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A tale of two species: vermilion and sunset rockfish in the Southern California Bight

Aimee A. Keller^{1*}, John H. Harms^{1*}, Anna Elz², John R. Wallace¹, Jim A. Benante³, and Aaron Chappell⁴

*equal first co-authors

¹Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA

²Lynker Technologies, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112, USA (current address: Fred Hutchinson CRC 1100 Fairview Ave. N. S5-153, Seattle, Washington 98109, USA)

³Pacific States Marine Fisheries Commission, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington, 98112, USA

⁴Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, Oregon 97365, USA

Abstract

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The vermilion rockfish complex consists of two distinct species, vermilion rockfish (*Sebastes miniatus*) and sunset rockfish (*S. crocotulus*) with clear haplotypic differences. Due to a one-way mitochondrial introgression from vermilion into sunset rockfish a high proportion (20-30%) of fish with a vermilion haplotype are characterized as sunset based on nuclear genotype (introgressed sunset, hereafter, introgressed). Here we examined differences in the distribution and biological attributes of vermilion and sunset rockfish (including introgressed individuals) collected during a fisheries independent groundfish survey conducted with hook and line gear in the Southern California Bight in 2014. We saw significant differences in spatial distribution (latitude, depth, and distance from the nearest port and mainland) and biological characteristics (average size, size frequency distribution, weight-length and size-depth relationships) between vermilion rockfish and both introgressed and sunset rockfish but no differences between sunset and introgressed fish. Our analyses established that introgressed and sunset rockfishes shared similar biological and geographic characteristics, with no significant differences based on the features we examined. Consequently, we explored the relationship between the catch of vermilion rockfish collected per site, relative to the combined presence of vermilion, introgressed and sunset rockfishes, and a suite of co-located environmental and geographic variables using binomial generalized additive models (GAMS). The best model explained 95.0% of the deviance, indicating that the occurrence of vermilion, introgressed, and sunset rockfishes depended on latitude, longitude, depth, dissolved oxygen, temperature and distance from port.

46 **1. Introduction**

47 Cryptic speciation appears somewhat common among rockfishes (genus *Sebastes*) in
48 the NE Pacific Ocean with examples including rougheye (*Sebastes aleutianus*) and
49 blackspotted (*Sebastes melanostictus*) rockfish (Gharrett et al., 2005), vermilion (*Sebastes*
50 *miniatus*) and sunset (*Sebastes crocotulus*) rockfish (Hyde et al., 2008), blue (*Sebastes*
51 *mystinus*) and deacon (*Sebastes diaconus*) rockfish (Frable et al., 2015), and others. In
52 general, rockfishes are economically valuable species supporting commercial and
53 recreational fishing ventures along the US west coast (Love et al., 2002; Warlich et al.,
54 2018). Since rockfish life history characteristics (long life, slow growth, low fecundity)
55 make them particularly vulnerable to overexploitation (Love et al., 2002), successful
56 management of rockfish cryptic pairs, in particular, may benefit from identification to the
57 level of species. Taxonomic ambiguity, coupled with life history differences may otherwise
58 result in inappropriate pooling of data, impacting reliability of information on life history
59 parameters, distribution and catch used to inform stock assessments (Garvin et al., 2011;
60 Love, 2011; Hicks et al., 2014). For cryptic species complexes, which cannot be
61 distinguished visually, genetic analyses remains one of the best avenues for separation into
62 individual species (Rocha-Olivares et al., 1999; Rocha-Olivares and Vetter, 1999). Nominal
63 vermilion rockfish, which includes the two sister species (vermilion and sunset rockfish) that
64 cannot be reliably separated by anglers or port samplers in the field, is a valuable
65 recreational groundfish fishery on the west coast (MacCall, 2005) and when not separated
66 into component pairs is the most abundant groundfish collected during the Northwest
67 Fisheries Science Center's Southern California Shelf Rockfish Hook and Line Survey
68 (hereafter called H&L survey) (Keller et al., 2019). Uncovering potential biological,

69 environmental and geographic differences for the vermilion and sunset rockfishes is thus
70 particularly important for successful management of this heavily exploited species complex.
71 Once identified, such differences may help clarify historic catch and landings data, generate
72 more accurate life history profiles and reduce uncertainty for stock assessments. Without
73 definitive species identification, management measures based on spatial or depth restrictions
74 could favor one component of the complex over the other and lead to overexploitation (Hyde
75 et al., 2008).

76 Hyde et al. (2008) recognized vermilion rockfish (*S. miniatus*) as a cryptic species
77 pair and proposed naming the second species, *S. crocotulus*, sunset rockfish. Despite this
78 speciation, a reproductive barrier did not exist between these two species. Specifically, they
79 found that all sunset rockfish had haplotypes and genotypes that assigned together with high
80 likelihood. However, many (>35%) of the fish with the vermilion haplotype in deeper water
81 (>100 m) also assigned to the same genotype as sunset rockfish. Hyde et al. (2008)
82 attributed this second group of vermilion rockfish, i.e. those with disagreement between
83 mitochondrial DNA (mtDNA) haplotype and nuclear genotype, to a one-way mitochondrial
84 introgression from vermilion into sunset rockfish (introgressed sunset, hereafter
85 introgressed).

86 Because of the relatively recent discovery of cryptic speciation within
87 nominal vermilion rockfish (i.e. the vermilion complex), the distribution and
88 biology of the component species pair, as well as introgressed forms, remains
89 largely undescribed (Love and Passarelli, 2020). Prior to separation, Love et al.

90 (2002) reported a geographic range for the combined species complex from
91 Prince William Sound, Alaska to Islas central Baja California with a depth
92 range from 12–478 m. Love et al. (2002) further noted a maximum size of 76
93 cm and maximum age of 60 years for vermilion rockfish, with females larger
94 and longer lived than males. Following separation, Hyde and Vetter (2009)
95 describe true vermilion rockfish as abundant from central Oregon to Punta
96 Baja, Mexico at depths <100 m. Sunset rockfish, however, occurred primarily
97 south of Pt. Conception, CA at depths >100 m with both species thought to
98 display high site fidelity following the pelagic larval and juvenile life stages.
99 Both vermilion and sunset rockfishes associate with rocky, high relief habitat
100 but Hyde and Vetter (2009) noted that adult vermilion rockfish occur
101 primarily at shallower depths (usually <100 m) than sunset rockfish (usually
102 >100 m).

103 On the US west coast, the vermilion-sunset complex is economically very
104 valuable, particularly within the recreational sector. In 2019, the complex was the third
105 most-commonly landed species on the coast among recreational anglers and the most commonly

106 landed recreational species in California (RecFIN, extracted 12/13/2021). Annual removals have
107 increased steadily in recent years (2011 to 2019) (Dick et al., 2021). A recent federal stock
108 assessment reported the combined catch for the complex south of Pt.
109 Conception, CA and noted that the recreational fleet accounted for the majority
110 of historical catch (Dick et al., 2021). The vermilion complex is currently managed
111 in aggregate with other minor shelf rockfish species and contributes to the
112 combined overfishing limit (OFL) for this group, which is not being exceeded.
113 Total mortality of the vermilion complex, however, has exceeded their
114 component OFL contribution in southern California from 2015–2019. Harvest
115 rates for the vermilion complex peaked in southern California in the 1990s, and
116 then declined to near-target fishing levels for the past two decades, though rates
117 have been elevated in recent years (Dick et al., 2021).

118 Management measures enacted to protect overfished rockfishes in the
119 early 2000s (such as the Rockfish Conservation Area and Cowcod Conservation
120 Areas), often relied on depth restrictions (PFMC, 2008, 2011; Mason et al., 2012). By
121 limiting fishing to depths less than 36 to 110 m, these spatial closures may have

122 unintentionally afforded greater protection to the deeper-dwelling sunset
123 rockfish versus vermilion. Recently elevated recreational harvest rates may
124 indicate that overexploitation of the complex is a potential concern in the near
125 future in a scenario where impacts on vermilion rockfish may be obscured by a
126 more abundant sunset rockfish population responding to the disparate protection
127 afforded by spatial management measures. The recent increase in recreational catch
128 highlights a need to separate this highly sought after complex into individual
129 species for management purposes.

130 Here we examined the distribution and biological characteristics for vermilion and
131 sunset rockfish to add to the sparse information currently available on size, weight, depth,
132 weight-length relationship and frequency distributions (latitude, depth, distance from
133 mainland and port, length, weight). We used data collected during the 2014 H&L survey
134 conducted in the Southern California Bight (SCB) since genetic sequencing data for the
135 vermilion-sunset complex are currently unavailable for additional years. Our goal was to
136 examine the distribution and biology of vermilion and sunset rockfish and evaluate if
137 introgressed fish were more similar to vermilion or non-introgressed sunset rockfish. We
138 conducted a rigorous comparison of their respective spatial and depth distributions as well as
139 various biological attributes to answer questions on how vermilion and sunset rockfish differ
140 and to what degree introgression manifests as a biologically intermediate form of the two

141 species. Definitive species identification for the vermilion/sunset complex, with updated
142 information on distribution and biology, will provide an essential step in improving future
143 species-specific stock assessments for these recreationally and commercially important
144 groundfish.

145 **2. Materials and Methods**

146 *2.1 Survey design and samples*

147 In 2014, the NWFSC conducted an annual fishery independent survey in untrawlable
148 habitat (reefs, banks, and hard-bottom) off the southern California coast (Harms et al., 2008,
149 2010; Keller et al., 2019). Sampling occurred at fixed sites from late September through early
150 October aboard vessels chartered from the local sportfishing fleet, also commonly referred to as
151 commercial passenger fishing vessels (CPFV). Sampling sites were located via a differential
152 global positioning system (DGPS) navigation unit (Garmin 152, Garmin International Inc.,
153 Olathe, Kansas, USA) with each site visited once. Vessel captains fished between depths of 37–
154 229 m (median 103 m, IQR 55 m) within a 91.4 m (100-yard) radius established around each site
155 to allow flexibility in response to prevailing wind and weather conditions.

156 At each site, three deckhands made five coordinated drops with hook and line gear set
157 using rod and reel. Fishers used a vertical, five-hook gangion similar to recreational gear often
158 used to capture shelf rockfishes in the study area. Both a shrimp fly lure (red and yellow bucktail
159 bristle) and a frozen squid strip were used to bait each hook. Each drop had a maximum soak
160 time of 5 minutes with a combined maximum catch of 75 fish per site. Following each set, we
161 recorded the total number of recovered hooks relative to the 75 deployed hooks per site.
162 Following capture, scientists subdivided the catch into managed versus non-managed species.
163 For managed species, such as the vermilion complex, we then identified, counted, sexed,

164 measured (length, cm) and weighed (kg) each fish. In addition, we collected otoliths and tissue
165 samples from all federally managed species.

166 We deployed a Sea-Bird SBE 19plus V2 SeaCAT Profiler CTD (Sea-Bird Electronics
167 Inc., Bellevue, Washington) equipped with a calibrated SBE 43 polarographic membrane-type
168 oxygen sensor at each site to provide water column profiles for dissolved oxygen (DO, mL L⁻¹),
169 salinity (S, ppt), temperature (T, °C) and on bottom depth (Z, m).

