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ARTICLE

Growth, distribution, and mortality of Light Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands

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Abstract

Objective: Along the Aleutian Islands, Light Dusky Rockfish *Sebastes variabilis* and Harlequin Rockfish *S. variegatus* are two of the more abundant species within the "Other Rockfish" management complex of this region. Many *Sebastes* spp. are assessed in multispecies complexes due to a lack of basic biological information to inform management. In an effort to address data gaps, we investigated age, growth, and natural mortality for both species. The larger abundance of Light Dusky Rockfish allowed for an examination of distribution across different areas of the Aleutian Islands.

Methods: Otoliths from Light Dusky Rockfish and Harlequin Rockfish were used for age determination to describe growth parameters and subsequent maximum ages used for calculating rates of natural mortality from a mean of updated age-based estimators. Generalized linear models were developed to describe the depth distribution of Light Dusky Rockfish.

Result: Ages ranged from 3 to 79 years for Harlequin Rockfish and 3 to 70 years for Light Dusky Rockfish. Maximum ages were corroborated by multiple analyses providing estimates for natural mortality (Light Dusky Rockfish = 0.084; Harlequin Rockfish = 0.075). The von Bertalanffy growth model for Harlequin Rockfish indicated sex-specific differences, with females attaining larger maximum sizes and a lower growth coefficient. Light Dusky Rockfish showed no differences in growth by area or sex. Length distributions among areas for each species were different. Light Dusky Rockfish tended to occur in deeper water in the central and western areas of the Aleutian Islands. The presence of Light Dusky Rockfish in deeper water is influenced, through the effect in terms of odd ratios, by maturity status and area and is variable by year.

Conclusion: These results contribute to our understanding of the management and biology of *Sebastes* spp. within their complex, but additional investigations are needed, especially with how traits may differ within and between regions.

KEYWORDS

age and growth, fisheries management, life history, natural mortality

INTRODUCTION

Stocks in multispecies fisheries or complexes often lack basic biological or life history information that is required for single-species assessments. Approaches to managing data-limited stocks have included using known information from congeneric or related species to fill in data gaps for important life history parameters (García-Carreras et al. 2015). However, such proxy information for basic stock assessment parameters (e.g., age, growth, mortality) introduces additional uncertainty in assessments. This may be especially true when closely related species with diverse life histories are grouped into a single multispecies fishery or complex (e.g., Wakeford et al. 2004; Currey et al. 2013). For many species, it may not be feasible to develop harvest control rules on an individual basis, but understanding their life history allows managers to make informed decisions on whether current practices are the most appropriate. In addition, life history parameters may help to identify separate management stocks (e.g., Begg and Waldman 1999).

In Alaska, Light Dusky Rockfish *Sebastes variabilis* and Harlequin Rockfish *S. variegatus* are managed within a rockfish multispecies complex ("Other Rockfish"; *Sebastes* spp. and *Sebastolobus* spp.) in the Bering Sea–Aleutian Islands management region (https://apps-afsc.fisheries.noaa.gov/refm/docs/2021/BSAIintro.pdf, accessed June 2022). Management for this complex relies on reference points computed by multiplying an overfished level (F_{OFL}) by the recent estimate of exploitable biomass, where natural mortality (M) is used as a proxy for F_{OFL}. Both species form a subcomponent within the complex that includes all species, except Shortspine Thornyhead *Sebastolobus alascanus*. Light Dusky Rockfish and Harlequin Rockfish are the most abundant within this subgroup. They are found primarily in waters off the Aleutian Islands and are significantly less abundant in the eastern Bering Sea (Hoff 2016; Lauth et al. 2019). Light Dusky Rockfish is distinguished from Dusky Rockfish *Sebastes ciliatus* by color and morphometric characteristics and its occurrence in deeper waters (Orr et al. 2000; Orr and Blackburn 2004). Light Dusky Rockfish is distributed across the Aleutian Islands, with the highest biomass estimates in the eastern Aleutian Islands. Light Dusky Rockfish is the dominant species within the component without Shortspine Thornyhead, contributing between 85% to 90% of the estimated annual biomass of 2500 metric tons (Sullivan et al. 2020). Harlequin Rockfish is the second most abundant species but is less common (von Szalay et al. 2017); similar to Light Dusky Rockfish, its population is likely underestimated due to its documented presence in untrawlable areas (Jones et al. 2012, 2021).

Impact statement

Age and growth data was analyzed from otoliths to develop initial growth parameters and rates of natural mortality for Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands. In addition, an analysis of the depth distribution of Dusky Rockfish was conducted to further understand its management and biology.

Annual fishery catches for Light Dusky Rockfish and Harlequin Rockfish have been variable in volume, but recent years suggest an increase in exploitation (Figure 1). Both species are primarily caught in bottom trawl gear across the continental shelf of the Aleutian Islands (Sullivan et al. 2020). Light Dusky Rockfish has consistently had the highest annual fishery catch of all the species within the entire complex since 2003 (with a high of 571 metric tons in 2018; Figure 1). An increase in landings in the Aleutian Islands since 2010 suggests that the catch of this species might be contributing to the F_{OFL} being exceeded for this subcomponent of the complex (Sullivan et al. 2020), necessitating an understanding of its biology in the region. Light Dusky Rockfish is currently identified as a species with increased conservation concerns in the assessment (Sullivan et al. 2020). Mean catch for Harlequin Rockfish has been approximately 44 metric tons since 2003, but this number has approached 100 metric tons in each year for the last three reported years (2018–2020; Sullivan et al. 2020; Figure 1).

Life history data for Light Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands are limited. To date, there has been no published information on age and growth and a limited understanding of the spatial or temporal effects of the aforementioned traits, including the distribution of these species. Although Light Dusky Rockfish and Harlequin Rockfish are not assessed using age-structured models in the Aleutian Islands, estimates of age and growth, including maximum age, can provide basic knowledge on the age and size structure of the populations, as well as the data needed to estimate important life history parameters such as M (e.g. Then et al. 2015; Maunder et al. 2023). For both species, more information exists from the Gulf of Alaska, where they are much more abundant. From this area, Light Dusky Rockfish maximum age has approached the mid-60s (Williams et al. 2022) and growth does vary among areas (Malecha et al. 2007). Harlequin Rockfish also exhibit variable growth across Gulf of Alaska areas, with ages known to be greater than 70 years and larger-sized fish occurring in cooler, deeper waters (TenBrink and Helser 2021).

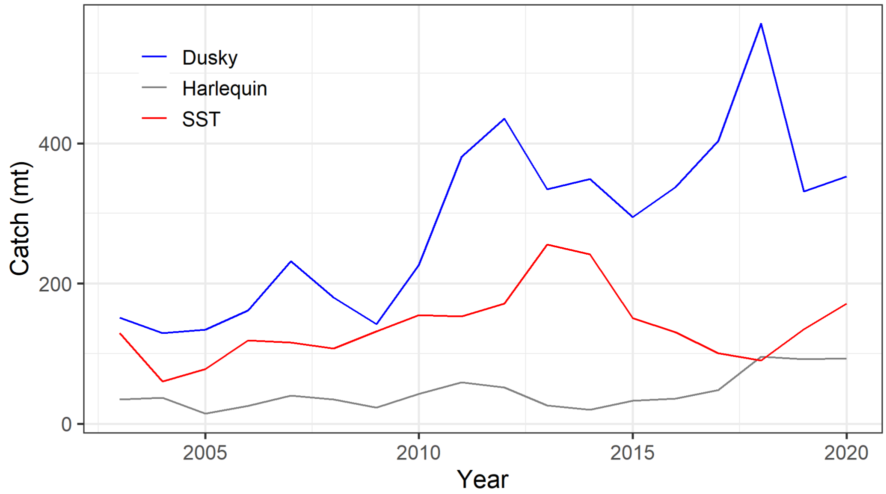

FIGURE 1 Time series of annual fishery catch in metric tons (mt) for Light Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands from 2003 to 2020. Fishery catch for Shortspine Thornyhead (SST) is provided for comparison. The mean annual catch for the entire complex, including Shortspine Thornyhead, is 541 metric tons during this period.

