ENVIRONMENTAL, ECOLOGICAL, AND FISHERY EFFECTS ON GROWTH AND

SIZE-AT-AGE OF PACIFIC HALIBUT (*HIPPOGLOSSUS STENOLEPIS*)

By

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Abstract

Size-at-age of Pacific Halibut (*Hippoglossus stenolepis*) has declined significantly since the 1980s. For instance, the average weight of a 20-year-old female declined from 55 kg in 1988 to 20 kg in 2014. The decline in size-at-age corresponds to a period of declining Pacific Halibut recruitment, spawning biomass, and reductions in catch limits for the directed commercial Pacific Halibut longline fishery. The causes of changes in Pacific Halibut size-at-age are poorly understood. Our project investigates several hypotheses related to declines in size-at-age, including the effects of environmental and ecological variability on growth, and the cumulative effects of harvest and size-selective fishing. Specific potential environmental covariates include the Pacific Decadal Oscillation, which is an index of basin-wide sea surface temperatures, and summer sea surface temperatures along the continental shelf of the Gulf of Alaska. Specific ecological variables include annual biomass estimates of Arrowtooth Flounder (*Atheresthes stomias*) and Pacific Halibut to investigate the potential role of inter- and intraspecific competition, respectively. We used a population modeling approach to simulate the effects of fishing on size-at-age. We found that the large increase in Arrowtooth Flounder biomass since the 1970s corresponds to declines in Pacific Halibut size-at-age. Our results also suggest that periods of high Pacific Halibut biomass relates to poor growth and low size-at-age. Finally, we found that harvest and size-selective fishing explains between 30 and 65% of observed declines since the 1980s in the Gulf of Alaska, and up to 100% of the declines in Southeast Alaska and British Columbia where harvest rates were high in the 1990s and 2000s. Our findings have implications for fisheries management, including balancing tradeoffs associated with size limits, and understanding how changes in environmental and ecological conditions can shift management reference points such as maximum sustainable yield.

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General Introduction

Pacific Halibut (*Hippoglossus stenolepis*) are a culturally and economically important flatfish species that is widely distributed throughout the North Pacific Ocean from California to the Chukchi Sea in the northeast and from Hokkaido (Japan) to the Gulf of Anadyr (Russia) in the northwest. Pacific Halibut have been managed since 1923 by the International Pacific Halibut Commission (IPHC), which was formed by a treaty between Canada and the United States (Keith et al. 2014).

Pacific Halibut are an iconic fish in the Pacific Northwest due to their enormous size. They are the largest flatfish in the world, reaching lengths up to 2.5 m and weighing up to 230 kg. They are also one of the longest-lived flatfish, attaining maximum ages over fifty years old. Despite their reputation as a large and long-lived fish, the size-at-age of Pacific Halibut has experienced significant declines in recent decades. For instance, the average weight of a 20-year-old female Pacific Halibut has declined from more than 45 kg in 1993 to less than 18 kg in 2011. Interestingly, the current small sizes-at-age are comparable to sizes-at-age experienced by Pacific Halibut in the 1920s. Maximum size-at-age of Pacific Halibut was observed in the 1970s and 1980s.

Causes of changes in Pacific Halibut size-at-age are poorly understood. The decrease observed over the past two decades has been hypothesized to result from both population dynamics of the Pacific Halibut stock (e.g., intraspecific competition through density dependence), interspecific competition with other species (e.g., Arrowtooth Flounder, *Atheresthes stomias*), as well as environmental variability (e.g., temperature), other ecological changes (e.g., influences of changes in prey field on bioenergetics), and anthropogenic impacts, such as harvest, bycatch, and the effects of size-selective fishing (Loher 2012). The examination of these potential causes of

variability in size-at-age requires a thorough understanding of the ecology and biology of Pacific

Halibut, including interactions with other organisms at various life history stages and an

understanding of how growth varies with changes in temperature or food availability. It also

requires in-depth knowledge of the fishery, including population dynamics, history of removals,

and different sources of mortality.

Pacific Halibut are demersal on the continental shelf of the North Pacific Ocean and most

frequently captured between 27 and 274 m (Keith et al. 2014). They are generally found in water

temperatures ranging from 3°C to 8°C (Keith et al. 2014). Pacific Halibut spawn throughout the

continental shelf of the Gulf of Alaska, Aleutian Islands, and Bering Sea. The eggs and larvae

are advected by the Alaska Coastal Current, which flows counter-clockwise around the Gulf of

Alaska and southwestward along the Aleutian Islands. Juvenile Pacific Halibut migrate long

distances to compensate for larval advection, moving east and south to inhabit areas of Southeast

Alaska, British Colombia, and the northwestern United States (St-Pierre 1984, Keith et al. 2014).

During winter months, Pacific Halibut undergo an offshore migration to spawn and return to

shallower depths in the summer to feed. Tagging studies provide evidence of both site fidelity

(adult Pacific Halibut returning to similar areas each summers), as well as a continued net

migration southward (Loher and Seitz 2006, Webster et al. 2013). Studies of temporal or spatial

variability of Pacific Halibut size-at-age need to bear in mind that they are highly mobile

organisms and individuals may occupy different regulatory areas from year to year.

Recruitment and growth of Pacific Halibut has been highly variable over the last century.

Recruitment and growth may be linked to climate variability and density-dependence,

respectively (Clark et al. 1999, Clark and Hare 2002), based largely on research focused on the

climate regime shift in 1976/1977 when the Pacific Decadal Oscillation switched from a period

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of cool to warm temperatures in the North Pacific Ocean (Mantua et al. 1997). The period of warm temperatures after the regime shift was associated with high recruitment but low growth (Clark et al. 1999). Moreover, these trends were associated with a strong density-dependent effect, in which periods of high biomass were associated with low growth, and vice versa. The combined influence of climate and density dependence on Pacific Halibut growth and recruitment remains a leading hypothesis.