170 *2.2 Tissue collection and DNA techniques*

171 During the 2014 H&L survey, we collected tissue (~1 cm²) for DNA extraction from
172 individuals identified in the field as nominal vermilion rockfish. Tissue samples from left
173 pectoral fins were stored and dried on chromatography paper without alcohol preservative
174 (LaHood et al., 2008). Initially we used mtDNA to separate vermilion and sunset rockfish to
175 species but following Hyde et al. (2008), who identified a one-way introgression of mtDNA from
176 vermilion into sunset (thus rendering a species call of vermilion rockfish ambiguous), we used
177 the mtDNA marker results to delineate non-introgressed sunsets from individuals with vermilion
178 haplotypes. Using microsatellite markers, we further examined individuals with vermilion
179 haplotypes for evidence of introgression to delineate true vermilion from introgressed sunset
180 rockfish.

181 We extracted genomic DNA from 2-mm discs punch-cut from each paper-mounted
182 finclip (LaHood et al., 2008) using a Chelex-100 (Bio-Rad Laboratories) and proteinase-K
183 boiling technique altered to accommodate a 96-well format (Miller and Kapuscinski, 1996; Hyde
184 et al., 2005). We completed the initial separation of the vermilion-sunset species complex into
185 species via single nucleotide polymorphism (SNP) assays. We sequenced 1141 base pair (bp) of
186 the cytochrome *b* (*cytb*) mitochondrial locus (mtDNA) (Roches-Olivares and Vetter, 1999 and

187 references therein) for three vermilion vouchered tissues, and additional sequences from
188 GenBank for known species, including the closely related canary rockfish (*S. pinniger*).

189 Based on sequence information we chose two-mtDNA *cytb* SNPs to differentiate vermilion
190 and sunset rockfishes into species and a third SNP that excluded canary rockfish. Diagnostic
191 sites were developed into 40X custom Taqman-minor-groove binding allelic discrimination
192 assays (Applied Biosystems, Foster City, CA) which included the following primers for sunset
193 rockfish (forward: 5'ACCGTTATCACCAACCTACTCTCT 3'; reverse: 5'GTAAGGGTT
194 GCATT GTCTACTGAGA 3') and vermilion rockfish (forward: 5'CCCGATTCTTTGCTTT
195 CCACTTC 3'; reverse: 5'GGAAAAGGAGGTGGACTATGGTT) and fluorescent probes for
196 sunset rockfish (VIC: 5'CCACCTCAGATTCATT 3'; FAM: 5'CCACCTCAAATTCATT 3')
197 and vermilion rockfish (VIC: 5'CCCTTTGTGATTGCAG3'; FAM: 5'CCCTTTGTAATTGCAG
198 3'). Real-time polymerase chain reaction (PCR) was conducted in 384-well plates in 5 μ L
199 reactions containing 2 μ L DNA, μ L 2.5 μ L 2X Taqman Master Mix, 0.25 μ L 20X SNP mix and
200 0.25 μ L of water and included positives and negatives for each assay. Thermal-cycling was
201 performed on an Applied Biosystems (Foster City, CA) ABI-7900 sequence detection system.

202 We used the results from the mtDNA SNPs to separate individuals into one group
203 composed of suspected, non-introgressed sunsets and a second group that we believed included
204 both true vermilion rockfish (e.g. vermilion haplotype and genotype) and introgressed sunset
205 (with a vermilion haplotype but a sunset nuclear genotype) (Hyde et al., 2008). A microsatellite
206 multiplex containing Sra7-7-PET, Sra7-25-NED (Westermen et al., 2005), Sra15-23-VIC
207 (GenBank: AF269060.1, Westermen unpublished), and Spi6-FAM (Gomez -Uchida et al., 2003)
208 was developed to assign a nuclear genotype to the mtDNA SNP identified vermilion samples
209 (which included introgressed sunset) and complete their separation into introgressed sunset and

210 vermilion rockfish. As a QA-QC measure, we also ran a small subset of the known, non-
211 introgressed sunset samples (also originally identified by mtDNA SNPs) using the same
212 method. Vermilion rockfish mtDNA, sunset rockfish mtDNA, and two controls of each species
213 were separately amplified at each locus using PCR in 10 μ L reactions consisting of 1X buffer, 2
214 mM MgCl₂, 1X BSA (bovine serum albumin), 200 μ M dNTPs, 0.2 μ M forward primer, 0.5 μ M
215 reverse primer, 0.05 units of *Taq* polymerase, and 2 μ L of DNA. PCRs were diluted such that
216 two loci were included in each dilution volume (1:50 for Sra7-25-NED and Sra7-7-PET; 1:150
217 for Sra15-23-VIC and Spi6-FAM). Each 1 μ L dilution was combined in 10 μ L of LIZ500
218 (Applied Biosystems, Foster City, CA), denatured and analyzed using an ABI-3730 automated
219 capillary sequencer (Applied Biosystems, Foster City, CA) for fragment analysis.

220 To assign groups based on allele frequency, samples with complete or one missing
221 nuclear genotype were included in *Structure* analyses (version 2.1) with 50,000 burn-in steps,
222 100,000 iterations and two inferred clusters ($k = 2$) (Pritchard et al., 2000; Hyde et al., 2008).
223 Nominal vermilion rockfish were assigned as either true vermilion or introgressed using an
224 assignment criteria $>90\%$.

225 *2.3 Distribution and CPUE*

226 To examine geographic distributions for the three subgroups we calculated site-specific
227 CPUE rates in 2014. We calculated CPUE ($n \text{ site}^{-1}$) for vermilion, introgressed and sunset
228 rockfishes as the total number of individuals caught divided by the proportion of the full
229 complement of 75 hooks recovered at the end of each set (i.e. $75 \times \text{catch}/\text{hooks recovered}$). This
230 standardization allowed for comparisons in catch among sites if recovery of the full complement
231 of 75 deployed hooks did not occur following a set, hooks were lost, or a drop not conducted due
232 to logistical issues. To provide information on differences in the distribution of vermilion,

233 introgressed and sunset rockfishes as sampled during the 2014 H&L survey, we also examined
234 catch-weighted average latitude ($^{\circ}$ N), depth (m), distance from mainland and distance from port
235 (nm) for each subgroup.

236 To test the null hypothesis of no significant differences in distribution among subgroups,
237 we next statistically compared latitude, depth and distance (from mainland and port) among the
238 three subgroups of the vermilion complex using ANOVAs with unequal variance (PROC GLM
239 in SAS) with significant results followed by multiple comparison of means tests (Student-
240 Newman-Keuls test, SNK). To control for unequal variance we used natural log transformed
241 variables. Based on these analyses we then combined homogeneous subgroups (i.e. subgroups
242 not found significantly different in the first analysis) and repeated the analyses to assess overall
243 differences in distribution. We evaluated distance from port among subgroups as a proxy for
244 fishing effort since catch and effort tend to decrease in recreational fisheries when travel time
245 and fuel costs increase (Bellquist and Semmens, 2016; Frid et al., 2016).

246 We also compared frequency distributions for latitude, depth and distance (from
247 mainland and port) between paired subgroups (initially vermilion versus sunset; vermilion versus
248 introgressed; sunset versus introgressed) using non-parametric, two-sample Kolmogorov-
249 Smirnov (K-S) analysis (SAS PROC NPAR1WAY, SAS v. 9.3, SAS Institute, Inc., Cary, North
250 Carolina; Daniel, 1990). We used this analysis to test the assumption that the frequency
251 distributions for each variable are the same among subgroups. Based on the initial K-S analysis,
252 we next combined data in subgroups with no significant differences and repeated the analysis,
253 for each variable, comparing the combined data to the remaining pair (e.g. sunset plus
254 introgressed versus vermilion). We plotted binned frequency distributions (depth, latitude and
255 distance) for subgroups with significant differences utilizing eleven bins for depth (60 to 225 m

256 by 15 m), 6 bins for latitude (32.2 to 34.6 °N by 0.4°N), and 7 bins for distance (0 to 105 bins by
257 15 nm).

258

259 *2.4 Biological characteristics*

260 2.4.1. Size analysis

261 We compared size information among the three subgroups as mean, minimum and
262 maximum length (cm) and weight (kg) separated by sex and with sexes pooled. We also
263 statistically compared average weight and length by subgroups and sex using ANOVAs with
264 unequal variance followed by a multiple comparison of means test (SNK Student-Newman-
265 Keuls Test). To control for unequal variance we used natural log transformed variables.

266 2.4.2 Weight – length relationship

267 We examined weight-length relationships for vermilion, sunset and introgressed
268 rockfishes using the allometric equation:

$$269 \quad W = aL^b \quad (1)$$

270 with weight, W in kg; fork length, L in cm; and constants a and b . After natural log
271 transformations for both weight and fork length, we fit equations via generalized linear models
272 (GLM) using R ver. 4.0.2 with an identity link function and normally distributed errors (Le Cren,
273 1951; R Core Team, 2020). We next examined if weight-length regressions varied among the
274 subgroups and by sex (female, male). We initially fit equations using all data, then with and
275 without sex, then combinations within subgroups. We compared these weight-length models
276 using analysis of covariance (ANCOVA), with sex and subgroups as covariates. We determine
277 relative support among all competing models with Akaike's Information Criterion (AIC_i) after
278 calculating Δ_i as:

279 $\Delta_i = AIC_i - AIC_{\min}$ (2)

280 with AIC_{\min} the minimum AIC-value and the best model defined as $\Delta_i = 0$.

281

282 2.4.3 Size – depth relationship

283 Since rockfishes often exhibit ontogenetic migrations resulting in species-specific habitat
284 depths with size (Love et al., 2002), we also examined variations in length and weight versus
285 depth among the three subgroups of the vermilion-sunset complex. We used a procedure similar
286 to that described above for weight versus length relationships to test the hypothesis of no
287 difference in size with depth among subgroups. We compared length (L , cm) versus depth (Z , m)
288 as:

289 $L = a Z^b$ (3)

290 and weight (W , kg) versus depth (Z , m) as:

291 $W = a Z^b$ (4)

292 with constants a and b for each relationship. We used natural log transformed variables (length,
293 weight, depth) and fit the equations via GLM using the identity link function and normally
294 distributed error (R Core Team, 2020). We tested the null hypothesis that covariates
295 (subgroups and sex) have no effect on size versus depth via ANCOVA. We fit
296 models in stages starting with a fit to all data without accounting for other
297 effects, followed by adding the gender effect and then accounting for subgroups
298 (two or three). We combined covariates (sex and subgroups) with no significant differences
299 based on the ANCOVA analysis and summarized variations in size (length and weight) versus

300 depth. We determined relative support among models via AIC-values. For models with $\Delta_i < 2$,
301 that have substantial support relative to the best model (Burnham and Anderson, 2002), we
302 calculated weighted AIC-values (w_i) following Wagenmakers and Farrell (2004).

303 To statistically examine length and weight frequency distributions we used non-
304 parametric, two-sample K-S analysis as previously described. Based on the analyses we grouped
305 homogeneous samples and examined paired differences for subgroups. We subsequently lumped
306 subgroups with no significant differences to display results graphically and summarized length
307 frequency distributions using twenty-four, 2-cm bins from 16 to 64 cm. Similarly, we divided
308 weight into twenty-four, 0.2 bins from 0.02 kg to 4.66 kg.

