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Reproductive Biology, Size, and Age Structure of Harlequin Rockfish: Spatial Analysis of Life History Traits

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Abstract

Many rockfish (genus *Sebastes*) species within multispecies complexes have lacked basic biological data hindering their fisheries management. In this study, we provide essential information for stock assessment decision making for one of these species, Harlequin Rockfish *Sebastes variegatus*. We analyzed aspects of reproduction, size structure, and growth of Harlequin Rockfish in waters off Alaska using historical survey data and recent field collections. Results are reported primarily from the Gulf of Alaska (GOA) region, but important findings are noted from the Aleutian Islands (AI). Harlequin Rockfish reached an observed maximum age of 76 years in the AI, a new estimate for this species. Females exhibited group-synchronous oocyte development; the parturition period occurred in the spring in both regions, ceasing as late as July in the GOA. Females from the GOA had an estimated length and age at 50% maturity of 187.6 mm (95% confidence limits [CL] = 152.0–215.6 mm; $n = 318$) and 4.7 years (95% CL = 1.6–6.2 years; $n = 188$), respectively, indicating that the Harlequin Rockfish is one of the earliest maturing rockfishes. We analyzed a 14-year time series of bottom trawl survey data to examine the relationship between Harlequin Rockfish length and selected covariates. Spatial heterogeneity existed, with size showing a relationship with bottom temperature and ocean color (productivity index) across the GOA. The comparison of Harlequin Rockfish length at age indicated that larger fish were present in the western GOA but variable growth occurred across the region. Our findings contribute to understanding Harlequin Rockfish biology within multispecies management complexes, and our results demonstrate that key life history traits vary spatially, possibly influenced by regional environmental conditions. This study represents the most comprehensive biological examination for Harlequin Rockfish.

Rockfish *Sebastes* spp. are found throughout the North Pacific Ocean and are valuable components of commercial and recreational fisheries (Love et al. 2002). Due to their unique life history characteristics, such as longevity, moderate to late maturation, and slow growth, and given their relatively low productivity and fairly high susceptibility to overfishing (Musick 1999), they are a high priority for research. Effective management for many rockfishes, however, has been problematic due to a lack of basic biological data and reliable fishery catch and abundance indices.

Reducing biological uncertainty is a key objective in improving fisheries management. Under data-limited situations, life history traits can be used as indices for population viability and biological productivity (Rochet 2000). An understanding of stock structure is improved as new life history data becomes available, which ultimately leads to increased confidence in stock management decision making. Additionally, an understanding of how life history traits (e.g., growth and maturity) vary spatially and temporally is critical to understanding population

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dynamics (Babcock et al. 2005). Variation in life history traits, either along micro or macroscale and temporal scales, have been well documented in *Sebastes* species (e.g., Dick 2009; Keller et al. 2012; Wilson et al. 2012; West et al. 2014).

Here, we examined the biology of Harlequin Rockfish *Sebastes variegatus*, a species managed within multispecies rockfish complexes in Alaska. In the Gulf of Alaska (GOA), Harlequin Rockfish fishery catches have represented approximately 50% of total landings in the “other-rockfish” complex since 1991 (Tribuzio and Echave 2015). Harlequin Rockfish generally inhabit continental shelf waters in the northeast Pacific Ocean (Eschmeyer et al. 1983). In Alaska, this species is most abundant in the GOA (von Szalay and Raring 2016), though its range extends across the Aleutian Islands (AI; von Szalay et al. 2017). Life history data for this species are sparse; more information is needed regarding maturity, growth, and size structure, including spatial variability within these traits. The only known estimate of maturity for this species was from fish captured off Southeast Alaska and British Columbia. In that study, the length at 50% maturity for Harlequin Rockfish females was estimated to be 23 cm using only macroscopic examinations (Westheim 1975). Age determination and growth of Harlequin Rockfish have not been fully described. Harlequin Rockfish exhibit sexual dimorphism in size with females being larger than males. Although rockfishes have been shown to exhibit length at age differences among sexes (e.g., Boehlert and Kappenman 1980; Gertseva et al. 2010; Keller et al. 2012), this has not been analyzed in Harlequin Rockfish.

Alaskan waters are characterized by regional oceanographic and biological influences that may contribute to life history variability (Mueter and Norcross 2002; Mueter et al. 2007; Waite and Mueter 2013; Coffin and Mueter 2016). It has been shown that variability in rockfish size and growth may be related to productivity patterns from unique physical and climate boundaries (e.g., Black 2009; Keller et al. 2012). In Alaska, Rooney et al. (2018) showed that ocean color, measured as sea surface pigmentation from carbon (^{14}C) production from phytoplankton, was an important spatial predictor for Harlequin Rockfish abundance. Bottom temperature also appears to be an important predictor for rockfish abundance (Rooper and Martin 2012) and recruitment (Rooney et al. 2018). Additionally, differences in mean bottom depth habitat has been known to be a factor for juvenile and adult rockfish (e.g., Rooper 2008).

Data gaps in the biology of Harlequin Rockfish have made management difficult, and recent information highlights the need to investigate the life history of this species to better inform future stock assessments. Biomass estimates appear to be underestimated for Harlequin Rockfish which may affect fishing reference points (Tribuzio and

Echave 2015). Given this information, knowledge of productivity attributes (life history parameters) of the Harlequin Rockfish stock—including maturity at age information for calculations of spawning stock biomass—is necessary for management. Knowledge of spatial variability within the Harlequin Rockfish stock is also important given the potential area apportionment to its management (Tribuzio and Echave 2015). Furthermore, there is a need to determine how similar or different the life history traits of each species are within multispecies complexes to reduce management uncertainty when new information becomes available (DeMartini 2019).

Our specific objectives were to examine and report on (1) general aspects of Harlequin Rockfish reproduction by examining maturity, seasonal oocyte development, and presence of reproductive anomalies; (2) age determination and growth of Harlequin Rockfish; and (3) spatial variation of Harlequin Rockfish reproduction, size, and growth. Our spatial analysis included an examination of how Harlequin Rockfish size structure relates to certain environmental variables. We analyzed these parameters with an emphasis on fish collected from the GOA. We also report pertinent findings from specimens collected in the AI.

METHODS

Study areas and field collections.—Specimens of Harlequin Rockfish were collected aboard fishery-dependent and independent sampling platforms from several different sampling years in the GOA and AI (Table 1). Fishery-independent samples were collected from bottom-trawl surveys in the GOA, which employed a random-stratified sampling design stratified by depth, bottom terrain, and statistical area. Survey operations were conducted in compliance with national and regional protocols detailed in Stauffer (2004). The number of stations per stratum was determined from a modified Neyman optimal allocation strategy (Cochran 1977). Within each stratum, the allocated stations were randomly selected without replacement from polygons formed from the intersection of a grid composed of cells (5×5 km) and the stratum boundaries (von Szalay and Raring 2016). Numbers and weights in catch of all taxa were recorded for each haul. At each station, bottom temperature ($^{\circ}\text{C}$) and bottom depth (m) were recorded. These surveys were conducted to assess groundfish resources and have provided a time series on distribution, abundance, and various biological characteristics of commercially important species for fisheries management.

Data were extracted from the survey databases to examine Harlequin Rockfish length distributions among areas within the GOA survey area. We used the period from 1984 to 2015, totaling 14 surveys. From 1984 to 1999, the survey was conducted every 3 years and on a biennial basis beginning in 2001. The GOA survey is

TABLE 1. Total numbers of Harlequin Rockfish analyzed during this study, separated by sampling collection type and sex in the five areas of the Gulf of Alaska and Aleutian Islands. Sampling years analyzed for length and age were 1984–2015 and for ovaries were 2009, 2010, and 2014–2016. All samples were collected from bottom-trawl gear.