Pacific Halibut have a diverse diet. Juveniles feed mostly on small invertebrates, but their diets shift to larger crustaceans (e.g., Giant Pacific Octopus, *Enteroctopus dofleini*, and Tanner Crab, *Chionoecetes bairdi*) and fish (e.g., Pacific Sand Lance, *Ammodytes hexapterus*, and Walleye Pollock, *Gadus chalcogrammus*) with increasing size (Best and St-Pierre 1986). They consume or are consumed by other Pacific Halibut, Arrowtooth Flounder, Pacific Cod (*Gadus macrocephalus*), Walleye Pollock, Spiny Dogfish (*Squalus suckleyi*), and numerous other flatfish species. Notably, adult Arrowtooth Flounder and Pacific Halibut have significant overlap in their diets (the diets of both species are dominated by Walleye Pollock), which implies the potential for competition between the two species if prey resources are limited (Yang 1995). Competitive interaction may be enhanced by the dramatic increase in Arrowtooth Flounder that occurred in the Gulf of Alaska since 1975 (Spies and Turnock 2013).

Pacific Halibut experienced a long history of exploitation by commercial, recreational, and subsistence fisheries. A commercial fishery for Pacific Halibut began in 1888 and, due to its firm texture, mild flavor, and ease of transport of the fish, the fishery rapidly developed in the U.S. and Canada (Keith et al. 2014). Commercial harvest of Pacific Halibut has been relatively stable since 1900, with periodic declines in catch during the 1910s, 1960s, 1980s, and 2000 to present. In addition to harvest in the directed commercial fishery, wastage also contributes to a significant

portion of total fishery removals of Pacific Halibut. Wastage is the incidental mortality of Pacific Halibut in the directed commercial fishery, and it includes the proportion of fish smaller than the commercial size limit (≤ 81.2 cm) that are released and subsequently die, as well as Pacific Halibut that die from lost or abandoned gear (Gilroy and Stewart 2013). Pacific Halibut are also harvested by recreational anglers, including a large charter fleet in Alaska and British Columbia particularly since the 1980s. Regulations governing bag limits and size limits for sport harvest of Pacific Halibut in Canada and the U.S. are quite variable, and tensions between commercial and sport fishermen have risen as catches in both fleets have declined. Pacific Halibut are taken by subsistence fishermen throughout coastal communities in this region. Finally, indigenous peoples inhabiting coastal waters of Alaska, British Columbia, and Washington have harvested Pacific Halibut for millennia.

In addition to being targeted by commercial, recreational, and subsistence fisheries, Pacific Halibut are also commonly caught as bycatch in trawl (e.g., Walleye Pollock, flatfish), longline (e.g., Pacific Cod), and troll fisheries (salmon). Pacific Halibut caught as bycatch in non-target fisheries in U.S. and Canadian fisheries must be discarded without additional injury, but inevitably a portion of these fish die from injuries sustained during catching or handling (Williams 2014). Discard mortality rates of Pacific Halibut caught in non-target fisheries are estimated using condition factors recorded by on-board observers (Williams 2014). In unobserved fisheries, discard mortality rates are fixed based on similar fisheries with known discard mortality rates. Because many fisheries are either unobserved or only partially observed, the total bycatch estimates reflect significant uncertainty.

Recent reduced catches in commercial, sport, and subsistence fisheries and high levels of bycatch are associated with stock declines since 1995 (Stewart and Martell 2014). Declining

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stock biomass has been attributed to two factors: (1) recent year classes are much smaller on average compared to those observed through the 1980s and 1990s, and (2) decreases in individual size-at-age (Stewart and Martell 2014). In recent years it takes longer for the Pacific Halibut to grow to sizes vulnerable to exploitation by the longline fishery. Thus, Pacific Halibut are vulnerable to bycatch and natural mortality over a more protracted period of time, with concomitant greater losses in spawning biomass. Additionally, some groundfish fishermen have suggested that smaller Pacific Halibut tend to co-mingle with other groundfish species (e.g., other flatfishes) in some instances, leading to higher bycatch rates. Moreover, wastage in the directed Pacific Halibut longline fishery is an increasing concern with a growing preponderance of sublegal-sized Pacific Halibut that must be discarded. Estimated mortality associated both with bycatch in non-target fisheries and wastage in the commercial Pacific Halibut fishery has comprised >20% of the total stock removals (by weight) in recent years (Stewart et al. 2014). In IPHC Area 4CDE in the Bering Sea and Aleutian Islands (BSAI) region, bycatch represented 66% of the total removals in 2013 (Stewart et al. 2014).

The present study is organized into two chapters to address a suite of hypotheses related to environmental, ecological, and fishery effects on growth and size-at-age of Pacific Halibut in the northeast Pacific Ocean. In Chapter 1, trends in growth and size-at-age of Pacific Halibut were examined using fisheries-independent length-at-age from the International Pacific Halibut Commission from 1914 to 2014. The objectives of this chapter were to 1) describe patterns in temporal and spatial variability in size-at-age and growth of Pacific Halibut and 2) identify potential environmental and ecological covariates influencing growth of Pacific Halibut, including intra- and inter-specific competition and temperature effects. In Chapter 2, we used a sex-, age-, and size-structured equilibrium model to examine the cumulative effects of size-

selective fishing on Pacific Halibut size-at-age. The objective of this chapter was to determine whether observed changes in size-at-age can be explained by fishery removals.

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Chapter 1. Spatial and temporal trends in growth and size-at-age of Pacific Halibut (*Hippoglossus stenolepis*) related to environmental and ecological variability in the North Pacific Ocean[1]

1.1   Abstract

Size-at-age of Pacific Halibut (*Hippoglossus stenolepis*) has declined significantly since the 1980s. For instance, the average weight of a 20-year-old female Pacific Halibut declined from 55 kg in 1988 to 20 kg in 2014. Our study uses fishery independent length-at-age data from the International Pacific Halibut Commission to explore spatial and temporal patterns in growth and size-at-age of Pacific Halibut from 1914 to 2014 in the northeast Pacific Ocean. We investigated hypotheses related to declines in size-at-age, including the effects of environmental and ecological variability on growth using linear mixed models. We developed an index of proportional growth, which we defined as the median annual change in length conditioned on initial size for unique combinations of sampling year, cohort, and sex. Environmental covariates included the wintertime (November to March) mean Pacific Decadal Oscillation, an index of large-scale climate variability in the North Pacific Ocean, and summer (May to August) mean sea surface temperatures along the continental shelf of the Gulf of Alaska. Ecological covariates included annual biomass estimates of Arrowtooth Flounder (*Atheresthes stomias*) and Pacific Halibut to investigate the potential role of inter- and intraspecific competition, respectively. We found no relationship between growth and environmental variables, which is consistent with previous findings. Results suggest a negative correlation between Arrowtooth Flounder and

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[1] Sullivan, J.Y., Kruse, G.H. Mueter, F.J. 2016. Spatial and temporal trends in growth and size-at-age of Pacific Halibut (*Hippoglossus stenolepis*) related to environmental and ecological variability in the North Pacific Ocean. Prepared for submission to Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science.

proportional growth, as well as some support for a negative relationship between Pacific Halibut and proportional growth. Our best fitting model explained only 28% of the observed variability in growth, which suggests that other factors (e.g. bioenergetics or size-selective fishing) are more important contributors to variability in size-at-age. Future work examining relationships between climate and biological processes such as growth should focus on integrated effects instead of annual variability.