Information about fish distribution is valuable both for understanding possible effects of ecological processes and for informing fisheries management decisions. The core depth distributions for both Light Dusky Rockfish and Harlequin Rockfish are within the depth range typically sampled by bottom trawl surveys in the Aleutian Islands (<500 m; von Szalay et al. 2017). They inhabit areas near the edge of the continental shelf between the depths of 100 and 300 m. For Light Dusky Rockfish, the most abundant species in its complex subgroup, historical time series data from surveys is available for use in describing spatial and temporal distribution patterns for those captured. Due to our limited biological knowledge of Light Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands to support stock assessment, the goals of this study were to provide initial age and growth parameters, including updating estimates of *M* that may be used in calculating management reference points, to determine if any spatial differences exist in age and growth parameters between distinct areas of the Aleutian Islands, and to assess patterns of depth distribution, focusing on the more abundant Light Dusky Rockfish.

METHODS

Survey area and field collections

Specimens in this study were mainly collected aboard triennial (1997–2000) and biennial (since 2000 through 2022, excluding 2008) bottom trawl surveys conducted by the Alaska Fisheries Science Center in the Aleutian Islands. The survey area extends across the continental shelf and upper slope from Islands of Four Mountains (170°W longitude) to Stalemate Bank west of Attu Island (170°E longitude), including Petrel Bank (180° longitude), and on just the northern side of the archipelago between Unimak Pass (165°W longitude) and the Islands of Four Mountains (Figure 2). This survey ranges across regions exhibiting distinct oceanographic and biological effects. The Aleutian Islands is divided by eastern, central, and western ecoregions (areas) within this marine ecosystem, which also encompasses primary management areas (Ortiz and Zador 2021; Figure 2). One of the major biogeographical breaks in this ecosystem lies at Samalga Pass (Figure 2). East of Samalga Pass (169°W), waters derived from the Alaska Coastal Current predominate, whereas west of Samalga Pass, waters of the Alaskan Stream predominate (Hunt and Stabeno 2005). Hunt and Stabeno (2005) further suggested a cline in productivity, with lower rates of production in the western Aleutian Islands. Additionally, longitudinal trends in distribution and growth patterns have been observed for major commercial species across the Aleutian Islands, including Northern Rockfish *Sebastes polyspinis* (Logerwell et al. 2005).

The bottom trawl surveys employed a random-stratified sampling design, divided into strata that are defined by depth and area (latitudinal and longitudinal boundaries). Survey operations were conducted in compliance with national and regional protocols detailed by Stauffer (2004). The surveys were randomly stratified designs of trawlable areas (von Szalay and Raring 2020). Surveys employed Nor'Eastern high-opening bottom trawls with a headrope measurement of 27.2 m and footrope measurement of 36.3 m (Stauffer 2004). The operational goal of each tow was a standard towing speed of 3 knots and good bottom contact, with a maximum of 20-m change in depth, for 15 min of on-bottom time. Survey depths ranged from

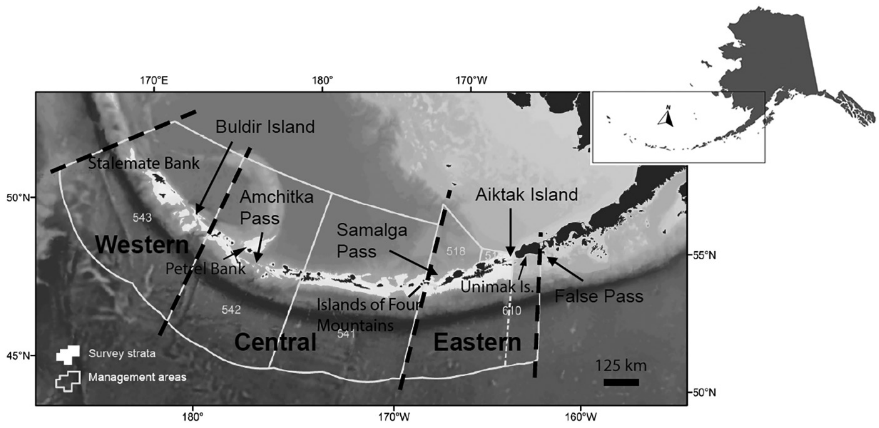

FIGURE 2 A map of the Aleutian Islands survey area within Alaska (inset map) and recognized spatial areas (Ortiz and Zador 2021).

nearshore waters of <50–500 m. Numbers and weights in catch of all taxa were recorded for each haul. A random subsample of up to 150 specimens was collected and measured to generate length frequencies, and a subset of these fish were utilized for otolith collection, with a maximum of three per centimeter per sex for each haul. Fork length (cm) and whole fish weights (g) were recorded in association with the otolith collections.

Data from commercial fishing vessels across the Aleutian Islands was used to augment samples collected from the bottom trawl survey. Otoliths from Light Dusky Rockfish were collected from random subsampling of bottom trawl gear from three different years (2009, 2019, and 2021). Fork length (cm) and whole fish weights (g) were recorded in association with the otolith collections. Sampling was conducted from a predetermined priority list of predominant *Sebastes* spp. in the catch (Alaska Fisheries Science Center 2022). When Light Dusky Rockfish were encountered in the sampled hauls, the frequency of otoliths collected ranged from one otolith pair if they were the thirdmost dominant species in the haul to up to three otolith pairs if the most dominant in the catch. No otoliths from Harlequin Rockfish were collected from commercial fishery catches for this study.

Age determination

Rockfish otoliths have largely been aged from two primary preparation methods: the traditional break and burn and a variation of this method, the break-and-bake technique, which has been used more frequently for *Sebastes* spp. in recent years (Matta and Kimura 2012). For this study, the aging process began with sagittal otoliths (either left or right) transversely sectioned through the core using a low-speed saw. The cut otolith prepared using break and burn was passed over an open flame, while the break-and-bake technique used a conventional toaster oven to "bake" the otolith for 35 min at 500°F. Examination of whole otolith surfaces provided supplemental information in the age determination process. Age determination by two independent age readers was performed with reflected light under a dissecting microscope (Leica MZ 95; Leica Microsystems) and selected otoliths imaged at 25× magnification with a digital microscope camera (Leica DMC4500). Growth increments from otoliths were annotated by both age readers and enhanced using Adobe Photoshop Elements (version 18.0) software. Scale bars (mm) were added to the otolith image to aid with early year increment size estimation. For Harlequin Rockfish, the bomb radiocarbon work of Kastelle et al. (2020) necessitated a reexamination of the currently used preparation method, which indicated an underaging by 3–4 years with the break-and-burn method. We addressed the biased aging for Harlequin Rockfish by modifying the preparation method by baking the otoliths rather than the traditional break and burn.

Age precision between readers was estimated and evaluated using percent agreement, average percent error (Beamish and Fournier 1981), coefficient of variation (CV) (Chang 1982; Kimura and Anderl 2005), and age bias plots (Campana et al. 1995). Between-reader variability was calculated using Bowker's test of symmetry (Bowker 1948; Evans and Hoenig 1998). For Harlequin Rockfish, the quality control procedure involved a 100% test sample. For Light Dusky Rockfish, an additional reader tested a 20% random subsample. For the oldest specimens, multiple expert analysts recorded independent age estimates for corroboration. An examination of age discrepancies was conducted to resolve potential differences or biases prior to recording final ages.