Type	Sex	Area					Aleutian Islands
		Southeast	Yakutat	Kodiak	Chirikof	Shumagin	
Length	Male	1,789	1,297	3,439	848	758	
	Female	1,922	1,429	3,146	881	1,024	
Age	Male	141	96	102	33	71	
	Female	159	114	97	41	44	
Ovary	Female			292	26		167

divided into five major areas across the region, from 133°W to 170°W (Southeast, Yakutat, Kodiak, Chirikof, and Shumagin; Figure 1). The extent of the survey is from the Islands of Four Mountains in the west to Dixon Entrance in the east, to the outer continental shelf (1,000-m isobath) and has occurred during late May through early August. Total catch of Harlequin Rockfish from each haul was weighed to the nearest 0.01 kg. Sex and fork length were recorded (mm) for each Harlequin Rockfish caught per haul. If the total number of individuals caught exceeded the target sample size of up to 150 specimens per haul, then a random subsample was taken. Otoliths were extracted for subsequent age determination from a length-stratified sampling scheme that did not exceed two specimens per cm/sex/haul. For females, ovaries were removed from specimens in the Kodiak and Chirikof areas during the 2015 survey to study aspects of reproduction.

Female Harlequin Rockfish were collected from fishery-dependent samples at inshore processing plants and aboard bottom trawling vessels off Kodiak Island in the GOA (Figure 1) and aboard bottom-trawling vessels in the AI. Sampling at processing plants was conducted in May 2016 and during fishing operations throughout several months in 2009 and 2010 and in May 2014. For AI collections, Harlequin Rockfish were sampled primarily during fishing operations targeting Atka Mackerel *Pleurogrammus monopterygius* in October 2014, April and July 2015, and April 2016. Sample locations from the AI were near Seguam Island, Kiska Island, and Petrel Bank. For each female, fork length (mm) was recorded. With the exception of samples collected in 2009, 2010, and 2015, otoliths were also removed.

Age determination.—Otoliths were aged via the break-and-burn method (Beamish 1979) by readers experienced in rockfish age determination. Age readers applied the same age determination protocol and independently assigned an age based on visual examination of the otolith (Matta and Kimura 2012). A large percentage of the specimens were precision tested by a second age reader

(tester). Age reader precision was measured using standard statistical tools. Precision was estimated and evaluated using percent agreement, average percent error (APE; Beamish and Fournier 1981), coefficient of variation (CV), and age bias plots (Campana et al. 1995). Specimens without agreement between age estimates were re-examined, and any remaining discrepancies were resolved between reader and tester.

Reproductive biology.—Histological assessments were used to describe seasonal oocyte stage development and reproductive anomalies and to estimate maturity. To determine ovarian development organization and identify oocyte synchrony (Murua and Saborido-Rey 2003), we examined oocyte size-frequency distributions from five randomly selected females (size range: 270–370 mm) exhibiting newly fertilized (mature) ova as the leading cohort. Oocyte development stages in the histological analysis were defined according to Shaw et al. (2012; Supplementary Table S1 available separately online). Reproductive phases described by Shaw et al. (2012) and Brown-Peterson et al. (2011) were also documented. Observations of ovarian atretic stages were based on histological characteristics following Hunter and Macewicz (1985). Early-stage (alpha) and late-stage atresia (beta, gamma, and delta) were documented when describing Harlequin Rockfish ovarian atresia. Reproductive anomalies such as abortive maturation and skipped spawning (Rideout et al. 2005) were recorded. Females exhibiting abortive maturation were mainly characterized by resorption of initial oocyte development, identified by the presence of extensive alpha atresia with no evidence of prior spawning. Skipped spawning was defined by evidence of a prior spawning, such as postovulatory follicles, and/or presence of late-stage atresia. Oocyte size-frequency distributions were determined from measurements of oocyte count and diameter using ImageJ software (version 1.48, National Institute of Health) and the ObjectJ plug-in (version 1.03, University of Amsterdam). Program-digitized images were analyzed to count and measure individual oocytes from a subsample of fixed ovarian tissue evenly distributed into small, water-filled wells after

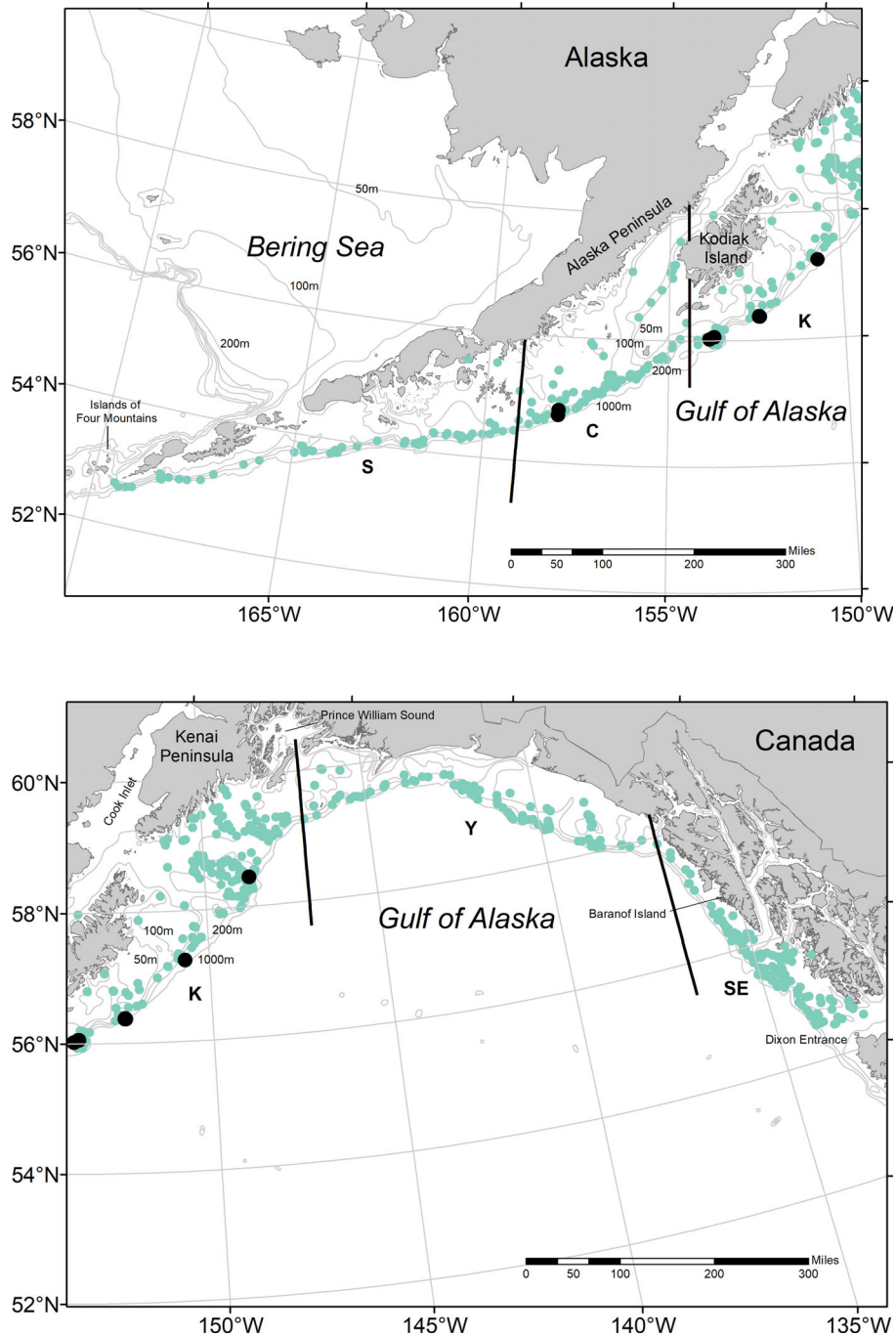


FIGURE 1. Map of the principal study area—Gulf of Alaska (GOA)—separated by the five survey areas from west to east (S = Shumagin, C = Chirikof, K = Kodiak, Y = Yakutat, SE = Southeast). Data points in green represent locations where all Harlequin Rockfish were caught and measured during bottom-trawl surveys from 1984 to 2015; black circles represent locations of ovary collections used to describe Harlequin Rockfish reproductive biology and maturity estimation.

removing connective tissue. A minimum of 250 oocytes were measured for each fish.