1.2   Introduction

Pacific Halibut (*Hippoglossus stenolepis*) are widely distributed throughout the North Pacific Ocean, in the northeast from California to the Chukchi Sea, and in the northwest from Hokkaido (Japan) to the Gulf of Anadyr (Russia) (Keith et al. 2014). In the northeast Pacific Ocean, Pacific Halibut have been managed by the International Pacific Halibut Commission (IPHC) since 1923 and are the target of an important commercial longline fishery in the United States and Canada. They are also prized by recreational anglers, taken by subsistence fishermen in coastal communities, and incidentally caught as bycactch in other commercially important groundfish fisheries for Pacific Cod (*Gadus macrocephalus*), flatfish, and other species.

Pacific Halibut are among the largest flatfish in the world, reaching lengths of 2.5 m (> 8 feet). However, size-at-age of Pacific Halibut has experienced a significant decline since the 1980s. For instance, the average weight of a 20-year-old female has declined from more than 55 kg in the 1980s to 20 kg in 2014. Interestingly, the current small sizes-at-age are comparable to sizes-at-age experienced by Pacific Halibut in the 1920s. Although declining size-at-age has been noted by the IPHC since the 1990s, causes of long-term variability and recent declines in size-at-age remain poorly understood. This decrease over the past two decades has been hypothesized to result from both population dynamics of the Pacific Halibut stock (e.g. density dependence) and

extrinsic factors, such as competition with other species (e.g. Arrowtooth Flounder, *Atheresthes stomias*), environmental variability, changes in bioenergetics, and anthropogenic impacts, such as over-harvest, bycatch, and the effects of size-selective fishing.

The goals of this paper are two-fold. First, we aim to provide a comprehensive description of the available fisheries-independent length-at-age data for this species. We describe spatial and temporal trends in length-at-age at multiple spatial scales from 1914 to 2014, and then test for significant differences in growth parameters between sexes and areas. We expected to find differences in growth parameters between males and females and among areas through time because these differences have been documented previously (e.g. Martell et al. 2013). Second, we attempted to identify variables that influence growth, including environmental variables, density dependence, and interspecific competition. Because length-at-age data reflect single observations of multiple individuals and not repeated measures of length from a single individual, there are inherent difficulties associated with using length-at-age data to describe growth. For this reason, we developed an index of growth that represents the median change in length from one year to the next, relative to the starting length, for unique combinations of age, sex, and cohort. We used this as a response variable in a regression analysis and tested for potential year and cohort effects.

A priori hypotheses related to environmental and ecological covariates were developed through literature review. We expected Pacific Halibut growth to be negatively related to Pacific Halibut biomass owing to intraspecific competition (density dependence) for limited prey resources. This hypothesis is supported by previous research demonstrating that mean size-at-age is negatively correlated to Pacific Halibut biomass and abundance (Clark and Hare 2002). We also expected Pacific Halibut growth to be negatively related to Arrowtooth Flounder biomass owing to

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interspecific competition for limited shared prey resources. Diets of adult Arrowtooth Flounder and Pacific Halibut have significant overlap (the diets of both species are dominated by Walleye Pollock, *Gadus chalcogrammus*), which implies the potential for competition between the two species when Walleye Pollock abundance is limited (Yang 1995). A competitive interaction would be enhanced by the dramatic increase in Arrowtooth Flounder in the Gulf of Alaska since 1975 (Spies and Turnock 2013).

Hypotheses related to environmental effects (namely temperature) on Pacific Halibut growth were more challenging to develop, because there is conflicting evidence for a positive, negative, or neutral effect of temperature on growth. In general, warmer temperatures promote faster rates of most physiological processes resulting in faster growth up to an optimum after which thermal limits are reached (Pörtner and Knust 2007). Hagen and Quinn (1991) found a statistically significant positive relationship between Pacific Halibut otolith growth in zones 0-2 (young juveniles) and sea surface temperatures (SSTs), but this relationship eroded after otolith zone 2, suggesting no relationship between temperature and growth for adult Pacific Halibut. Laboratory experiments found that age-0 Pacific Halibut reared at 2°C experienced only 25% of the growth of fish reared at 10°C over a 26 week period in the laboratory (Hurst et al. 2005). However, no laboratory experiments have examined temperature effects on growth of adult Pacifc Halibut. Such experiments may be of limitted value because of the large body size and highly mobile nature of this species. Pacific Halibut tagged in waters of 3.8-11.6°C were most commonly recovered in waters of 5-7°C, suggesting colder waters may be optimal for feeding and growth (Loher and Seitz 2006). Taken together these Pacific Halibut observations are consistent with the observation that the optimal temperature for growth declines with increasing size for many marine species (Árnason et al. 2009). For example, juvenile Atlantic Halibut (*Hippoglossus*

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hippoglossus) of size 5-10 g had an optimum growth at 14.9°C, whereas those of size 60-70 g grew optimally at 12.7°C (Imsland and Jonassen 2001). Interoperculum growth of English Sole (*Parophrys vetulus*) is negatively related to shelf temperatures during the cool summer upwelling season in the California Current system (Kreuz et al. 1982). Finally, there was no relationship between Pacific Halibut growth and the Pacific Decadal Oscillation (PDO), a regional index of sea surface temperatures in the North Pacific Ocean, using an earlier (albeit shorter) version of the IPHC length-at-age dataset (Clark and Hare 2002). Given the disparate evidence for a positive, negative, or no relationship between temperature and Pacific Halibut growth, we adopted a null hypothesis of no relationship.

