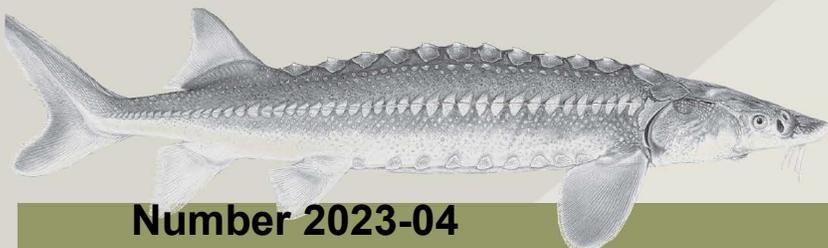
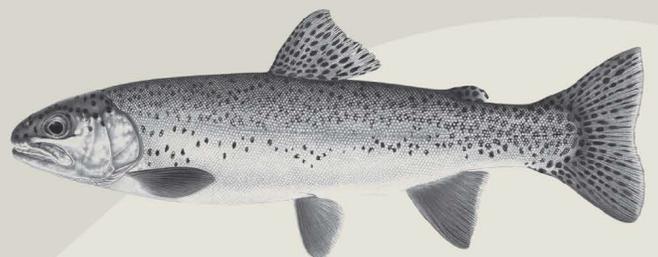




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The Search for Oregon's Older Female Rockfishes



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The Search for Oregon's Older Female Rockfishes



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SUMMARY

Recent stock assessments for Black Rockfish (*Sebastes melanops*), Canary Rockfish (*Sebastes pinniger*) and Yellowtail Rockfish (*Sebastes flavidus*) have shown that there is a lack of old female rockfish in these populations from California to Alaska. This absence is based on the lack of old females in both fisheries-dependent and fisheries-independent collections, a surprising fact considering these three species live across an extreme depth range and are therefore captured by a diversity of fisheries (hook and line, long line, midwater trawl and bottom trawl). To explore potential explanations for why older females are absent from fisheries-dependent data, we examined commercial and recreational catch data as well as surveyed the commercial and recreational fleets for their expert knowledge. Neither effort resulted in a consistent pattern or association with the lack of old females in any of the three populations. Based on our analysis of fisheries-dependent data and fleet survey responses, we present multiple hypotheses for the absence of old females, each with associated arguments for, and against; as well as a short description of how each hypothesis could be tested in the future. We consider these hypotheses using the principle of parsimony, where the reason for the absence of old females in each species is assumed to be the same. Ultimately, we hypothesize that elevated natural mortality (mortality unrelated to fishing) of females relative to males is the most likely cause of their absence. The most notable fact in support of this hypothesis being that these three species occupy a wide geographic range, a diversity of habitat types, are captured in multiple fisheries, and yet, old females are consistently absent in all three species throughout their geographic ranges. Moreover, we pose that the question of “why aren’t there old females” be reframed to ask “why are there old males” for these three species? Finally, we suggest the importance of the Big Old Fat Fecund Female (BOFFF) hypothesis be reframed to impart emphasis on the Bigger Older Fatter Fecunder Females. We feel that the original phrasing gives way to only considering the oldest fish important, while the reality is reproductive output increases linearly with age, such that a middle-aged fish is increasingly more important than a younger-aged fish. The implication being that BOFFF-related reproductive benefits increase with age and are not limited to only the oldest individuals.

BACKGROUND

Understanding the reproductive output of a population is key to effective fisheries management (Hilborn and Walters 1992; Maunder and Punt 2013). Assuming all females reproduce, reproductive output is positively correlated with the number of females in the population (He et al. 2015). Further, increased survival of offspring may occur when older females provide greater maternal investments (Bobko and Berkeley 2004; Beyer et al. 2015; Dick et al. 2017).

Stock assessments for some semi-pelagic rockfishes (Black Rockfish, Canary Rockfish, and Yellowtail Rockfish) on the West Coast of North America have demonstrated a pattern of declining proportion of females with increasing age. In other words, older individuals of these species are more likely to be male. These patterns are consistently observed in the data from

Alaska to California. However, these data come from fisheries-dependent sources, so there is uncertainty over whether the absence of old females is due to selectivity of the fisheries, or if females are not present in the population.

The uncertainty regarding the disposition of older females greatly influences the result of stock assessment models. During the most recent assessment of Black Rockfish (Cope et al. 2015), stock assessors ran two separate models, one where larger (older) females were dead, and one where they were alive but unavailable to the fishery; the results were strikingly different with approximately 30% difference in spawning stock biomass. While there are many opinions in the scientific and public communities about where these older females are, their true presence or absence in the population remains unknown.

Although declining percentage of females with age is observed throughout the geographic range of all three species, Oregon represents a unique location to attempt to address this question. Historically, Oregon has had very active commercial and recreational fisheries, and over time, most areas have been fished and a variety of gear types utilized. Therefore, to determine if these trends were associated with any historic fleet or fishery management changes, we examined trends in Oregon's historic fisheries data. We also conducted a written survey of members of Oregon's commercial and recreational fishing fleets to see if fishers had knowledge of where these older individuals may be. Based on our analysis of fisheries-dependent data and fleet survey responses, we generated a list of most likely hypotheses, discussed their merits and downfalls, and considered best ways to approach each hypothesis. Additionally, double-read age data was examined to determine if ageing error was higher for old females than old males.

Herein, we focus on Black Rockfish; however, as noted above, Yellowtail Rockfish and Canary Rockfish also exhibit this pattern. As such, we examined data from fisheries that encounter all three species, but the fleet survey focused on Black Rockfish. We use the law of parsimony when considering our results. In this case, the law of parsimony assumes that factors driving patterns observed in Black Rockfish are likely the same for Yellowtail Rockfish and Canary Rockfish. Widow Rockfish and Blue/Deacon Rockfish were also included in our initial analyses as controls because these species live in similar habitats, are phylogenetically similar, and yet do not display the same trends as Black Rockfish, Canary Rockfish and Yellowtail Rockfish.

Black Rockfish commonly occur in waters < 55 m deep (Love et al. 2002), and are a common target of both the commercial nearshore and recreational fisheries. Yellowtail Rockfish commonly occur in waters 90-180 m, whereas Widow Rockfish commonly occur between 140-210 m depth (Love et al. 2002). Both are primarily targeted by the commercial midwater trawl fishery. Canary Rockfish are commonly found across a wide range of depths, 80-200 m, and are caught in both trawl (commercial) and hook and line fisheries (commercial and recreational). Finally, Blue/Deacon Rockfish are found primarily in the nearshore < 50 m, but can occupy greater depths, often collocated with Yellowtail Rockfish and Widow Rockfish. Blue/Deacon Rockfish are primarily targeted with recreational hook and line gear. Blue and Deacon Rockfish have only recently been recognized as separate species, but are still managed as a stock complex by the

Pacific Fisheries Management Council. Therefore, we combined these two species into a single species group for our analysis.

ANALYSIS

Historic Fisheries Data

Commercial fishery age data for Black Rockfish, Blue/Deacon Rockfish, Canary Rockfish, Widow Rockfish, and Yellowtail Rockfish were downloaded from (<https://pacfin.psmfc.org/>), and recreational fishery age data were downloaded from (<https://www.recfin.org/>). Only ages generated using the break and burn method were used in our analysis, as this is the method considered acceptable for ageing rockfish by the Committee of Age Reading Experts (Committee of Age-Reading Experts, 2006). Data from both fisheries were generated by multiple age readers from multiple production laboratories. The data obtained for this study are available from the lead author upon request.

Data Exploration

For the purpose of our analysis, we grouped age samples into two categories, recreational or commercial fisheries. Depending on the species commercial fisheries may include hook and line, long line, and trawl. For all species, except Blue/Deacon Rockfish, the annual sample sizes of aged individuals were approximately evenly split between male and female samples. However, more females were aged for Blue/Deacon Rockfish, likely due to the sexual dimorphism in the species, resulting in reduced retention of males. Black Rockfish otoliths started being collected around 2000 and Blue/Deacon Rockfish collections began in earnest around 2010. For each species and fishery, potential sampling bias may occur due to sample sizes, most notably a decline in the number of samples taken from each fishery in the last decade, especially for Canary Rockfish and Yellowtail Rockfish (**Fig. 1**). Age data for Canary Rockfish generated from sampling commercial and recreational fisheries began around 1980, while sampling species caught by commercial trawl (Widow Rockfish and Yellowtail Rockfish) started around 1990 (**Fig. 2**).

For the remainder of the analysis (Figures 3-7), age data were binned into four-year age bins [0,4), [4,8) etc., and length data were binned into 4 cm length bins. For each species, we calculated proportion of females for each age or length bin. These data were plotted for each decade.