Maturity data from GOA females were combined and fitted with a two-parameter weighted logistic regression to estimate length and age at 50% maturity using generalized linear modeling based on binomial data for maturity

status (0 = immature, 1 = mature) using a logit link function. The lack of samples at the very young ages (or smaller sizes) resulted in unrealistically high estimates of the proportion of mature fish. We chose the weighted maximum likelihood method for rare logistic regression events to resolve this, where all rare (or “immature”) events were

weighted and a random fraction of the “mature” events were weighted (King and Zeng 2001). Weights were also given at a theoretical age and length at “0” and assigned as “immature.” Confidence intervals (CIs) were estimated through bootstrapping methods by resampling cases 10,000 times (Ogle et al. 2018). A total of 318 females were available for estimates of length at maturity. Of this total, 188 otoliths were collected and aged for the maturity-at-age ogive. Females were considered functionally mature if there was evidence that spawning would occur during the current or approaching reproductive year or if evidence suggested that they had spawned in the previous reproductive cycle when sampled in a postparturition or reproductively inactive period. Females that exhibited abortive maturation or skipped spawning were considered to be in a nonreproductive phase. Estimates for the AI were not possible due to the absence of immature females, but we report on observations of mature females sampled.

Spatial analysis.—We tested for spatial heterogeneity in Harlequin Rockfish length distributions across the five main areas in the GOA. First, we examined the overall length distributions, identifying Harlequin Rockfish presence by haul throughout the survey period (1984–2015). Pairwise two-sample Kolmogorov–Smirnov tests were used to determine whether between-area length distributions by sex were identical. Data points used in the spatial analysis exhibited nonindependence (Zuur et al. 2009), as multiple fish were caught in the same haul; therefore, we applied linear mixed-effects models with mean fork length as the response variable. We considered the influence of sex, area, bottom depth, bottom temperature, and average ocean productivity (an index expressed as ocean color = $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Rooney et al. 2018) on Harlequin Rockfish size structure. For ocean productivity, data were extracted from Rooney et al. (2018) and were based on satellite-based moderate-resolution imaging spectroradiometer (MODIS) ocean productivity data from 1993 to 2013 which encapsulated the spring–summer phytoplankton blooms. Average ocean color values ($\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were calculated for each haul during this period for the entire GOA survey area, averaged by grid cell and month, and then averaged again by cell and year (to account for differences in the number of samples within each cell; Rooney et al. 2018). To address collinearity, final model covariates were examined using Pearson’s product-moment correlation coefficient, with maximum scores of 0.7 being the limit for model incorporation (Dormann et al. 2013). Ocean productivity and area were moderately correlated (0.67), so we compared full models alternating between these two variables using the Akaike information criterion corrected for small sample sizes (AIC_c). The models with ocean productivity were chosen.

Linear mixed-effects models with random intercepts were used with sex, ocean productivity, bottom depth, and

bottom temperature treated as fixed effects. Haul was assigned as the random effect variable. The analysis used the GOA survey years of 1993–2013 with available ocean productivity data. Since model comparisons involved different fixed effects, maximum likelihood methods were used, rather than restricted maximum likelihood (McCulloch et al. 2008). Candidate models of varying complexity were fitted to the data. Model parsimony was compared using AIC_c . Model selection was based on the lowest AIC_c value and largest Akaike weight indicating the best model fit. Akaike weights are used in model averaging and represent the relative likelihood of the model (Bolker et al. 2009). Diagnostics tests were run for the best-fitting model. Marginal and conditional coefficients of determination (R^2) were calculated (Nakagawa and Schielzeth 2013), referring to the percent deviance explained by the (1) fixed and (2) fixed and random effects, respectively. We ran our best-fitting mixed model while also testing for overall significance of the fixed effects using type III ANOVA. Our models were built from a general matrix notation of linear mixed-effects models (Laird and Ware 1982):

$$Y = X\beta + Zu + \varepsilon,$$

where Y is the vector of observations, β is the vector of fixed effects ($\beta_{0\dots}$), u is the vector of random effects, ε is the random error, and X and Z are design matrices associated with β and u , respectively.

For growth analysis of length-at-age data, we analyzed two GOA survey collections that had age determinations (1996, $n = 647$; and 2011, $n = 255$). An age–length key was constructed from the length distributions where ages were assigned to individual fish when ages were not available, partitioned by year, area, and sex. Age–length keys were developed using the semirandom age assignment method of Isermann and Knight (2005) using length bins of 10 mm.

Rockfish species typically have followed a growth pattern best fit by the von Bertalanffy growth function (e.g., Katsanevakis 2006; Gertseva et al. 2010; Keller et al. 2012; West et al. 2014). Therefore, when describing Harlequin Rockfish growth, length-at-age data were fit using the common parameterization version of the von Bertalanffy growth function (Beverton and Holt 1957), using nonlinear least-squares estimation:

$$L_t = L_\infty[1 - e^{-k(t-t_0)}],$$

where L_t is fish length (FL in mm) at age t ; L_∞ is the asymptotic maximum fish length (FL in mm); k is the instantaneous growth coefficient; t is the age (years); and t_0 is the theoretical age (years) at $L_t = 0$. Due to a low number of small and young individuals, we constrained t_0 to 0. We focused on the comparison of asymptotic maximum lengths and growth rates from the von Bertalanffy

growth function. Estimates from the age-length keys were used for fitting growth parameters. Confidence intervals were estimated via nonparametric bootstrapping (Baty et al. 2015). Likelihood ratio tests were used to compare GOA area-specific von Bertalanffy growth parameters (Kimura 1980). Pairwise comparisons by area for male and female growth were evaluated separately. We analyzed common age groups by sex (males = 7 to 29 years; females = 7 to 30 years) to assure validity with the comparisons.

Statistical procedures and plots were conducted using R programming, version 3.6.3 (R Core Team 2019) with the following packages: AICcmodavg (Mazerolle 2019); effects (Fox and Weisberg 2018); fishmethods (Nelson 2018); fsa (Ogle et al. 2018); ggplot2 (Wickham 2016); lme4 (Bates et al. 2015); lmerTest (Kuznetsova et al. 2017); MuMIn (Bartoń 2018); and nlstools (Baty et al. 2015).