1.3   Materials and methods

1.3.1   Data

Our study area covers a large region in the northeast Pacific Ocean, from Oregon to the eastern Bering Sea. The IPHC manages Pacific Halibut as one stock, and divides the area into ten management areas and one closed area in the Bering Sea (Figure 1.1). Length-at-age data comprised more than 390,000 fisheries-independent observations collected from 1914 to 2014 (Table 1.1). They include observations from the modern IPHC setline survey (1996-2014), historical IPHC trawl and setline survey (1961-1996), and samples from IPHC special research projects, which are comprised predominately of individual fish taken during tagging or gear experiments (1914-1959). Ageing methodology has improved over the last century, and the IPHC now relies on the break-and-bake method to age otoliths instead of reading surface ages. The method of break-and-bake has shown to reduce aging bias in older fish (>16 years) (Forsberg and Stewart 2015). We used individuals between age-8 and age-16 to represent long-term temporal and spatial variability in size-at-age, because they are well represented in the

survey data and appear to suffer from minimal bias in surface ageing. We used break-and-bake age estimates when they are available, otherwise surface ages were used.

1.3.2 Spatial and temporal patterns in growth and size-at-age

To describe spatial and temporal trends in size-at-age, we obtained the mean and standard deviation of length-at-age by sex, year, regulatory area, and statistical area, which were examined visually. Statistical areas are much smaller than regulatory areas and have been used to tabulate catch, biological and biometric data. To describe variability in growth over the time series, we fit a standard three-parameter Ludwig von Bertalanffy growth model to length-at-age data by sex, decade, and regulatory area:

$$\text{(1.1)} \qquad L_a = L_\infty(1-\exp(-k(a-t_0)))+\varepsilon,$$

where L_a is length at a given age (cm), L_∞ is the mean asymptotic length (cm), k is proportional to the rate at which L_∞ is reached (year^{-1}), and t_0 is the theoretical age at length zero (years). We assumed a normal error structure and examined residual plots to ensure that assumptions were not violated. We tested for statistically significant differences between sexes and among regulatory areas within each decade by comparing the full model (different L_∞, k, and t_0) to simpler candidate models (e.g. two parameters the same, one parameter the same, no parameters the same) using the Akaike Information Criterion (AIC) (Akaike 1974). Because Pacific Halibut appeared to demonstrate linear growth, we also fit a simple linear model to length-at-age data by sex, decade, and regulatory area:

$$\text{(1.2)} \qquad L_a = \beta_0 + age\beta_1 + \varepsilon.$$

We compared fits of the linear and corresponding von Bertalanffy models using AIC. A summary of the sample sizes, years and areas represented, and maximum age in each sample are found in Table 1.1.

1.3.3 Analyses of environmental and ecological covariates

We used a multiple regression approach to test hypotheses related to intraspecific competition (i.e. density dependence), interspecific competition between Pacific Halibut and Arrowtooth Flounder, and environmental variability. The response variable used in regression analyses, termed proportional growth (G), was obtained by taking the difference between the median length $\bar{L}$ at a given age a in sampling year i and the median length of the previous age in year i-1 divided by the median length in year i-1 for unique combinations of sampling year, cohort year j, and sex k:

$$(1.3) \qquad G_{a,i,j,k} = (\bar{L}_{a,i,j,k} - \bar{L}_{a-1,i-1,j,k}) / \bar{L}_{a-1,i-1,j,k} \,.$$

We limited our analyses to fish sampled in areas 2B, 2C, 3A, and 3B, because they were best represented in our sample. Using this procedure we obtained 490 observations of proportional growth between 1964 and 2013. We used annual estimates of Pacific Halibut (*HAL*) and Arrowtooth Flounder biomass (*ATF*) from stock assessments to test for intra- and interspecific competition, respectively (Spies and Turnock 2013, Stewart and Martell 2014). Challenges associated with obtaining regional estimates of Pacific Halibut and Arrowtooth Flounder biomass prevented us from testing for differences in growth between regions; therefore, we conducted a coastwide analysis for the entire Gulf of Alaska. To test for environmental effects, we used wintertime PDO values (November to March) at 2 lags, including year *i (PDO* corresponding to November of year *i-1* through March of year *i)* and year *i-1* (*PDO_1*). The

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wintertime PDO is potentially a good descriptor of environmental conditions experienced by Pacific Halibut during summer feeding periods in the North Pacific because summer conditions are established during this winter period (Mantua et al. 1997). Similarly, we included sea surface temperatures (SSTs) at 2 lags (*SST* and *SST_1*) to test for direct temperature effects on growth. We obtained the SSTs from the Extended Reconstructed SST (ERSST) database, a global monthly SST analysis covering a 2.0 degree latitude by 2.0 longitude grid from 1854 to present (NOAA_ERSST_V4 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at http://www.esrl.noaa.gov/psd/). The annual SST value is the mean summer time SST (May to August) obtained from 12 "stations" (points along the 2.0 grid) on the Gulf of Alaska continental shelf and includes roughly 3 stations for each regulatory area (2B, 2C, 3A, 3B). Our measure of proportional growth was negative about 20% of the time, which may be partially attributed to harvest of faster growing individuals. To account for this probable mechanism, we included annual harvest rates of Pacific Halibut as a covariate in our model, which we estimated as the ratio of total catch (M mt) in a given year to the estimated biomass (Stewart and Martell 2014). Time series of all covariates used in our model can be found in Figure 1.2.