For Black Rockfish, Canary Rockfish, and Yellowtail Rockfish, analysis of all fishery-dependent data showed that regardless of decade, as fish got older, the proportion of females declined (**Fig. 3**). However, this pattern was not observed for Blue/Deacon Rockfish or Widow Rockfish. For all five species analyzed, as fish got larger, the proportion of the population which was female increased (**Fig. 4**). In other words, although large females exist, old females are missing in Black, Canary, and Yellowtail Rockfish populations. However, these observations are somewhat misleading because males do not attain the larger lengths females do, consequently larger length classes are dominated by females, regardless of the number of females in those larger length classes.

The pattern of declining proportion of females with age was never observed in Blue/Deacon or Widow Rockfish populations and was therefore excluded from further analyses. Remaining data were separated by commercial and recreational fisheries and analyzed by decade. The hypothesis being tested now was whether age patterns observed were due to selectivity in one of the fisheries. This analysis revealed that the pattern of declining proportion of females with age persisted, regardless of fishery or decade (**Fig. 5**).

Next, we combined data from all years to test the hypothesis that the lack of old females is due to seasonal selectivity. By analyzing seasonal selectivity, we are trying to determine whether fishing dynamics or fish behavior may change between summer and winter months. Due to low catch numbers in the winter, commercial and recreational data were combined for this analysis, and we considered two seasons: winter (October through March) and summer (April through September). This analysis revealed that the pattern of declining proportion of females with age persisted, regardless of the season (**Fig. 6**).

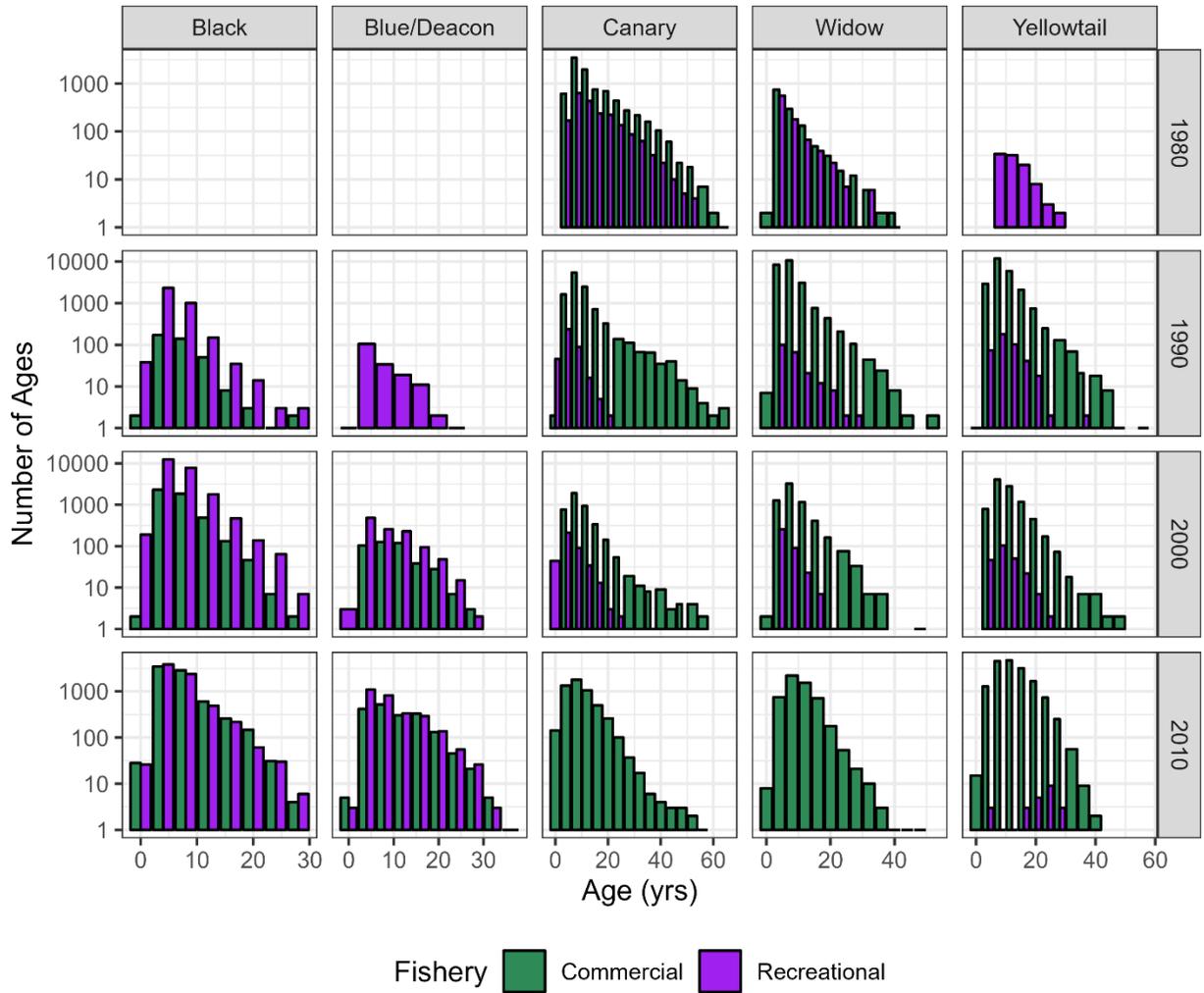


Figure 1. Number of aged structures by age (years) for five rockfish species captured in the commercial and recreational fisheries each decade age samples were collected. Note: scale on x- and y-axis are unique to each species and y-axis is log10. The width of bars does not depict any patterns in the data and is an artifact of the plotting software.

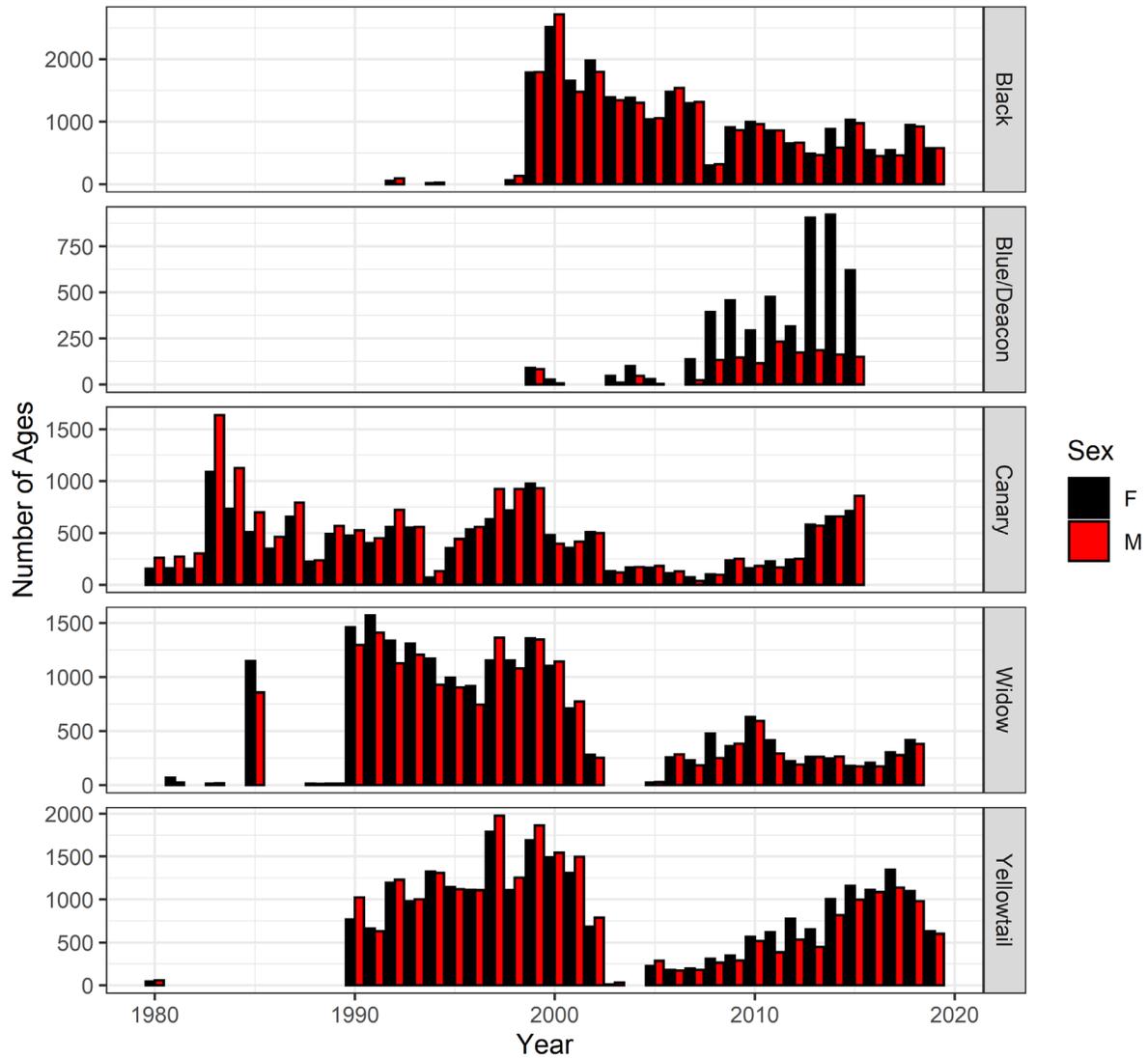


Figure 2. Annual number of aged structures from fisheries-dependent samples (commercial and recreational fisheries combined) for five semi-pelagic rockfish species, separated by male and female. Note: scale on y-axis is unique to each species.