Size and growth analysis

We assessed patterns of length distributions for both Light Dusky Rockfish and Harlequin Rockfish. Separate two-sample Kolmogorov–Smirnov tests were used to determine if there was a significant difference among length distributions. Pairwise comparisons were conducted between areas (western, central, eastern) of the Aleutian Islands.

Growth models of the length-at-age data were fit using nonlinear least squares from the following common parameterization of the von Bertalanffy equation (equation 1; Beverton and Holt 1957):

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

where L_t is the expected length (mm) at age t, L_∞ is the asymptotic length, k is the growth rate coefficient, and t_0 represents the theoretical age when length was zero. Growth parameters were estimated through the *nlsLM* function in R (version 4.0.4; R Core Team 2021) using the Levenberg–Marquardt algorithm from packages *minipak.lm* (Elzhov et al. 2013) and *FSA* (Ogle et al. 2021). We chose this function as it was more robust with less than optimal starting values compared to the Gauss–Newton algorithm associated with the *nls* function (*nlstools*; Baty et al. 2015). Confidence intervals for each of the von Bertalanffy growth parameters were estimated via bootstrapping based on normal distribution theory using 1000 iterations (Ogle et al. 2021). Likelihood ratio tests were used to compare sex-specific or area-specific growth (Kimura 1980; *fishmethods*, Nelson 2018). Due to limited sample sizes in the western Aleutian Islands, area comparisons among length-at-age data for Light Dusky Rockfish was made between east and west of Samalga Pass.

Distribution

We used generalized linear models (GLMs) to explore the depth distribution of Light Dusky Rockfish caught in the bottom trawl surveys of the Aleutian Islands. Bottom depth was determined to be one of the best predictors of suitable habitat for Light Dusky Rockfish in the Aleutian Islands (Turner et al. 2017). In order to visualize depth segregation across the Aleutian Islands among primary life history stage (maturity status = immature, mature), we separated the data using the midpoint for length at 50% maturity (33 cm) between the estimates of Turner et al. 2017 (29.5 cm) and Chilton 2010 (36.5 cm). *Sebastes* spp. have been shown to exhibit differences in bottom depth habitat between juvenile and adult rockfish, indicating that larger-sized fish prefer deeper water (e.g., Rooper 2008; Frey et al. 2015). The GLMs were fit using a binomial distribution with a logit link to evaluate the effects of Light Dusky Rockfish presence at depths greater than 100 m (≥100 m = 1; absence ≤ 100 m; R Core Team 2021). We chose to quantify the binary outcome with the odds ratio (Gallis and Turner 2019), which represents the relative association to the response variable using a ratio measure. The odds ratios are the exponential form of the model coefficient estimates (Burnham and Anderson 2002). An odds ratio > 1 indicates an increased occurrence of an event, while an odds ratio < 1 indicates a decreased occurrence or negative association. Maturity status, survey year (cruise), and area were chosen as covariates in the model and treated as factor variables to describe their effect on the response variable. The full model followed this structure:

$$Depth \sim \beta_0 + area + maturity\ status + cruise, \quad (2)$$

where β_0 is the intercept; *depth* is the bottom depth of capture (m), with the binomial response being presence and absence of Light Dusky Rockfish captured at greater than 100 m; *cruise* represents temporal effects, proxy for year; *area* was divided into three subareas across the Aleutian Islands (west, central, east). The model with the lowest Akaike information criterion (AIC; Akaike 1973) value was selected as the most appropriate model after considering all combinations of covariates. Model diagnostics, such as assumption checking and outlier detection, were performed.

Mortality

Then et al. (2015) used a comprehensive approach to evaluate the predictive performance of estimators based on combinations of life history parameters and found that maximum-age-based (t_{max}) estimators were superior to those methods associated with growth or water temperature (e.g., Alverson and Carney 1975; Pauly 1980; Jensen 1996). Their analysis estimates values of M, while validating these values through comparison of M from direct methods. We use their updated methods based on modifications to the Hoenig (1983) method using linear (equation 3) and nonlinear models (equation 4). Additionally, we used Hamel's (2015) formula representing a median value from an M prior (equation 5) currently used for U.S. West Coast *Sebastes* spp. that fits the Then et al. (2015) one-parameter estimate under a log–log transformation (Cope et al. 2021; Langseth et al. 2021). The formulas for the aforementioned estimators are as follows:

$$\log(M) = 1.717 - 1.01 \log(t_{max}) \quad (3)$$

$$M = 4.899 t_{max}^{-0.916} \quad (4)$$

$$M = 5.4 / t_{max} \quad (5)$$

RESULTS

Age determination

A total of 227 Harlequin Rockfish and 1047 Light Dusky Rockfish ages were assigned from fishery-independent otolith samples. In addition, 332 Light Dusky Rockfish ages were assigned from fishery-dependent samples. For Harlequin Rockfish, no systemic biases occurred between age readers throughout its age range (3–79 years; Bowker's test of symmetry: $X^2 = 57.1$, $p = 0.799$; Figure 3). The overall CV for Harlequin Rockfish age was 4.61% based on the updated preparation method ($n = 227$; Table 1). Overall mean observed age for readers 1 and 2 was 18.35 and 18.71 years, respectively (Table 1). For early year interpretation in the age determination of Harlequin Rockfish, the first two annual marks generally followed a typical *Sebastes* spp. pattern (Figure 4A). The third interpreted growth zone was narrower and bordered closer to the second annuli, often represented by dark marks. Clarity in annuli interpretation near the otolith edge among some samples was observed (Figure 4A). Maximum age was estimated to be 79 years from multiple readings (Figure 4B, C), but older specimens (>40 years) only accounted for approximately 6% ($n = 14$) of the total sampled. There was no age reader bias for Light Dusky Rockfish (Bowker's test of symmetry: $X^2 = 37.2$, $p = 0.552$; Figure 3). Light Dusky Rockfish had an age range from 3 to 70 years (Figure 3). Clearer growth zones from Light Dusky Rockfish otoliths were evident throughout the observed age range, especially for those fish with ages ≤20 years (Figure 5A). Independent age analysts corroborated the maximum age (Figure 5B, C). Age precision for Light Dusky Rockfish from fishery-independent samples resulted in a CV of 2.26%, with both age readers agreeing to nearly 67% of the samples tested ($n = 259$; Table 1). The CV between readers for those fish ≥20 years was 3.44%. The overall CV from ages of Light Dusky Rockfish collected from fishery-dependent sources was slightly higher (3.65%) from older samples.

Size and growth analysis

A total of 2950 Light Dusky Rockfish and 1021 Harlequin Rockfish had recorded length measurements during trawl surveys of the Aleutian Islands. The survey appeared to catch a larger size range of Light Dusky

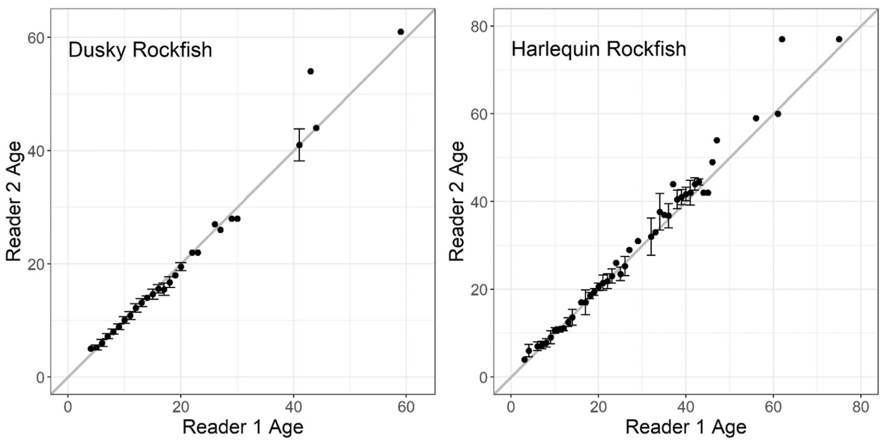

FIGURE 3 Age bias plots comparing original ages between readers prior to evaluating age discrepancies. Deviance from the linear 1:1 equivalence line indicated bias. Error bars represent SE.