We explored relationships between proportional growth and environmental and ecological covariates with a generalized additive modeling (GAM) approach using the 'mgcv' package in the statistical computing software R version 3.2.5 (Wood 2006, R Core Team 2016). Preliminary results from the GAM suggested that relationships could be adequately described by a simple linear or quadratic model. The exception was harvest rate, which we modeled using a third order polynomial. The full multiple linear regression model took the following form:

$$(1.4) \quad \begin{aligned} G_t = {} & \alpha + sex_k + \beta_1 age + \beta_2 PDO + \beta_3 PDO^2 + \beta_4 PDO\_1 + \beta_5 PDO\_1^2 + \\ & \beta_6 SST + \beta_7 SST^2 + \beta_8 SST\_1 + \beta_9 SST\_1^2 + \beta_{10} HAL + \beta_{11} HAL^2 + \\ & \beta_{12} ATF + \beta_{13} ATF^2 + \beta_{14} HR + \beta_{15} HR^2 + \beta_{16} HR^3 + \varepsilon_t. \end{aligned}$$

Models were fit using weighted least squares regression to account for the much higher variance of observations prior to the modern survey period, which began in 1996. Observations were weighted by the inverse of the variance in proportional growth during the two periods ($\sigma^2_{\text{pre-1996}}$ =0.0047, $\sigma^2_{\text{post-1996}}$ =0.00049). Because observations of proportional growth were more likely to be similar within years or cohorts, we considered random effects models to account for random differences among sampling years and cohort years using the 'nlme' package for linear mixed effects models (Pinheiro et al. 2016). We compared the full model (no random effects) with models containing a random cohort effect, a random sampling year effect, and both a cohort and year effect, and retained the best random effects structure throughout the model fitting process. Candidate models were selected using AIC. To describe the predictive power of candidate models, we used the 'piecewiseSEM' package in R to calculate a marginal R^2 and conditional R^2, which indicate the proportion of variance explained by the fixed effects and the proportion of the variance explained by the combination of fixed and random effects, respectively (Nakagawa and Schielzeth 2013, Lefcheck 2015). The marginal R^2 and conditional R^2 are given by:

$$(1.5) \quad R^2_{LMM(m)} = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_l + \sigma^2_\varepsilon}$$

and

$$(1.6) \quad R^2_{LMM(c)} = \frac{\sigma^2_f + \sigma^2_l}{\sigma^2_f + \sigma^2_l + \sigma^2_\varepsilon},$$

where σ_f^2, σ_l^2, σ_e^2 represent the variance of the fixed effect components (predicted values), random effects, and residuals, respectively.

1.4   Results

1.4.1   Spatial and temporal patterns in growth and size-at-age

Plots of length-at-age by sex demonstrate long-term trends and variability in size-at-age (Figure 1.3). Length-at-age data for ages-8 and older suggest that size-at-age was small in the 1920s, gradually increased into the 1970s and 1980s, and declined through 2014. These trends appear to be consistent between males and females, but were not detected in ages < 6 (Figure 1.3 A and B).

Lengths-at-age by IPHC regulatory area were grouped by region due to low sample sizes and poor spatial coverage in early years. Area 2 includes 2A, 2B, and 2C, Area 3 includes 3A and 3B, and Area 4 includes 4A, 4B, 4C, 4D, 4E, and the closed area in the Bering Sea. Regional summaries reveal that the most extreme changes in size-at-age occurred in Area 3 (Figure 1.4). For example, the mean ($\pm$SE) fork length of an age-15 female in Area 3 was 110 cm ($\pm$6.7) in 1925, 165 cm ($\pm$2.5) in 1985, and only 95 cm ($\pm$1.1) in 2014. In contrast, available data suggest that length-at-age was more stable in Area 2 between 1914 and 1980, and low size-at-age was not observed until post-1980 (Figure 1.4). Although relatively few samples were available from Area 4 prior to 1990, the data suggest that temporal trends in size-at-age were more similar to Area 3 than Area 2. During the period of peak size-at-age (1970s and 1980s), the highest observed size-at-age occurred in Area 3 for both males and females (Figure 1.4). In 2014 size-at-age was lowest in Area 3 for both sexes, highest in Area 2 for females, and comparable in Area 2 and 4 for males. Regardless of long-term trends, all areas have exhibited steep declines since 1990.

Using age-15 females as a reference age and sex, summaries by IPHC statistical area show decadal changes in size-at-age at a finer spatial scale (Figure 1.5). These finer scale summaries highlight the extreme changes in length-at-age in the western Gulf of Alaska, especially near Kodiak Island and extending west past the Alaska Peninsula.

At least two von Bertalanffy growth parameters differed statistically between males and females and among decades. Females had a higher L_∞ (asymptotic length) and lower k (proportional to the rate at which L_∞ is reached) than males in most decades (Figure 1.6). Further, growth parameters changed over time, with declines in both L_∞ and k for both males and females in recent decades. Results from comparisons of von Bertalanffy growth models by regulatory area, sex, and decade using AIC were somewhat less consistent, although all best model fits suggest that at least one growth parameter was different among regulatory areas (Appendix 1.A). In general, von Bertalanffy parameter estimates and standard errors should be regarded with caution due to high parameter correlation.

Of more interest perhaps is the finding that a simple linear model performed better by AIC than the three-parameter von Bertalanffy model 24% of the time (32 of the 136 models). In particular, the early decades (1910 to 1950) were well described by a linear trend for both sexes and in all regulatory areas. Two things may be contributing to this phenomenon: (1) the maximum ages in the samples from early decades are much lower than later decades, and (2) sample sizes are much greater in later decades (Table 1.1). Related to the first point is the fact that Pacific Halibut appeared to demonstrate linear growth until age-25, and an apparent asymptotic length (L_∞) is not achieved until much later in life. For example, a visual examination of sex-specific models in the 1920s and 2000s shows that a linear trend fit better for the 1920s and a von Bertalanffy growth curve fit better for the 2000s because older ages are represented in the sample from the

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2000s (Figure 1.7). To compare linear model estimates across decades, we truncated the data at age ≤ 25 because growth was well described by a linear trend up to this age (Figure 1.8). The intercept and slope parameters for both sexes exhibited strong temporal trends, with the highest estimates for the slope parameter corresponding to the period of high size-at-age between 1960 and 1980 (Figure 1.8). These estimates should not be used for predictions beyond age-25, because they would imply infinite growth.

1.4.2 Environmental and ecological effects on growth

Preliminary exploration of the covariates used in regression models showed moderately high correlations among Pacific Halibut biomass (*HAL*), Arrowtooth Flounder biomass (*ATF*) and harvest rate (*HR*) (Table 1.2). This was not surprising because these indices displayed strong trends over time (Figure 1.2), and *HAL* was used to estimate *HR*.

The best fit model by AIC suggests that proportional growth was higher in females, decreased linearly with age and *ATF*, remained relatively constant from low to intermediate *HR*s, and decreased rapidly at the highest *HR* (Table 1.3, Figure 1.9). The best fit model included a random intercept for sampling year, and the estimates for standard deviation of the random intercept and residuals for sampling year suggest that the within-year variability in growth (i.e. variability among ages) was nearly four times larger than between-year variability (Table 1.4). Predicted annual deviations from the mean intercept indicated that random effects did not appear to violate any assumptions, although proportional growth in 2012 appeared to be unusually large (Figure 1.10).

