., 2014), plasma Igf-1 concentration showed a statistically significant positive association with body length in Blue Rockfish (**Fig. 6a**) ($r^2 = 0.009$, $F_{1,1264} = 11.8671$, $p = 0.0006$). Nonetheless, body length variation explained little of the Igf-1 variability among Blue Rockfish. The pattern of Blue Rockfish body length variation between the regions showed a pattern dissimilar to that for Igf-1 (**Fig. 5a,b**), and covariate analyses (see **Appendix 1**) accounting for body size influences on Igf-1 continued to indicate a robust regional difference in Igf-1 values (**Fig. 6b**) as well as similar annual variation in Igf-1 across both regions (**Fig. 6c**) suggesting that fish size is not a major driver of variation in Igf-1 in Blue Rockfish in the Piedras Blancas and Point Buchon regions.

3.3. Igf-1 variation within areas

In each sampling year, Blue Rockfish collected in the Piedras Blancas region also exhibited greater variability in Igf-1 values among individual fish compared to variability among fish from the Point Buchon region (Brown-Forsythe tests: 2016: $F_{1,340} = 4.2993$, $p = 0.0389$; 2017: $F_{1,452} = 14.7582$, $p = 0.0001$; 2018: $F_{1,475} = 15.2646$, $p = 0.0001$). Those geographic differences in variance in Igf-1 concentrations among individual rockfish was especially pronounced in the Point Buchon MPA, where the % coefficient of variation (CV) for Igf-1 values among fish collected from that location was lower in all three sampling years (**Fig. 7a**). Body length variation, however, did not mirror those same patterns of Igf-1 variation, and in all years was variation in Blue Rockfish body length statistically similar across the MPA and reference locations of both regions (**Fig. 7b**)

(2016: $F_{1,340} = 0.2797$, p = 0.8401; 2017: $F_{1,450} = 2.0359$, p = 0.1081; 2018: $F_{1,473} =$ 1.0259, p = 0.3808).

3.4. Fine scale spatial and temporal variation in Igf-1

Igf-1 concentrations were also observed to vary significantly over smaller geographic scales as variation in mean Igf-1 between different 500 m^2 fishing area cells sampled within the same region on the same or consecutive days (**Fig. 8**). That fine scale spatial variation was detected among 500 m^2 fishing cells sampled in the Piedras Blancas MPA That fine scale spatial variation was observed among 500 m^2 fishing cells sampled in the Point Buchon MPA on July 24th 2017 ($F_{3,82} = 8.0992$, p < 0.0001), in the Point Buchon MPA on August 7th 2017 ($F_{3,49} = 3.1379$, p = 0.0336), and in the Piedras Blancas MPA on July 23rd 2018 ($F_{3,94} = 4.6182$, p = 0.0047). Length did not have a significant impact on Igf-1 for any of the dates (July 24th 2017: $F_{1,82} = 0.0667$, p < 0.7968, 08/07/2017: $F_{1,49} = 3.7858$, p = 0.0574, July 23rd 2018: $F_{1,94} = 1.3763$, p = 0.2437).

Comparisons of Igf-1 concentrations between sampling dates for the sixteen 500 m^2 fishing cells resampled on a 2nd date within the same year revealed short-term changes across weeks in Igf-1 concentrations between dates for eight of those cells, but no change in mean Igf-1 values across dates for another eight cells (**Table 3**). Further examination of the locations and sampling times for those cells suggests a pattern of declining Igf-1 values from mid-July to early-September in 2016 in both the Point Buchon and Piedras Blancas regions (**Fig. 9**). In 2017, similar declines in Igf-1 again appeared to occur in both regions from late-July to early/mid-August, followed by a stabilizing of that pattern of decline to stability in Igf-1 levels in the Point Buchon region from early/mid-August to late-August. However, in 2018, Blue Rockfish in the Piedras Blancas region showed at

trend of increasing Igf-1 concentrations from July to September, which fish in the Point

Buchon region did not seem to experience an increase in Igf-1 over that same time period

(**Fig. 9**).

4. DISCUSSION

Changes in somatic growth rate can impact the productivity of marine fish populations as changes in body size impact stock biomass, reproduction, and survivorship (Duffy and Beauchamp, 2011; Audzijonyte et al., 2013; Beamish and Neville, 2021). Here, we used variation in concentrations of the hormone Igf-1 as a novel tool to examine short-term growth rate variation in wild Blue Rockfish in nearshore central California. Variation in levels of Igf-1 in blood circulation has been demonstrated to be a reliable indicator for short-term growth rate in a wide taxonomic variety of teleost fishes (Beckman, 2011), and captive studies with *Sebastes* rockfishes have demonstrated that an individual's concentration of Igf-1 correlates positively with the rate of somatic growth of the fish (Hack et al., 2018, 2019). That positive relationship between Igf-1 and growth rate arises because Igf-1 has a direct mechanistic relationship with food intake and growth: when a fish consumes food, that consumption of food induces the pituitary gland to secrete growth hormone (GH), which then stimulates the liver to synthesize and release Igf-1 into blood circulation (Duan et al., 1993; Schmid et al., 2000; Leung et al., 2008; Bergan-Roller and Sheridan, 2018). The direct physiological link between nutritional condition (i.e., food consumption), Igf-1 hormone production, and growth results in Igf-1 serving as a robust indicator for growth rate variation in many fish species (Pérez-Sánchez et al., 1995; Picha et al., 2008; Beckman, 2011), including *Sebastes* rockfishes and other scorpaeniform fish (Hack et al., 2018, 2019; Strobel et al., 2020).

In this study, we documented variation in Igf-1 concentrations among wild Blue Rockfish on multiple spatial and temporal scales. Significant spatial variation in Igf-1 concentrations was detected between the Piedras Blancas and Point Buchon regions,

which are separated by ~60 km, but also at more localized scales as differences in mean Igf-1 levels among Blue Rockfish collected from different 500 m^2 sampling locations on the same day (**Fig. 3, Fig. 8**). Regionally, Igf-1 concentrations were observed to be higher in the Piedras Blancas region than in the Point Buchon region. That regional difference in Igf-1 was consistently observed in each year of the 2016-2018 sampling period, despite annual variation in mean Igf-1 concentrations in both regions (**Fig. 3**).

Even though circulating Igf-1 correlates with body size in Blue Rockfish as in other fishes (Shimizu et al., 2009; Ferriss et al., 2014; Hack et al., 2019; Strobel et al., 2020), the minimal amount of variation in Blue Rockfish Igf-1 explained by body size (r^2 = 0.009) suggests that the observed regional differences in mean Igf-1 are not simply due to variation in fish size (**Fig. 6**). Rather, these Igf-1 differences likely represent growth rate differences linked to regular spatial variation in food availability and/or quality between the Piedras Blancas and Point Buchon regions. Controlled laboratory studies in other fishes have found that recent food intake has a larger effect on Igf-1 than body size (Beckman, 2011). In Copper Rockfish (*S. caurinus*), for instance, fish of the same cohort grown to larger size on higher rations had significantly reduced plasma Igf-1 when deprived of food for 12 d, compared to similar sized fish continuously fed, indicating that recent food consumption experience has larger contributions to blood Igf-1 concentration than body size variation (Hack et al., 2019). Similar results were obtained with juvenile Chinook salmon (*Oncorhynchus tshawytscha*), in which fish divided into 'large' and 'small' bodied groupings and then reared under 'high' and 'low' ration amounts showed Igf-1 levels associated with their feeding treatment, and not with their body size group (Beckman et al., 1998, 2003).

The time span over which plasma Igf-1 concentrations best represent growth rate variation is not well documented in rockfish. Given the mechanistic physiological relationship between food consumption, Igf-1, and growth, variation in plasma Igf-1 concentrations likely best relates to 'recent growth' on the scale of weeks (Beckman, 2011). In juvenile Coho salmon (*O. kisutch*), plasma Igf-1 related best to growth rate calculated as change in length over the course of the last month (Beckman et al., 2004b). And, in two studies with other scorpaeniform fishes related to the Blue Rockfish studied here, Igf-1 significantly decreased in Copper Rockfish and Cabezon at times 12 d and 14 d, respectively, following the start of food restriction (Hack et al., 2019; Strobel et al., 2020). While positive relationships between plasma Igf-1 and growth have been recorded for fishes over time periods spanning from two weeks to several months (for review, see: Beckman, 2011), Igf-1 is best considered an indicator of 'recent' variation in food intake and growth rate on the scale of days to weeks.