309 *2.5 Modeling Species Composition*

310 We evaluated the proportion of vermilion rockfish (P_V) as CPUE ($n \text{ site}^{-1}$) relative to the
311 sum of vermilion, introgressed and sunset CPUE ($n \text{ site}^{-1}$) using a binomial Generalized Additive
312 Model (GAM), fitted to P_V as a function of environmental and spatial variables (Wood, 2006). In
313 general, GAMs allow incorporation of non-linear relationships in the model through non-
314 parametric smoothers thus offering some potential advantage relative to linear regression models
315 (Hastie and Tibshirani, 1990). We included environmental measurements (salinity, temperature,
316 dissolved oxygen, and bottom depth) and spatial elements (latitude, longitude and distance from
317 the nearest major port or mainland) as explanatory variables in the model. We evaluated
318 collinearity among predictor variables (environmental and spatial) for inclusion in GAMs, by
319 calculating Pearson's correlation coefficients using R ver. 4.0.2 but retained all variables during
320 the model exploration phase (R Core Team, 2020). We fit a binomial GAM with a logit link
321 function using the "mgcv" package (version 1.28–34; Wood, 2011). To avoid losing information
322 about the site-level precision of each proportion, we fit the model with prior weights equal to the

323 denominator of P_V (note: this is a special use of prior weights for GLM/GAMs with binomial
324 errors in R, see `stats::glm help`, R Core Team, 2020). The model structure was:
325 $\text{logit}(P_V) \approx a + s_1(\text{Long}, \text{Lat}) + s_2(\text{DO}) + s_3(\text{S}) + s_4(\text{Z}) + s_5(\text{T}) + s_6(\text{D})$ (weights not shown) (5)
326 where a binomial GAM with a logit link function (logit) is used to relate P_V (vermilion CPUE
327 versus the sum of vermilion, introgressed and sunset CPUE) to the intercept term (a), longitude
328 (Long, °W) and latitude Lat, °N), dissolved oxygen (DO, mL L⁻¹), salinity (S, ppt), temperature
329 (T, °C), depth (Z, m) and distance (D, nm), s_1 and s_{2-6} are two-dimensional and one-dimensional
330 smooth functions respectively, in this case thin plate regression splines (Wood, 2006). The
331 degrees of freedom for each smooth term in the GAM was constrained to four ($k = 4$), based on
332 sensitivity analyses.

333 The most parsimonious model was selected based on AIC-values ($\Delta_i = 0$) by adding or
334 removing covariates until no further reduction in AIC occurred. The rank degrees of freedom for
335 AIC-values used in the analyses were adjusted following Wood et al. (2016). During the model
336 exploration stage, we progressively evaluated which covariates produced the best model, based
337 on reduction in AIC value, for each step in the analysis. In addition, we developed a
338 parsimonious set of models with increasing number of variables to evaluate their use in
339 management when a full suite of environmental measures may not be available.

340 **3. Results**

341 *3.1 Hook and Line Survey and sampling in 2014*

342 In 2014, we successfully sampled 162 sites from Point Arguello, CA (34°30' N) to the
343 US Mexico border (32°00' N (Fig. 1). Sampling occurred from Sept. 28, 2014 to Oct. 8, 2014
344 aboard three chartered CPFVs, the *F/V Mirage*, *F/V Toronado* and *F/V Aggressor* (58 to 72 ft
345 length overall). On average, we recovered 73 (± 5.2 SD) of the 75 hooks deployed at each site.

346 In 2014, we recovered a full complement of hooks ($n = 75$) at the majority of sites (58%) where
347 the vermilion complex was captured. We recovered greater than 61 hooks at 116 sites and a low
348 number of hooks ($n = 45$) at a single site. We captured nominal vermilion rockfish at 117 of the
349 162 sites sampled in 2014 with a maximum catch of 60 per site (depth range 49.2 to 211 m). We
350 recorded environmental data (depth, temperature, salinity, dissolved oxygen) at 106 to 117 of the
351 sites where individuals of the vermilion complex were present.

352 *3.2 DNA*

353 The initial separation of the 2014 vermilion-sunset samples ($n = 1730$) into species via
354 SNP within the mtDNA genome revealed the presence of 839 vermilion, 887 sunset rockfishes,
355 one canary rockfish and three failed assays due to insufficient DNA. Based on nuclear
356 microsatellite markers, 550 of the 839 nominal vermilion rockfish were identified as true
357 vermilion and 239 as introgressed fish with the remainder either classified as intermediate
358 hybrids ($n = 31$) or with insufficient tissue or DNA to complete separation via microsatellites. A
359 subset of sunset SNP mtDNA samples ($n = 49$) were also evaluated with microsatellite markers
360 and confirmed the majority ($n = 33$) as true sunset. We excluded all intermediate hybrids,
361 misidentifications and incomplete separations from further analyses.

362 *3.3 Distribution and CPUE*

363
364 We observed geographic variability in site-specific CPUE ($n \text{ site}^{-1}$) in 2014 between
365 vermilion (Fig. 1a) versus introgressed (Fig. 1b) and sunset rockfish (Fig. 1c). Distribution charts
366 visually indicate a more northerly occurrence of vermilion rockfish, particularly near Point
367 Conception, CA (Fig. 1a). The high CPUE of vermilion rockfish in and around Pt. Conception
368 also contributes to the difference in catch-weighted distance from the mainland relative to the
369 other two subgroups (Fig. 2) given this area's remoteness from the closest fishing port.

370 Distributions for introgressed (Fig. 1b) and sunset (Fig. 1c) rockfishes appear very similar, despite
371 the higher CPUE observed for sunset rockfish (note difference in scale).

372 When adjusted by the number of hooks recovered per site, we observed a total catch of
373 1740 for the vermilion complex overall with 566 vermilion rockfish, 249 introgressed, and 925
374 sunset rockfish taken in 2014 (Table 1). We collected vermilion rockfish at 61 sites, introgressed
375 at 59 sites, sunset at 87 sites (Table 1) and a combination of introgressed plus sunset rockfish at
376 97 sites. Based on catch-weighted averages, vermilion rockfish occurred at shallower depths
377 (Fig. 2a), further north (Fig. 2b), and closer to the mainland relative to sunset and introgressed
378 sunset rockfishes (Fig. 2c). We saw a low correlation ($r = 11$) between depth and distance from
379 the mainland at the sites ($n = 106$) where the vermilion complex occurred in 2014. Although
380 average catch-weighted distance from the nearest port was similar among the three subgroups
381 (Table 1), both introgressed and sunset rockfishes exhibited substantially greater interquartile
382 ranges for this metric relative to vermilion catch (Fig. 2d).

383 Significant differences existed in both means and frequency distributions (K-S test, see
384 below) among the three subgroups for geographic location and depth. Statistical comparisons via
385 ANOVA revealed highly significant differences ($p < 0.0001$) in depth, latitude and distance from
386 both mainland and port for the vermilion-sunset species complex by subgroup (Table 2). When
387 followed by multiple comparison tests (Student Newman-Keuls, SNK), we noted that vermilion
388 rockfish were significantly shallower, further north, closer to the mainland and farther from
389 fishing ports relative to both introgressed and sunset rockfish as separate subgroups. For
390 significant ANOVAs, we subsequently combined subgroups with no differences (i.e.
391 introgressed and sunset) and repeated the analysis. SNK tests revealed that depth, latitude and

392 distance from the mainland and port remained significantly different for vermilion rockfish
393 compared to the combined introgressed and sunset rockfish group (Table 2).

394 Comparison of frequency distributions indicated highly significant differences (described
395 below) between vermilion rockfish versus introgressed ($p < 0.0001$) and vermilion rockfish versus
396 sunset rockfish ($p < 0.0001$) based on non-parametric, two-sample Kolmogorov-Smirnov analyses
397 for depth, latitude, distance from the mainland and port but not between introgressed and sunset
398 rockfish (Table 3). Similarly, we observed significant differences when we pooled data for
399 introgressed and sunset and repeated the comparison with vermilion rockfishes (Fig. 3a). The
400 depth frequency distribution for vermilion rockfish exhibited a generally normal pattern
401 extending from ~70 to 135 m with peak occurrence centered at ~100 m and none at depths >133
402 m (Fig. 3a). By comparison, introgressed plus sunset rockfish displayed a relatively uniform
403 depth frequency distribution from ~90 to ~165 m then decreased frequency at greater depths and
404 very few at the shallowest depth interval (Fig. 3a). The latitudinal distribution for vermilion
405 rockfish exhibited increasing frequency at higher latitudes while the significantly different
406 distribution for sunset plus introgressed appeared uniform within the latitudinal range sampled
407 with a slight peak ~33.8° N (Fig. 3b). All subgroups exhibited a decline in frequency of
408 occurrence with distance from the mainland; however, introgressed plus sunset rockfishes
409 occurred at greater distances from the mainland than vermilion rockfish (Fig. 3c). Both vermilion
410 rockfish and introgressed plus sunset rockfishes exhibited peak frequency of capture at ~60 nm
411 from the nearest port, but vermilion rockfish rarely occurred beyond this distance (Fig. 3d).
412 Introgressed plus sunset rockfishes occurred at higher frequencies both closer to and further from
413 port relative to vermilion rockfish (Fig. 3d).

414 *3.4 Biological characteristics*

415 3.4.1 Size analysis

416 Fork lengths (cm) and weights (kg) were available for 543 vermilion, 877 sunset and 235
417 introgressed rockfishes in 2014. For all subgroups, females attained greater maximum lengths
418 and weights than males and on average tended to weigh more (Table 4). In general, the average
419 size for vermilion rockfish (females, males and overall) also tended to be smaller with lower
420 mean lengths (Fig. 4a) and weights (Fig. 4b) than sunset or introgressed rockfishes.

421 Based on ANOVAs, we found significant differences in size for the vermilion – sunset
422 species complex by subgroups and sex (Table 5). Initial analyses revealed that both length and
423 weight of vermilion rockfish (females and males) were significantly smaller than sunset and
424 introgressed rockfish. Based on the SNK multiple comparison of means tests we saw no
425 differences in size (length and weight) by sex between sunset and introgressed rockfish. After
426 pooling these two subgroups we confirmed that vermilion rockfish were significantly smaller and
427 weighed less when also compared by sex with the combined sunset plus introgressed subgroup
428 (Table 5).

429 3.4.2 Weight – length relationship

430 ANCOVAs for weight-length relationships, based on measurements from vermilion
431 (male = 274, female = 267), introgressed (male = 120, female = 115), and sunset rockfishes
432 (male = 403, female = 473), indicated differences by subgroup and sex (Table 6a). Model
433 selection via the minimum AIC-value ($\Delta_i = 0$), suggested the best model incorporated two
434 subgroups (vermilion and a combination of introgressed plus sunset) in addition to sex (Table
435 6a). Predicted weight at length was greatest for females relative to males regardless of subgroup
436 (Table 6b). Additionally, weight of vermilion rockfishes tended to increase more rapidly as a
437 function of length relative to the combined introgressed plus sunset subgroup (Table 6b).

438 Vermilion rockfish exhibited significantly different length and weight frequency
439 distributions compared with introgressed and sunset rockfishes (Table 7). Based on non-
440 parametric Kolmogorov-Smirnov analysis, size distributions for vermilion rockfish were
441 significantly different ($p < 0.0001$) when compared separately with either introgressed or sunset
442 rockfishes (Table 7). However, length ($p = 0.29$) and weight ($p = 0.09$) distributions were not
443 different between introgressed and sunset rockfishes. We subsequently pooled data for subgroups
444 with no differences (introgressed and sunset) and confirmed significant differences (described
445 below) between this combined group and vermilion rockfish for length ($p < 0.0001$) and weight
446 ($p < 0.0001$) distributions (Table 7). Length distributions for vermilion rockfish peak at a smaller
447 size (~46 cm) and exhibit a narrower size range relative to introgressed and sunset rockfish (Fig.
448 5a). In addition, vermilion exhibited a severe truncation above 52 cm in length, which we did not
449 observe in the combined introgressed plus sunset subgroup. We saw similar differences in weight
450 frequency distributions with weights of introgressed and sunset rockfish encompassing a greater
451 range and a more gradual decrease in frequency at higher values relative to vermilion rockfish
452 (Fig. 5b).