RESULTS

Age Determination

A total of 1,231 Harlequin Rockfish were aged. Of this total, 742 ages were tested by a second reader, representing 60.3% of all age determinations (GOA: $n = 657$; AI: $n = 96$). Age estimation uncertainty measured by between-reader precision showed an overall percent agreement of 45.7% (± 0) from break and burn otoliths (Figure 2). The absolute difference between readers showed that 91.4% of all ages were within ± 2 years. General biases were not observed between readers except for older individuals. The largest deviations from the 1:1 equivalence line occurred mainly in those estimated at ≥ 30 years (Figure 2), due primarily to differences in interpretation of annuli near the otolith edge. Overall mean age for readers 1 and 2 was 13.79 and 13.76 years, respectively. Combined precision statistics yielded an average percent error of 3.59 and a

CV of 5.07. Better precision between readers occurred at the younger ages (< 10 years; $n = 253$), where PA was 71.8% with an average percent error of 3.42 and CV of 4.84. The maximum age was 76 years; the youngest specimen was estimated to be 2 years old.

Reproductive Biology and Maturity

Reproductive biology in the GOA and AI regions exhibited similar seasonal trends in ovary development and reproductive phases. In the GOA, females were undergoing development from August through January and spawning in May (Figure 3). Histological analysis in May indicated migratory nucleus and prematuration oocytes, mature ova, embryonic development stages, and postovulatory follicles. For the AI, collections occurred mainly during 3 months, with spawning and regressing phases observed in April, regressing females observed in July, and developing females observed in October. It was unclear if those caught in the AI were undergoing spawning earlier than those caught in the GOA due to few samples collected from the AI in May and few from GOA in April. Immature females were characterized by primary growth oocytes and/or oil vacuole stages, thin ovarian wall, and with no previous evidence of spawning (Figure 4A). Developing females from both regions were characterized by primary or secondary vitellogenesis and possibly late-stage atresia (Figure 4B). Spawning-capable females were present from December through February, exhibited by larger oocyte sizes, greater yolk presence, and integration of oil vacuoles and yolk globules that completely filled the cytoplasm (Figure 4C, D). Regressing females were present beginning in May, characterized by abundant postovulatory follicles, primary vitellogenesis, and residual embryonic development stages (Figure 4F). Ovarian development for Harlequin Rockfish was determined to be group-synchronous, with females extruding a single annual brood, exhibited by a leading cohort to be spawned (Figure 4G, H). Measured oocytes

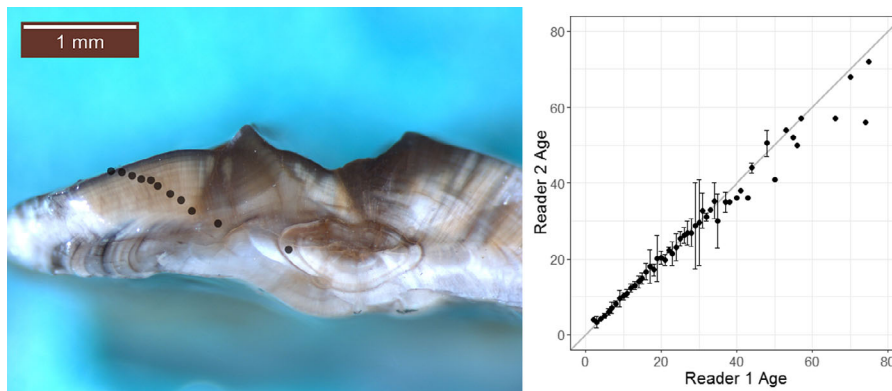


FIGURE 2. Image of a Harlequin Rockfish otolith aged from the break and burn method in this study. Age estimate was 11 years; to the right, a bias plot comparing ages between reader 1 (\pm SD) and reader 2 ($n = 742$). Deviance from the linear 1:1 equivalence line indicated bias.

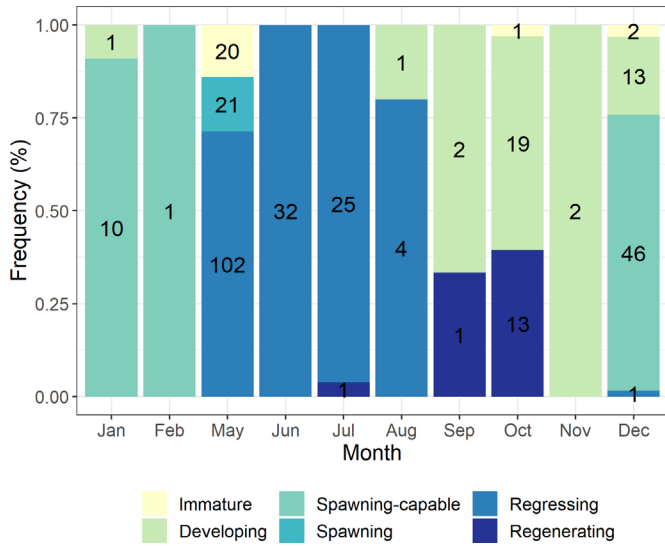


FIGURE 3. Proportion of Gulf of Alaska Harlequin Rockfish females in each reproductive phase by collection month. Sample sizes for each reproductive phase are indicated within each month.

from five randomly selected females ranged in size from 82 to 1,933 μm ($n = 1,647$), with the leading cohort at the mature ovum development stage with a mean size of 1,308.5 μm ($\pm 151.0 \mu\text{m}$ SD).

Overall, few observations of reproductive anomalies in Harlequin Rockfish were recorded. Females from the GOA were examined, and four were determined to have undergone abortive maturation, representing 16.7% of the nonreproductive females ($n = 24$; age range: 4 to 8 years). These females had no previous evidence of parturition; they were characterized by mass alpha-stage atresia of the most advanced vitellogenic group of oocytes, minimal or no late-stage atresia presence, and no postovulatory follicles. Skipped-spawning females in the GOA were rare, with only a single observation.

Collections of female specimens yielded a wide size range for maturity ogive estimation (160–430 mm; Figure 5). Ages ranged from 3 to 45 years. Females matured at a 50% length and age at maturity estimate of 187.6 mm (95% confidence limits [CL] = 152.0–215.6 mm; $n = 318$) and 4.7 years (95% CL = 1.6–6.2 years; $n = 188$), respectively (Figure 5). Furthermore, 90% of female Harlequin Rockfish were mature by an estimated length of 242.0 mm (95% CL = 217.7–252.1 mm) and at an age of 7.4 years (95% CL = 6.3–9.5 years). The earliest and smallest mature female was 4 years old at a size of 167 mm.

An important finding from mature females sampled in the AI was the older ages estimated (Supplementary Figure S1 available separately online). Of the 96 Harlequin Rockfish females with assigned age determinations, 15 were at least 50 years old. The maximum age observed in this study of 76 years was estimated from a mature female