Even though food consumption and nutrition (i.e., changes in feeding rate, food quality) are the primary drivers of variation in plasma Igf-1 concentrations in teleost fishes, other factors can influence the relationship between Igf-1 and growth (Reinecke, 2010; Beckman, 2011). Studies to date indicate that plasma Igf-1 concentrations are largely unaffected by daily cycles of photoperiod (Ayson and Takemura, 2006; Small, 2005; Shimizu et al., 2009), so time-of-day of sampling is likely not a major influence on Igf-1 values. Sexual maturation, however, can alter Igf-1 concentrations in teleost fish. Sexually mature fish make gametes and perform behaviors associated with reproduction, and these processes require energetic resources such that energy often shifts away from growth toward reproductive processes. Sexual maturation has been documented to affect

the relationship between Igf-1 and growth rate in salmon (Beckman et al., 2004a,c), and in several fish species, mature male and female fish have been found to differ in plasma Igf-1 concentrations (Riley et al., 2002; Davis and Peterson, 2006; Davis et al., 2008). For that reason, in the current study we limited our analysis of Igf-1 variation in Blue Rockfish to individuals ≤ 22 cm in total length (TL). That body length of 22 cm was reported as the size at 50% maturity for the species by Schmidt (2014) and was reported as the minimum size for sexual maturity in both males and females by Echeverria (1987). Importantly, Wales (1952) reported that Blue Rockfish in the area of Monterey Bay in central California spawned in the months of Dec-Feb; our sampling occurred each year in Jul-Sept outside of the spawning season. Notably, the statistical conclusions for regional, protection status, and yearly variation in Igf-1 values derived using Blue Rockfish of lengths 14 cm to 35 cm (**Appendix 1**) do not differ from the statistical conclusions derived from fish that were ≤ 22 cm. That consistency suggests that – rather than any confounding influences of sex differences or sexual maturation status – the observed spatial and temporal patterns of Igf-1 variation in wild Blue Rockfish likely represent growth rate differences from variation in diet quantity or quality.

Information about Blue Rockfish diet in central California is limited, although studies have reported gut content analyses for Blue Rockfish collected from two nearby locations in California: the Santa Barbara region ~130 km to the south (Love and Ebeling, 1978), and Carmel Bay located ~170 km to the north (Hallacher and Roberts, 1985) of our current study area. Love and Ebeling (1978) reported the diet of Blue Rockfish (lengths: 7.8 cm to 26.2 cm total length) caught between March 1971 and June 1972 to consist primarily of tunicates (51.5%; % volume), hydroids (13.1%), kelp with

encrusting bryozoans (10.5%), and both squid (8.3%) and fish (7.4%). Love and Roberts (1978) also reported that Blue Rockfish exhibited greater seasonal variation in diet compared to another rockfish species studied concurrently, the Olive Rockfish, *Sebastes serranoides*. Similar seasonal variation was observed for Blue Rockfish studied in Carmel Bay (Hallacher and Roberts, 1985). Hallacher and Roberts (1985) observed that Blue Rockfish exhibited dietary differences between the upwelling (April - August) and non-upwelling seasons (September - March). During the Spring and Summer upwelling season, gut content consisted of primarily pelagic tunicates (79%; % mass), hydroids (8%), and euphausids (3%), but shifted to algae (88%) and caridean shrimp (11%) during the non-upwelling season. Markedly, fish contributed only a small proportion of the Blue Rockfish diet in both of those studies and – of the six species of rockfishes surveyed in Carmel Bay by Hallacher and Roberts (1985) – Blue Rockfish had the most distinctive diet and altered their different vertical distribution patterns relating to upwelling season. Also notably, those studies by Love and Ebeling (1978) and Hallacher and Roberts (1985) were both completed before Blue Rockfish (*S. mystinus*) and Deacon Rockfish (*Sebastes diaconus*) were diagnosed as distinct species in 2015. It is therefore possible that the dietary data reported is to some extent confounded by measurements on both of these species. Even so, it is likely that more than 80% of rockfish collected for those reported dietary studies were Blue Rockfish based on ratios of Blue Rockfish and Deacon Rockfish in Morro Bay and Monterey California (Schmidt, 2015).

While the consistent difference in Igf-1 levels for Blue Rockfish between Piedras Blancas and Point Buchon point to different feeding and growth rate dynamics between these regions, there is limited information available about what environmental

dissimilarities between the regions might mediate that growth variation. Data derived from the California Seafloor and Coastal Mapping Project (Johnson et al., 2017) summarized by Dodgen (2020) indicates that while mean depth does not differ between our sampling areas in these regions, the Point Buchon region does have a higher mean bottom slope and vector ruggedness measure (VRM, an index for rugosity) than the Piedras Blancas region. Notably, neither slope, VRM, nor percent rough bottom cover differed between MPAs and associated reference areas within each respective region (Dodgen, 2020). While we have limited ability to assess differences in oceanographic parameters between regions, monthly mean surface temperature differed between regions by an average of only 0.4°C and depth temperature varied by only 0.2°C across the regions and did not show patterns of variation consistent with the patterns of variation in Igf-1 (**Table 4**). While the exact environmental differences that drive this pattern are beyond the scope of this project, this result provides an example of how Igf-1 could be used to identify highly productive habitats for fisheries populations and could significantly augment existing evaluations of productivity.

Despite our prediction that MPA protection status would have a significant impact on Igf-1 levels, we did not observe consistent patterns of Igf-1 variation in Blue Rockfish between MPAs and adjacent unprotected reference areas (**Fig. 5**). For example, in 2018, Igf-1 values were found to be greater in Blue Rockfish collected from the reference area than in the MPA in the Piedras Blancas region. However, that difference was only observed in 2018 and not in 2016 or 2017. Nor were any differences in Igf-1 detected in any year between MPA and reference locations in the Point Buchon region. The absence of a positive effect of MPA protections for Blue Rockfish growth rate are similar to

findings reported by Andrews et al. (2011) for Lingcod (Ophiodon elongatus), another species of groundfish with high site fidelity. Andrews et al. (2011) examined the impact of MPAs and fine scale site differences on Igf-1 in Lingcod in Puget Sound, Washington, USA, and found that even though male Lingcod mean Igf-1 levels varied across fine spatial scales, that spatial variation did not occur in patterns consistent with MPA protections. While Andrews et al. (2011) did, however, observe that individual variation in Igf-1 was greater in MPAs, individual variation in Igf-1 in Blue Rockfish in the current study was instead lower in the Point Buchon MPA in all three years of sampling (**Fig. 7**).

MPAs are often established to protect and restore habitat as well as a fisheries management tool with the intention of restoring fish stocks and conserving biodiversity (Micheli et al., 2004). The MPAs sampled in the current study were established in 2007 as the first part of a network of MPAs designated between 2007-2012 to protect marine biodiversity and improve fisheries in California (Gleason et al., 2013; Kirlin et al., 2013). MPAs have been shown to impact fish populations and communities in multiple ways, including variation in biomass, abundance, diversity, and body size (Lester et al., 2009). For example, Thompson et al. (2017) detected increased larval fish abundances for several species of Sebastes rockfishes including Blue Rockfish in MPAs established in 2001 in southern California. There is a paucity of data regarding the impact of MPA implementation on fish growth and often information regarding MPA effects on fish growth are compounded by the fact that growth in fish is influenced by a multitude of factors, including food quality and community-level interactions such as competition for food resources that can lead to density-dependent interactions. Such density-dependent processes have been predicted to occur as fish abundance increases in newly established

MPAs (Levin et al., 1997; Gårdmark et al., 2006). For example, Taylor and McIlwain (2010) observed that the heavily targeted Indo-Pacific reef fish species *Lethrinus harak* showed a decreased size-at-age for fish collected from protected MPA locations compared to those from non-protected locations, suggesting that density related impacts on growth rate occurred with the increased fish density in MPAs. Whether similar density-dependent effects on Blue Rockfish growth might be occurring in MPAs along California's coast is not clear. It is possible that any effects of MPA protections on the growth of Blue Rockfish were overshadowed by the influences of other factors, such as finer scale spatial variation among individual 500 m² sampling cells, or fluctuations in ocean environmental conditions across the three year duration of the study.