453 3.4.3. Size – depth relationship

454 Length and weight varied significantly by depth within the vermilion-sunset complex
455 with smaller individuals occurring at shallower depths ($p < 0.0001$). We initially used ANCOVA
456 to determine if sex and subgroup should be included in the analyses of size versus depth. Results
457 indicated that the most appropriate models included significant effects among subgroups
458 ($p < 0.05$) but no significant effects for sex. Model selection, based on AIC, indicated that the
459 most parsimonious models for both length and weight versus depth included separation into two
460 subgroups (vermilion rockfish versus a combination of introgressed and sunset rockfishes)

461 without separation by sex (Table 8a). There was substantial support ($\Delta_i < 2$) for secondary models
462 that included separation into two subgroups, as above, but with separation by sex (Table 8a).
463 Weighted AIC-values (w_i , not shown) indicated the most parsimonious models were 1.4 (length
464 versus depth) and 2.6 (weight versus depth) times more likely to be better than the second best
465 models (Wagenmakers and Farrell, 2004). Predicted length and weight for vermilion rockfish
466 both increased more rapidly at depth relative to introgressed and sunset rockfishes (Fig. 6a, b).
467 Depth explained 27% of the variation in length and 27% of the variation in weight for vermilion
468 rockfish (Table 8b). For introgressed and sunset rockfishes combined, regression analysis
469 indicated that 46% of the variation for weight and length were explained by depth.

470 *3.5 Modeling species composition*

471 We initially evaluated both distance from port and distance from the mainland for
472 inclusion in GAM models. But since they were highly correlated ($r = 0.89$), we eliminated
473 distance from the mainland for further consideration since distance from port produced lower
474 AIC-values during the model exploration phase. We also observed high correlation coefficients
475 ($r > 0.75$, absolute value) for salinity with other covariates (depth, dissolved oxygen and
476 temperature) (Table 9). But we retained this covariate during model exploration because of
477 potential value to fishery managers during future modeling exercises when the full suite of
478 variables may not be available. The best GAM relating the proportion of vermilion rockfish (P_v)
479 to environmental and geographic variables included latitude, longitude, depth (Z), distance from
480 nearest port (D), dissolved oxygen (DO), and temperature (T) (Table 10). The optimal model
481 explained 95% of the deviance with an $r^2 = 0.947$. Salinity was eliminated from the final model
482 based on AIC analysis.

483 The average percent deviance explained by the models increased from 55.7% as
484 covariates were added (range 55.7 to 95.0%). The greatest improvement in deviance explained (+
485 35.4%) occurred with the addition of depth to the GAM. Unbiased risk estimator (UBRE) values
486 varied with addition of covariates. UBRE-values ranged from 0.35 for the optimal model to 5.16
487 for latitude and longitude and indicated that overfitting did not occur (Table 10). AIC-values and
488 UBRE-values were highly correlated ($r = 1.00$, $n = 8$) for the best models shown in table 10.

489 We plotted the functional form of the relationships for depth, distance from port,
490 dissolved oxygen and temperature with the predicted proportion of vermilion rockfish (P_v) based
491 on the GAM analysis. Partial GAM plots, identifying the additive effects of significant
492 covariates, indicate an increase in P_v with dissolved oxygen and distance from port (Fig. 7). The
493 relationships with distance to port appear linear while a more complex relationship occurred with
494 DO. In contrast, predicted P_v significantly decreased with both depth and temperature and
495 displayed non-linear response curves (note: shaded areas represent 95% confidence intervals).
496 Note that ranges on x- and y-axes differ among panels. The y-axis reflects the effect of each
497 covariate on P_v . The relative density of data is shown by the “rug” along the x-axis.

498 We further examined relationships among the covariates that explained a high percentage
499 of deviation (>93%) in binomial GAM models by examining the proportion of CPUE for
500 vermilion rockfish and introgressed plus sunset rockfishes relative to latitude, distance from port
501 and dissolved oxygen versus depth at each site (Fig. 8).

502 Results demonstrate that the highest proportions of vermilion rockfish CPUE occurred in
503 a narrow band of sites north of $\sim 34^\circ\text{N}$ and shallower than ~ 110 m. Elevated proportions of
504 introgressed plus sunset rockfish CPUE occurred at depths >125 m in the most northern extent of
505 their range ($>34^\circ\text{N}$) (Fig. 8a). South of $\sim 33.5^\circ\text{N}$, a high proportion of introgressed plus sunset

506 rockfish CPUE occurred throughout their full depth range but rarely in shallow water (<80 m)
507 north of 34 °N. Results further indicated that vermilion rockfish and the combined introgressed
508 plus sunset subgroup were unevenly distributed with respect to distance from port and dissolved
509 oxygen, particularly at shallow depths (Fig. 8b, 8c). Vermilion rockfish were concentrated in an
510 area greater than 40 nm from the nearest port at depths <110 m (Fig. 8b). Introgressed plus
511 sunset rockfishes dominated areas <20 nm from the nearest fishing ports at relatively shallow
512 depths (<100 m) and areas >40 nm from ports but at depths deeper than 120 m (Fig. 8b). Sites
513 with high dissolved oxygen concentrations (>4 mL L⁻¹) were characterized by CPUEs dominated
514 by the sunset plus introgressed rockfish subgroup (Fig. 8c) while vermilion rockfish CPUE was
515 concentrated at depths <110 m and oxygen levels from ~ 2 to 4 mL L⁻¹. The sunset plus
516 introgressed rockfish subgroup also occurred at a range of dissolved oxygen levels from ~1.5 to
517 3.5 mL L⁻¹ at depths >110 m (Fig. 8c).

518 **4. Discussion**

519 This study focused on life-history characteristics and population ecology (catch and
520 distribution) for the recreationally and commercially important vermilion-sunset cryptic species
521 pair in southern California. We provided preliminary biological information on the individual
522 components of the species complex while also examining whether the subgroup identified as
523 introgressed sunset rockfish possessed characteristics more closely aligned with either sunset or
524 vermilion rockfish. Our results suggest that, based on distribution and the biological
525 characteristics examined here, introgressed fish do not represent an intermediate form between
526 vermilion and sunset rockfish but rather behaved in all cases as sunset rockfish. In addition, our
527 results indicate that the characteristics for introgressed and sunset rockfish examined here are
528 statistically different from vermilion rockfish. The introgressed subgroup represented a

529 substantial proportion (~21%) of the total sunset rockfish catch (n = 1174) in 2014 within the
530 SCB. Based on a smaller sample size, Hyde et al. (2008) estimated introgressed sunset rockfish
531 comprised ~34% of the overall sunset rockfish catch within a similar latitudinal and depth range
532 sampled from 1993 through 2006. While vermilion and sunset rockfishes were found to be
533 genetically distinct in 2008, this study demonstrates that significant distributional and biological
534 differences exist between this cryptic pair. Our research suggests that without careful scrutiny,
535 depth and/or area-based fishing restrictions might place disproportionate effort on the two
536 species. In addition, this research suggests the need to incorporate additional years of data,
537 examine a wider portion of the coast and consider separate management of these important
538 groundfishes.

539 The biology and distribution information presented here supplement the relatively few
540 prior publications devoted to the distinct taxonomic components of this cryptic species pair along
541 the US West Coast (Hyde, 2007; Hyde et al., 2008; Hyde and Vetter, 2009). Because of the
542 confusion between the two species, most prior studies on biology and ecology likely included
543 data pooled across both species rather than species-specific information. Love et al. (2002) noted
544 that vermilion rockfish, inclusive of sunset, extended from central Baja California to Alaska at
545 depths of 12 to 478 m. Following separation, vermilion rockfish was described as abundant from
546 central Oregon to Mexico at depths <100 m while sunset rockfish dominated the region south of
547 Pt. Conception, California at depths >100 m (Hyde et al., 2008; Hyde and Vetter, 2009). The
548 north-south variation in distribution between the components of the vermilion complex reflects
549 similar latitudinal differences reported for other cryptic rockfish pairs such as blue (*Sebastes*
550 *mystinus*) and deacon rockfish (*Sebastes diaconus*) off Oregon and California (Frale et al.,
551 2015; Vaux et al., 2019). Our results support Hyde et al.'s (2008) findings that sunset rockfish

552 dominant the species complex south of Pt. Conception, particularly in deeper waters. Hyde et al.
553 (2008) observed that sunset rockfish accounted for 54% of the total catch of this cryptic pair
554 south of 34.5 °N in 1993–2006 (n = 428) while we identified 67.5% of the complex as sunset
555 rockfish plus introgressed individuals south of Pt. Conception in 2014 (n = 1740). This increase
556 in the proportion of the complex attributable to introgressed plus sunset rockfish within the SCB
557 could reflect differences in sampling between the two studies or perhaps greater exploitation of
558 vermilion rockfish in recent years as fishing pressure shifted to shallower waters following depth
559 based management closures.

560 Hyde et al. (2008) reported a common depth range for vermilion rockfish from 30 to 100
561 m and a deeper range for sunset rockfish, primarily from 100 to 200 m. They noted few sunset in
562 water shallower than 100 m and emphasized a high degree of bathymetric segregation between
563 vermilion and sunset rockfishes at 100 m. Here we observed a depth range of 64 to 133 m for
564 vermilion rockfish with an average catch-weighted depth of 98 m. Introgressed and sunset
565 rockfish occurred at depths from 49 to 211 m with an average depth of 131 m but exhibited
566 considerable overlap with vermilion rockfish in waters <133 m. We found 29% of the sunset plus
567 introgressed rockfish catch at depths <100 m, 25% within the 100–133 m depth range and 46%
568 deeper than 133 m. We found more overlap between the components of the cryptic pair in
569 shallower water relative to that reported by Hyde et al. (2008) and that complete separation
570 occurred at depths >133 m. Whether this apparent shift in depth distribution over time is
571 attributed to fishery removals, shifts in prey distribution, differences in sampling distribution or
572 changing oceanographic profiles, remains to be explored.

573 In addition to differences in depth, we found significant differences in average latitude
574 and distance from the mainland and fishing ports between vermilion rockfish and introgressed

575 plus sunset rockfish, consistent with Hyde et al.'s (2008) observation that vermilion rockfish
576 occur further north and closer to the coast. Geographic comparisons of CPUE further emphasized
577 differences in distribution between the species. Elevated CPUE for vermilion rockfish occurred
578 near Pt. Conception and the northern Channel Islands. Introgressed plus sunset rockfish exhibited
579 greater prevalence and were generally evenly distributed throughout the SCB with elevated
580 CPUE near Pt. Conception, across the outer Channel Islands region, along the mainland, and
581 within the Cowcod Conservation Areas (CCAs).

582 We also observed significant differences in frequency distributions for latitude, distance
583 from mainland and distance from the nearest port. Frequency distributions for latitude indicate
584 increased frequency of occurrence for vermilion rockfish further north with sunset rockfish more
585 evenly distributed throughout the SCB. Both species exhibited similar distribution patterns for
586 distance from the mainland with highest frequency at sites closest to the mainland, decreased
587 occurrence offshore but with vermilion rockfish not found as far from land as their sister species.
588 In contrast, vermilion rockfish, unlike introgressed plus sunset, exhibited their highest frequency
589 of occurrence at their greatest distance from port (60 nm). As distance from port represents a
590 proxy for fishing effort (Miller et al., 2014; Bellquist and Semmens, 2016; Frid et al., 2016), our
591 results suggest that Pt. Conception, the region with the highest vermilion rockfish catch from the
592 H&L survey, in fact experiences decreased fishing pressure from the recreational fleet and
593 perhaps serves as a refuge for vermilion rockfish in the SCB. The introgressed plus sunset
594 rockfishes did not exhibit this pattern with no apparent correlation between elevated fishing
595 pressure and distance from port.