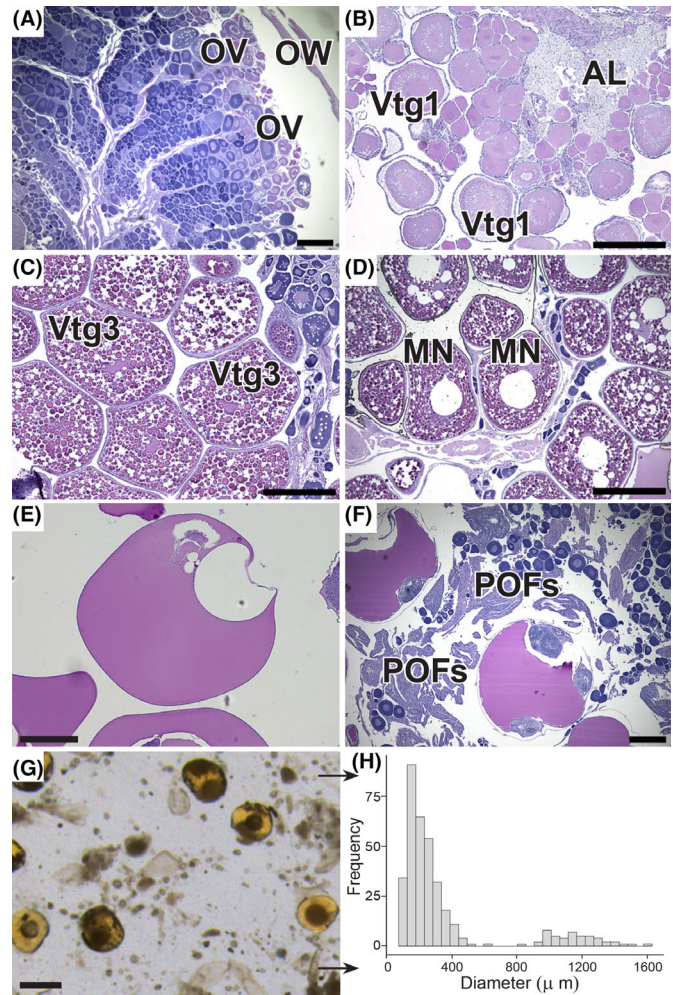


FIGURE 4. Primary oocyte development stages and their reproductive phases in female Harlequin Rockfish, including (A) immature female showing only primary growth oocytes, with oil vacuoles present along the periphery, and a thin ovarian wall; (B) developing female exhibiting primary vitellogenesis and late-stage atresia; (C) a spawning-capable female with ovaries exhibiting tertiary vitellogenesis; (D) a spawning-capable female exhibiting migratory nucleus oocyte stages just prior to maturation, characterized by large oil vacuoles; (E) a mature ovum after fertilization; (F) regressing female, with abundant postovulatory follicles and residual embryonic development stages; (G) a mature ovum as the leading cohort, surrounded by primary growth oocytes and connective tissue, to determine oocyte synchrony; and (H) a histogram of the oocyte size-frequency distribution associated with panel G. Abbreviations are as follows: AL = late-stage atresia, MN = migratory nucleus stage, OV = oil vacuole stage, OW = ovary wall, POFs = postovulatory follicles, Vtg1 = primary vitellogenesis, and Vtg3 = tertiary vitellogenesis. Scale bars represent 0.250 mm (0.500 mm for panel D).

captured in this region. Each of these older females were functionally mature, contributing to the current year's reproductive cycle. Their ovaries were characterized by tertiary vitellogenic oocytes, migratory nucleus stage oocytes, embryonic developmental stages, eyed larvae, and/or postovulatory follicles.

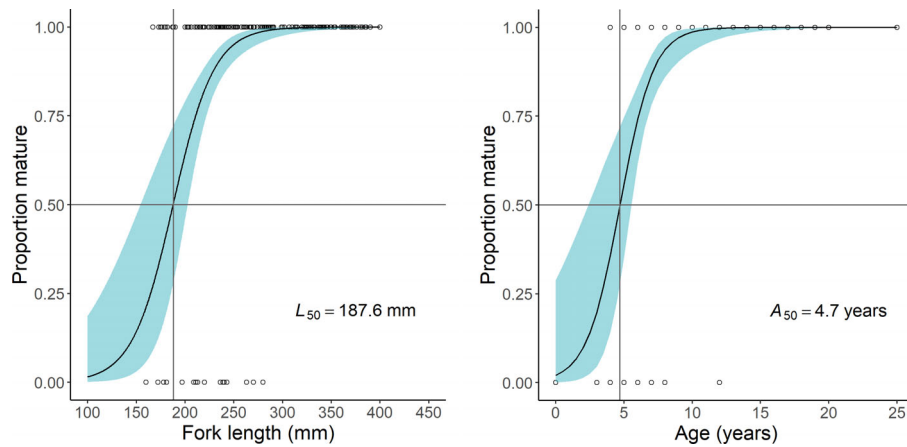


FIGURE 5. Estimates of length ($n = 318$; 187.6 mm at 50%) and age ($n = 188$; 4.7 years at 50%) at maturity for Gulf of Alaska Harlequin Rockfish females. Shaded areas denote the 95% CIs; gray lines represent the intersection where 50% of the specimens were observed to be mature. Note that the x -axis for the age plot is truncated at 25 years (age range: 3 to 45 years) for the purposes of illustration.

Spatial Analysis

Analysis of the Harlequin Rockfish length distributions collected during fishery-independent surveys in the GOA indicated variability by area and sex for all comparisons examined (Kolmogorov–Smirnov tests, $P < 0.001$; Figure 6). A total of 17,749 specimens were caught in 555 different hauls. Ocean productivity, as indicated by ocean color, had a general increasing trend from the west to the southeast (Supplementary Figure S2A). The area farthest west (Shumagin) had the lowest mean bottom temperatures, with Chirikof exhibiting the largest variation (Supplementary Figure S2B).

The linear mixed-effects model showed that the model with sex, ocean color, and bottom temperature was the most parsimonious model describing mean length (Table 2). Bottom temperature was more important than bottom depth as a factor affecting Harlequin Rockfish length. The final model was fitted based on a total of 425 hauls, accounting for 8,933 Harlequin Rockfish caught. The criterion for model fitting, marginal and conditional R^2 , yielded coefficients of 0.25 and 0.78, respectively (Table 3). Most of the model deviance was explained by the addition of the random haul effect. Females were larger than males across the GOA. Larger fish were associated with lower bottom temperatures and areas of lower productivity. Smaller fish were associated with warmer bottom temperatures and areas of higher productivity (Figure 7).

Length-at-age analyses showed growth differences from a total of 2,621 samples (Table 4; Figure 8). Ages ranged from 2 to 47 years. The growth rate differed significantly between males and females based on an evaluation of all growth parameters using the likelihood ratio test ($P < 0.001$), so regional comparisons were separated by sex. Maximum size for both males and females, as indicated by their asymptotic lengths L_{∞} , exhibited an eastward

decline. Female growth rates exhibited more pronounced differences between areas. For example, females were much larger in size at age 10 to 20 years than females from the Southeast (Table 4). Females from the Kodiak, Yakutat, and Southeast areas at younger ages (≤ 10) tended to be smaller in size. Growth rates (k) were variable across the GOA (Table 4). Male growth rates appeared similar in the eastern and western areas. For females, growth rates were slower in the Yakutat and Kodiak areas. For males, growth rates were similar in the Southeast and Shumagin areas.

Using likelihood ratio tests, pairwise comparisons rejected the null hypothesis of no growth differences for nearly all model comparisons, indicating regionally dimorphic growth within each sex (Table 5). The majority of the model comparisons, however, did not exhibit statistical significance when evaluating individual parameters. There were significant differences in maximum size among areas, as indicated by the parameter L_{∞} . The lone regional comparison that did not exhibit differences in growth was between Shumagin and Chirikof Harlequin Rockfish males (Table 5; $P > 0.05$).