TABLE 1 Age precision statistics for Light Dusky Rockfish and Harlequin Rockfish. Abbreviations are as follows: CV = coefficient of variation, APE = average percent error, and PA = percent or exact agreement between readers (±0 years). Source refers to the sampling platform.

Species	Source	Age *N*	Test *N*	Mean read age	Mean test age	CV	APE	PA	PA (± 2 years)
Light Dusky Rockfish	Survey	1047	254	13.06	13.21	2.29	1.62	66.8	98.5
	Fishery	332	80	15.69	15.77	3.65	2.58	40.9	95.4
	Total		334	13.62	13.60	2.61	1.85	61.4	97.6
Harlequin Rockfish	Survey	227	227	18.35	18.71	4.61	3.26	35.2	90.0

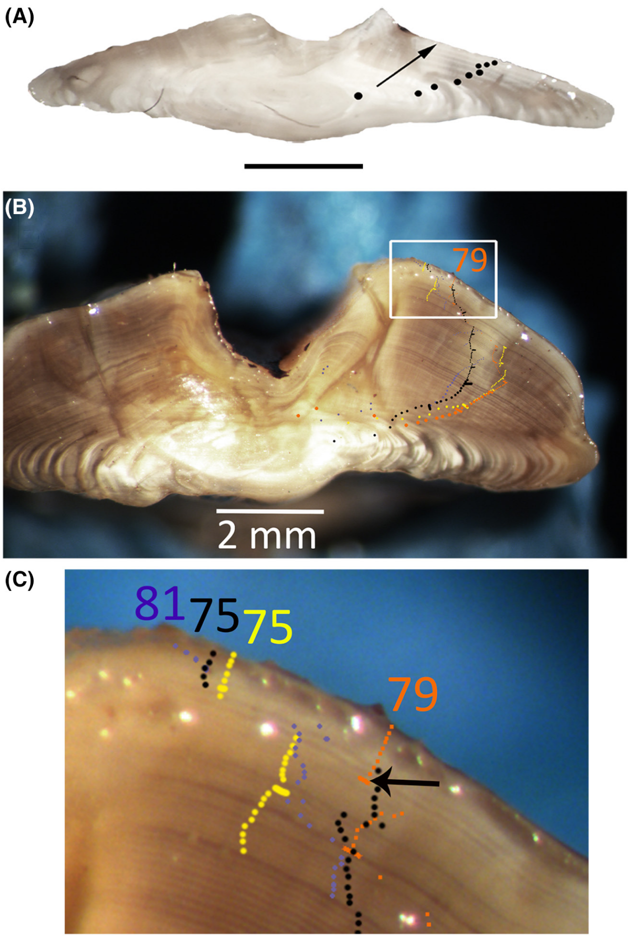

FIGURE 4 Images of representative otoliths for Harlequin Rockfish: (A) an otolith from a 10-year-old fish, aged along the primary reading axis (arrow; scale bar = 1 mm); (B) the oldest specimen from this study (79 years), aged independently by four experienced rockfish age readers; and (C) zoomed image of each independent age (the arrow denotes the mark at year 70 in orange).

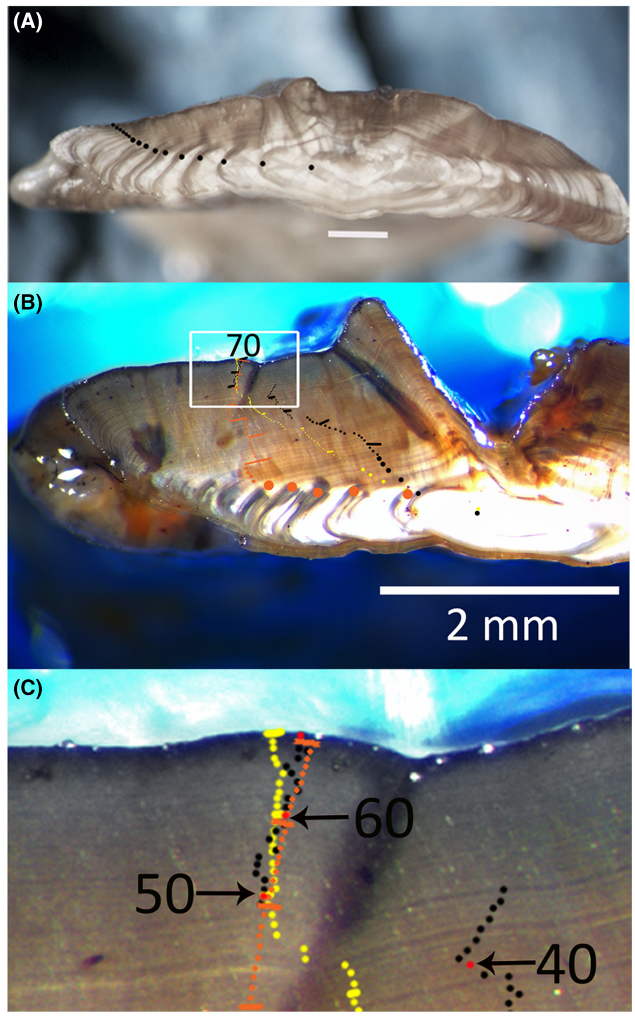

FIGURE 5 Images of representative otoliths for Light Dusky Rockfish: (A) an otolith from a 16-year-old fish (scale bar = 1 mm); (B) the oldest specimen from this study (70 years), aged independently by three experienced rockfish age readers (each age was identical); and (C) zoomed image of each independent age (the arrows denote marks at year 40, 50, and 60 years from the annotation in black).

Rockfish than Harlequin Rockfish (Figure 6). For Light Dusky Rockfish, fork lengths ranged between 15 and 53 cm and their distributions between each of three areas of the Aleutian Islands were significantly different (two-sample Kolmogorov–Smirnov tests: $p < 0.001$; Figure 6). Mean fork length for Light Dusky Rockfish in the central area (mean = 40.8 cm; SD = 3.3; range = 23–53 cm) was higher than those in the western area (mean = 39.9 cm; SD = 2.9; range = 23–50 cm) and eastern area (mean = 38.3 cm; SD = 5.8; range = 15–51 cm). Length distributions for Harlequin Rockfish were also significantly different among areas (Figure 6). Lengths ranged between 17 and 39 cm in the central area (mean = 32.4 cm; SD = 3.7 cm), 20 to 42 cm in the eastern area (mean = 32.5 cm; SD = 2.6), and 19 to 38 in the western area (mean = 30.8 cm; SD = 3.2; two-sample Kolmogorov–Smirnov test: $p < 0.001$; Figure 6).