Alternative candidate models included *HAL*, quadratic terms for *ATF* and *HAL*, and/or for *PDO*. The best fit model had a marginal R^2 of 0.23 and a conditional R^2 of 0.28, which indicates that

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approximately 23% of the observed variance in the data can be explained by the fixed effects and 28% can be explained by the fixed and random effects combined. Alternative candidate models boasted similar or better marginal and conditional R^2 values, but did so at the cost of additional parameters (Table 1.3). No candidate models included *SST* at either lag or *PDO_1* (*PDO* lagged -1 year).

1.5   Discussion

Temporal trends in length-at-age were consistent with other studies indicating that size-at-age of Pacific Halibut was low in the 1920s, steadily increased until the 1970s and 1980s, and declined after 1990 (Clark et al. 1999, Clark and Hare 2002). Since these earlier studies, length-at-age has continued to decline in all areas of the northeast Pacific Ocean, although it may have stabilized during 2013 to 2015 (Stewart et al. 2016). Interestingly, these long-term trends were not detected in ages < 6, either because younger ages were not fully selected to the sampling gear or because growth has not changed for younger ages over this time period (Figure 1.3 A and B). Our study demonstrates that historical trends in size-at-age are dependent on relatively low sample sizes and incomplete spatial coverage in available fisheries-independent data (Table 1.1, Figure 1.5); however, the trends are consistent with fisheries-dependent observations over the same period (Stewart and Monnahan 2016). We found that Pacific Halibut growth can be well explained by a simple linear trend up to age-25. A linear model outperforms the von Bertalanffy growth model if older ages are not represented in the sample, because asymptotic length is not well estimated. For this reason, examination of linear model coefficients shows temporal trends in Pacific Halibut growth more clearly than von Bertalanffy coefficients (Figure 1.8), although these parameter estimates should not be used for predicting growth beyond age-25.

Trends in length-at-age by area showed strong regional patterns (Figure 1.4). In addition, von Bertalanffy growth parameters were statistically different between sexes and areas, consistent with previous analyses of growth (e.g. Martell et al. 2013). Differences in growth and size-at-age between areas could be attributed to differences in habitat quality, prey availability, or temperature differences. For example, preliminary results from bioenergetics modelling suggest that growth rates may be higher for Pacific Halibut in the western Gulf of Alaska due to cooler temperatures and access to more energy rich prey items (e.g. Walleye Pollock) (K. Holsman, NMFS, Alaska Fisheries Science Center, personal communication). These results explain historical patterns in size-at-age, when size-at-age in the central and western Gulf of Alaska was high, but do not explain current trends in size-at-age that show fish were larger at age in the eastern Gulf of Alaska than in the west (Figure 1.4, Figure 1.5). Alternatively, recent tagging studies suggest that this pattern may be driven by size-dependent migration, with larger fish migrating from the west to the east (Webster et al. 2013).

Pacific Halibut biomass was not included as an ecological covariate in our best model for explaining variability in growth (Table 1.3). However, it was included in the next four candidate models, which provides some support for our hypothesis that Pacific Halibut growth is negatively related to Pacific Halibut biomass (density dependence). Moreover, Pacific Halibut biomass was correlated with Pacific Halibut harvest rates, which suggests that the latter term may explain a portion of the variability associated with a density-dependent effect (Table 1.2). Previous studies found a strong negative relationship between mean weight at age-8 and abundance of age-8 Pacific Halibut (Clark and Hare 2002). While numerical abundance is a better indicator of density dependence than biomass in some cases, we found that model formulations using biomass estimates for both Pacific Halibut and Arrowtooth Flounder

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outperformed those using abundance. Additionally, we found no significant cohort effect in this analysis, which can likely be attributed to the fact that Pacific Halibut recruitment has been stable over time, with the exception of an extremely large recruitment event in 1987.

Our results support the hypothesis that Pacific Halibut growth would be negatively related to Arrowtooth Flounder owing to interspecific competition for limited shared prey resources (Figure 1.9 C). Though difficult to observe directly, a competitive interaction between Pacific Halibut and Arrowtooth Flounder, if one exists, would be intensified by (1) the near five-fold increase in Arrowtooth Flounder biomass in the Gulf of Alaska (Spies and Turnock 2013), which is like related to extremely low harvest rates of Arrowtooth Flounder (e.g. in 2013 Arrowtooth Flounder harvest was < 9% of the acceptable biological catch) (Spies and Turnock 2013), and (2) the decline in Walleye Pollock, a shared dominant prey item of Pacific Halibut and Arrowtooth Flounder, from 1986 to 2008 (Dorn et al. 2013). The population increase in Arrowtooth Flounder since the 1960s is similar to trends observed in other groundfish species in the Bering Sea/Aleutian Islands and Gulf of Alaska that could also act as competitors to Pacific Halibut, including Pacific Cod, Northern Rock Sole (*Lepidopsetta polyxystra*), and Flathead Sole (*Hippoglossoides elassodon*) (Walters et al. 2000, Wilderbuer et al. 2002, Spencer 2008, A'mar and Palsson 2013). Although we did not use regional indices of biomass for Pacific Halibut or Arrowtooth Flounder, there is strong evidence from bottom trawl surveys that densities of both of these species are markedly higher in the western than eastern Gulf of Alaska, suggesting that competition could be more prominent in the west (von Szalay et al. 2010).

We found no evidence that SST at either lag or PDO at a lag of -1 year had an effect on growth, which is consistent with our null hypothesis of no relationship between temperature and Pacific Halibut growth, at least for the ages investigated in this study. This finding is supported by a

previous study that found no relationship between PDO and growth (Clark and Hare 2002). It is

also consistent with a previous finding of no significant relationships between Pacific Halibut

survey catch-per-unit-effort and environmental variables (Ames 2007). However, there may be

an indirect or lagged response of growth to environmentally-driven population dynamics. For

instance, although the underlying mechanisms remain poorly understood, it appears that warm

ocean temperatures are related to strong year classes, which lead to delayed density-dependent

growth as cohorts become recruited to the fishable stock of Pacific Halibut (Parker et al. 1995,

Clark et al. 1999, Clark and Hare 2002). Future research into environmental or climate effects on

Pacific Halibut growth, recruitment, or biomass may benefit by focusing on low frequency trends

or integrated effects (sensu Di Lorenzo and Ohman 2013).