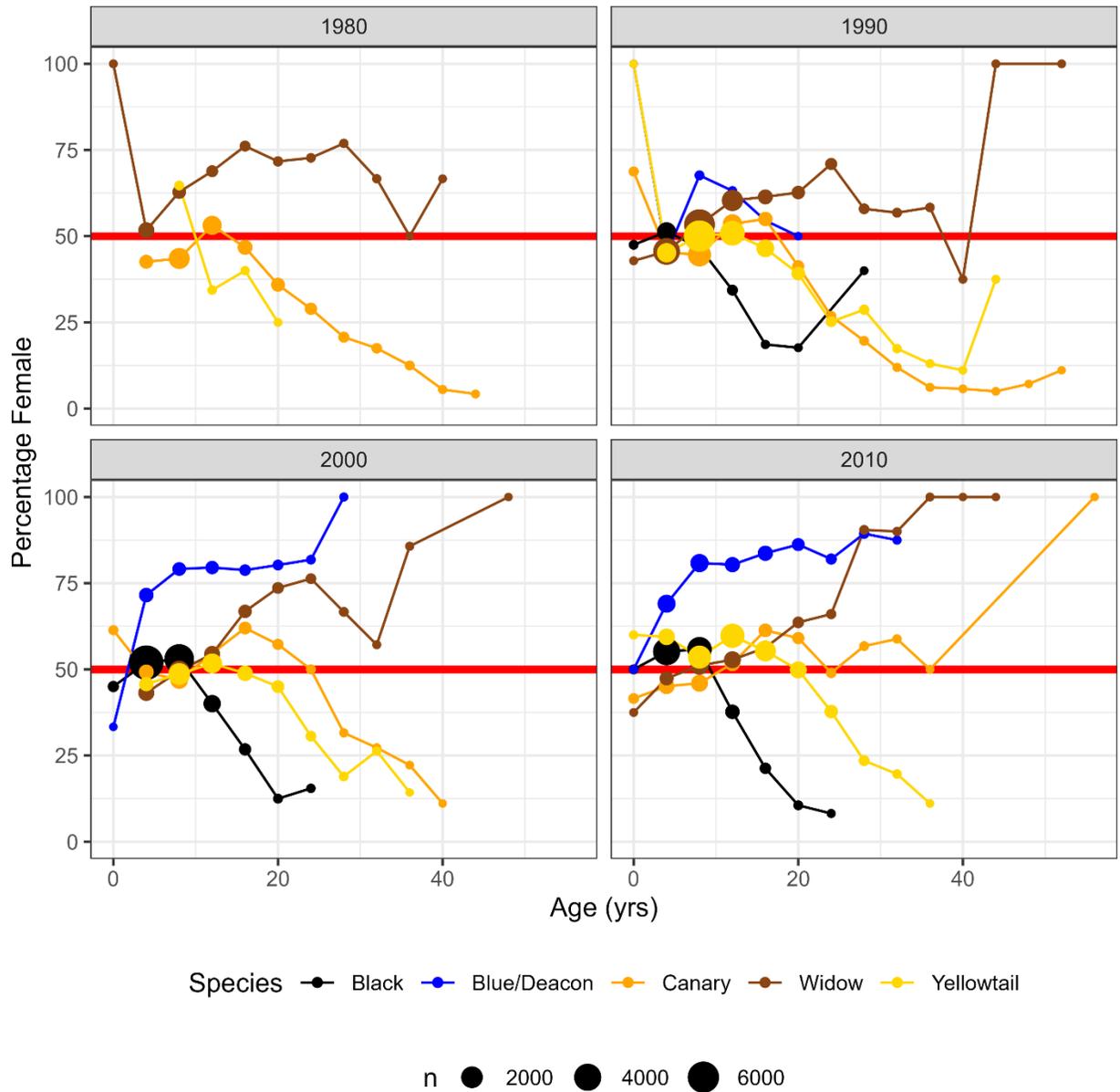


Figure 3. Percentage of the catch which is female by age (years) for five rockfish species per decade. Graphs combine commercial and recreational fisheries. Bubble size represents the total number of samples observed in each age class (males and females combined). Note: small bubbles at the oldest ages represent very small sample sizes (Fig. 1 & 2).

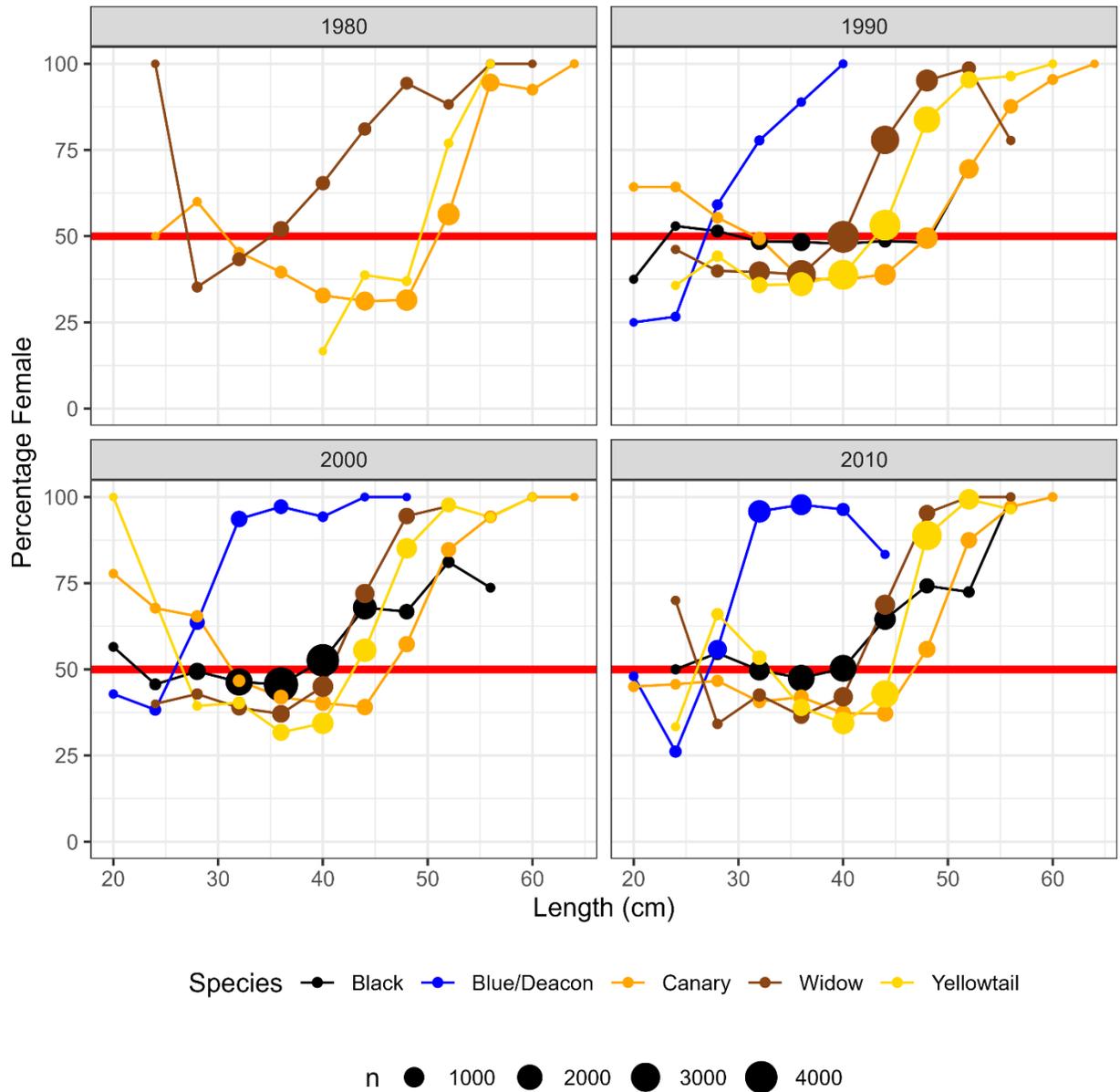


Figure 4. Percentage of the catch which is female by length (cm) for five different semi-pelagic rockfish species per decade. Graphs combine commercial and recreational fisheries. Bubble size represents the total number of samples observed in each age class (males and females combined). Note: small bubbles at the oldest ages represent very small sample sizes (**Fig. 1 & 2**).