Length-at-age analysis showed growth differences for Harlequin Rockfish by sex (likelihood ratio test: $p < 0.001$; Figure 7A), but a combined von Bertalanffy model best represented Light Dusky Rockfish length at age as sex and area (Samalga Pass, east versus west) had no effect on growth (likelihood ratio test: $p > 0.05$; Figure 7B). The growth coefficient (k) for Harlequin Rockfish was 0.235 for females and 0.457 for males, with females growing slower than males after approximately 10 years (Table 2; Figure 7A). The asymptotic length of Harlequin Rockfish males was approached several years younger compared with females (Figure 7A). Light Dusky Rockfish growth showed a 10-year-old fish reaching approximately 35 cm. The asymptotic length was approached at approximately 20 years at 45 cm (Figure 7B).

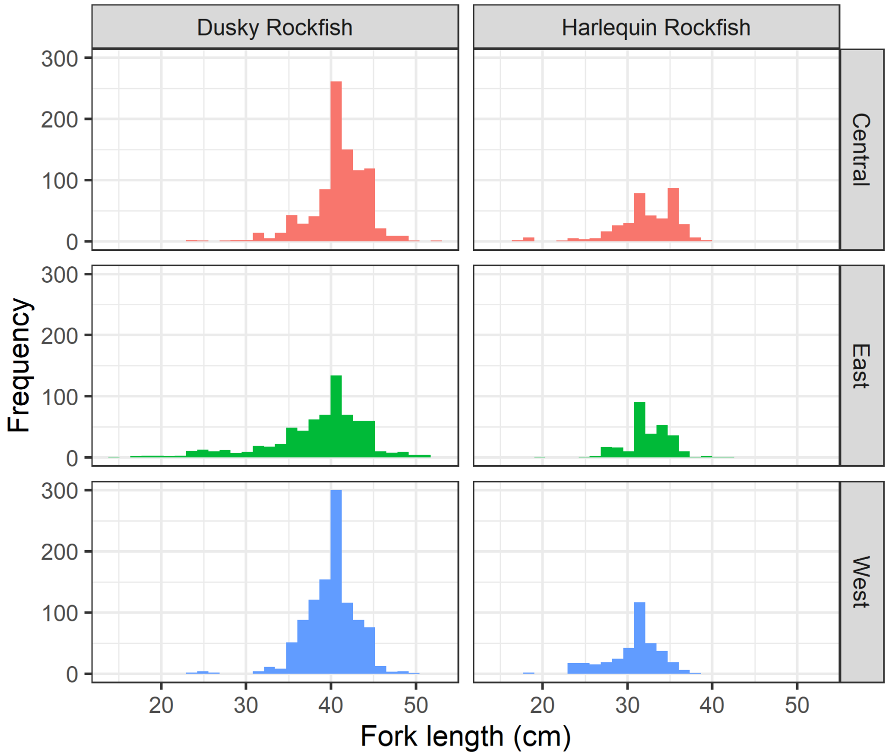

FIGURE 6 Length-frequency distributions for Light Dusky Rockfish and Harlequin Rockfish caught in the west, central, and eastern areas of the Aleutian Islands during bottom trawl surveys.

Distribution

When describing the depth distribution, the variance in depth generally increased as a function of size for captured Light Dusky Rockfish (Figure 8). At 100 m and approximately at the reported size at maturity (33 cm) there appears to be a shift in depth preference, although this pattern appears to be slightly different for each area. In the western area, nearly all Light Dusky Rockfish greater than 35 cm were captured between 100 and 250 m. Larger numbers of Light Dusky Rockfish in the eastern area were captured near 100 m and were found to be present in shallower waters. In the central area, large-sized Light Dusky Rockfish were present in shallower depths, but there was an overall trend towards deeper water with increasing size. The full GLM model with predictors of area, maturity status, and cruise was the best model (AIC = 1713.6), compared with the next highest model with covariates area and cruise (ΔAIC = 117.3). Each covariate was able to highly predict the value of the response variable in the full model (Table 3; Figure 9). Odds ratios suggest that maturity status (mature fish) is the most influential predictor (Figure 9). Fish captured in the western area, where much of the sampled population was located greater than 100 m, also exhibited strong association with deeper depths. In the eastern area of the Aleutian Islands, an odds ratio of 0.14 suggests that presence of Light Dusky Rockfish at increasing depth was less likely to occur (Figure 9). The odds of different survey years (cruises) of capturing Light Dusky Rockfish deeper than 100 m was greater in some years than others.

Mortality

Estimates of *M* based on maximum age showed some variation among the methods. Estimates from the nonlinear model of Then et al. (2015) were higher than those from Hamel (2015) and the linear model of Then et al. (2015) (Table 4). The mean estimate of *M* for Harlequin Rockfish for the maximum observed age of 79 years was 0.075/year (Table 4). For Light Dusky Rockfish, the mean estimate of *M* from the maximum observed age of 70 years was 0.084/year (Table 4).

DISCUSSION

This study provides the most comprehensive biological examination for both Light Dusky Rockfish and Harlequin Rockfish in the Aleutian Islands. Results here will provide critical information to inform management in the assessment of these two data-limited species, particularly aspects of age and growth, including maximum age, which may be used to estimate rates of *M*. Also, our distribution analysis suggested differences in ontogenetic movement from Light Dusky Rockfish across the Aleutian Islands, important in understanding spatial dynamics in this region.

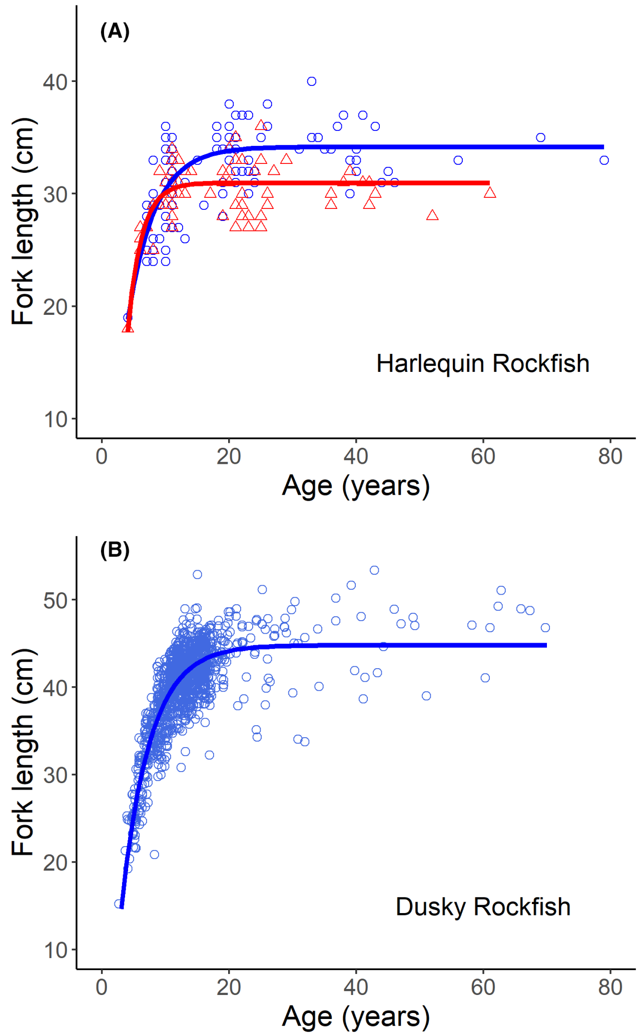

FIGURE 7 Fitted curves of the von Bertalanffy growth equation from age–length data for (A) Harlequin Rockfish and (B) Light Dusky Rockfish captured in the Aleutian Islands. For Harlequin Rockfish, males are in red, females are in blue.