There are a number of caveats with our results. First, as indicated earlier, length-at-age data used

in this study do not reflect repeated measures of length from a single individual. Instead, we

analyzed trends in median length-at-age of the survivors each year after natural and selective

fishing mortality, which may vary from year to year. Second, our analysis was confined to

length-at-age data instead of weight-at-age data because the latter are not routinely collected in

surveys. It is difficult to relate environmental conditions in a given year to changes in length-at-

age because fish are not likely to shrink as a result of an unfavorable environment in a given

year. It is more probable for a fish to gain or lose weight in response to favorable or unfavorable

conditions, so weight may be a better metric than length to examine changes in growth. This is

an important factor to consider in light of studies demonstrating variability in the weight-length

relationship of Pacific Halibut, which is assumed constant in the stock assessment (Courcelles

2012). Fourth, it should be noted that biomass estimates for Arrowtooth Flounder and Pacific

Halibut, as well as the sources used to obtain harvest rates of Pacific Halibut, are estimates from

stock assessment models, and are potentially problematic because they suffer from high autocorrelation and do not account for uncertainty in these estimates. Pitfalls associated with using point estimates from stock assessments as model inputs include the detection of spurious relationships and potential overconfidence in the precision and significance of results (Brooks and Deroba 2015). Finally, given the highly migratory life history of Pacific Halibut, individuals are likely to experience a wide range of thermal regimes, competitor densities, and prey fields seasonally and inter-annually. The resultant complexity of feeding regimes confounds studies such as ours in which relationships are sought among broad spatially averaged measures of fish densities and environmental conditions.

In summary, our model results indicated that a relatively low proportion of variability in Pacific Halibut growth could be explained by the environmental and ecological variables examined in this study (28%), which suggests that other factors are more influential (Table 1.3). Alternative explanations for variability in Pacific Halibut growth and size-at-age include size-selective fishing (Parma and Deriso 1990), including the negative effects of genetic selection related to fishing (Munch et al. 2005, Walsh et al. 2006). Recent work investigating the cumulative effects of size-selective fishing on size-at-age of Pacific Halibut found that fishing explains between 30 and 65% of observed declines in size-at-age since the 1980s in the Gulf of Alaska, and up to 100% in Southeast Alaska and British Columbia where harvest rates were high in the 1990s and 2000s (Sullivan 2016). Alternatively, variability in size-at-age could be the result of changes to bioenergetic processes affecting halibut growth, and ongoing research using otolith increment data to evaluate temperature effects on physiology and prey availability will contribute to our understanding of this complex system (K. Holsman, NMFS, Alaska Fisheries Science Center, personal communication).

Our study provides motivation for a more thorough investigation into physiology and heritability of Pacific Halibut growth, the ecological interactions among Pacific Halibut and other species like Arrowtooth Flounder, and the influence of climate on the population dynamics of this and other species in the North Pacific. Future planned work at the IPHC includes the identification of growth markers for Pacific Halibut, which will greatly improve our understanding of stock dynamics, as well as the potential for fishing and environmental effects on growth. Other ongoing studies at the University of Alaska Fairbanks are examining the spatial and dietary overlap of Arrowtooth Flounder and Pacific Halibut, which will help elucidate this complex trophic interaction. Current management of the Pacific Halibut fishery uses an ensemble approach to single-species stock assessment with the aim of accounting for multiple sources of uncertainty that should be considered in management decisions (Stewart et al. 2016). However, because predation and competition are not considered in a single-species context, the current ensemble approach could benefit from adding a multispecies assessment that accounts for interactions between Pacific Halibut and Arrowtooth Flounder (e.g. Van Kirk et al. 2010). Another informative tool would be the development of a spatially explicit stock assessment model that accounts for the high degree of migration that occurs throughout the lifetime of Pacific Halibut (Skud 1977, Loher and Seitz 2006, Webster et al. 2013). Finally, a helpful contribution to future work would be the development of more spatially discrete estimates of environmental variables and biomass and abundance for Arrowtooth Flounder, Pacific Halibut, and other species.