Spatial variation in mean Igf-1 was detected among individual 500 m² sampling cells within the same MPA or reference location (**Fig. 8**). That observation suggests a fine-scale heterogenous structure of feeding ecology in Blue Rockfish, wherein localized differences in food availability and/or feeding success may be generating spatial structure in growth rates. While such fine scale spatial variation likely arises from heterogeneity in the habitat, the observation of Igf-1 variation among sampling cells also suggests that Blue Rockfish have limited movement, otherwise variation in Igf-1 signal would probably not be detectable at such small geographic scales. Multiple studies have assessed the movement patterns of Blue Rockfish on the central Coast (e.g., Starr et al., 2015, Jorgensen et al., 2016, Green et al., 2014); however, due to the difficulties of studying fish movement in marine environments, sample sizes are limited. Starr et al. (2015) reported movement of 12 Blue Rockfish tagged and released using floy tags as part of CCFRP monitoring, for which Blue Rockfish migrated an average of 1.2 km ± 0.7

(SD) over the course of between one and 623 d. Both Jorgensen et al. (2016) and Green et al. (2014) used acoustic tags to show that Blue Rockfish activity was concentrated in core areas. Green et al. (2014) surveyed 20 Blue Rockfish in Carmel Bay for 445 d and found the mean home range to be 0.23 km^2. Thirty percent of Blue Rockfish in that study shifted their home range up to 3 km, but those shifts occurred across time durations of seven months and more than one year after release. Taken together, the limited movement of Blue Rockfish in tagging studies coupled with our observation of detectable variation in Igf-1 across individual 500 m^2 fishing cells – which are about five times the size of the mean home range for Blue Rockfish reported by Green et al. (2014) – points to fine-scale spatial structure in the feeding and growth ecology of this species in nearshore California.

Variation in mean Igf-1 was detected over the course of the three years of the study; specifically, we observed significantly higher mean Igf-1 concentrations in 2016 than in 2017 and 2018 in both regions (**Fig. 3**). Since Blue Rockfish feed primarily in the water column on drifting prey, those temporal patterns of Igf-1 variation possibly reflect changes in food availability or quality resulting from differences in oceanographic parameters. There is evidence that Blue Rockfish can be significantly impacted by sources of ocean climate variation such as El Niño-Southern Oscillation (ENSO), which, on the central coast of California, is associated with increased sea surface temperature and a depression in upwelling intensity (VenTresca et al., 1995). VenTresca et al. (1995) showed that Blue Rockfish exhibited reduced body condition during ENSO events when compared to non-ENSO years. The differences in ocean climate during the course of this study could have impacted prey availability or quality and thus influenced Igf-1

concentrations in Blue Rockfish. It is also notable that anomalous ocean conditions were documented in 2015 during a severe Marine Heat Wave event (García-Reyes and Sydeman, 2017, Hobday et al., 2018), which could also have impacted Blue Rockfish prey and caused a delayed impact on Igf-1 concentrations due to complex trophic interactions. While the exact explanation of the inter-annual variation we observed is beyond the scope of this study, it is likely that variation in oceanography has a significant impact on Blue Rockfish Igf-1 concentrations.

We also observed temporal variation in Igf-1 concentrations across a period of just weeks for some locations. The similar patterns of decreasing mean Igf-1 observed in 2016 between late-July and early-September in cells from both the Point Buchon and Piedras Blancas regions – and again in 2017 between late-July and early/mid-August – is suggestive of changes in food availability during those times that spanned a geographic area broader than the ~60 km between the two sampling regions. Those changes might be attributed to the relaxation of upwelling that typically occurs from June to September in central California (García-Reyes and Largier, 2012). In 2018, however, more regional-scale changes in food availability instead seem to have occurred as Blue Rockfish from Point Buchon showed no change in mean Igf-1 from late-July to early-September, while Igf-1 levels in fish from Piedras Blancas increased over that same time period (**Fig. 9**). Geographic variation in upwelling intensity associated with local topography and variation in wind strength has been documented along the central California coast, and semi-permanent plumes and eddies of upwelled waters can arise in patterns dependent on coastline headlands and embayments (García-Reyes and Largier, 2012), which may impact general region-scale variation in food availability for Blue Rockfish.

The results presented here provide important insight into the spatial and temporal variation in growth rate of Blue Rockfish from central California. The multi-year approach of this study allowed us to evaluate the consistency of our observations and examine variation in short-term growth rate across years. In particular, the Piedras Blancas region appears to be consistently more productive in terms of Blue Rockfish short-term growth than the Point Buchon region. While a significant body of literature exists that addresses habitat variation impacts on Blue Rockfish abundance and spatial use (e.g., Jorgensen et al., 2016, Green et al., 2014, Hanan and Curry 2012, Young and Carr, 2015), more research is necessary to address the impact of habitat variation on growth rate. The majority of fisheries population assessment efforts, both for identifying productive habitats and assessing fisheries management tools such as MPAs, involve quantifying abundance, community diversity, and size variation. However, growth rate does not necessarily correlate with these well documented metrics including abundance and size. Growth rate is an important metric of individual and population success and its wider inclusion in population monitoring would facilitate a more holistic approach to population assessments and fisheries management practices. The identification and subsequent protection of productive habitat, using short-term growth rate in addition to traditional metrics, could help restore exploited populations and thus benefit the communities that rely on them. Further, a more extensive understanding of the impacts of oceanographic cycles, events, and trends on short-term growth rate could aid in predictions of fish population trends. The findings presented here provide evidence that Igf-1 can be an effective tool for monitoring growth rate in wild fish populations on multiple spatial and temporal scales and, in certain metrics such as the ability to obtain

growth rate information from a large sample size of fish, can greatly exceed the

capabilities of traditional methods of quantifying growth rate. In addition, Igf-1 as an

indicator of short term growth rate has the potential to significantly contribute to existing

monitoring and management efforts of culturally and economically important fisheries

species.

Table 1. Sample sizes (*n*) of blood samples collected for Igf-1 quantification in Blue Rockfish (*Sebastes mystinus*), from Piedras Blancas and Point Buchon from 2016-2018.

Year 2016	July 18, 19		July 25, 26		August 1, 2		August 8, 9		August 15, 17		August 29		September 6, 7		September 8, 9		September 12, 13	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas	4	17			32	31			41	22			28	13				
Point Buchon			23	15			41	24			5				49	30	48	17

2016	July 17, 18		July 24, 25		July 31, August 1		August 7, 8		August 14, 16		August 28, 29	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas	39	36			47	42			39	30		
Point Buchon			98	32			67	30			35	37

2018	July 16, 17		July 23, 24		July 30, 31		September 4, 5		September 6, 7		September 10, 11	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas			119	54			97	90	112	43		
Point Buchon	34	30			88	45					90	38

Total 1812

Table 2. Sample sizes (*n*) of blood samples collected for Igf-1 quantification in Blue Rockfish (*Sebastes mystinus)* that were less than 23cm in length, from Piedras Blancas and Point Buchon from 2016-2018.

Year 2016	July 18, 19		July 25, 26		August 1, 2		August 8, 9		August 15, 17		August 29		September 6, 7		September 8, 9		September 12, 13	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas	3	8			17	16			30	17			28	13				
Point Buchon			9	12			28	22			5				48	27	43	16

2016	July 17, 18		July 24, 25		July 31, August 1		August 7, 8		August 14, 16		August 28, 29	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas	27	21			41	36			36	26		
Point Buchon			90	29			57	23			33	35

| 2018	July 16, 17		July 23, 24		July 30, 31		September 4, 5		September 6, 7		September 10, 11	
	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF	MPA	REF
Piedras Blancas			102	26			53	45	55	19		
Point Buchon	17	13			42	30					52	23

Total 1273

Table 3. Results of pairwise statistics comparing Igf-1 levels between two sampling dates from the same cell for cells of at least n = 5 fish.

| year	Total number of cells repeatedly sampled per year	Number of cells repeatedly sampled with at least n = 5 fish both times sampled
2016	8	3
2017	10	6
2018	11	6