Reliable age estimates are required to determine life history traits such as maximum age, growth rates, and *M*, all of which are crucial for stock assessment and management. Prior to this study, Harlequin Rockfish ages have been determined through the break-and-burn method. Our results suggest that otoliths prepared via the break-and-bake technique might be a more suitable method, with slightly higher precision than age estimates from the Gulf of Alaska that were prepared by the break-and-burn method (4.61% CV, this study; 5.07% CV in TenBrink and Helser 2021). Our maximum age of 79 years represents the oldest published estimate for Harlequin Rockfish. In a recent study, TenBrink and Helser (2021) found one specimen to reach 76 years from a limited collection of the Aleutian Islands. For Light Dusky Rockfish, age compositions from the Gulf of Alaska are reported biennially in the stock assessment of that region (Williams et al. 2022). Maximum ages from the survey and fishery are 75 and 66 years, respectively. In the Aleutian Islands, the maximum corroborated age from the Aleutian Islands was 62 years (https://www.fisheries.noaa.gov/resource/tool-app/fish-species-maximum-age-data; accessed May 2023).

Light Dusky Rockfish is routinely aged on an annual or biennial basis to support an age-structured assessment for the Gulf of Alaska stock (Fenske et al. 2020). Although ages and the aging method for Light Dusky Rockfish have not been validated, historical age reader precision suggests that ages from this species are precise, resulting in the highest percent agreement and lowest CV for any production-aged *Sebastes* spp. (https://www.fisheries.noaa.gov/alaska/science-data/alaska-age-and-growth-precision-statistics; September 2022). Nevertheless, aging error is accounted for in the Gulf of Alaska stock assessment as aging error matrices are constructed by assuming that ages were unbiased but had normally distributed age-specific error based on between-reader percent agreement tests (Fenske et al. 2020). In this study, we were confident in our aging estimates (relatively low CV and average percent error) and that Light Dusky Rockfish is long-lived with a maximum age reaching 70 years, an age derived independently from multiple

TABLE 2 Predicted growth parameters from the von Bertalanffy equation for Aleutian Islands Light Dusky Rockfish and Harlequin Rockfish. Numbers in parentheses represent the bootstrapped 95% confidence intervals.

Data	L_{inf} (cm)	*K*	t_0	*N*
Light Dusky Rockfish				
Combined	44.81 (44.39, 45.27)	0.224 (0.208, 0.240)	1.236 (0.865, 1.547)	1379
Harlequin Rockfish				
Male	30.98 (30.53, 31.48)	0.457 (0.331, 0.625)	2.143 (0.747, 2.913)	108
Female	34.18 (33.46, 34.97)	0.235 (0.164, 0.305)	0.595 (−2.283, 2.061)	119
Combined	32.64 (32.19, 33.14)	0.296 (0.235, 0.366)	0.115 (−0.319, 2.143)	227

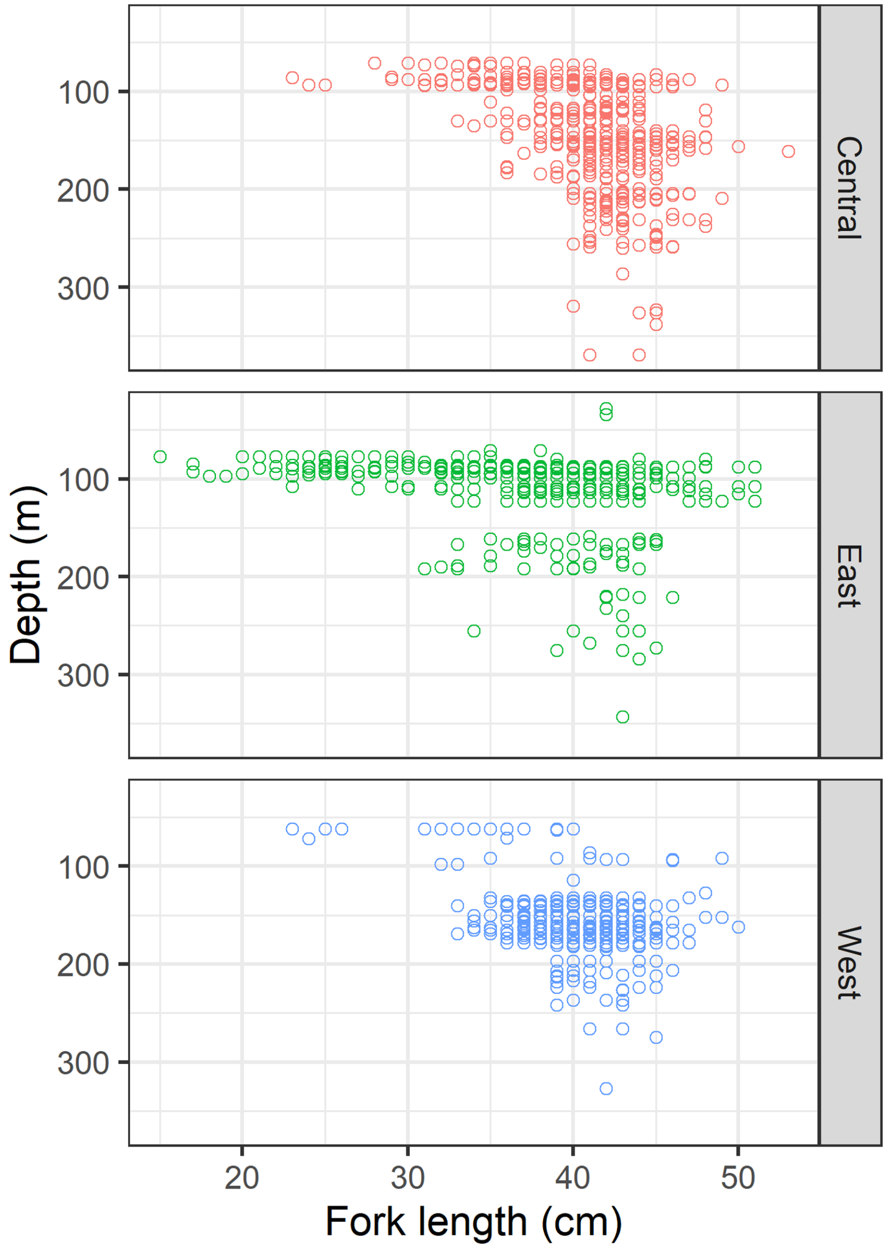

FIGURE 8 Plot of depth versus length for Light Dusky Rockfish captured in the bottom trawl surveys in the three Aleutian Islands areas.

TABLE 3 Deviance table for the best-fitting generalized linear model (binomial GLM) for predicting presence or absence of Light Dusky Rockfish (>100 m) in the Aleutian Islands.