DISCUSSION

Our age determination of Harlequin Rockfish resulted in a new estimate of longevity for this species. A specimen estimated to be 76 years old in the AI was substantially older than the previously known maximum age of 47 years from a specimen in the GOA (Malecha et al. 2007). The considerable age difference observed between the new and the earlier estimate may be due to two primary reasons. Fishery-induced changes to Harlequin Rockfish longevity in the GOA may be occurring resulting in the truncation of the age structure. The majority of commercial fishing

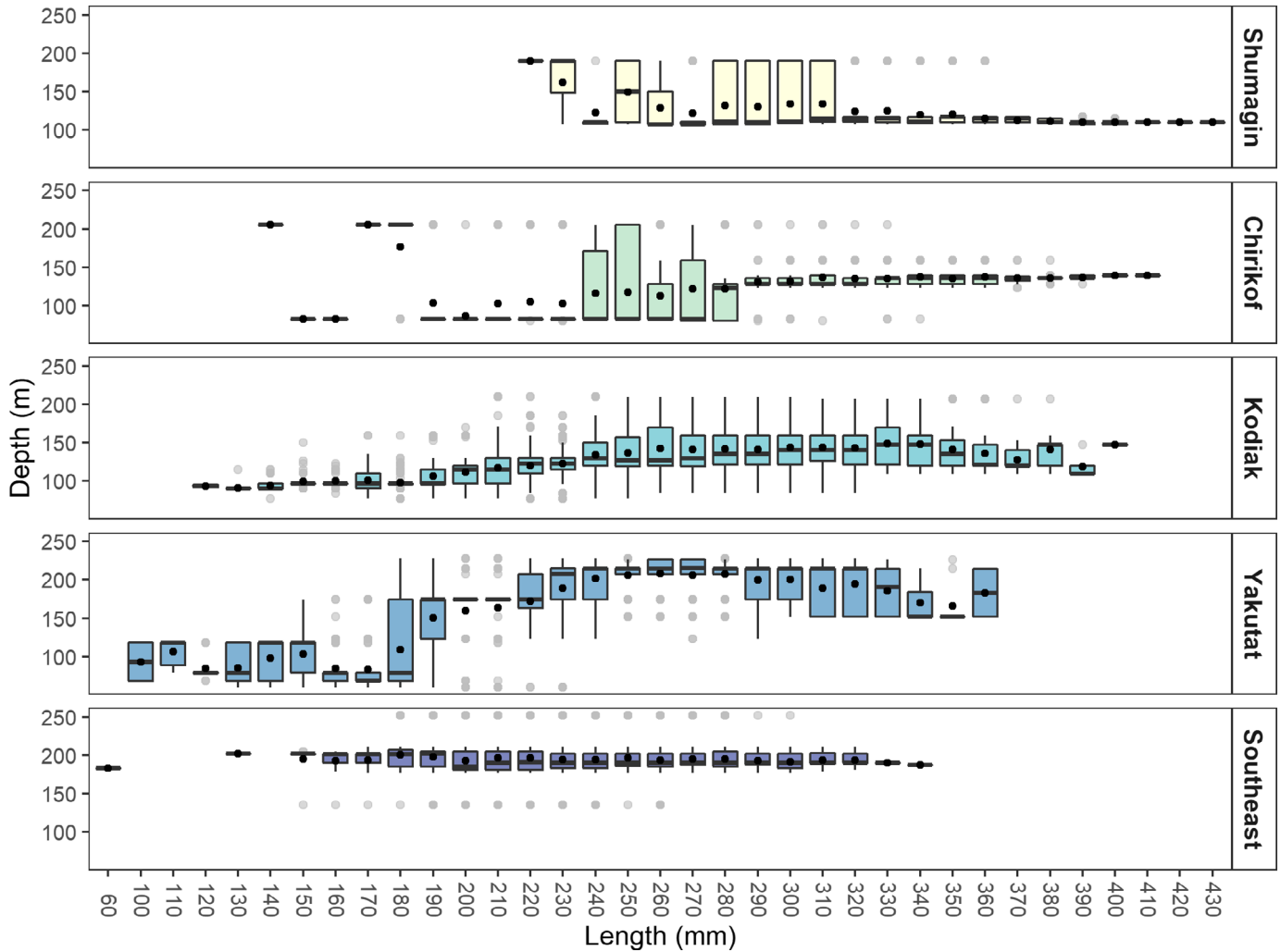


FIGURE 6. Length (FL in mm) distribution of Harlequin Rockfish specimens captured by depth in Gulf of Alaska areas from 1984 to 2015. Sampling stations covered the depth range of 60–252 m. The horizontal line of each box represents the median; points in black represent the mean; points in gray represent outliers. The box limits indicate the 25th and 75th percentiles and whiskers represent horizontal lines at the 1.5 interquartile range of the upper/lower quartiles. Gulf of Alaska areas are listed from west (Shumagin) to east (Southeast).

landings of Harlequin Rockfish occur in the western GOA. The oldest previous Harlequin Rockfish specimen (47 years) was caught in the southeast GOA, an area with minimal fishing (Tribuzio and Echave 2015). Furthermore, age determinations of Harlequin Rockfish have been limited in scope, both spatially and temporally, suggesting that populations have not previously been adequately sampled, especially in the GOA where Harlequin Rockfish are more abundant. Malecha et al. (2007) did not examine variability in age or growth due to paucity of data. It is unclear how much older the AI population is than those found in the GOA given our observations of only three fish exceeding 60 years. Nonetheless, the new estimate of longevity in the AI represents a critical component in the stock assessment.

Ages and longevity of long-lived species, such as *Sebastes* species, have often been underestimated, emphasizing the importance of age validation (Cailliet and Andrews 2008). Unlike age estimation which measures reliability and reproducibility of age assignment, age validation measures the accuracy of age estimation and describes how well ages determined from counting annuli compare with known ages (i.e., statistical bias). In a recent study involving Harlequin Rockfish, Kestelle et al. (2020) used bomb radiocarbon (^{14}C) and determined that for moderately old to the oldest specimens (mean assigned age of specimens = 32 years), there was a high probability of under-aging by 3–4 years. A lack of between-reader precision of older Harlequin Rockfish in our study was observed more than younger specimens, leading to

TABLE 2. Summary of Akaike's information criterion (bias-corrected for small sample sizes; AIC_c) performance from the top six candidate linear mixed-effects models testing the influence of sex, ocean color (productivity), bottom depth, and bottom temperature on Harlequin Rockfish mean fork length. Haul was the random effect. The difference in AIC_c between the best-fitting model and subsequent models (ΔAIC_c) and the Akaike weight (w) are given.

Model	df	ΔAIC_c	w
Sex + Productivity + Bottom temperature	6	0	0.72
Sex + Productivity + Bottom depth + Bottom temperature	7	1.9	0.28
Sex + Bottom depth + Bottom temperature	6	333.1	0.00
Sex + Bottom temperature	5	334.1	0.00
Sex + Productivity + Bottom depth	6	855.4	0.00
Sex + Productivity	5	970.5	0.00

TABLE 3. Results of the best-fitting linear mixed-effects model for predicting mean fork length (mm) for Harlequin Rockfish across the Gulf of Alaska; P -values were calculated using Satterthwaite's t -test approximation method. Ocean color is an index of average ocean productivity ($g \cdot C \cdot m^{-2} \cdot d^{-1}$). The final model was fitted based on 425 hauls ($n = 8,933$ Harlequin Rockfish). Marginal and conditional R^2 yielded coefficients of 0.25 and 0.78, respectively. Most of the model deviance was explained by the addition of the random haul effect (variance = 1,652.1; $SD = 40.7$) with residual variance = 701.1 ($SD = 26.5$).

Fixed Effects	Estimate	SE	t -value	$P < (t)$
Intercept	505.92	21.55	23.43	0.000
Sex	-18.84	0.59	-32.01	0.000
Ocean color (productivity)	-0.06	0.07	-8.16	0.000
Bottom temperature	-23.89	3.97	-6.02	0.000

questions of interpreting the otoliths' more problematic late-growth zone areas, rather than the early-growth zones. Later years were difficult due to break-and-burn irregularities where the compact nature of growth zones blurred opaque and translucent zones. Based on the aforementioned validation study, it appears that a number of Harlequin Rockfish aged in this study could be slightly older. Revisions to preparation methods and criteria for older specimens may need to be addressed.