Year	Region	Area	Cell #	Sampling Date (n)	t Ratio	P value
2016	Point Buchon	MPA	5	8 Sept 2016 (8) 12 Sept 2016 (25)	1.46	0.1590
	Point Buchon	MPA	10	25 Jul 2016 (6) 8 Sept 2016 (17)	-2.99	**0.0129***
	Point Buchon	REF	15	26 Jul 2016 (6) 9 Sept 2016 (11)	-2.46	**0.0362***
	Piedras Blancas	MPA	16	1 Aug 2016 (10) 6 Sept 2016 (11)	-3.10	**0.0090***
2017	Point Buchon	MPA	1	7 Aug 2017 (16) 28 Aug 2017 (9)	-1.59	0.1253
	Point Buchon	MPA	5	7 Aug 2017 (13) 28 Aug 2017 (8)	-0.71	0.4869
	Point Buchon	MPA	10	24 Jul 2017 (14) 7 Aug 2017 (16)	-4.36	**0.0002***
	Point Buchon	REF	12	25 Jul 2017 (16) 29 Aug 2017 (6)	-2.90	**0.0111***
	Point Buchon	REF	17	8 Aug 2017 (9) 29 Aug 2017 (6)	0.31	0.7696
	Piedras Blancas	REF	54	18 Jul 2017 (5) 14 Aug 2017 (20)	**3.31**	**0.0031***
2018	Point Buchon	MPA	6	16 Jul 2018 (6) 11 Sept 2018 (10)	1.58	0.1399
	Point Buchon	MPA	8	30 Jul 2018 (26) 11 Sept 2018 (13)	-1.79	0.0825
	Point Buchon	MPA	11	30 Jul 2018 (9) 11 Sept 2018 (8)	-0.28	0.7815
	Point Buchon	REF	17	31 Jul 2018 (9) 10 Sept 2018 (10)	-0.69	0.5006
	Piedras Blancas	MPA	13	23 Jul 2018 (29) 4 Sept 2018 (8)	4.42	**0.0009***
	Piedras Blancas	REF	40	24 Jul 2018 (6) 7 Sept 2018 (7)	-2.49	**0.0347***

Table 4. Monthly mean sea surface temperature and temperature collected at depth for months in which temperature was available.