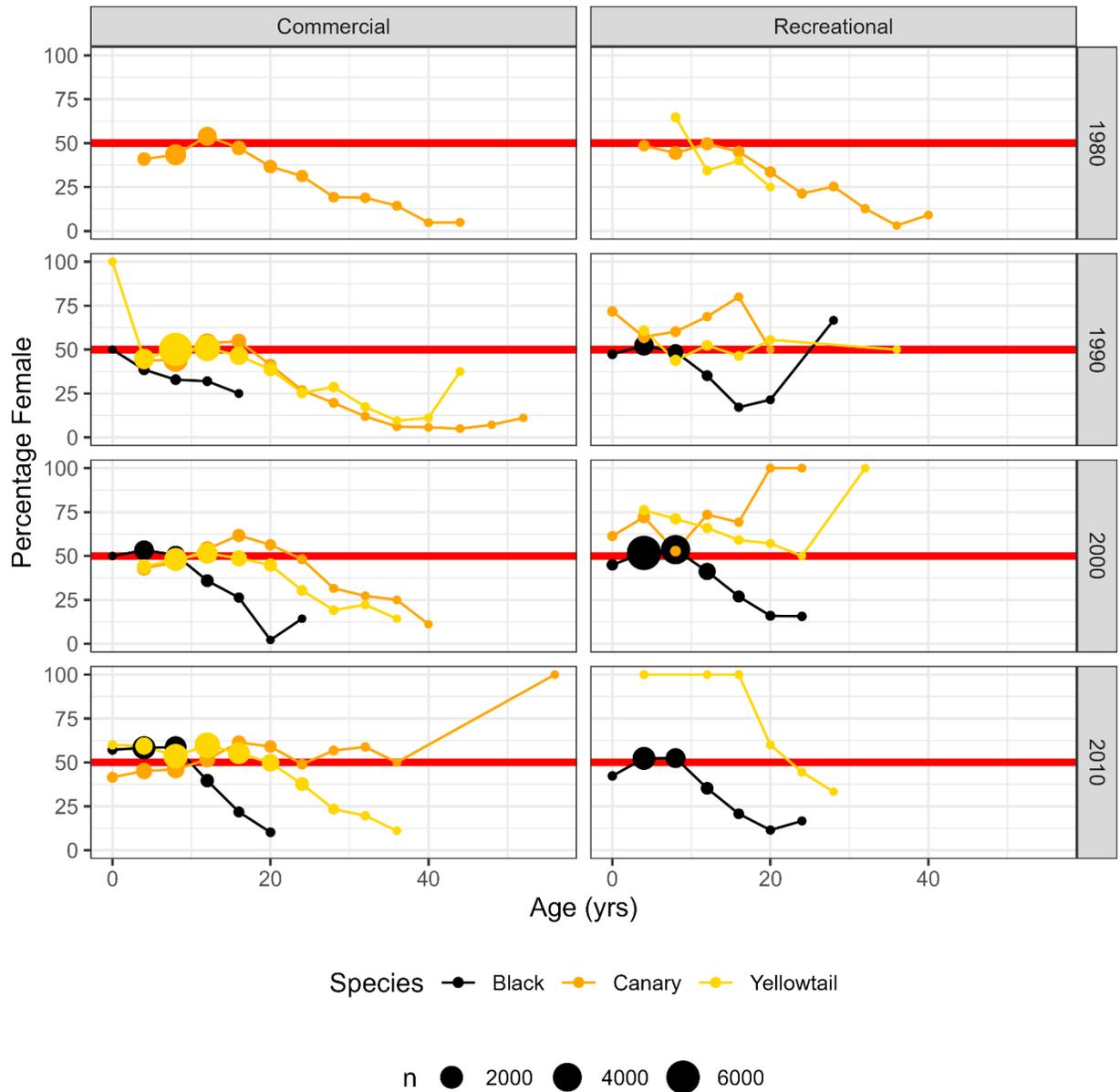


Figure 5. Percentage of the catch which is female by age (years) for the three different semi-pelagic rockfish species showing declining proportion female with age. Plots show trends for recreational and commercial fisheries independently. Bubble size represents the total number of samples observed in each age class (males and females combined). Note: small bubbles at the oldest ages represent very small sample sizes (Fig. 1 & 2).

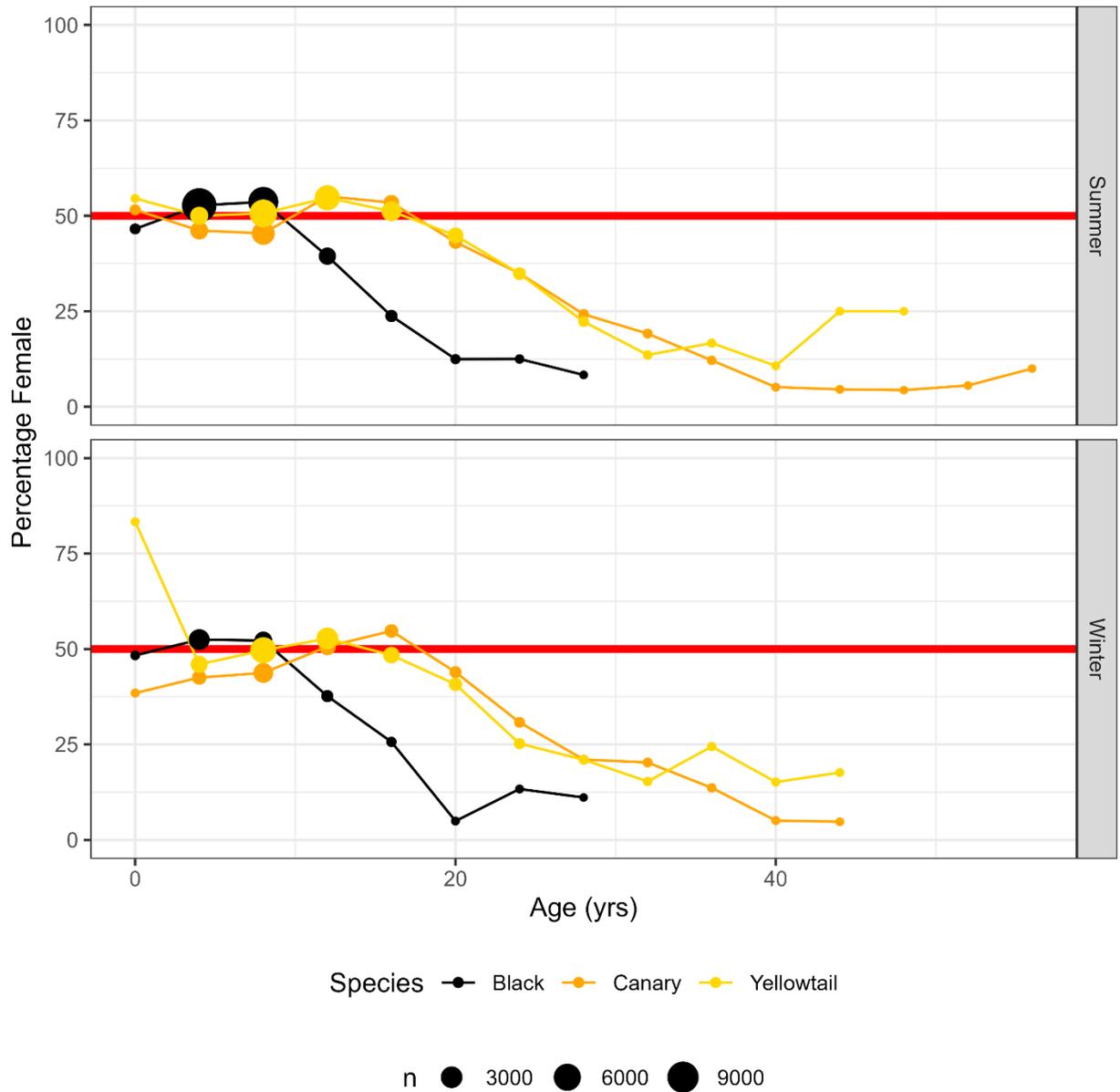


Figure 6. Seasonal percentage of the catch which is female by age (years) for the three different semi-pelagic rockfish species showing declining proportion female with age. The goal here was to test whether season impacted prevalence of old females in the fishery. Plots combine the recreational and commercial fisheries for all data since the 1980s. Bubble size represents the total number of samples observed in each age class (males and females combined). Note: small bubbles at the oldest ages represent very small sample sizes (**Fig. 1 & 2**).