596 Love et al. (2002) reported a maximum length of 76 cm and weight of 6.8 kg for the
597 complex with females larger than males. MacCall (2005) found lengths up to ~70 cm for

598 nominal vermilion rockfish caught in southern California fisheries, particularly in years prior to
599 1986. We also found that the maximum size for females was greater than males following
600 separation by species but somewhat lower than prior reported maxima (56 to 63 cm). We
601 additionally observed that average lengths and weights for introgressed and sunset rockfish were
602 greater than for vermilion rockfishes. When examining larger size classes, MacCall (2005) noted
603 that fish exceeding 54 cm occurred regularly through 1986 but rarely afterwards. Here less than
604 1% of vermilion rockfish exceeded 54 cm compared to ~13.7% of sunset plus introgressed
605 rockfish larger than 54 cm. MacCall (2005) further found that the largest vermilion seen in
606 southern California catch from 1987 to 2004 rarely exceeded 46–48 cm. In contrast, we recorded
607 20% of vermilion and ~8.5% of introgressed plus sunset rockfish catch in the 46 to 48 cm size
608 range. Length composition data from Dick et al. (2021) suggest increased catch of larger fish
609 (50–60 cm) from 2018 to 2021 within the commercial hook and line fishery but little change in
610 size of recreational catch. Since we found no species-specific size data for comparison with our
611 results, we cannot determine if these differences reflect variation in sampling area or depth or if
612 they indicate that size has increased for both components of the complex since the period of
613 heavy exploitation in the 1980s. Additionally, some of the apparent increase may be tied to the
614 H&L survey sampling areas that have been closed to fishing for 20+ years. Prior to depletion of
615 the vermilion population in the 1980s–early 1990s, Miller and Gottshall (1966) reported a long-
616 term average weight of 1.77 kg fish⁻¹ along the west coast south of Oregon. We found an average
617 weight of 1.36 kg for vermilion rockfish and a higher average (1.73 kg) for introgressed plus
618 sunset rockfish. Differences between the historical and current averages can be attributed to
619 variation in geographic area and separation into component species.

620 Both length and weight frequency distributions differed significantly between vermilion
621 and introgressed plus sunset rockfishes with no prior species-specific data available for
622 comparison. However, similar to what we saw here for vermilion, MacCall (2005) and more
623 recently, Dick et al. (2021) reported truncated length distributions for the complex overall,
624 particularly at sizes greater than 46 cm. Importantly, although the vermilion rockfish length
625 frequency distribution appears severely truncated as in the past, truncation now occurs at an
626 overall larger size (>52 cm) relative to earlier years. Introgressed plus sunset length and weight
627 frequency distributions did not exhibit severe truncation at larger sizes but gradually declined
628 from peak to maximum size. Since truncation in size often associates with exploitation, our
629 results suggest that vermilion rockfish may currently be more highly exploited than their species
630 pair (see below).

631 Our analyses revealed significant differences in weight-length relationships between
632 vermilion and introgressed plus sunset rockfish with the best model incorporating sex. Data
633 indicated that weight, by sex, increased faster as a function of length for vermilion rockfish
634 relative to introgressed plus sunset, perhaps reflecting their more northerly distribution in cooler,
635 more productive waters near Pt. Conception. Results also indicated that females increased weight
636 faster than males regardless of species. Earlier studies reported no difference in weight-length
637 relationships by sex for vermilion rockfishes (Phillips et al., 1990; Love et al., 1990; MacCall,
638 2005; Dick et al., 2021). However, studies on the closely related canary rockfish (*Sebastes*
639 *pinniger*) reported differences in weight-length relationships by sex (McClure, 1982; Thorson
640 and Wetzel, 2015; Keller et al., 2018), as similarly reported for multiple other species of
641 rockfishes (Love et al., 1990). For vermilion rockfish, differences between sexes demonstrated
642 here may have been masked by fitting earlier data to the species complex rather than its distinct

643 taxonomic components (MacCall, 2005; Dick et al., 2021), highlighting a common error when
644 neglecting to manage cryptic pairs as individual species. Prior coefficients reported for the
645 complex (e.g. intercept = -10.957, slope = 2.995) fall between the species-specific values
646 reported here (Love et al., 1990; MacCall, 2005).

647 We saw significant differences in length and weight versus depth relationships between
648 vermilion rockfish and introgressed plus sunset rockfish but no differences between males and
649 females for either subgroup. Very little historical information exists on these relationships for the
650 vermilion complex. Love et al. (2002) noted that small nominal vermilion rockfish commonly
651 occurred at depths of 6 to 36 m with juveniles gradually found deeper. Hyde et al. (2008)
652 similarly noted that sunset rockfish taken at depths less than 100 m were young of year or
653 subadult fish (<25 cm). Here we saw an average length of 32.8 cm for introgressed and sunset
654 rockfish from depths of 68 to 100 m but smaller subadult fish (average length 27.2 cm) present at
655 depths from 68 to 80 m. Within both depth ranges vermilion rockfish tended to be somewhat
656 larger than sunset rockfish. On average, vermilion rockfish were 5.6 cm larger in water less than
657 100 m and 8.0 cm larger at depths less than 80 m. Similar to other rockfish species, including
658 closely related canary rockfish, nominal vermilion rockfish undergo an ontogenetic migration
659 with increasing size at depth (Boehlert, 1977, 1978, 1980; Love et al., 2002; Sampson, 1996).

660 Based on GAM analysis, we saw that the proportion of vermilion rockfish relative to
661 overall catch of the species complex could be explained as a function of environmental and
662 geographic covariates. We found that the proportion of vermilion rockfish within the SCB was
663 related to latitude, longitude, depth, dissolved oxygen, distance from port and temperature.
664 Geographic location (latitude, longitude) produced the best initial GAM followed by the greatest
665 improvement in fit with the addition of depth. The inclusion of other environmental variables

666 (dissolved oxygen and temperature) as well as distance from nearest port further improved the
667 ability to predict the proportion of vermilion rockfish relative to the overall catch of the species
668 complex. In general, the proportion of vermilion rockfish increased with dissolved oxygen
669 concentration and distance from port but decreased with depth and temperature. We are hopeful
670 that our modeling exercise provides a potential framework for separation of historical data in the
671 absence of DNA evidence provided some of these ancillary data exist.

672 Among recreational fisheries, the vermilion complex ranks as one of the highest in value
673 along the US west coast. Based on data collected in the SCB during the NWFSC's annual H&L
674 surveys from 2014 to 2016, the vermilion-sunset complex represented 30% of the overall catch
675 and was the survey's most abundant species (Keller et al., 2019). The complex was captured at
676 170 of the 196 sites sampled during these three years with only bocaccio (*Sebastes paucispinis*)
677 occurring at more frequent sampling sites (n = 185). With the complex separated into two
678 distinct taxonomic subgroups, the sunset-introgressed subgroup comprised 20% of the total catch
679 and vermilion rockfish 10%. With this separation into component species, bocaccio becomes the
680 most frequently caught species in the 2014 H&L survey (30%). He and Field (2017) similarly
681 noted that bocaccio accounted for 25–30% of the historical catch in southern California over the
682 last century.

683 An initial stock assessment for vermilion rockfish occurred in 2005, prior to the
684 discovery that vermilion was in fact a species complex (MacCall, 2005; Hyde et al., 2008).
685 Despite the recognized commercial and recreational value for the vermilion species complex, the
686 assessment was not formally accepted for management purposes by the Pacific Fishery
687 Management Council (PFMC). A second assessment, planned in 2013 was abandoned due to the
688 lack of sufficient data to separate the cryptic pairs into component species (PFMC, 2013). The

689 most recent assessment was also based on the complex rather than a separation into vermilion
690 and sunset rockfish (Dick et al., 2021). During the interim between the first two attempted
691 assessments, Hyde et al. (2008) provided information on the depth and geographic distribution of
692 the complex's component species. Although these species should be separated, it is not
693 straightforward to do so in historical data sets.

694 Like many single species of rockfishes, abundance for the vermilion complex declined
695 through the 1990's due to excessive exploitation. MacCall (2005) presented results for two
696 vermilion assessment models off California (subdivided at Pt. Conception), that at the time
697 incorporated more than one genetically distinct species. The 2005 assessment, based on
698 MacCall's (2005) single species assumption, indicated that the complex was recovering due in
699 part to a strong 1999 year class and would be above a precautionary exploitation rate of 30% for
700 regions north and south of Pt. Conception by 2007 (MacCall, 2005). The 2005 assessment
701 revealed the highest proportion of both recreational (57%) and commercial (65%) catch occurred
702 south of Pt. Conception relative to overall catch off California. The southern model was based on
703 the geographic area where both sunset and vermilion distributions significantly overlap and
704 notably the only model that indicated a precautionary biomass level for a lower bound model
705 (MacCall, 2005). The California Department of Fish and Wildlife reported significant increases
706 in recreational catch for the vermilion complex in recent years (increasing from ~100 mt in 2008
707 to ~400 mt in 2019). Dick et al. (2021) also reported increased recreational catch for the
708 complex in recent years (2015–2019) but that overfishing is most likely not currently occurring.
709 However, increased recreational catch coupled with a presumed higher level of protection
710 afforded to deeper dwelling introgressed and sunset rockfish, suggests that assessment of the

711 vermilion complex as distinct species would likely provide better guidance for management of
712 these important resources.

713 As noted by Hyde (2007), failure to recognize the differences in depth and geographic
714 distribution between the distinct taxonomic components of the vermilion-sunset cryptic pair
715 impacts management, particularly since strategies enacted in the early 2000s to protect multiple
716 overfished rockfish species often incorporated spatial and depth closures. The Rockfish
717 Conservation Area (RCA), the CCAs and other marine reserves restricted fishing in deep waters
718 off California (PFMC, 2008, 2011; MacCall, 2005). Within the extensive CCAs (11,138 km²),
719 catch of all groundfish was restricted in depths deeper than 36.6 m while other closures, such as
720 the RCA, provided seasonal, annual or geographic limits at depths deeper than 55 to 120 m. Both
721 of these geographic and depth-based fishing restrictions likely afforded greater protection to the
722 deeper dwelling and more southerly sunset and introgressed subgroups while potentially
723 exposing vermilion rockfish to the same or higher level of exploitation. Further, the closure of
724 these deeper waters likely shifted some fishing effort into the more nearshore areas inhabited by
725 vermilion rockfish possibly further exacerbating the exploitation of the two sister species relative
726 to one another.