| Year	Month		Sea Surface Temperature	Temperature At Depth
2016				
	July	Piedras Blancas	13.1	11.8
		Point Buchon	13.3	11.6
	August	Piedras Blancas	14.0	12.2
		Point Buchon	13.8	11.9
	September	Piedras Blancas	13.8	11.9
		Point Buchon		
2017				
	July	Piedras Blancas		
		Point Buchon		
	August	Piedras Blancas	13.4	11.9
		Point Buchon	15.0	12.5
	September	Piedras Blancas	16.4	13.7
		Point Buchon	16.9	14.3
2018				
	July	Piedras Blancas	12.8	11.9
		Point Buchon	12.8	11.6
	August	Piedras Blancas		
		Point Buchon		
	September	Piedras Blancas	14.4	13.2
		Point Buchon	14.8	13.7
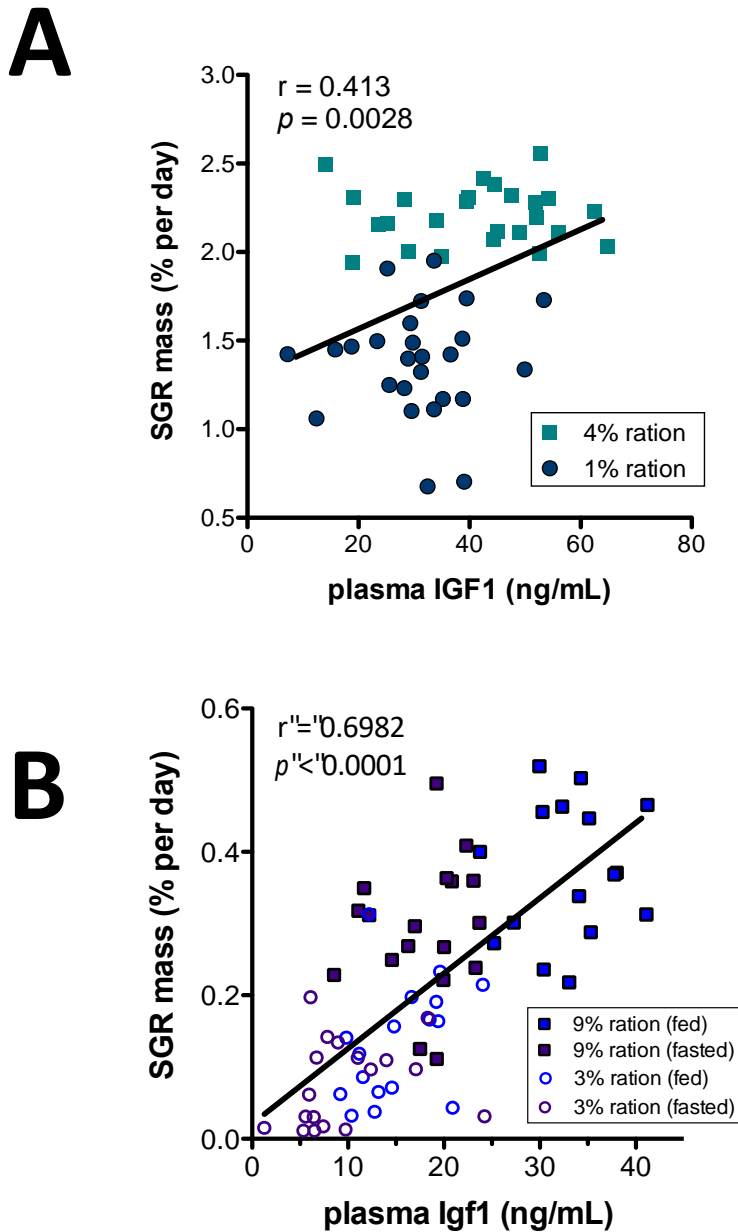
Figure 1. Individual variation in plasma Igf-1 concentration correlates positively with individual differences in mass-specific growth rate (SGR) as measured in (**a**) Olive Rockfish (*Sebastes serranoides*) fed either a high or low ration of food (Hack et al., 2018), and (**b**) Copper Rockfish (*Sebastes carinus*) experiencing either a high or low ration of food combined with 2 weeks of continued feeding or fasting (Hack et al. 2019).
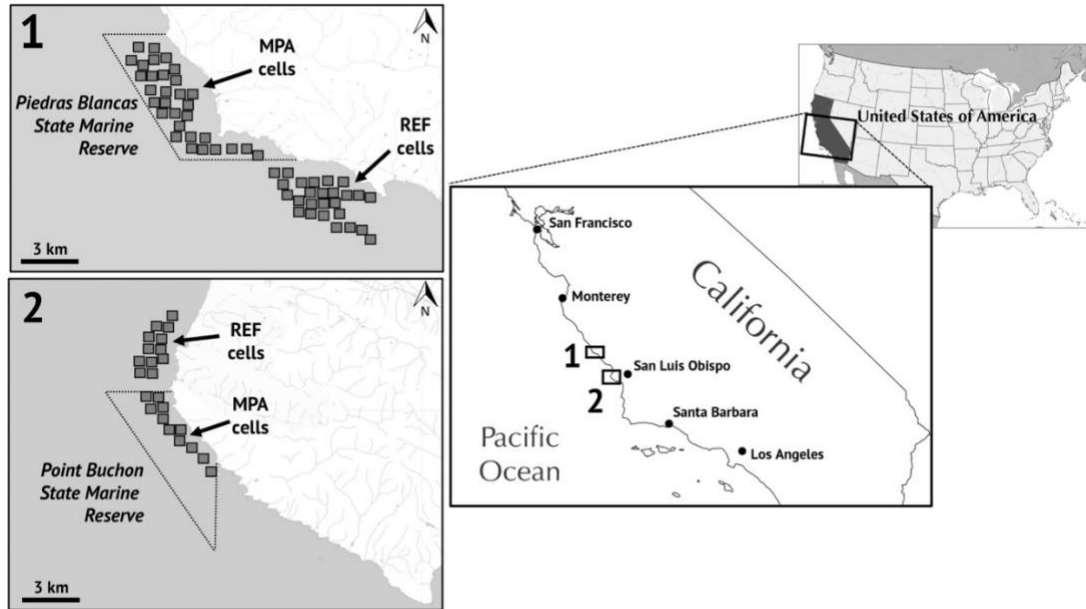
Figure 2. Maps of the Piedras Blancas and Point Buchon study regions, including MPAs and adjacent reference areas (REF). The Piedras Blancas MPA (26.9 km^2) and the Point Buchon MPA (17.4 km^2) are both marine reserves where no take of marine resources has been allowed since 2007. Blue Rockfish blood samples were collected by hook-and-line fishing within 500 m^2 sampling cells shown (dark gray rectangles) inside the MPAs and reference areas.
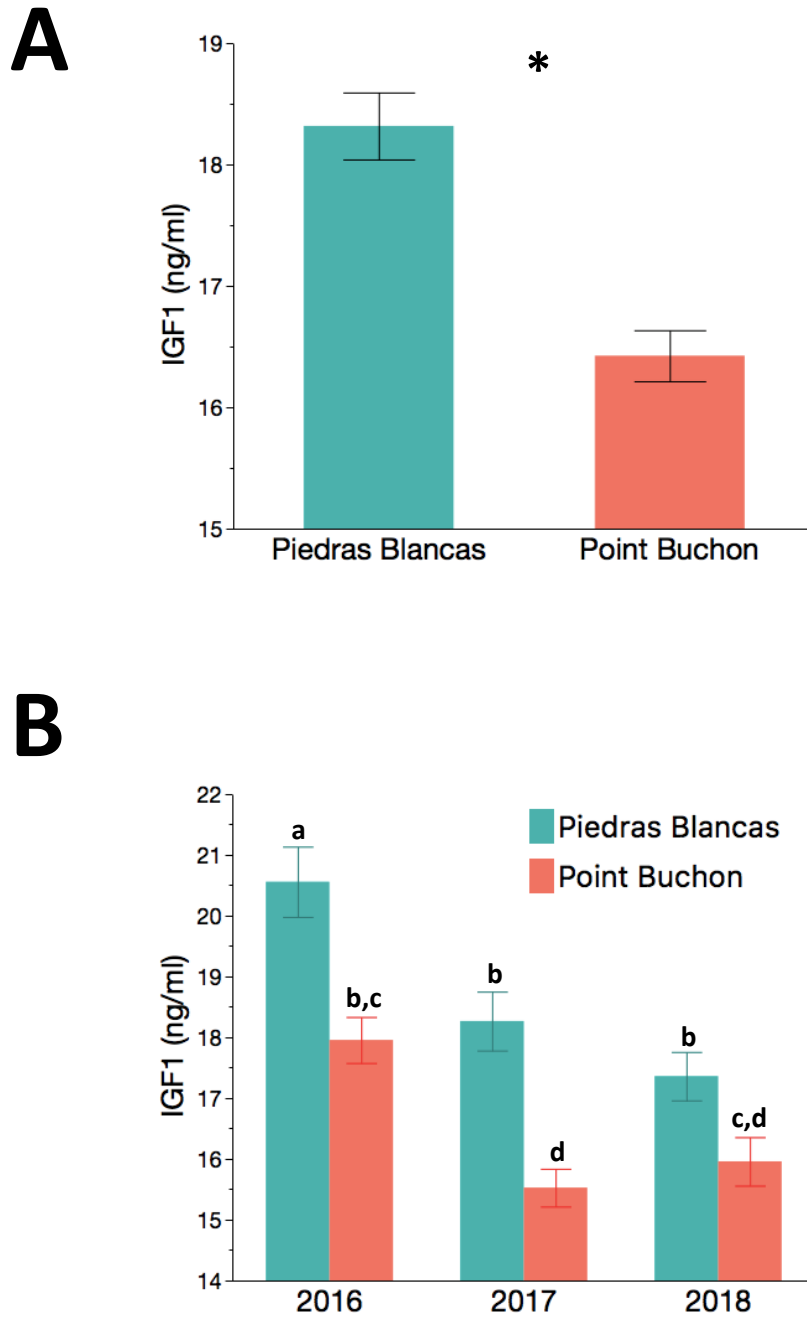