Statistical Analysis

Generalized additive models (Wood 2006) were used to explore the effect of the categorical variables (species, decade, and fishery) on the proportion of females at each age (in four-year age bins). All models included the age data (in four-year bins) and we tested all possible interactions with species, decade, and fishery. The data were fit using a quasibinomial distribution and the models were weighted by the number of samples used to inform each age class. Eight models were compared using delta AICc. None of the categorical variables tested were included in the best fit model (**Tables 1-2**). In the best fit model, the proportion of females in the population dropped below 50% at 16 years of age (**Fig. 7**). Confidence intervals at older ages were large due to the relatively small sample sizes of those age groups.

We then tested the hypothesis that the age at which the proportion of females dropped below 50% declines over time. In other words, one would hypothesize a progressive decline in the age at which 50% of the population is female if the fishery was removing the oldest females. For this analysis we combined the recreational and commercial fisheries data and examined the data in four-year bins. For each bin we determined the age at which the percentage of females fell below and remained below 50%. We then fit these data with a line using the *lm* package in R and a gaussian distribution. For both Black Rockfish and Canary Rockfish there was no significant trend in the age at which the proportion of female rockfish dropped below 50%, and surprisingly for Yellowtail Rockfish it has increased since the 1980s (**Fig. 8**). Expressly, declining female presence as these populations age remains consistent across species, despite inconsistencies in female interactions between the fisheries, suggesting that there is not systematic removal of old females by the fishery.

In addition to fishery impacts, it is also important to consider data processing error as another potential explanation for the lack of older females, the most overt age data error source being from age reading. For example, if age structures were to become more difficult to age as fish got older, the lack of old females could be an artifact of increased ageing error with fish age. To explore ageing bias, we used the *FSA* package in R to analyze double read aging data. Double read data for Yellowtail Rockfish were provided by the Washington Department of Fish and Wildlife (WDFW) and by the Cooperative Ageing Project Northwest Fisheries Science Center (NWFSC) for Canary Rockfish. Data from two age readers employed over different time-periods were combined for this analysis. Results showed no significant trend in ageing error as fish got older and the only age at which the ageing estimate differed significantly was at age six (**Fig. 9**).

Table 1. Delta AICc values for model selection of the generalized additive models used to assess if species, decade, or fishery affected the trend in the proportion of female rockfish by age. Best fit models are noted by a Δ AICc value of 0.

Model Formula	ΔAICc
s(Age by Species X Decade X Fishery)	41.27
s(Age by Species X Fishery)	12.98
s(Age by Species X Decade)	28.2
s(Age by Decade X Fishery)	15.69
s(Age by Species)	6.57
s(Age by Decade)	1.41
s(Age by Fishery)	3.51
s(Age)	0

Table 2. Summary of best fit generalized additive model. The best fit model only contained age as a smoothed variable. All other categorical variables were excluded from analysis. The smooth was restricted to 5 knots and the age data was weighted by number of samples in each age class. The model was generated using a quasibinomial distribution.

* Significant <0.05, *** Significant <0.0001

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.3740	0.5301	-2.592	0.0258*

Approximate significance of smooth terms:

	Edf	Ref.df	F	p-value
s(Age)	3.445	3.743	32.95	3.11e-05***

R² (adjusted) = 0.861 Deviance explained = 92.7 %

GCV = 3.2607 Scale estimate = 2.3068 n=15

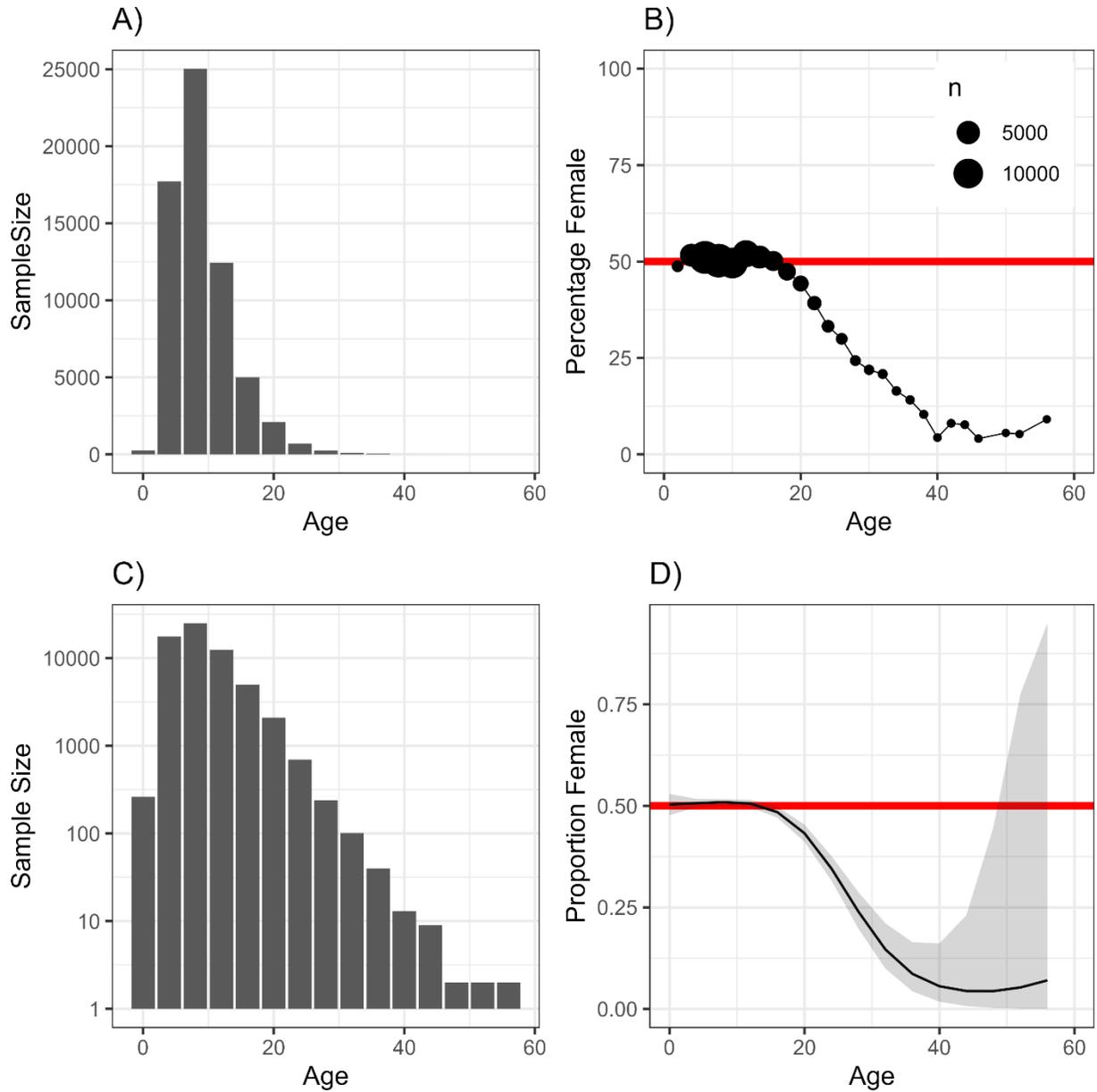


Figure 7. Sample sizes informing the best fit generalized additive model which combined all species, fisheries, and decades for each age class (A-raw scale, C-log 10 scale). Proportion females for each age class where sample size is indicated by bubble size (B). D shows the best fit generalized additive model fit to the data in B using a quasibinomial distribution and weighted for sample size. Horizontal red lines denote the 50% line, data below the line represents fewer females in the population than males for a given age class.