727 Two lines of evidence suggest that greater exploitation of vermilion rockfish relative to
728 sunset and introgressed rockfish may be occurring within the SCB. As noted previously the
729 proportion of the vermilion rockfish relative to the total catch of the species complex has
730 declined within the SCB compared to earlier years (Hyde et al., 2008), a topic we will explore
731 more fully when a time series of genetic sequencing data for nominal rockfish captured on H&L
732 surveys from 2004 to 2019 becomes available. Additionally, size frequency distributions seen
733 here for vermilion rockfish exhibit severe truncation at larger sizes, a pattern often correlated

734 with size selective fishing pressure (Frank et al., 2018). We did not observe a similar pattern for
735 introgressed and sunset rockfish. Based on observed and potential differences between vermilion
736 and sunset rockfish, this research suggests that the appropriate management of this cryptic
737 species complex should more explicitly consider the differences in their respective biology and
738 distribution. This should include research into additional aspects of their life history, including
739 age, growth and reproductive biology. Currently, we plan future studies that will incorporate
740 additional data on maturity and age based on samples collected during multiple years of the H&L
741 survey.

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755

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Table 1. Mean (weighted by catch), minimum and maximum latitude (Latitude, °N), Depth (m), distance from mainland (Main, nm), and distance from port (Port, nm) shown by subgroups within the vermilion – sunset species complex. Total CPUE (catch adjusted by the number of hooks) and the number of sites with positive catch (n) also shown.

Subgroup	Latitude			Depth			Main			Port			CPUE	Sites
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	n	n
Vermilion	34.04	32.45	34.52	98.3	68.4	133	16.6	0.9	84	42.6	2.4	88.7	566	61
Introgressed	33.45	32.01	34.53	132.9	49.2	211	33.7	0.9	87	42.4	3.7	90.6	249	59
Sunset	33.47	32.01	34.52	129.8	68.4	211	31.6	0.9	87	41.2	2.4	90.6	925	87

Table 2. Results from analysis of variance (ANOVAs) comparing natural log transformed latitude (N°), depth (m), distance (nm) from mainland (Main) and nearest port (Port) for the vermilion–sunset species complex by subgroups (vermilion: V, introgressed: I, sunset: S). We followed significant ANOVAs with the Student-Newman-Keuls (SNK) multiple comparison of means tests and demarcated significant differences among groups as V>S>I or, if equivalent, separated by commas, i.e. V>S, I. For significant ANOVAs (p<0.05), we subsequently combined subgroups with no differences, i.e. S + I and repeated the analysis.

Variable	F	p	df	SNK	r ²
Depth					
V, S, I	191.9	<0.0001	2, 1661	V<I, S	0.19
V, S + I	381.2	<0.0001	1, 1662	V<I + S	0.19
Latitude					
V, S, I	138.2	<0.0001	2, 1655	V>I, S	0.14
V, S + I	275.1	<0.0001	1, 1656	V>I + S	0.14
Main					
V, S, I	51.2	<0.0001	2, 1655	V<I, S	0.08
V, S + I	98.8	<0.0001	1, 1656	V<I + S	0.08
Port					
V, S, I	14.1	<0.0001	2, 1655	V>I, S	0.02
V, S + I	27.1	<0.0001	1, 1656	V>I + S	0.02

Table 3. Comparison of frequency distributions for depth (m), latitude (°N), and distance (nm) from the mainland (Main) and nearest port (Port) for the vermilion-sunset species complex (vermilion: V, introgressed: I, sunset: S) based on a non-parametric, two-sample Kolmogorov-Smirnov analysis. Shown are the Kolmogorov-Smirnov asymptotic statistics (KS_a) with p-values (p) between subgroups. Subgroups with no significant differences (p>0.05) were combined (S + I) and the analysis repeated.

Comparisons	Depth		Latitude		Main		Port	
	KS _a	p	KS _a	p	KS _a	p	KS _a	p
V vs S	9.478	<0.0001	8.465	<0.0001	4.950	<0.0001	3.574	<0.0001
V vs I	7.122	<0.0001	5.910	<0.0001	4.149	<0.0001	3.002	<0.0001
S vs I	0.965	0.310	0.758	0.617	0.867	0.440	0.537	0.934
S + I vs V	10.039	<0.0001	8.826	<0.0001	5.340	<0.0001	3.887	<0.0001

Table 4. Mean \pm (standard error, se), minimum (min), maximum (max) and count (n) for length (cm) and weight (kg) for vermilion, introgressed and sunset rockfishes by sex and overall.

Length	females				males				all
	mean (\pm se)	min	max	n	mean (\pm se)	min	max	n	mean (\pm se)
Vermilion	40.67 (0.42)	18	56	268	41.77 (0.36)	23	52	275	41.19 (0.28)
Sunset	43.23 (0.53)	17	63	473	43.81 (0.46)	22	60	404	43.37 (0.36)
Introgressed	44.97 (1.01)	16	63	115	44.74 (0.82)	21	58	120	44.77 (0.64)
Weight	mean (\pm se)	min	max	n	mean (\pm se)	min	max	n	mean (\pm se)
Vermilion	1.37 (0.04)	0.12	3.58	267	1.35 (0.03)	0.22	2.46	275	1.35 (0.03)
Sunset	1.77 (0.05)	0.08	4.54	473	1.63 (0.04)	0.18	3.66	403	1.69 (0.03)
Introgressed	1.94 (0.11)	0.08	4.66	115	1.75 (0.08)	0.18	3.48	121	1.83 (0.07)

Table 5. Results of analysis of variance (ANOVAs) comparing length (cm) and weight (kg) for the vermilion–sunset species complex by subgroups (vermilion: V, introgressed: I, sunset: S) and sex (female: F, male: M). We followed significant ANOVAs with the Student-Newman-Keuls (SNK) multiple comparison of means tests with significant differences among subgroups demarcated as V<S<I or, if equivalent, separated by commas, i.e. V<I, S. We subsequently combined subgroups with no differences, i.e. I + S and repeated the analyses.

Variable	F	p	df	SNK
Length (sex, subgroups)				
F (V, I, S)	8.52	0.0002	2, 852	V<I, S
M (V, I, S)	7.80	0.0004	2, 793	V<I, S
F (V, I + S)	14.36	0.0002	1, 853	V<I + S
M (V, I + S)	14.54	<0.0001	1, 794	V<I + S
Weight (sex, subgroups)				
F (V, I, S)	17.97	<0.0001	2, 852	V<I, S
M (V, I, S)	17.25	<0.0001	2, 793	V<I, S
F (V, I + S)	33.36	<0.0001	1, 853	V<I, S
M (V, I + S)	32.50	<0.0001	1, 794	V<I, S

Table 6. a) Delta AIC-values (Δ_i , the difference between Akaike's information criterion per model and the minimum AIC-value) for weight-length relationships for the vermilion rockfish complex. For fitted relationships, models incorporated sex (female, male) and evaluated combinations of three subgroups within the vermilion-complex: vermilion (V), sunset (S), and introgressed sunset rockfishes (I). The best model ($\Delta_i = 0$) included separation by sex and two subgroups (V and a combination of S + I). Models are shown in order of complexity (number of parameters, n); b) Estimated parameters for the best fit curves relating weight (ln kg) and length (ln cm) based on fitted allometric equations by sex (F: female, M: male) and two subgroups (V and S + I). Also shown are standard errors (\pm se), number of observations (n), F-values (F), and r^2 , $p < 0.0001$ for all equations.

a)

Model description	Δ_i	n
Without subgroup, sex	103.9	2
By sex, without subgroup	24.6	4
By subgroup, without sex		
with 2 subgroups (I, V + S)	105.8	4
with 2 subgroups (S, V + I)	98.5	4
with 2 subgroups (V, S + I)	81.2	4
with 3 subgroups (V, S, I)	102.6	6
By subgroup, with sex		
with 2 subgroups (I, V + S) and sex	26.4	8
with 2 subgroups (S, V + I) and sex	16.0	8
with 2 subgroups (V, S + I) and sex	0.00	8
with 3 subgroups (V, S, I) and sex	22.5	12

b)

sex	subgroup	intercept (\pm se)	slope (\pm se)	n	F	r^2
F	V	-11.316 (0.111)	3.112 (0.030)	267	10730	0.98
F	S + I	-11.087 (0.045)	3.045 (0.012)	588	62740	0.99
M	V	-10.833 (0.111)	2.968 (0.030)	274	9906	0.97
M	S + I	-10.652 (0.054)	2.919 (0.014)	523	40280	0.98

Table 7. Comparison of frequency distributions for length (cm) and weight (kg) for the vermilion-sunset species complex (vermilion: V, introgressed: I, sunset: S) based on a non-parametric, two-sample Kolmogorov-Smirnov analysis. Shown are the Kolmogorov-Smirnov asymptotic statistics (KS_a) with significant values (p) between subgroups. Subgroups with no significant differences ($p > 0.05$) were combined (S + I) and the analysis repeated.

Comparisons	Length (cm)		Weight (kg)	
	KS_a	p	KS_a	p
V vs S	5.523	<0.0001	4.646	<0.0001
V vs I	4.492	<0.0001	4.367	<0.0001
S vs I	0.978	0.294	1.246	0.09
S + I vs V	5.946	<0.0001	5.143	<0.0001

Table 8. a) Delta AIC-values (Δ_i , the difference between Akaike's information criterion and the minimum AIC-value) for length-depth and weight-depth relationships for the vermilion rockfish complex. For fitted relationships, models incorporated sex (female, male) and evaluated combinations of three subgroups within the vermilion-complex: vermilion (V), sunset (S), and introgressed sunset rockfishes (I). The best model ($\Delta_i = 0$) included separation into two subgroups (V and a combination of S + I). Models are shown in order of complexity (number of parameters, n); b) Estimated parameters for the best fit curves relating length (ln cm) and weight (ln kg) with depth (ln m) based on fitted allometric equations for two subgroups (V and S + I). Also shown are standard errors (\pm se), number of observations (n), F-values (F), and r^2 . $p < 0.0001$ for all equations.

a)

Model description	Δ_i length	Δ_i weight	n
Without subgroup, sex	124.3	134.4	2
By sex, without subgroup	123.2	136.3	4
By subgroup, without sex			
with 2 subgroups (I, V + S)	124.2	136.8	4
with 2 subgroups (S, V + I)	48.1	51.9	4
with 2 subgroups (V, S + I)	0.0	0.0	4
with 3 subgroups (V, S, I)	52.4	57.6	6
By subgroup, with sex			
with 2 subgroups (I, V + S) and sex	123.0	138.6	8
with 2 subgroups (S, V + I) and sex	48.5	54.5	8
with 2 subgroups (V, S + I) and sex	0.6	1.9	8
with 3 subgroups (V, S, I) and sex	52.0	59.6	12

b)

Length-depth	intercept (\pm se)	slope (\pm se)	n	F	r^2
V	0.985 (0.191)	0.595 (0.042)	541	203	0.27
S + I	0.545 (0.105)	0.664 (0.022)	1108	934	0.46

Weight-depth	intercept (\pm se)	slope (\pm se)	n	F	r^2
V	-8.073 (0.592)	1.806 (0.129)	541	195	0.27
S + I	-9.387 (0.314)	2.008 (0.064)	1108	956	0.46

Table 9. Pearson's correlation coefficients (r) among spatial (latitude, Lat, °N; longitude, Long, °W; distance from nearest port, D, nm) and environmental (dissolved oxygen, DO, mL L⁻¹; salinity, S, ppt; temperature, T, °C; bottom depth, Z, m) variables included in the binomial generalized additive models relating the proportion of vermilion rockfish to the sum of the vermilion, introgressed and sunset rockfish taken at sites within the study area (n = 106).