Model	df	Deviance residuals	df residuals	Deviance	*p*
Null			2689	3410.9	
Area	2	930.5	2687	2480.4	0.000
Maturity status	1	116.3	2686	2364.1	0.000
Cruise (survey year)	9	676.6	2677	1687.5	0.000

analyses. In summary, for some of the oldest specimens of any stock in question, we recommend ages be conducted at least through paired readings for corroboration whenever possible, especially when management reference points are based on age-based empirical methods for data-limited stocks. For both Light Dusky Rockfish and Harlequin Rockfish ages, we were within the CV standard of 5% that Campana (2001) suggests as an

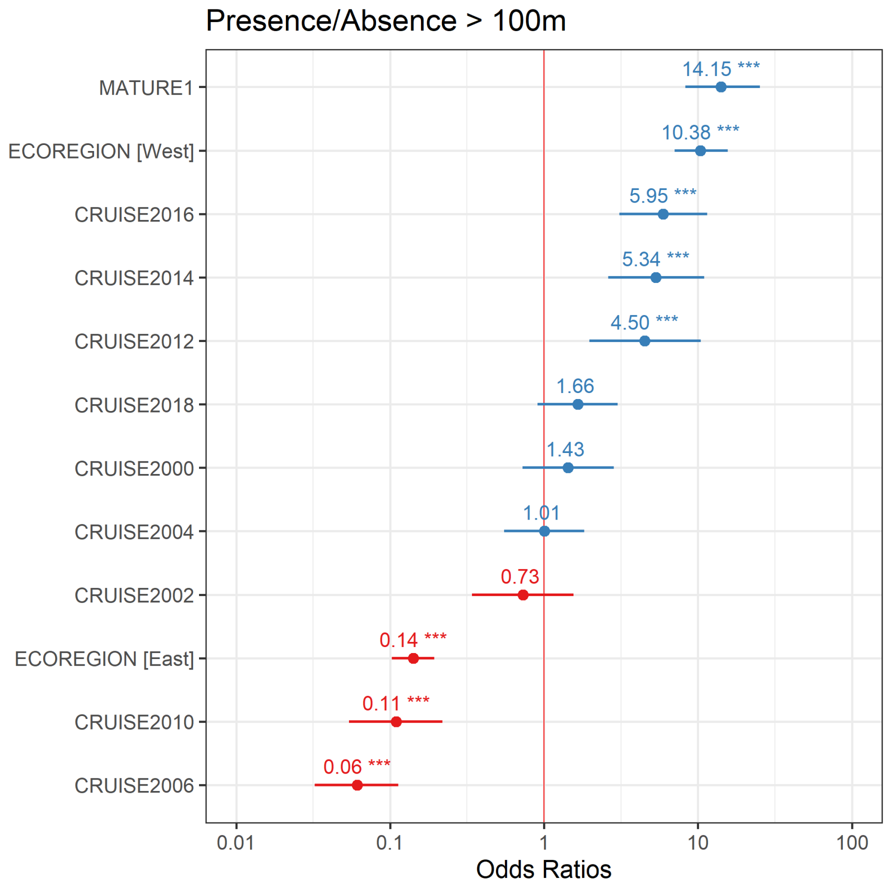

FIGURE 9 Odds ratios for the full binomial GLM used in the study. The variables to the left represent the factor variables (maturity status, area, cruise [survey year]). Asterisks indicate the significance level of the *p*-values for each variable (three asterisks indicates $p < 0.001$).

TABLE 4 Estimates of *M* for Harlequin Rockfish and Light Dusky Rockfish from three maximum-age-based (t_{max}) empirical methods. The current status quo estimate of *M* used for the assessment of the rockfish multispecies complex is 0.09. Variability around the estimates of *M* are based on the CV from age-reading precision for Harlequin Rockfish (4.61%; ≈5 years) and Light Dusky Rockfish (2.26%; ≈2 years). Maximum age for Harlequin Rockfish and Light Dusky Rockfish was 79 and 70 years, respectively. LM = linear model; NLS = nonlinear least squares.

Method	Harlequin Rockfish	Light Dusky Rockfish
Then et al. 2015 LM	0.067 (0.063, 0.072)	0.076 (0.074, 0.079)
Then et al. 2015 NLS	0.090 (0.085, 0.095)	0.100 (0.097, 0.103)
Hamel 2015	0.068 (0.064, 0.073)	0.077 (0.075, 0.080)
Mean	0.075	0.084

acceptable benchmark for precision among species of moderate longevity and aging complexity.

This study is the first to report on estimates of growth for both Harlequin Rockfish and Light Dusky Rockfish in the Aleutian Islands. For Harlequin Rockfish, the growth parameter (*k*) was less than what was reported in the Gulf of Alaska, although the estimated asymptotic lengths were similar (Malecha et al. 2007; TenBrink and Helser 2021). For Light Dusky Rockfish, our estimates were the result of a combined growth model. In the central Gulf of Alaska, Chilton (2010) reported differences between male and female growth. The current age-structured assessment model of Light Dusky Rockfish, however, uses combined von Bertalanffy growth parameters for all fish caught (Williams et al. 2022). Further sampling and additional ages would be needed to test for any spatial or temporal effects. Our predicted length-at-age estimates should be viewed as baseline information pending further studies.

A detailed 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. Our study increases our understanding of the function and complexity of Light Dusky Rockfish distribution. Light Dusky Rockfish clearly exhibits spatial distribution by depth across the Aleutian Islands, and this distribution is segregated by life history stage. Our observations for

Light Dusky Rockfish preference for deeper depths with increasing size has been reported in other studies of *Sebastes* spp. (e.g., Frey et al. 2015). Turner et al. (2017) indicated that, in addition to bottom depth, ocean color (a proxy for productivity) was also a predictor for Light Dusky Rockfish suitable habitat. Our initial analysis suggested that ocean color had no effect on depth at capture. The samples from this study were collected across a large-scale environment and it may be necessary to closely examine smaller-scale variation (e.g., within specific areas of the Aleutian Islands) in depth distribution to understand connectivity with various oceanographic and biological forces (e.g., Schaber et al. 2012). Very little diet or prey field information exists for Light Dusky Rockfish in the Aleutian Islands that might help explain an affinity for deeper water with increasing size (https://apps-afsc.fisheries.noaa.gov/REFM/REEM/WebDietData/Table1.php; May 2023).

For the management of many Alaskan rockfish stocks, indirect methods have been routinely used to estimate *M* for data-poor stocks. Then et al. (2015) updated Hoenig's (1983) use of least squares regression, with their nonlinear method providing the strongest predictive power from the maximum age-based estimators. However, Then et al. (2015) did note that there was no strong trend in model residuals from their cross validation prediction error approach on the best two maximum age-based estimators. Then et al. (2015) raised an important point concerning their comprehensive approach—the potential difficulty in obtaining a representative longevity value in heavily exploited stocks. For the oldest estimated age in heavily exploited stocks, an estimate of *M* may be considered the upper bound to the natural mortality rate (Hoenig 2017). The utility of adopting the *M* from Light Dusky Rockfish for the non–Shortspine Thornyhead portion of the complex is likely appropriate because most of the biomass of the non–Shortspine Thornyhead portion of the complex is Dusky Rockfish (Sullivan et al. 2020). Adoption of the Harlequin Rockfish *M* would be assuming that the other members of the complex (mostly Dusky Rockfish) have the same *M*.