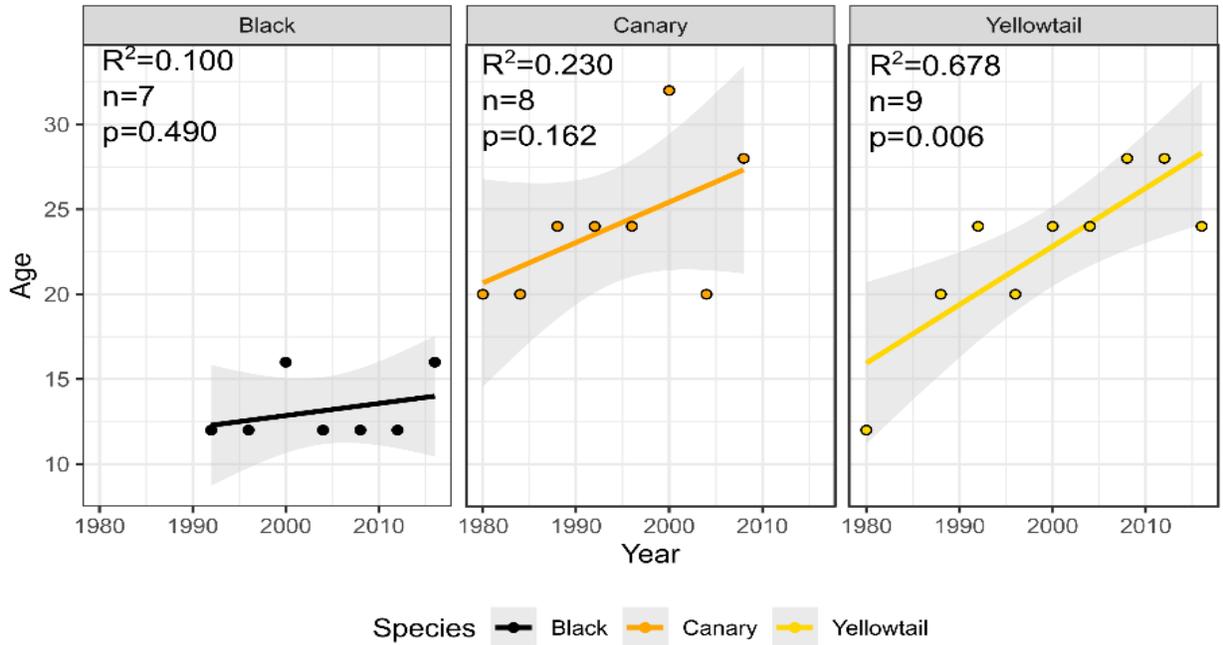


Figure 8. Age at which proportion female dropped below 50% and remained below 50% for each of the three species grouped in four-year age bins. Commercial and recreational fisheries were aggregated.

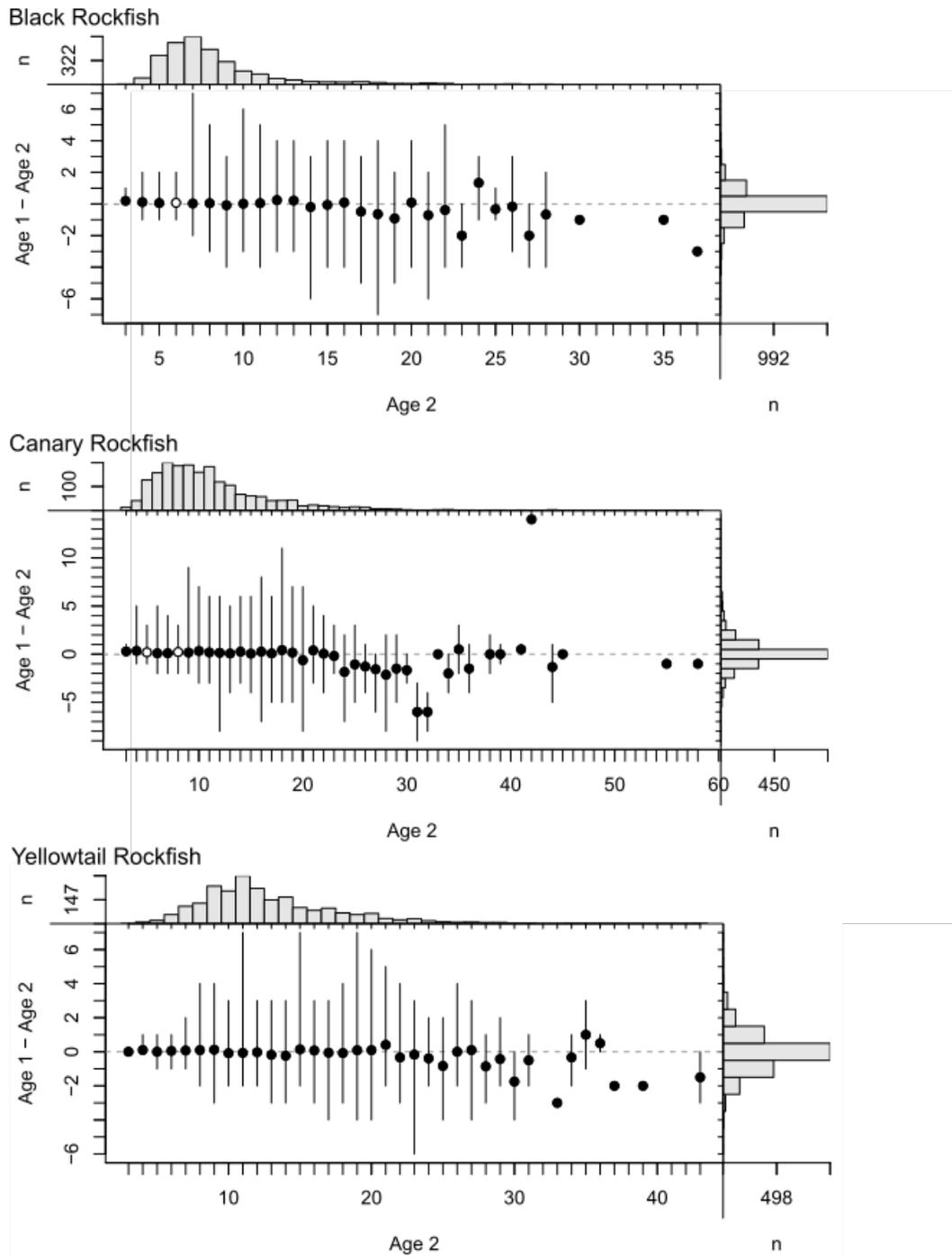


Figure 9. Average (points) and range (vertical lines) of differences in ageing estimates between the first and second read by the same reader (Black Rockfish) and different readers (Canary and Yellowtail Rockfish). Open points represent differences that are significantly different from zero. The histograms on the x and y axis depict sample sizes for the corresponding axes. Ages for Canary Rockfish and Yellowtail Rockfish were generously provided by NWFSC and WDFW, respectively.

Commercial and Recreational Fleet Survey

Prior to the historic fishery-dependent data analysis, we distributed a survey to the commercial and recreational fishing fleets that was designed to help impart some of the vast knowledge sustained by the fishing community to ODFW. The focus of the survey questioned the whereabouts of old Black Rockfish. The impetus for conducting this survey was to help inform the upcoming 2023 Black Rockfish stock assessment process. During the previous stock assessment process, assessors invested a significant amount of time into comparing model runs with older females either alive or hidden. These two models had complex differences that were not easily understood or disentangled. Therefore, knowing it was a significant investment of time for the assessors in the past, we attempted to preemptively answer some known questions regarding older female Black Rockfish. Although presented after the historic data in this manuscript, the survey was conducted in the spring of 2022 prior to the historic fishery-dependent data analysis.

Table 3. ODFW Survey questions sent to the commercial and recreational fleets.

Question Number	Question	Response Options
1	Do you think the older female black rockfish are dead or we just don't catch them?	Select: Dead/Don't catch them
2	If they aren't dead, do you think common current gear can catch old female black rockfish?	Circle: Yes/No
3	What is the best gear that could be used?	Write-in
4	Do the recreational power boat and commercial nearshore fisheries not commonly operate where old female black rockfish live?	Circle: Yes/No
5	If your goal is to fish for old female black rockfish, where would you fish? (All answers are confidential but only share what makes you comfortable, and even answers of depth contours or reef complexes are helpful.)	Write-in
6	Do you have any other idea why we don't see them in our catch data? If so please share below!	Write-in

Six questions were sent to members of the commercial and recreational fleet listservs with an associated letter (**Table 3** and Appendix). The goal was to determine: 1) if the fleet thought old female Black Rockfish were still alive and 2) if they are alive, why they aren't observed. The survey was sent to several ODFW listservs including: sport groundfish (21,439 subscribers); sport halibut (20,465 subscribers); recreational ocean salmon (24,356 subscribers); commercial troll salmon (14,656 subscribers); and commercial nearshore (13,842 subscribers). It is worth noting that: 1) there is cross membership in these listservs, so we do not have an accurate assessment of how many unique addresses were reached, and 2) there are dead end subscribers in each list. We received 278 responses. For question 1, most respondents assumed that old female Black Rockfish are present in the population but are not caught by either fleet (**Fig. 10**). Responses to

question 2 indicated an overall assumption that most anglers use the right gear to catch old Black Rockfish. However, question 4 revealed a nearly even split over whether commercial and recreational fleets operate in the right location to encounter older fish.