	Lat	Long	Z	D	DO	S	T
Lat	1.00						
Long	-0.68	1.00					
Z	-0.08	-0.04	1.00				
D	-0.55	-0.20	0.08	1.00			
DO	-0.31	0.38	-0.64	0.05	1.00		
S	-0.07	-0.19	0.78	0.05	-0.82	1.00	
T	-0.06	0.32	-0.72	-0.20	0.72	-0.75	1.00

Table 10. A suite of binomial general additive models (GAMs) analyzed by Akaike's information criterion (AIC) relating the proportion of vermilion rockfish (P_v) to environmental (dissolved oxygen, DO, mL L⁻¹; salinity, S, ppt; temperature, T, °C; bottom depth, Z, m) and spatial (latitude, °N, longitude, °W, Lat, Long; distance from nearest port, D, nm) covariates. Models shown represent the best models as covariates were added and removed during model exploration with the final model determined by the lowest Δ AIC value ($\Delta_i = 0$). A plus (+) indicates addition of covariates that progressively produced a more parsimonious model, based on reduction in AIC value, for each step in the analysis. A minus (-) indicates removal of a covariate from the analysis, based on a non-significant P-value ($p > 0.05$) and high correlation ($r > 0.72$) with other retained variables. The rank degrees of freedom (df) for AIC-values, deviance explained (%), unbiased risk estimator (UBRE), and r^2 are also shown for each model.

Covariate	AIC	Δ_i	df	% deviance	UBRE	r^2
Lat, Long	737.7	507.9	30.0	55.7	5.16	0.43
+ Z	261.6	32.0	28.0	91.1	0.66	0.91
+ D	248.2	18.6	33.9	92.9	0.53	0.93
+ DO	243.1	13.5	36.4	93.7	0.48	0.93
+ S	241.0	11.4	31.2	93.1	0.46	0.93
+ T, - D	236.1	6.5	33.2	93.8	0.41	0.94
+ S, D	234.9	5.3	33.6	93.9	0.40	0.94
- S	229.6	0.0	38.4	95.0	0.35	0.95

Figure Legends

Fig. 1. Geographic extent of the Northwest Fisheries Science Center's H&L survey showing location of the 2014 sample sites in the Southern California Bight relative to the coast of California. Charts show 2014 distributions and relative abundance (site-specific catch per unit effort (CPUE) for: (a) vermilion, (b) introgressed, and (c) sunset rockfish. For each subgroup, the sizes of the circles represent the CPUE ($n \text{ site}^{-1}$). Note that the range of CPUE varies as shown in the key for each chart; + represents zero catch. Base chart credits: Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors.

Fig. 2. Box-whisker plots for: (a) depth (m); (b) latitude ($^{\circ}\text{N}$); (c) distance from mainland (nm); and (d) distance from nearest port (nm) for vermilion, sunset and introgressed rockfish. Box limits represent 25% and 75% quartiles; line in center represents the median; X the mean, whiskers the minimum and maximum values and points represent outliers.

Fig. 3. Frequency distributions (%) comparing: (a) depth (m); (b) latitude ($^{\circ}\text{N}$); (c) distance from mainland (nm); and (d) distance from nearest port (nm) for vermilion (upper white bars) versus introgressed plus sunset rockfish (grey lower bars) in 2014.

Fig. 4. Box-whisker plots for: (a) length (cm); and (b) weight (kg) for female, male and all vermilion, sunset and introgressed rockfish. Box limits represent 25% and 75% quartiles; line in center represents the median; X the mean, whiskers the minimum and maximum values and points represent outliers.

Fig. 5. Frequency distributions (%) comparing: (a) length (cm); and (b) weight (kg) for vermilion rockfish (upper white bars) and introgressed plus sunset rockfish (lower gray bars) from the 2014 H&L survey.

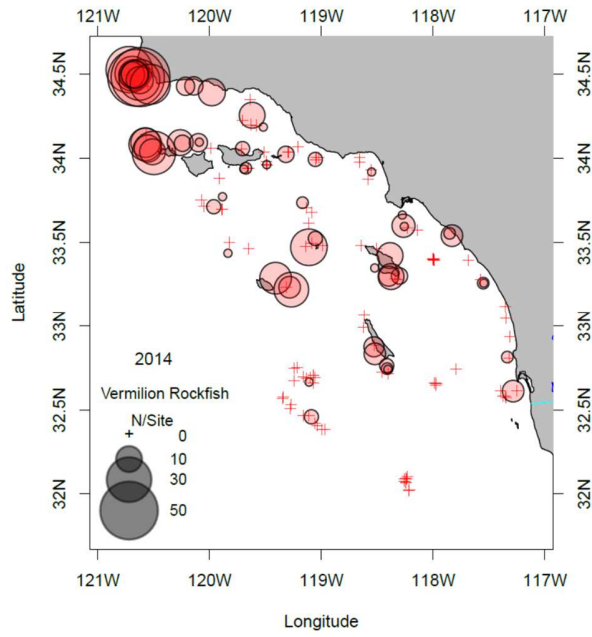
Fig. 6. Fitted allometric relationships for: (a) length (cm); and (b) weight (kg) versus depth (m) for vermilion (red circles) versus introgressed plus sunset rockfish (green circles) showing the

best fit models based on two subgroups: vermilion (solid line) and introgressed plus sunset rockfish (dashed line) from Table 8.

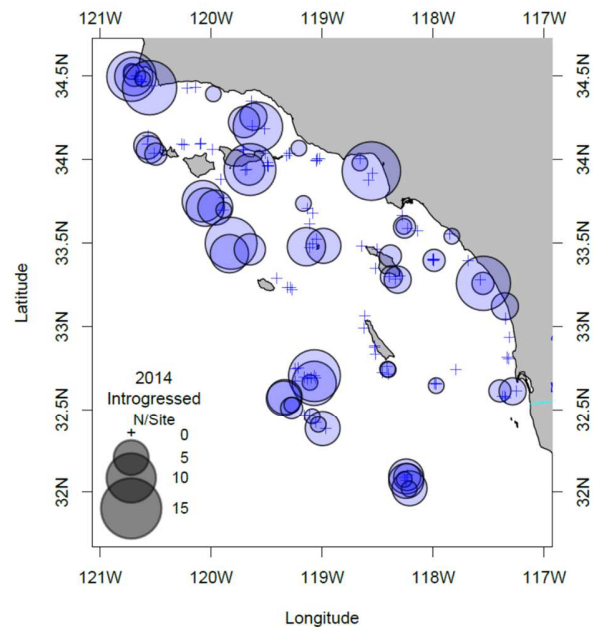
Fig. 7. Binomial generalized additive model (GAM) plots identifying the additive effects of significant covariates: (a) depth (m); (b) distance from port (nm); (c) dissolved oxygen (mL L^{-1}); and (d) temperature ($^{\circ}\text{C}$) on the proportion of vermilion rockfish (P_v) at sampling sites within the H&L survey area in 2014. Shaded areas reflect the 95% confidence intervals around response curves. Note that ranges on x- and y-axes differ among panels. The y-axis reflects the effect of each covariate on CPUE. The relative density of data is shown by the 'rug' along the x-axis.

Fig. 8. Plots of: (a) latitude ($^{\circ}\text{N}$); (b) distance from port (nm); and (c) dissolved oxygen, (mL L^{-1}) versus depth (m) where individual pie charts are scaled by total CPUE (n site^{-1}) and represent the proportion of vermilion rockfish versus introgressed plus sunset rockfish observed at each H&L site in 2014. Note key represents CPUE scaled for 50, 25 and 10 (n site^{-1}); asterisk (*) represents zero catch.

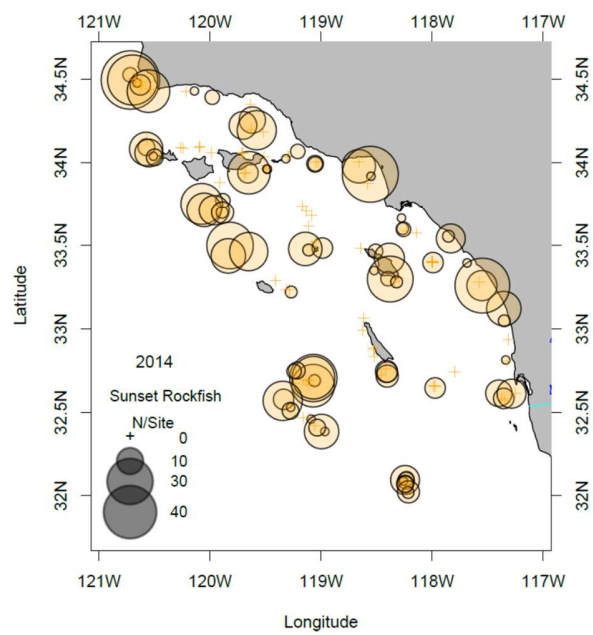
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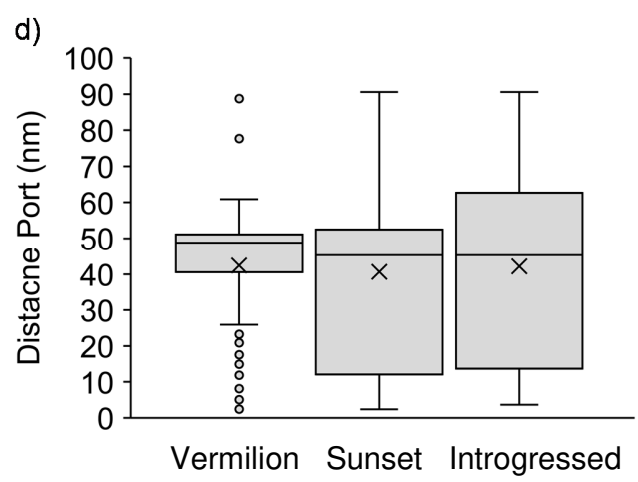
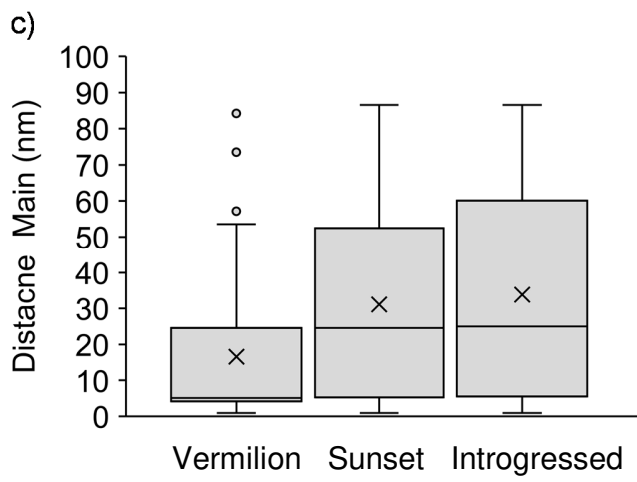
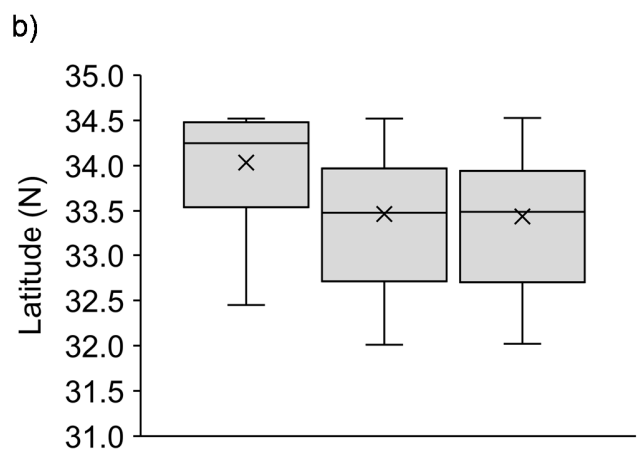
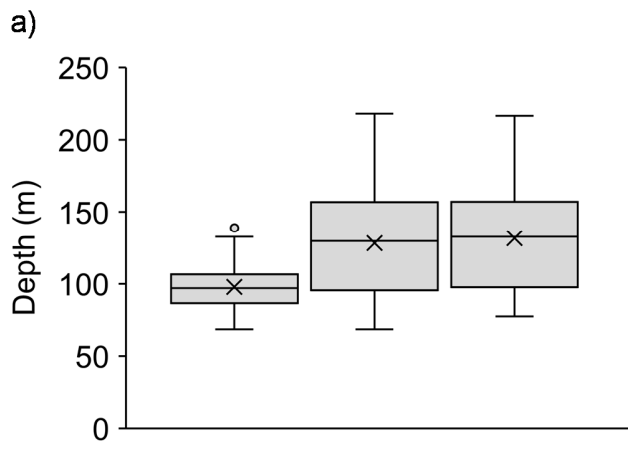


b)