Figure 3. (A) Mean (± SEM) values of plasma Igf-1 for Blue Rockfish collected from the Piedras Blancas and Point Buchon regions. Data are for MPA and reference locations combined within a region. Stars indicate statistically significant differences. **(B)** Mean (± SEM) values of plasma Igf-1 for Blue Rockfish collected from the Piedras Blancas and Point Buchon regions for 2016, 2017, and 2018. Letters indicate post-hoc Tukey's HSD groupings.
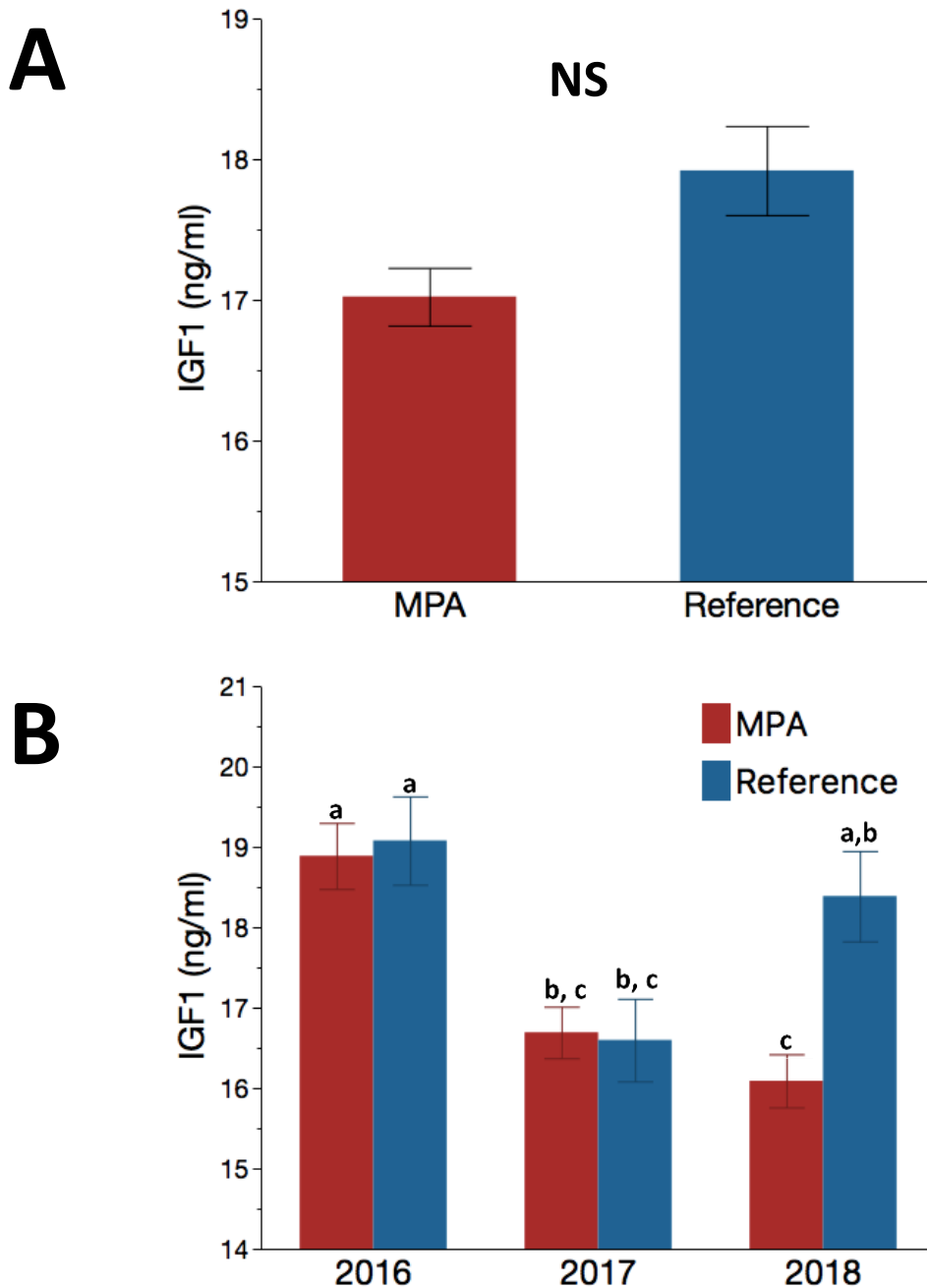
Figure 4. (A) Mean (± SEM) plasma Igf-1 concentrations for Blue Rockfish collected from MPAs and reference areas. NS indicates no statistically significant differences **(B)** Mean (± SEM) values of plasma Igf-1 for Blue Rockfish collected from MPAs and reference areas for 2016, 2017, and 2018. Letters indicate post-hoc Tukey's HSD groupings.
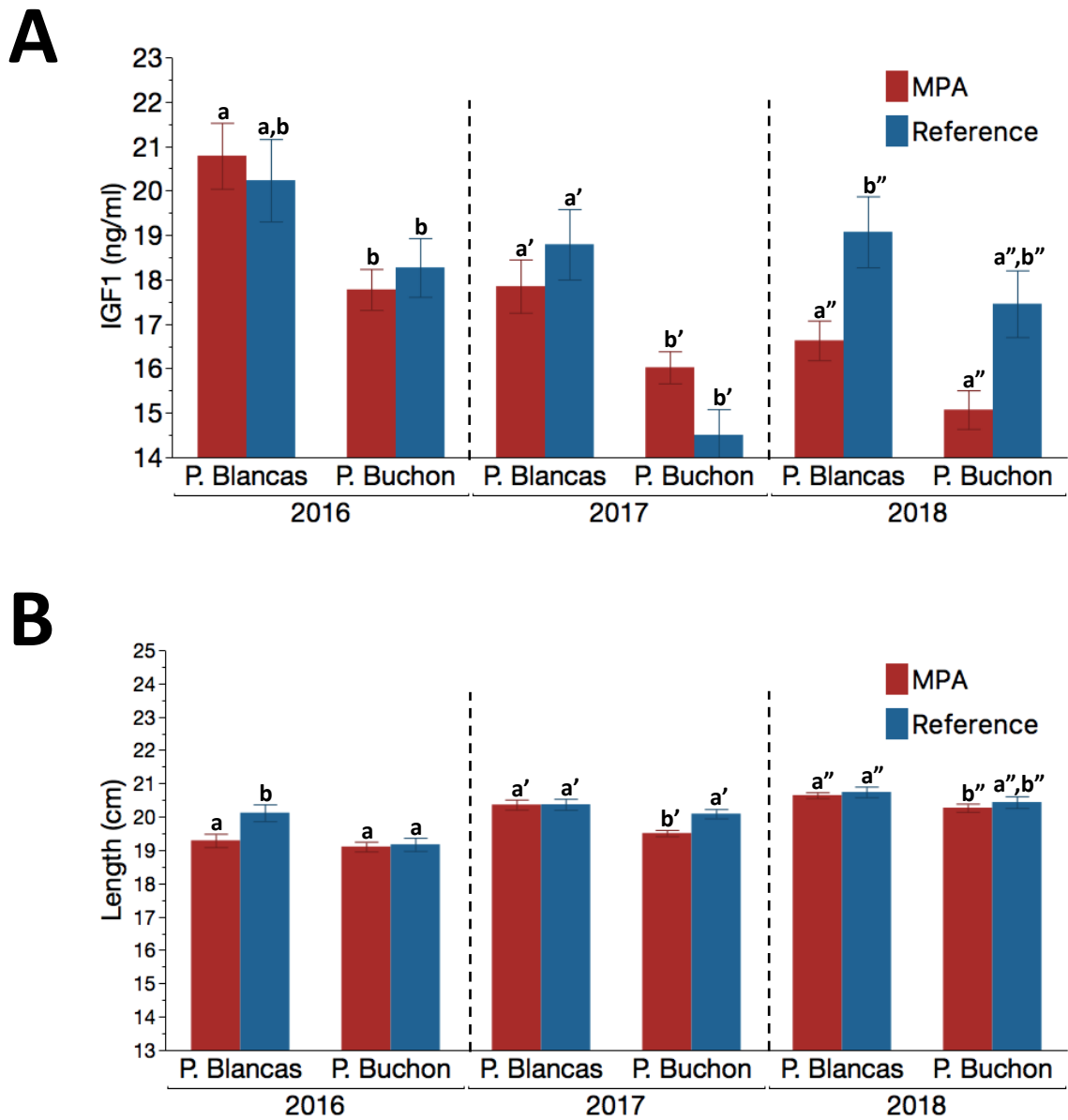
Figure 5. **(A)** Mean (± SEM) values of plasma Igf-1 for Blue Rockfish collected from MPAs and reference areas in both regions for 2016, 2017, and 2018. Letters indicate post-hoc Tukey's HSD groupings for each year tested separately. **(B)** Mean (± SEM) lengths of Blue Rockfish collected from MPAs and reference areas in both regions for 2016, 2017, and 2018. Letters indicate post-hoc Tukey's HSD groupings for each year tested separately.
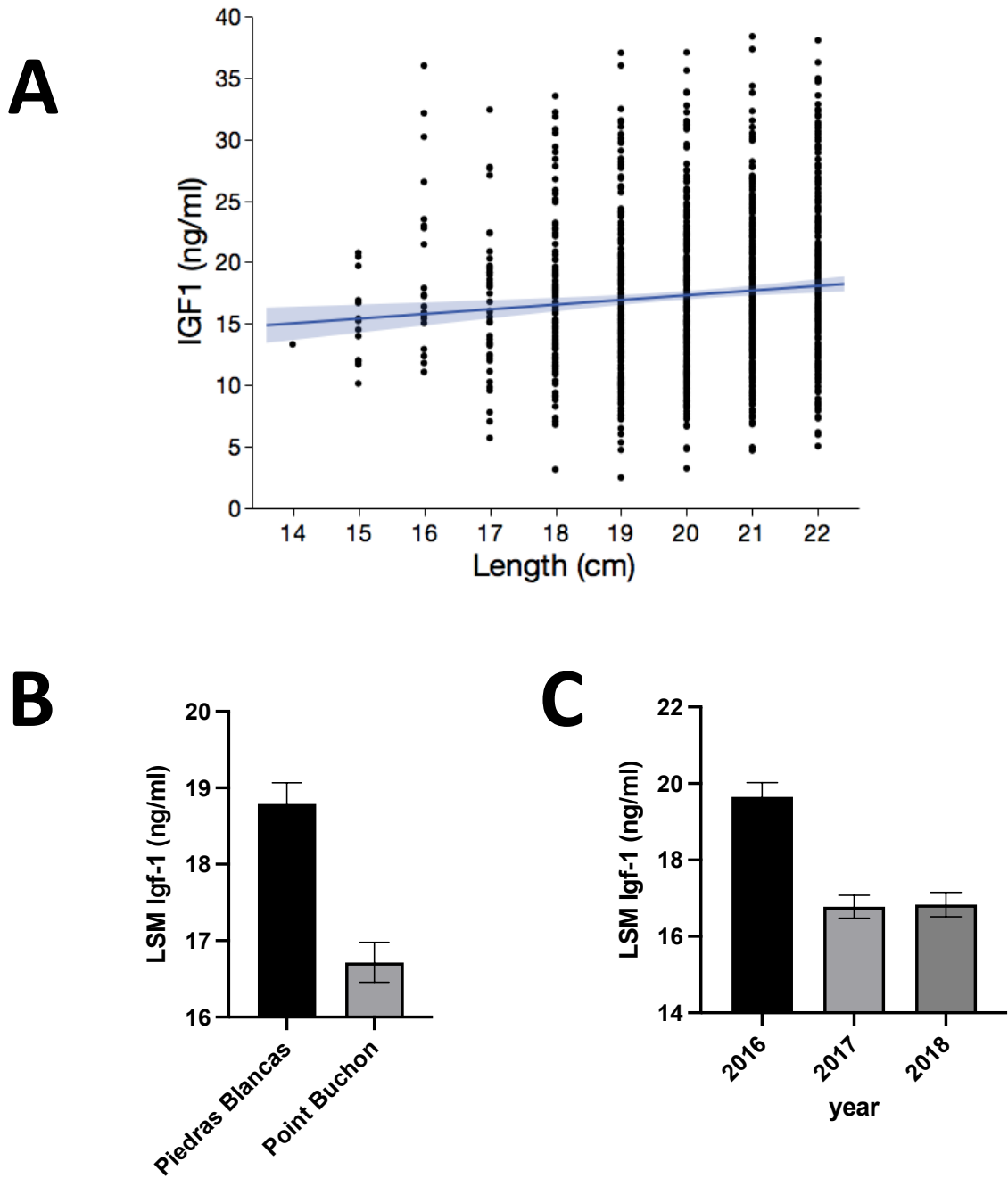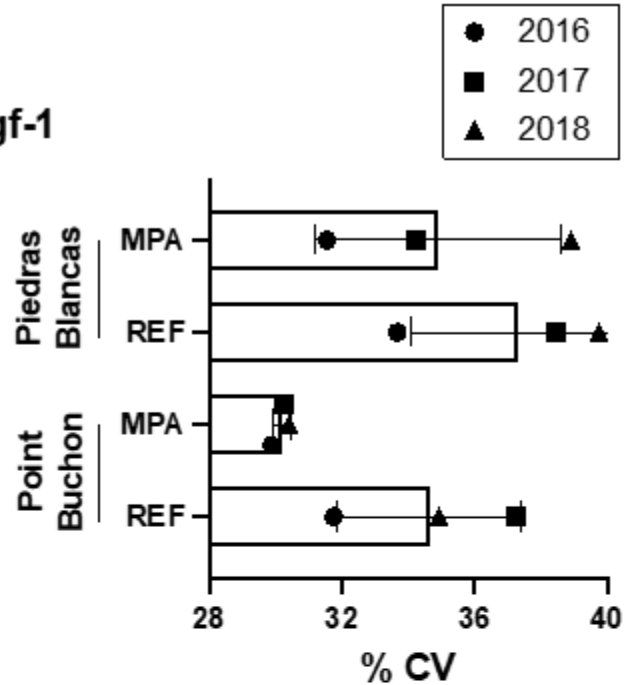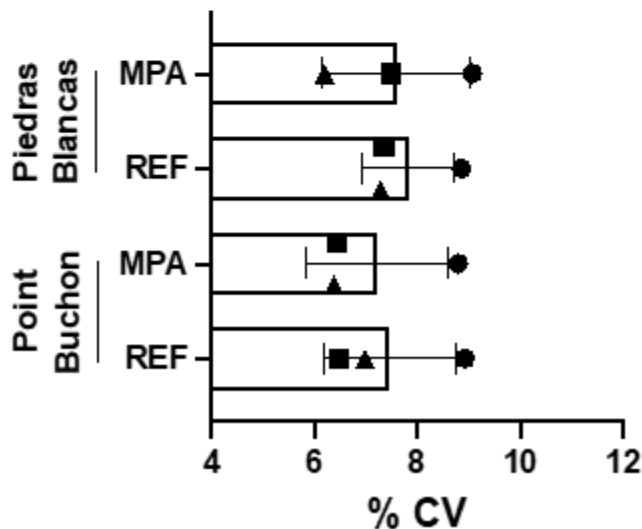
Figure 6 (A) Linear regression (r^2=0.009, p = 0.0006) and standard error (blue) of lengths by plasma Igf-1 for all fish that were less than 23 cm long. ANCOVA analyses using body length as a covariate continued to show a significant difference in Igf-1 between **(B)** geographic regions and **(C)** years. Data plotted as least squares mean (LSM) values (± SEM).