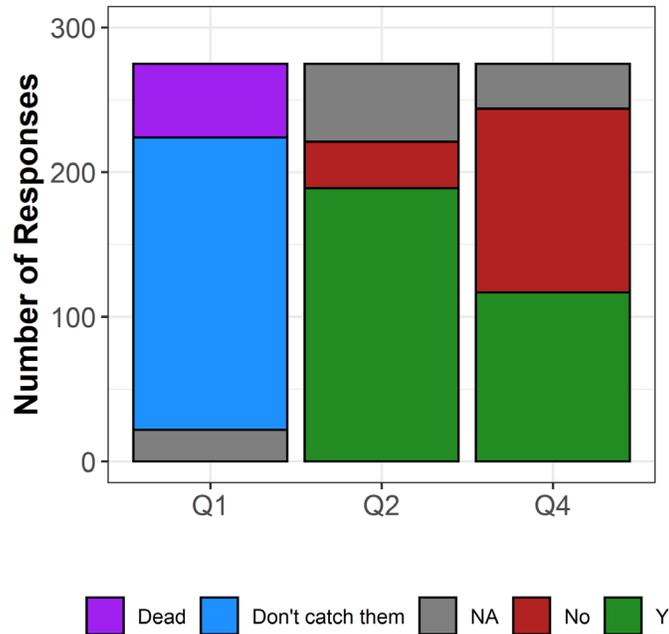


Figure 10. Number of responses to the check box questions in the survey.

Given the lack of nuance in the responses to the check box questions, we analyzed the responses to the written questions. To categorize the written answers, ODFW’s Marine Fisheries Research team identified commonalities in the answers to the write-in questions (3,5,6). For each question, we first identified keywords (e.g., shrimp flies in Q3). We then tallied the number of responses that matched with each keyword. If a response included multiple keywords, the response was coded multiple times. For example, shrimp flies with bait would get a tally for both shrimp fly and bait.

For question 3, regarding which gear to use, there were no consistent patterns observed (**Fig. 11**). For question 5, where to fish, most responses on this topic indicated deep waters to be the most likely location to capture older females. Other responses related to specific habitat characteristics such as on top of rock piles, rocky areas adjacent to large changes in depth, or areas with kelp. Question 6, other explanations, tracked similarly to question 5, with the assumption that most of the fishing occurs in the wrong spot.

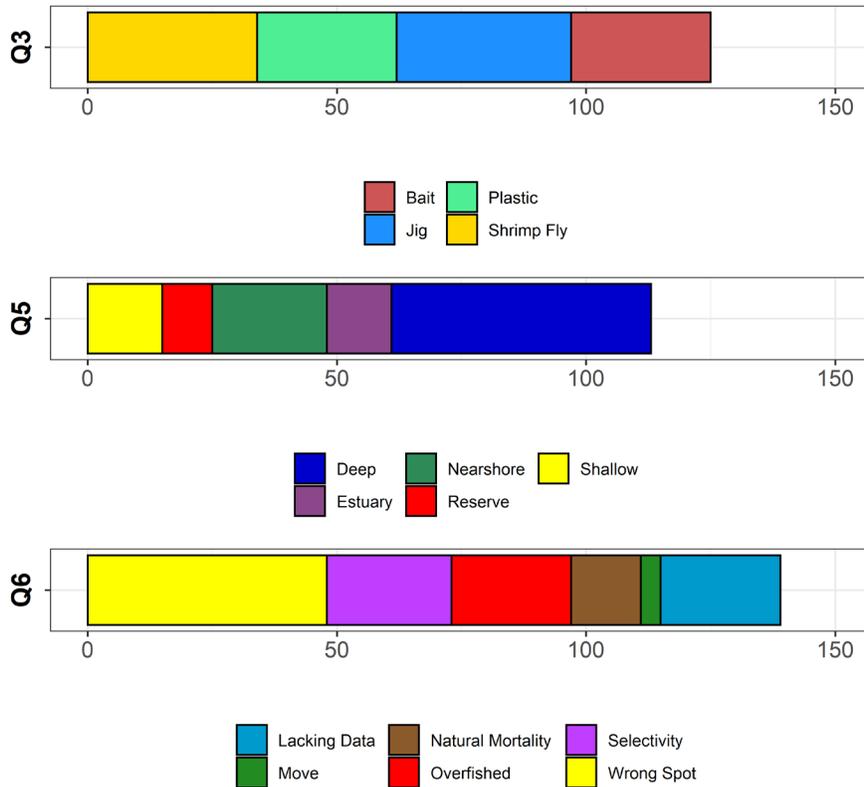


Figure 11. Number of responses to the written in survey questions. Most respondents did not respond to questions 3, 5 and 6, so non-responses were excluded from the plots to make it easier to find patterns in the responses provided.

SUMMARY AND PROPOSED HYPOTHESES

Four decades of fishery-independent data from Oregon was analyzed and the trend of declining female proportion with age was observed in Black Rockfish, Canary Rockfish, and Yellowtail Rockfish. It was present in both recreational and commercial fisheries across all studied decades. For Black Rockfish and Canary Rockfish, there was no observable trend in the age at which the proportion of females dropped below 50%. A survey of members of the Oregon fishing community revealed that in general, both the commercial and recreational fleets believe older females are present and that the gear currently used by each fleet is sufficient to catch them (recall that we only asked about Black Rockfish). The most consistent “trend” in survey responses was that we aren’t fishing in the right location.

It is rather notable to observe the same declining female proportion with age in three species (Black Rockfish, Canary Rockfish, and Yellowtail Rockfish) when they occupy such a broad range of habitats (both latitudinally and longitudinally), and experience varying selective pressures (i.e., fishery types) throughout their ranges. While Black Rockfish and Yellowtail Rockfish are phylogenetically similar (Li et al. 2006), the last common ancestor they shared with Canary

Rockfish was during the first quarter of the genus' existence. If declining percentages of females with age is a genetic trait that has been selected for in these three species, it would possibly be an example of convergent evolution or atavism. However, given the wide depth ranges and habitats occupied by these three species, such a consistent selective force between them seems highly unlikely, especially considering this trait reduces reproductive output and fitness.

A previous attempt to find older females was conducted by Sampson et al. (2008) who targeted Canary Rockfish in untrawlable habitat on the shelf. They found the mature canary rockfish caught in deep-water reefs off WA, OR, and CA were predominately female and relatively few old individuals were discovered. Neither previous research, nor the results of our analyses allow for conclusively stating whether old female rockfish are alive or dead. Alternatively, we present five hypotheses that endeavor to explain the lack of old females in fishery catches and discuss the evidence for and against each hypothesis. We considered two groups of hypotheses, ones where old females are alive, and alternatives where they are dead. In the development of these hypotheses, we assumed that the causality of reduced proportions of old females is the same for each of the three species (logic of parsimony). As we evaluated the evidence for and against each hypothesis, we also considered the diverse ecological differences between the species, as well as differences in how fisheries target them.

Hypotheses:

Alive Hypothesis 1: Old female rockfish move to, or live in, deep waters as they age.

Argument: Old females permanently or seasonally reside in deeper water than where the fisheries operate; this hypothesis is focused on Black Rockfish and primarily driven by public perceptions driven by depth restrictions in place for this fishery in recent years.

Support: Dunn and Hitz (1969) reported finding Black Rockfish in nearly 5,000 m of water, suggesting they are capable of residing at great depths, though it is worth noting this was water column depth and the fish were actually caught in the upper portion of the water column. Laurie Weitkamp (NMFS) reported finding a few large Black Rockfish during the recent International Year of the Salmon high seas salmon surveys.

Opposition: Nearshore, continental shelf, and slope habitats have all been fished extensively using many gear types throughout the history of fishing in Oregon. If fish were to move to deeper waters than where most fisheries are operated, they would have to move off the continental shelf into the North Pacific Gyre. Although not routinely fished, fishing that has occurred has yielded a few Black Rockfish, but Canary Rockfish or Yellowtail Rockfish have never been observed. If females are making these extreme offshore movements, they would have to also return to where males reside to spawn; if they do not, they are not contributing to the spawning stock.

How to test: Using similar methods to Sampson et al. (2008), targeted sampling could be conducted in habitats (e.g., deep water for Black Rockfish) hypothesized to be where fish are

present. If fish are found, researchers would need to assess how large the population is in these additional habitats to determine if the size of these populations is large enough to account for the missing older females. Identification of these habitats could be undertaken by using logbook and vessel monitoring system data to identify areas where relatively little effort has occurred across fisheries over the years.

Alive Hypothesis 2: As female rockfish age they conduct an ontogenetic along-shelf migration.

Argument: Rockfish are known to move along-shelf; this hypothesis states they move north or south out of fished waters as they age.

Support: Black Rockfish tagged in California have later been caught in Oregon and Washington indicating at least some individuals undergo along-shelf movement. Canary Rockfish and Yellowtail Rockfish are known to move large distances, although to date this movement appears to be more random than is suggested for Black Rockfish.

Opposition: Although there is a lot of evidence for along-shelf movement of these species, no clear evidence suggests that it is an ontogenetic migration. Further, the pattern of reduced proportions of older females is observed from Alaska to California. If these fish are indeed moving alongshore, one would hypothesize we would find them in a bordering state or country, which we do not.