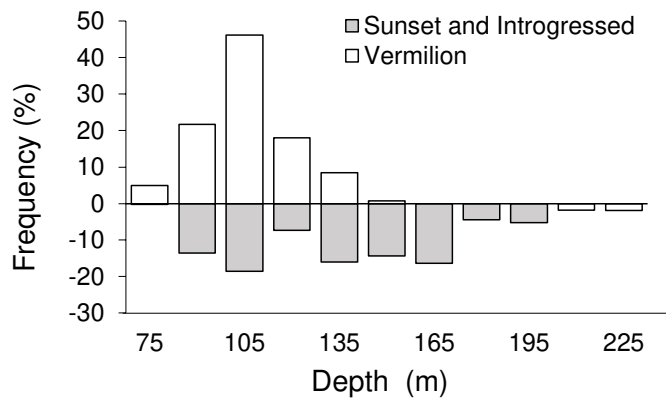


c)

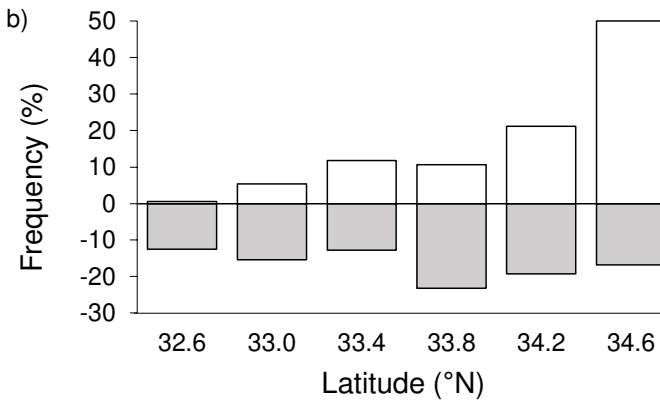




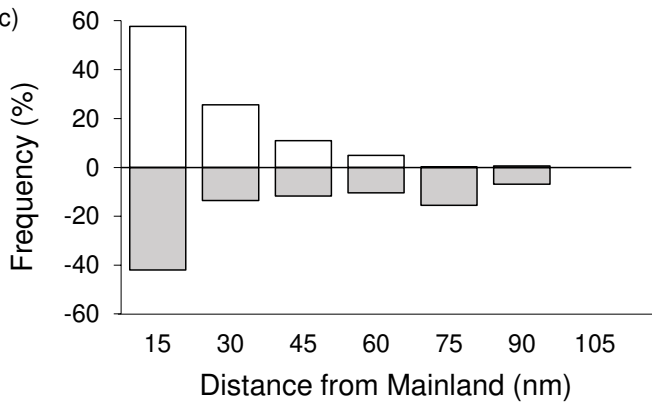
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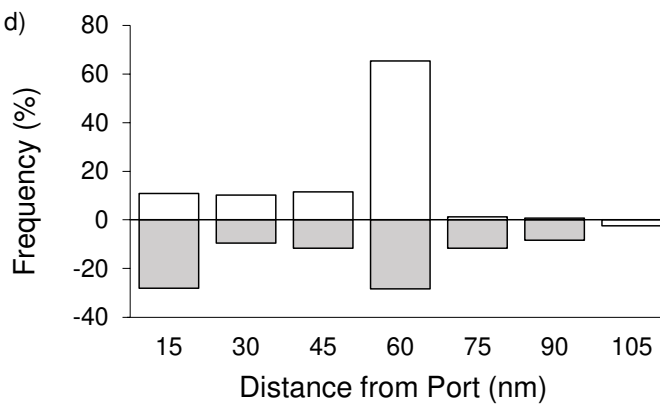
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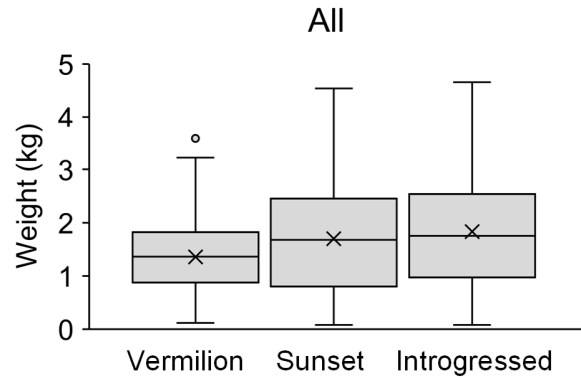
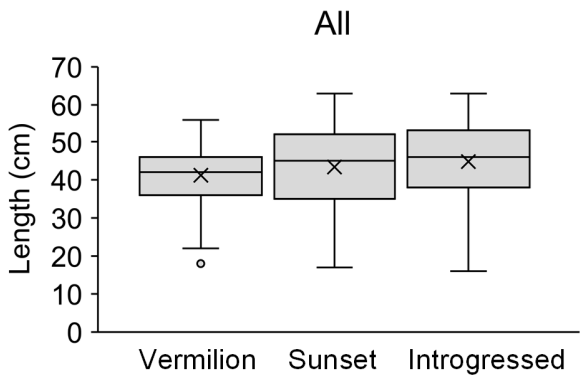
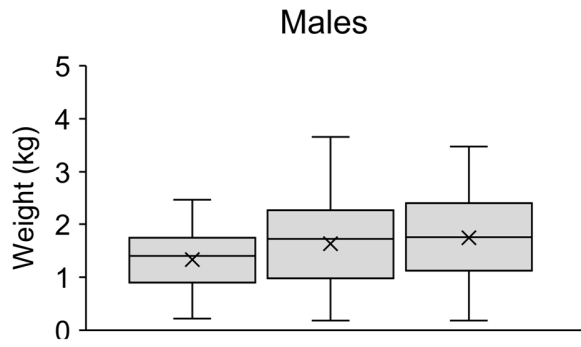
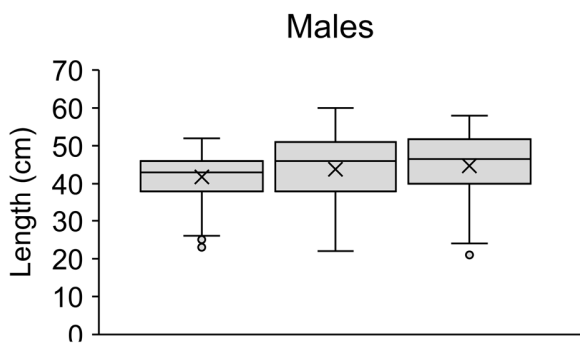
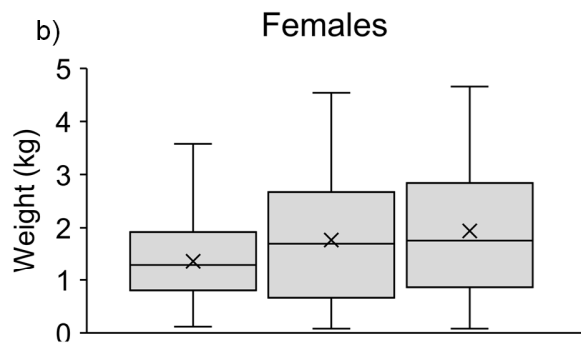
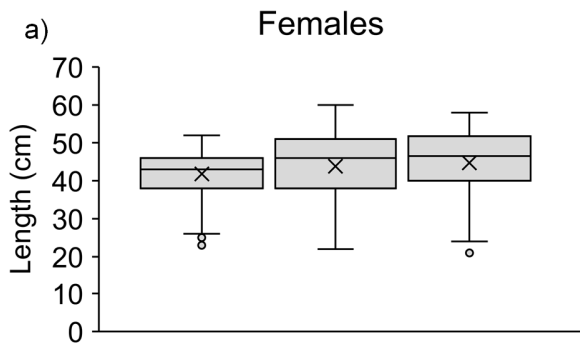


c)

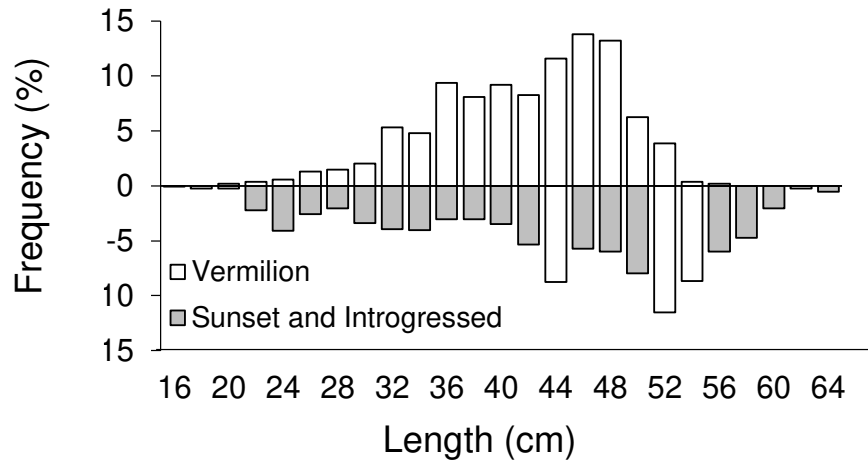


d)

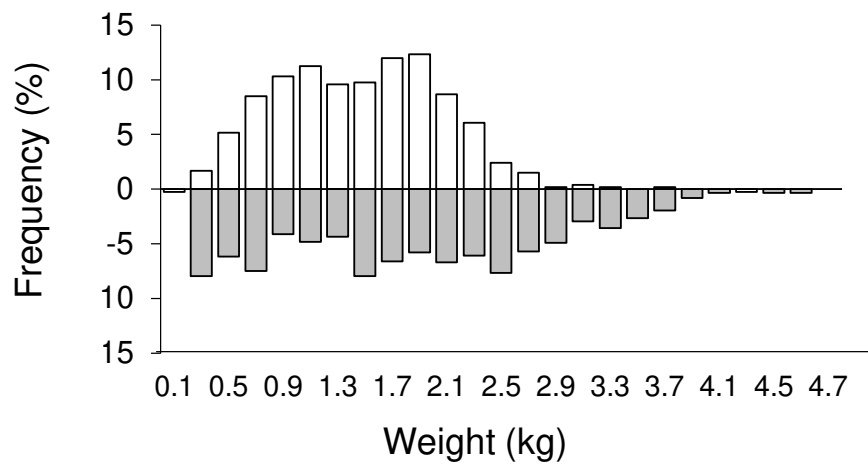




a)



b)



S + I

W i ht (k)

(g)

^

Length (cm)

2