This study is the first to report on estimates of both length and age at maturity for Harlequin Rockfish through histological analysis. Histological examination of fish gonads has been regarded as a more accurate method to determine reproductive characteristics than visual or macroscopic assessments (e.g., Vitale et al. 2006; Midway and Scharf 2012). Our sampling in the GOA was nearly year-round and during multiple seasons, but due to the

protracted period of oocyte development and evidence of parturition and postparturition, an assessment of functional maturity could be made for all samples. For example, females aged as young as 4 years were unambiguously mature due to clearly identified features such as postovulatory follicles and residual embryonic development, indicative of parturition. Rockfish reproduction has been known to exhibit evidence of parturition throughout the year within the same species (Conrath 2017), while early secondary-growth oocytes and abortive maturation events may also be present at any period (Lefebvre and Field 2015). Additional studies that target smaller and younger individuals, however, would likely result in an improvement in the length and age estimate and a decrease in model uncertainty. Our estimates should be viewed as baseline data pending further studies.

Our observations of other aspects of Harlequin Rockfish reproduction have been documented in other *Sebastes* species, but rockfish reproduction is known for its complexities and variation. Reproductive anomalies were not especially noted for Harlequin Rockfish. Abortive maturation and skipped spawning rates also do not appear to be widespread in other Alaskan *Sebastes* species (e.g., Pacific Ocean Perch *S. alutus*, Conrath and Knoth 2013; Northern Rockfish *S. polyspinis*, TenBrink and Spencer 2013; Dusky Rockfish *S. variabilis*, Conrath 2019). Conrath (2017) recently noted high percentages of skipped-spawning rates, however, in females of three Alaskan deepwater rockfish (Shortraker Rockfish *S. borealis*, Rougheye Rockfish *S. aleutianus*, and Blackspotted Rockfish *S. melanostictus*). Although these same species had abortive maturation rates similar to the aforementioned species, large percentages of the sampled population skipped spawning (37% to 94%), perhaps as a trait to increase survivorship during lean years (Rideout et al. 2005; Rideout and Rose 2006). Our observations of ovarian organization and oocyte synchrony appear to be common among *Sebastes* (e.g., Bowers 1992; Bobko and Berkeley 2004; Shaw et al. 2012), but multiple brooding has also been documented (Beyer et al. 2015; Lefebvre et al. 2018).

Our estimates of maturity for Harlequin Rockfish indicate that it is one of the earliest maturing rockfishes documented. As a group, *Sebastes* spp. show wide variation in age at maturity. Frey et al. (2015) reported a 50% maturity-at-age estimate of only 6.0 years for female Darkblotched Rockfish *S. crameri* off California, while Hannah (2014) reported an estimate of 5.6 years for Copper Rockfish *S. caurinus* off Oregon. Higher estimates are seen in Pacific Ocean Perch (9.1 years; TenBrink and Spencer 2013), Dusky Rockfish (9.2 years; Chilton 2010), and Northern Rockfish (7.6 years; TenBrink and Spencer 2013). Rougheye Rockfish and Blackspotted Rockfish mature much later at 27.4 and 19.6 years, respectively (Conrath 2017).

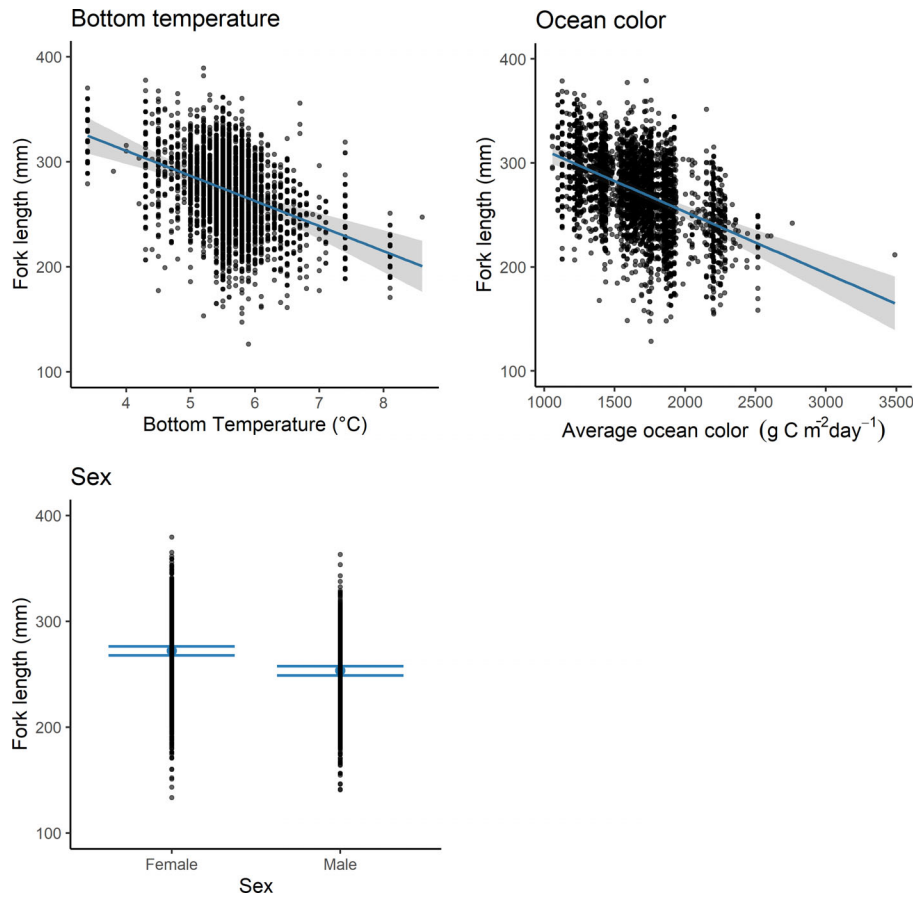


FIGURE 7. Partial residual plots showing the relationships from the best-fitting linear mixed-effects model of Harlequin Rockfish length and sex, bottom temperature, and average ocean color (productivity).

TABLE 4. Parameter estimates from the von Bertalanffy growth function for Gulf of Alaska Harlequin Rockfish in each of the five sub-areas. The bootstrapped 95% confidence limits are in parentheses. The parameter t_0 was constrained to 0 and is not shown.

Area	L_{inf} (mm)	K	N
Males			
Southeast	260.6 (257.6, 264.3)	0.222 (0.210, 0.235)	458
Yakutat	278.0 (272.4, 283.9)	0.196 (0.182, 0.211)	167
Kodiak	278.8 (269.2, 295.3)	0.218 (0.187, 0.240)	314
Chirikof	330.9 (323.2, 341.8)	0.187 (0.166, 0.212)	61
Shumagin	336.3 (328.3, 343.4)	0.225 (0.206, 0.252)	204
Females			
Southeast	277.9 (274.6, 281.8)	0.207 (0.194, 0.220)	541
Yakutat	315.2 (309.5, 321.0)	0.154 (0.144, 0.164)	185
Kodiak	340.2 (332.4, 349.3)	0.142 (0.136, 0.149)	366
Chirikof	346.4 (335.7, 357.2)	0.210 (0.185, 0.250)	66
Shumagin	395.1 (390.7, 400.3)	0.176 (0.168, 0.183)	259