Even with the update to the life history parameters here, the majority of the primary species within the multispecies rockfish complex continues to be data limited (Figure 10). The ratio (M/k) can play a role in evaluating data-limited or data-moderate fish stocks (Hordyk et al. 2015; Rudd et al. 2021). Information from this study (age-based *M*) allows a comparison with other *Sebastes* spp. and suggests that estimates of *M* for Light Dusky Rockfish and Harlequin Rockfish are moderate with respect with other stocks and the

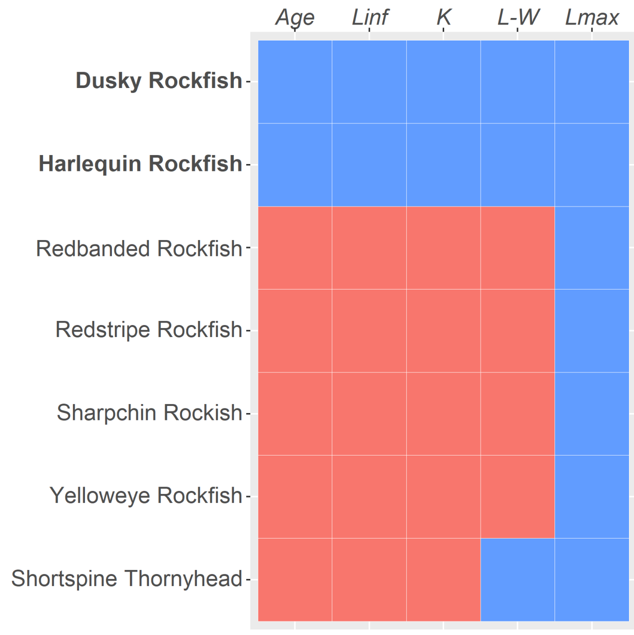

FIGURE 10 The level of data quality for selected life history traits for each major species in the multispecies rockfish complex of the Bering Sea–Aleutian Islands management region. Abbreviations are as follows: *Age* = maximum estimated age (t_{max}); *Linf* and *K* = asymptotic length and growth parameter, respectively, of the von Bertalanffy growth equation; *L-W* = length–weight relationship, as measured from fishery-independent or fishery-dependent data; and *Lmax* = recorded maximum fork length (cm). Shortspine Thornyhead is provided for comparison. Blue cells indicate where regional data has been collected, while red cells denote lack of information.

M/k ratio is similar to other stocks (Figure 11). Proxy information exists with the "borrowing" of life history data from adjacent regions that may be subject to entirely different environmental forcing mechanisms. An *M* rate of 0.09/year is currently used in the stock assessment for the non–Shortspine Thornyhead portion of the complex (Sullivan et al. 2020). Although a reduction in the rate of *M* to 0.08 found in this study appears to be relatively small, it can still have a large influence on management reference points. For example, if the fishery catch of Light Dusky Rockfish were 500 metric tons, the new estimate of *M* would decrease the F_{OFL} by 12%.

In Alaska, stocks without age-specific information on size and proportion mature continue to be managed where a harvest rate is computed by multiplying an exploitation rate by a biomass estimate. Information on size and maturity at age would allow target *F* rates to be based upon the conservation of reproductive potential. Improving the reliability of *M* under the current management scenario reduces uncertainty of fishing reference points. The F/M ratio in multispecies complexes

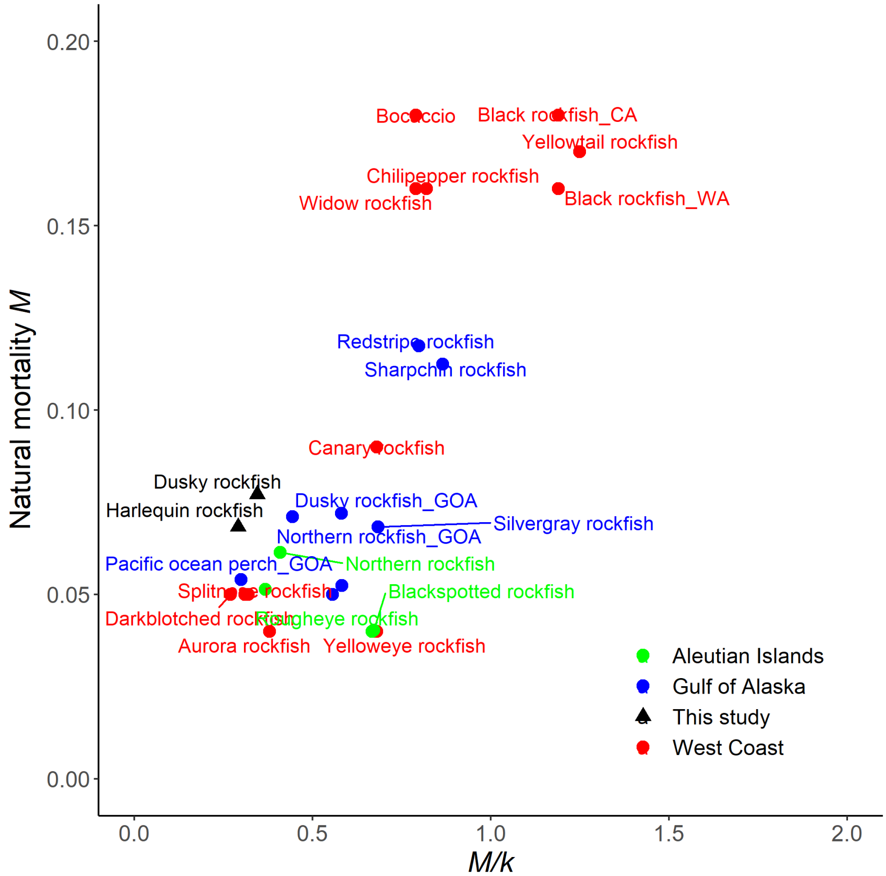

FIGURE 11 A comparison plot of *M* versus *M*/*k* with *Sebastes* spp. from areas of Alaska and the West Coast (from Sullivan et al. 2020; Rudd et al. 2021; Williams et al. 2022; this study). The following species are included: Light Dusky Rockfish, Harlequin Rockfish, Bocaccio *S. paucispinis*, Black Rockfish *S. melanops*, Yellowtail Rockfish *S. flavidus*, Chilipepper Rockfish *S. goodei*, Widow Rockfish *S. entomelas*, Redstripe Rockfish *S. proriger*, Sharpchin Rockfish *S. zacentrus*, Canary Rockfish *S. pinniger*, Northern Rockfish *S. polyspinis*, Silvergray Rockfish *S. brevispinis*, Pacific Ocean Perch *S. alutus*, Blackspotted Rockfish *S. melanostictus*, Darkblotched Rockfish *S. crameri*, Splitnose Rockfish *S. diploproa*, Rougheye Rockfish *S. aleutianus*, Aurora Rockfish *S. aurora*, and Yelloweye Rockfish *S. ruberrimus*.

provides an indication of the relative impact of fishing pressure due to the scalar multiple of *M* that is used as a proxy for fishing at maximum sustainable yield. Even under these current approaches to calculating management reference points, where a single species may represent an entire component or subgroup, our results have demonstrated that revisions are necessary. In addition to this, current methods of calculating *M* (i.e., from Hoenig 1983) have been updated and should be considered in future calculations. Although there are no plans to formally assess and manage rockfish stocks at the species level for Alaskan waters in the immediate future, new biological information allows for a review of the fishing effects on species for which sufficient information is available.

For Light Dusky Rockfish, the majority of the fishery catch from the Aleutian Islands is in the eastern area (Sullivan et al. 2020), adjacent to the western Gulf of Alaska, which is managed as a separate stock (Fenske et al. 2020). Defining stock structure is a critical piece in management decision making. The eastern portion of the Aleutian Islands management region lies east of Samalga Pass, a known ecological boundary (Ortiz and Zador 2021), and extends into the western portion of the Gulf of Alaska management region. A more thorough investigation of life history data for Light Dusky Rockfish between these two areas may be useful in determining if the apparent high exploitation rates are the result of a poorly defined stock structure or are a legitimate conservation concern. Filling life history data gaps can improve stock assessments, and it may be used as part of a multidisciplinary approach to delineate stocks (Begg and Waldman 1999) or assist in defining spatial structure (Cadrin 2020). Following this approach, future work may involve tools, such as otolith morphometrics (e.g., Canas et al. 2012; Rodgveller et al. 2017) and genetics (Buonaccorsi et al. 2005; Siegle et al. 2013), to determine population and regional-scale structure.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

All data are available upon request to the corresponding author.

ETHICS STATEMENT

All research and sampling met ethical guidelines, including legal and permitting requirements.

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