Figure 7. (A) Coefficient of variation (% CV) values for variability in plasma Igf-1 levels than among individual Blue Rockfish was lower in the Point Buchon MPA in all years compared to the reference (REF) area from the region and both the MPA and REF areas from the Piedras Blancas region. Symbols indicate % CV values for 2016, 2017, and 2018, and the bar is the mean % CV across those years **(B)** Mean % CV for body length variation among individual Blue Rockfish did not differ in any year among the MPA and REF areas of the two regions.
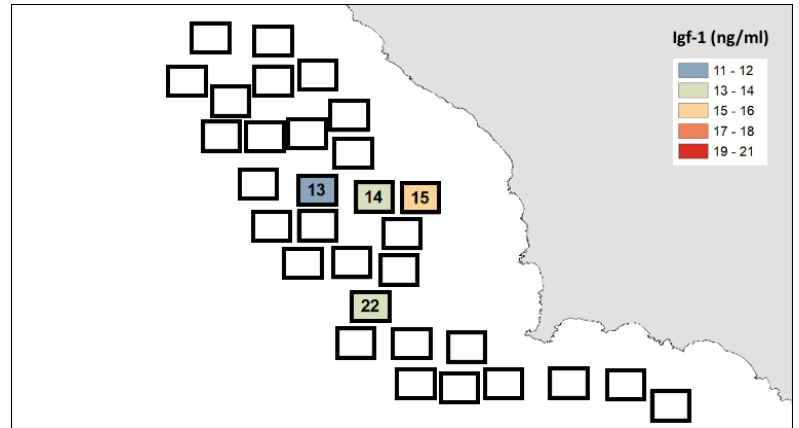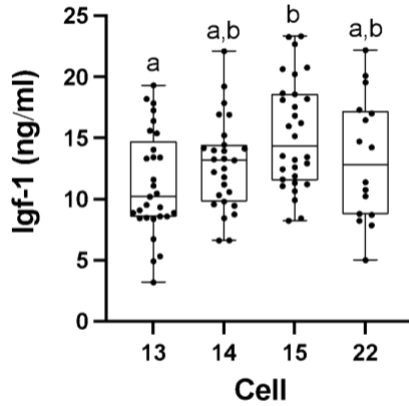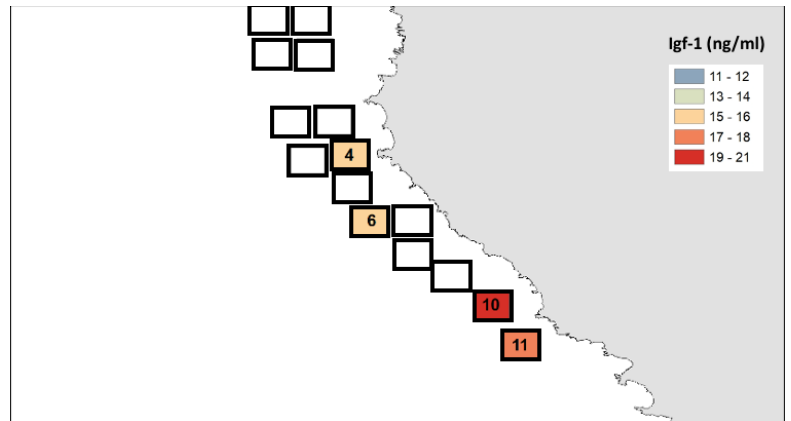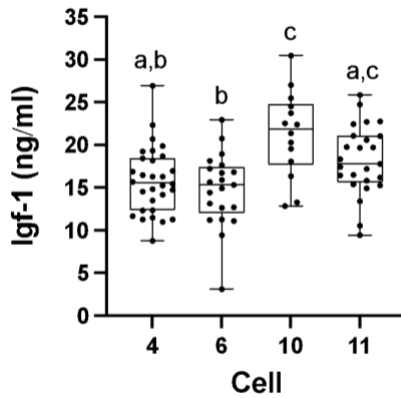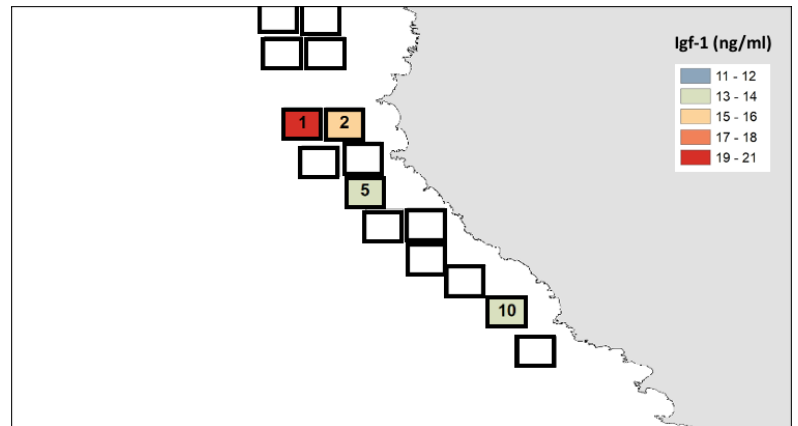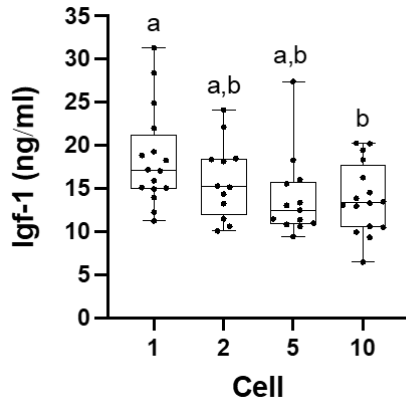
Figure 8. Igf-1 levels from cells sampled from **(A)** the Piedras Blancas MPA on 23 Jul 2018, **(B)** the Point Buchon MPA on 24 Jul 2017, and **(C)** the Point Buchon MPA 7 Aug 2017. Boxplots show first and third quantiles and the center line shows the median. Whiskers represent the range of values. Maps show color coded average Igf-1 levels in each cell sampled on that date.
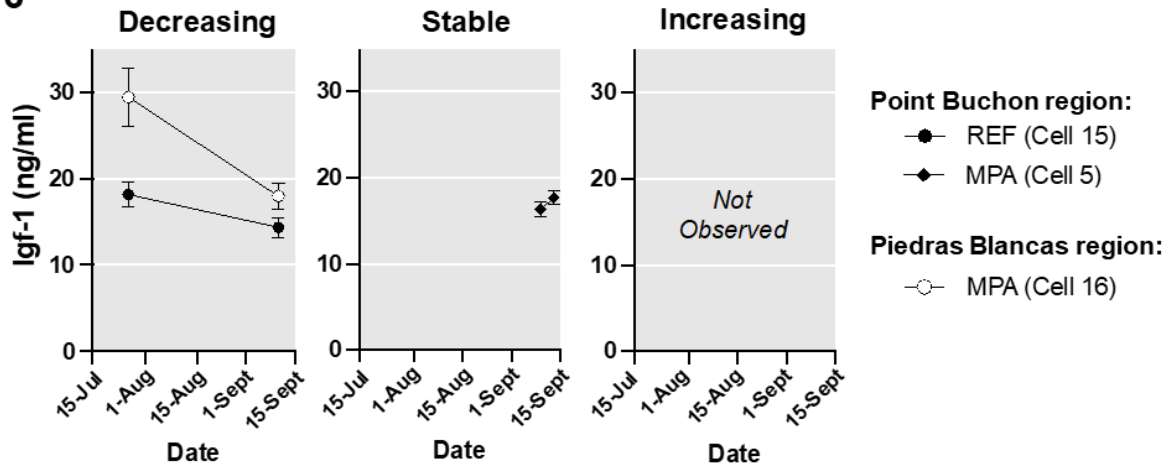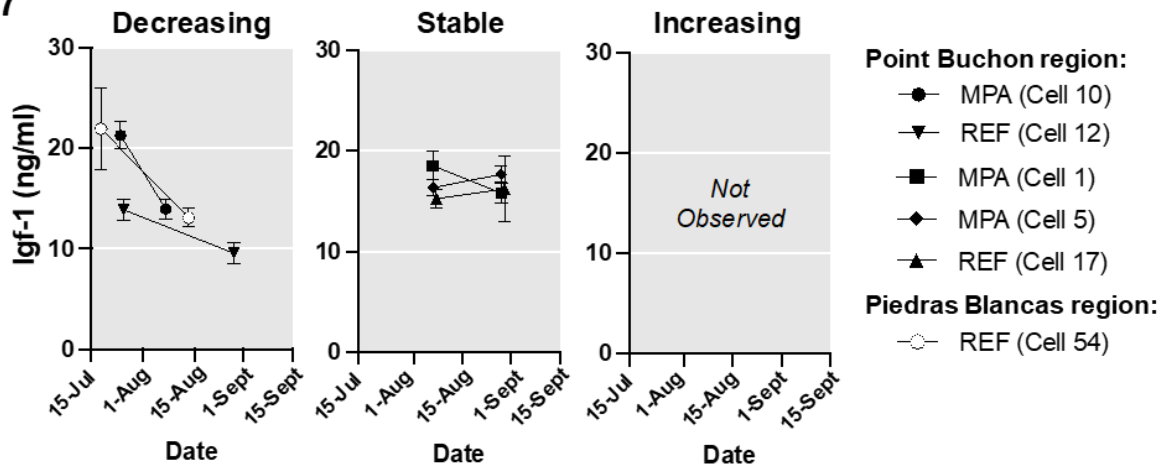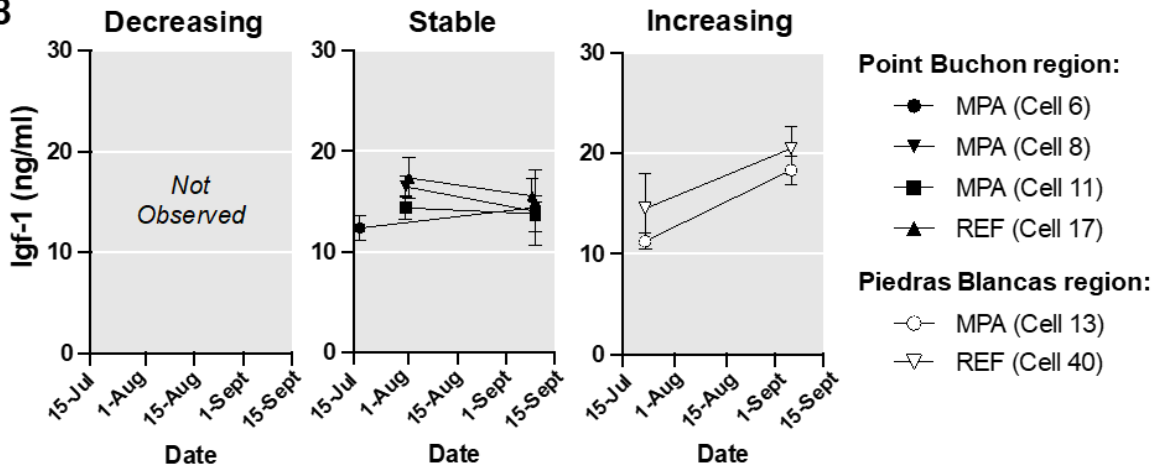
Figure 9. Mean (± SE) Igf-1 concentrations from 500 m^2 fishing cells resampled in the same year. Panels are separated by statistical outcomes of Igf-1 level stability or change across dates (decreasing, stable, or increasing). Symbols designate cell identity coded using color to indicate region (black = Point Buchon, white = Piedras Blancas).