How to test: This is perhaps the hardest hypothesis to test. Ideally, satellite tags would be the best tool; however, researchers would need to tag young (and therefore small) fish and monitor their movement over many years. Existing tag sizes and battery life would make this test difficult. The alternative would be to use a Floy Tag; however, since we do not observe these fish (as demonstrated by this study), it is unlikely we would be able to recapture tagged individuals. There may be some genetic or isotopic methods that could be used, currently unknown to the authors.

Alive Hypothesis 3: Sampling of fisheries does not represent the population.

Argument: Obviously when sampling fisheries, subsampling procedures need to be conducted. This hypothesis is that the subsampling is accidentally missing old females.

Support: In the recreational fishery, age structure sampling occurs mostly in the charter fleet, and less from privately owned recreational boats or shore-based fishermen. If older females reside at different locations on the reef than where the charter boats fish, it is possible that age structure sampling misses older females. In the commercial nearshore fishery, totes are sampled haphazardly if the catch is high. However, in many instances the catch is low enough that all fish are sampled. The commercial nearshore live fish fishery is not sampled for age due to the need to keep fish alive. In sampling the trawl fishery, selection of totes sampled is haphazard, and selection of fish to sample within those totes is also haphazard.

Opposition: Given that sampling procedures differ across fisheries, it seems very improbable that all of them ultimately result in an under-sampling of older females. Further, these species are also sampled by a highly standardized fisheries-independent research surveys: NOAA/NWFSC's

groundfish bottom trawl survey (which catches Canary Rockfish and Yellowtail Rockfish) and the ODFW Black Rockfish Survey. The pattern of a lower proportion of females at older ages is also observed across sampling agencies and methods. The trawl survey may miss certain age classes though because it cannot be operated in high relief habitats.

How to test: In the recreational fishery, researchers could simultaneously collect samples from both the charter and non-charter sectors of the fishery, then compare the distributions of ages from the two sectors to see if there are appreciable differences. In the commercial fishery, entire offloads could be sampled and compared to the subsamples that are taken to see if there are any appreciable differences in the data. For the live fish fishery, samples could be purchased and sampled to determine if a higher proportion of old females is present in this fishery than others.

Alive Hypothesis 4: Fisheries do not capture large old females.

Argument: As female rockfish age, something about their biology or ecology changes, resulting in lower selectivity in all fisheries.

Support: Fishermen and scientists alike hypothesize that female Black Rockfish's feeding behavior may change as they age, either by: becoming more lethargic and less likely to feed; only feeding at night to avoid competition/predation; or by searching for prey on the seafloor versus looking upward. These alternative feeding behaviors would result in lower availability to hook and line fisheries. Further, selectivity of trawl fisheries is well established in the literature (Lauth et al. 2004).

Opposition: Although there is evidence of selectivity in fisheries and evidence that older females may not as actively bite onto hooks, it seems highly improbable that selectivity is consistent across all gear types across all habitats where these three species live.

How to test: For each species individually, an equal proportion of large males and females from a single focal species could be held, in either a tank or large mesocosm. The held populations could then be fished (captured individuals replaced) and the proportion of males and females collected recorded. If this hypothesis were true, we would expect to see more males caught than females.

Dead Hypothesis 1: Fisheries remove females at a higher/faster rate than males.

Argument: Alternative to the previous argument, this hypothesis suggests fisheries selectivity is higher for female rockfish, resulting in a faster decline in the number of females in the population.

Support: Uneven selectivity of sexes in fisheries, especially hook and line fisheries, is well known (Kendall and Quinn 2013; Halvorsen et al. 2020), and attributed to differential resource needs associated with growth rate and reproduction.

Opposition: Effectively this is the hypothesis we have tested in this report and showed this is not the case. Assuming rockfish populations start with a 50/50 split of males to females (an

assumption well supported by evolutionary theory), if disproportional catch were causing the decline in females with age, then we would hypothesize, at younger ages, more females are removed than males. By removing more females at younger ages, as the population ages, the proportion that is male becomes greater than that of the females. In our current examination of historic fisheries data, at young ages we would observe a higher than 50% proportion of females being caught, and over time, we would observe a relatively constant decline in the proportion of females. However, we do not observe this pattern.

How to test: An equal proportion of small males and females from a single focal species could be held, in either a tank or large mesocosm. Then the held populations could be fished (captured individuals replaced) and the proportion of males and females collected recorded. If this hypothesis were true, we would expect to see more females caught than males resulting in greater selectivity of females than males.

Dead Hypothesis 2: Females experience a higher rate of natural mortality than males.

Argument: Females, due to some unknown aspect of spawning, experience higher rates of natural mortality than males. Also unknown is the age at which females experience this elevated natural (non-fishery related) mortality.

Support: Spawning associated mortality is well known in other species, with salmon perhaps being the most iconic (Quinn 2018). However, spawning mortality can occur because of a variety of factors other than the spawning process, such as increased predation during gestation (Hagmayer et al. 2020).

Opposition: Females dying before males is not observed in other rockfish species, suggesting convergent evolution as the most likely explanation, since Canary Rockfish are phylogenetically distant from Yellowtail Rockfish and Black Rockfish.

How to test: Natural mortality is inherently difficult to quantify. Perhaps the best way to quantify this would be to hold fish for multiple years in a laboratory setting and to determine if males or females senesce at different rates. Obviously, this is not ideal as it is a laboratory study, but given the difficulties with tagging work mentioned above, it may be the best option.

CONCLUSIONS

Analyses of historic fishing data and a fishery participant survey were used to determine if there were any consistent patterns as to why the proportion of females declines with age for Black Rockfish, Canary Rockfish, and Yellowtail Rockfish, and lead us to formulate six over-arching hypotheses about the disposition of old females. Overall, an examination of the fishery data did not suggest a temporal or a fishery-based cause. Additionally, analysis of a subset of age data did not indicate increased ageing error in older fish is to blame. A survey to members of Oregon's commercial and recreational fleets demonstrated that respondents thought fishing, in its current form, can capture old female Black Rockfish but fishing may not be occurring in the correct location or old females are missed due to fisheries sampling error. Within our consideration of

the alive versus dead hypotheses we presented ideas for further research that may help elucidate this question further; however, for the purposes of the upcoming stock assessment cycle, the authors of this manuscript hypothesize that natural mortality of females (Dead Hypothesis 2) is the most likely explanation for the lack of older females. We arrived at this hypothesis by using the laws of parsimony while attempting to find an answer that could explain the same trend in Black Rockfish, Canary Rockfish, and Yellowtail Rockfish. While we consider this the most likely hypothesis, we cannot say with absolute certainty that the natural mortality hypothesis is correct, and therefore strongly encourage further research that addresses the questions we've raised in the alive versus dead hypotheses section above.

Given our findings, it may be more interesting to reframe the overarching question from *why are old females are missing*, to *why do old males persist* in each population. While natural mortality in females may be reasonable in an evolutionary context, due to the high energetic costs of bearing live young, explaining which selective force(s) cause males to persist beyond females might be a more feasible research goal, resulting in an equally relevant outcome for these species.

Our conclusions may cause some to wonder if the Big Old Fat Fecund Females (BOFFF) hypothesis is incorrect, or at least does not apply to all rockfish species, we do not posit that is the case. While a review of the ecological literature may lead readers to the conclusion that a fish is either a BOFFF or not a BOFFF, the relationship is instead a continuum, with fish increasing in reproductive output as they age. Stock assessment models account for this by directly including the mathematical relationship in the model. To prevent the inadvertent association of the BOFFF hypothesis with a step function, we suggest that it is worth reframing the hypothesis as Bigger Older Fatter Fecunder Females and place emphasis on the continual increase of reproductive benefits with age.

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APPENDIX: SURVEY LETTER AND QUESTIONS

Dear Fisher,

We are looking for old female black rockfish and are hoping you can help us find them. We would appreciate it if you filled out the attached questionnaire to help guide the ODFW marine fisheries research team in finding them.

During the last stock assessment, scientists showed that the proportion of female black rockfish observed in fisheries catch data starts declining as fish reach ~10 years in age (17"). By age 20, the catch is almost entirely males. This begs the following questions. Do large older females die before they reach older ages, and therefore we don't catch them? Alternatively, if older female black rockfish exist, are we not catching them because we use the wrong gear or are we looking in the wrong spot? Knowing if the number of old female black rockfish is truly just a low number or if the catch data is not representing the population is very important. We use these data to determine reproductive output of the population.

The answers to these questions are critically important to black rockfish management. Rather than speculate on if they are dead or where they are, we are trying to use your knowledge to help provide better data for upcoming black rockfish stock assessments.

Sincerely,



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