The size and growth differences between Harlequin Rockfish caught in the GOA may be the result of different oceanographic effects in the region influencing life history

traits. Understanding the complexities involved in shaping these differences is difficult, but there are regional influences that are distinct that might account for some level of spatial variability observed in Harlequin Rockfish. Natural divisions or breaking points within the GOA ecosystem have been documented. The western GOA is a large coastal ocean system dominated by the Alaska Coastal Current. The eastern GOA has a narrow continental shelf influenced by the northward-flowing Alaska Current (Stabenot et al. 2004). A delineation near 148°W is created by two distinct downwelling regions (Coffin and Mueter 2016). Carbon (^{14}C) productivity, as measured through sea surface pigmentation from phytoplankton carbon fixation, also shows regional boundaries between the two areas (Behrenfeld and Falkowski 1997; Rooney et al. 2018). Our results correlating Harlequin Rockfish with ocean productivity suggest a relation between carbon production rates and size. For Harlequin Rockfish growth, although variable across the GOA, differences in growth were generally observed between the extreme western and eastern GOA areas, most noticeably in asymptotic sizes. Differences in growth of other rockfish species has

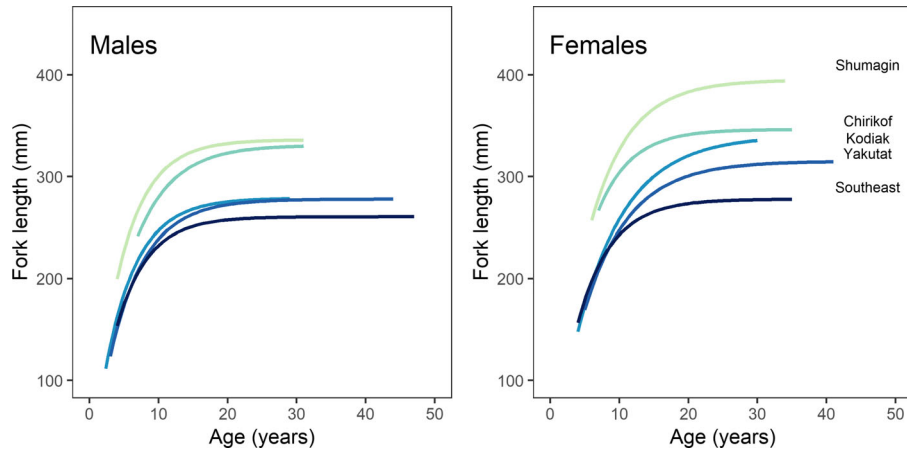


FIGURE 8. Fitted curves of the von Bertalanffy growth equation from age-length key construction for Harlequin Rockfish captured in the Gulf of Alaska, separated by area for males and females. Parameter values are listed in Table 4.

TABLE 5. Pairwise model comparisons of Gulf of Alaska regional von Bertalanffy growth parameters using likelihood ratio tests (Kimura 1980) by sex for Harlequin Rockfish. Regions are defined as: SH = Shumagin; CH = Chirikof; KO = Kodiak; YK = Yakutat; SE = Southeast. Chi-square (χ^2) statistics were used for each hypothesis, including testing the null hypothesis of no growth differences (Null = common). Statistical significance is denoted as one asterisk = $P < 0.05$, two asterisks = $P < 0.01$, and three asterisks = $P < 0.001$; vs = versus. Note: model comparisons based on common age ranges.

Model	Hypothesis		
	$L_{\infty 1} = L_{\infty 2}$ (H_0 vs H_1)	$K_1 = K_2$ (H_0 vs H_2)	Null = common (H_0 vs H_4)
Females			
SH-CH	0.005**	0.142	0.000***
SH-KO	0.000***	0.806	0.000***
SH-YK	0.222	0.072	0.000***
SH-SE	0.493	0.002**	0.000***
CH-KO	0.442	0.718	0.000***
CH-YK	0.823	0.014*	0.000***
CH-SE	0.168	0.002**	0.000***
KO-YK	0.617	0.007**	0.000***
KO-SE	0.216	0.001**	0.000***
YK-SE	0.179	0.119	0.001***
Males			
SH-CH	0.522	0.198	0.057
SH-KO	0.752	0.460	0.000***
SH-YK	0.029*	0.597	0.000***
SH-SE	0.206	0.256	0.000***
CH-KO	0.597	0.888	0.012*
CH-YK	0.026*	0.458	0.000***
CH-SE	0.191	0.999	0.000***
KO-YK	0.279	0.764	0.003**
KO-SE	0.543	0.920	0.000***
YK-SE	0.823	0.454	0.004**

similarly been reported between unique oceanographic boundaries (Gertseva et al. 2010; Keller et al. 2012). Our results indicate that size and growth vary across the GOA and that they may be influenced by productivity in the region.

The effect of temperature appeared to play a more important role than depth in the size structure of Harlequin Rockfish. Juvenile rockfish are known to prefer shallower depths than adults (e.g., Love et al. 1991; Rooper et al. 2007; Rooper 2008; Frey et al. 2015). The paradigm of larger-sized fish being present in deeper waters was not entirely supported by our analysis, perhaps partly due to the small number of juveniles analyzed. Along the regional edges in the areas of Shumagin and Southeast, there appeared to be little difference in the relationship between size-classes and depth. Within or near the GOA longitudinal transitional zones, ontogenetic movement appeared to be the greatest. Most of Harlequin Rockfish caught throughout the GOA region were at depths between 100 and 200 m, and what ontogenetic movement exists may be due to stronger oceanographic or biological influences in certain areas.

Regular monitoring of or periodic updates to biological traits are necessary for effective management, and future investigations should continue to explore spatial variability. Based on the size and growth analysis presented here, it would be reasonable to infer that there are differences in reproductive parameters (e.g., differences in size or age at maturity) between the western and eastern GOA. An in-depth analysis of the spatial structure within management regions that accounts for spatiotemporal variations has not been carried out for many species, especially those in multispecies complexes. Knowledge of this variation may necessitate a broader approach to data collection and priorities.

This study represents the first comprehensive investigation of life history parameters of Harlequin Rockfish. Data limitations for rockfishes in multispecies management complexes in Alaska have been widespread, and it is difficult to determine if the current management structure is appropriate given the considerable biological data gaps for a number of these species. As Tribuzio and Echave (2015) noted for Harlequin Rockfish in the GOA, gaps have included unvalidated age determination, and lack of data that adequately describe distribution and regional reproductive parameters. This study has filled some of those gaps. In the AI, Harlequin Rockfish are much less abundant, but the same management concerns exist (Spies et al. 2018).

With the revised life history information related to growth, longevity, and maturity presented here, there is the potential of elevating the management status for Harlequin Rockfish. Based on this study, new fishing reference points (such as total allowable catch and overfishing limits) could be generated for the GOA region, including a spawning stock biomass estimated based on the maturity-at-age estimate; an approach similar to that used for Sharpchin Rockfish *Sebastes zacentrus* (Tribuzio and Echave 2015). This study would also provide an individual estimate of natural mortality in the GOA, which for this species, is given a broad range with 17 other rockfishes. The natural mortality rate is important in setting fishing reference points; therefore, gaining knowledge on the life history of a species is a major step in improving management for a data-poor stock such as Harlequin Rockfish. Although the official overfishing definitions currently apply to the entire multispecies complexes that include Harlequin Rockfish, any effort to report separate fishing reference points provides managers with more sufficient management scrutiny to determine overfishing. In the AI, Harlequin Rockfish biology remains poorly understood, notably for its continued lack of a length or age-at-maturity estimate and insufficient region-wide growth analysis. The new estimate of longevity from the AI, however, necessitates a closer examination within its current management structure.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.