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Appendix 1. Summary of ANOVA results comparing Igf-1 values between years, locations, protection status, all associated interactions, and while accounting for date pair for Blue Rockfish that range in length from 14cm to 35cm. A p-value of 0.05 was used to establish significance and significant p-values are shown in blue.

Source	DF	F-value	p-value
Pair[year,Location]	15	25.6493	<.0001
year	2	13.3812	<.0001
Location	1	44.1165	<.0001
year*Location	2	12.2957	<.0001
Protection	1	1.5694	0.2105
year*Protection	2	4.1172	0.0164
Location*Protection	1	1.8613	0.1727
year*Location*Protection	2	5.1385	0.0060

Appendix 2. Summary of ANOVA results comparing Igf-1 values between years, locations, protection status, all associated interactions, and while accounting for both date pair and length for Blue Rockfish that range in length from 14cm to 22cm. A p-value of 0.05 was used to establish significance and significant p-values are shown in blue.

Source	DF	F-value	p-value
Location	1	51.7252	<.0001
Protection	1	0.1674	0.6825
Protection*Location	1	0.8002	0.3712
Length (cm)	1	16.5304	<.0001
year	2	16.1111	<.0001
Pair[Location,year]	15	17.2814	<.0001
Location*year	2	4.0806	0.0171
Protection*year	2	4.6148	0.0101
Protection*Location*year	2	3.4986	0.0305
Protection*Location*year*Length (	2	0.6983	0.4976
Length (cm)*year	2	0.2562	0.774
Length (cm)*Location	1	0.7805	0.3772
Length (cm)*Protection	1	0.0692	0.7925
Length (cm)*year*Protection	2	0.9205	0.3986
Length (cm)*Location*Protection	1	0.7252	0.3946
Length (cm)*year*Location	2	1.9207	0.1469