1.6   Acknowledgements

1.7 References

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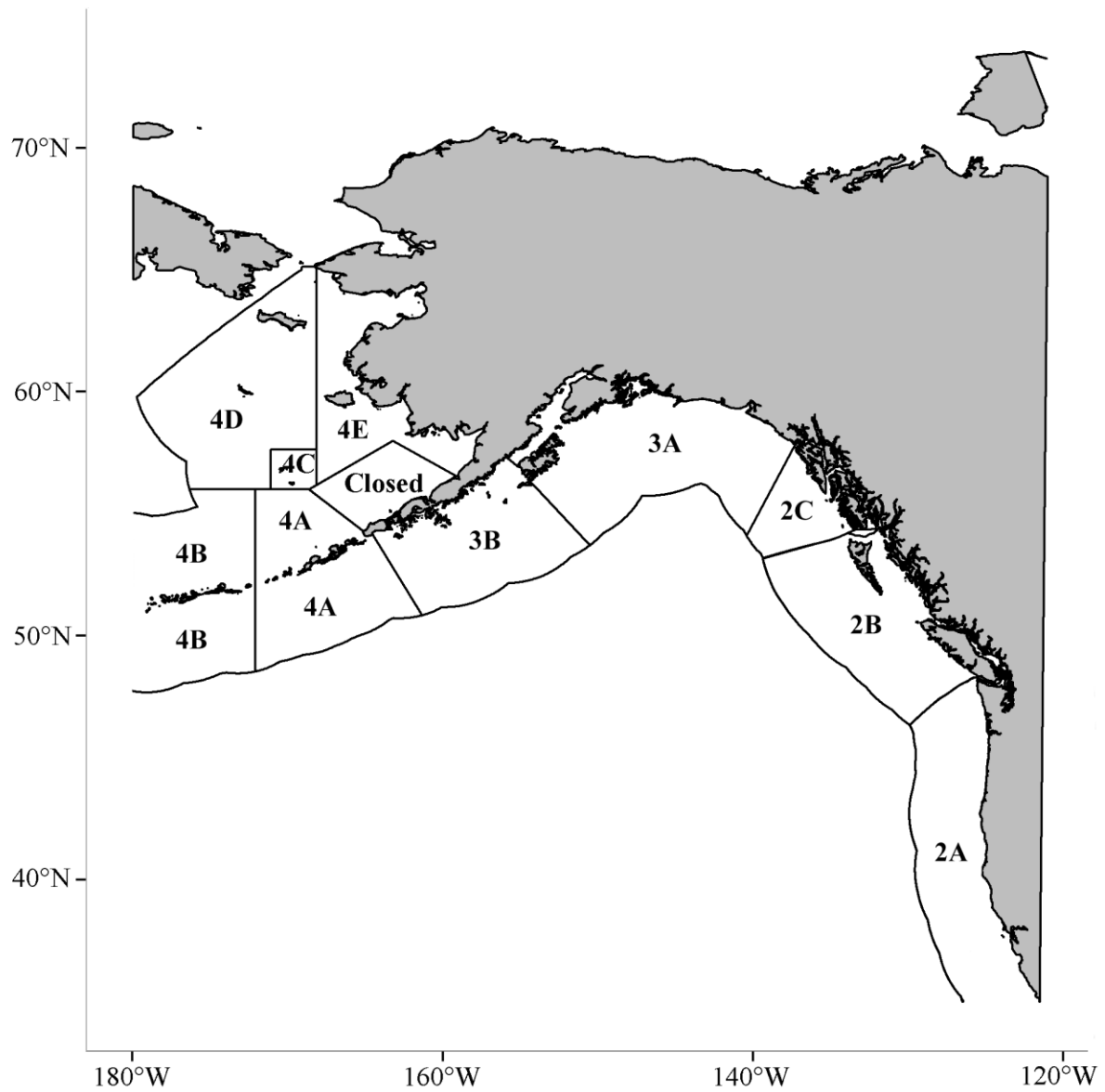
Figure 1.1. Map of IPHC regulatory areas (polygons) where Pacific Halibut length-at-age data were collected.
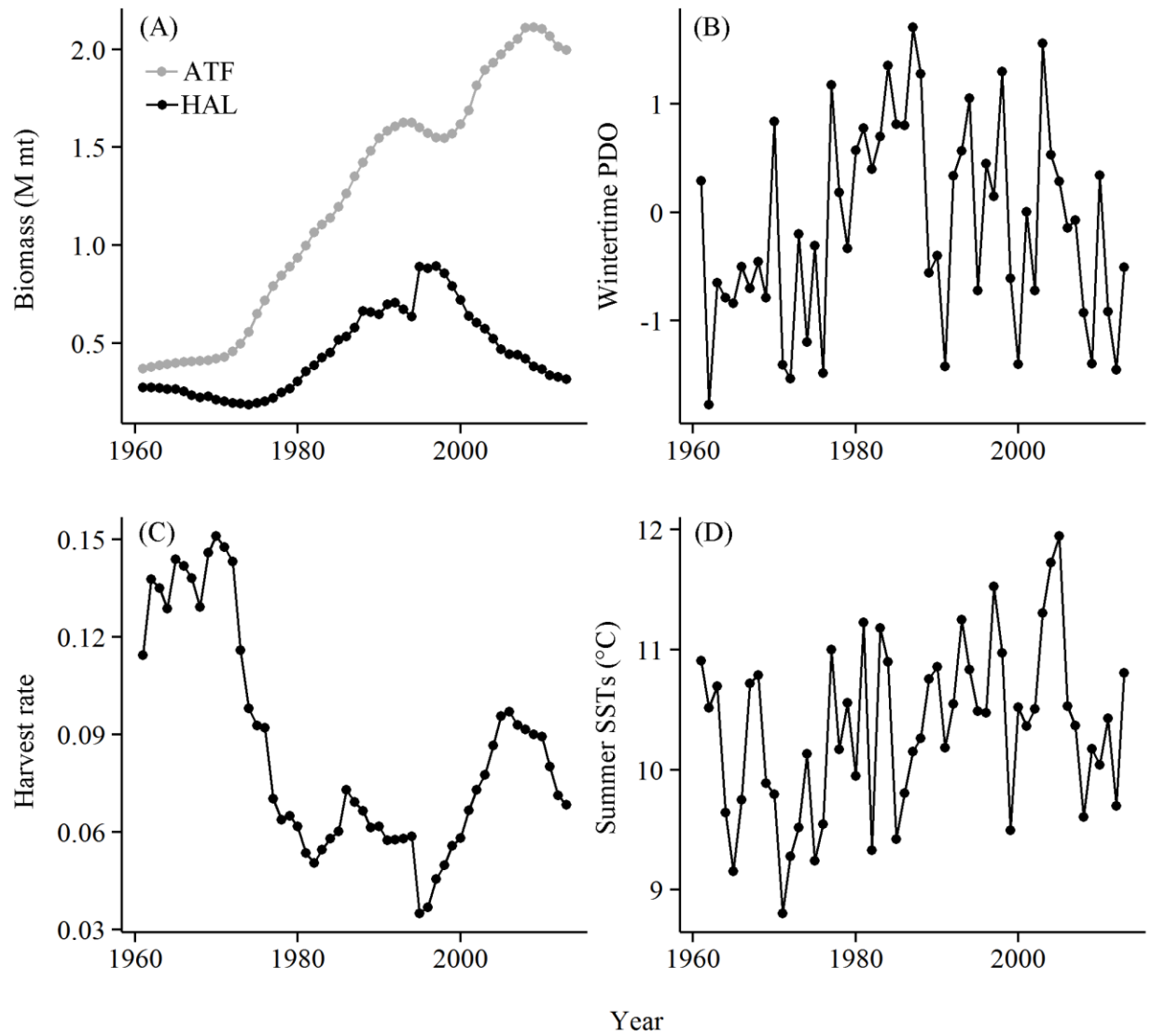
Figure 1.2. Time series of covariates used in regression analyses, including (A) biomass (M mt) of Arrowtooth Flounder (ATF) and Pacific Halibut (HAL) in grey and black, respectively; (B) mean wintertime (November to March) Pacific Decadal Oscillation (PDO) values; (C) harvest rate of Pacific Halibut (total removals/HAL); and (D) mean summer (May to August) sea surface temperatures (SSTs) in the Gulf of Alaska.
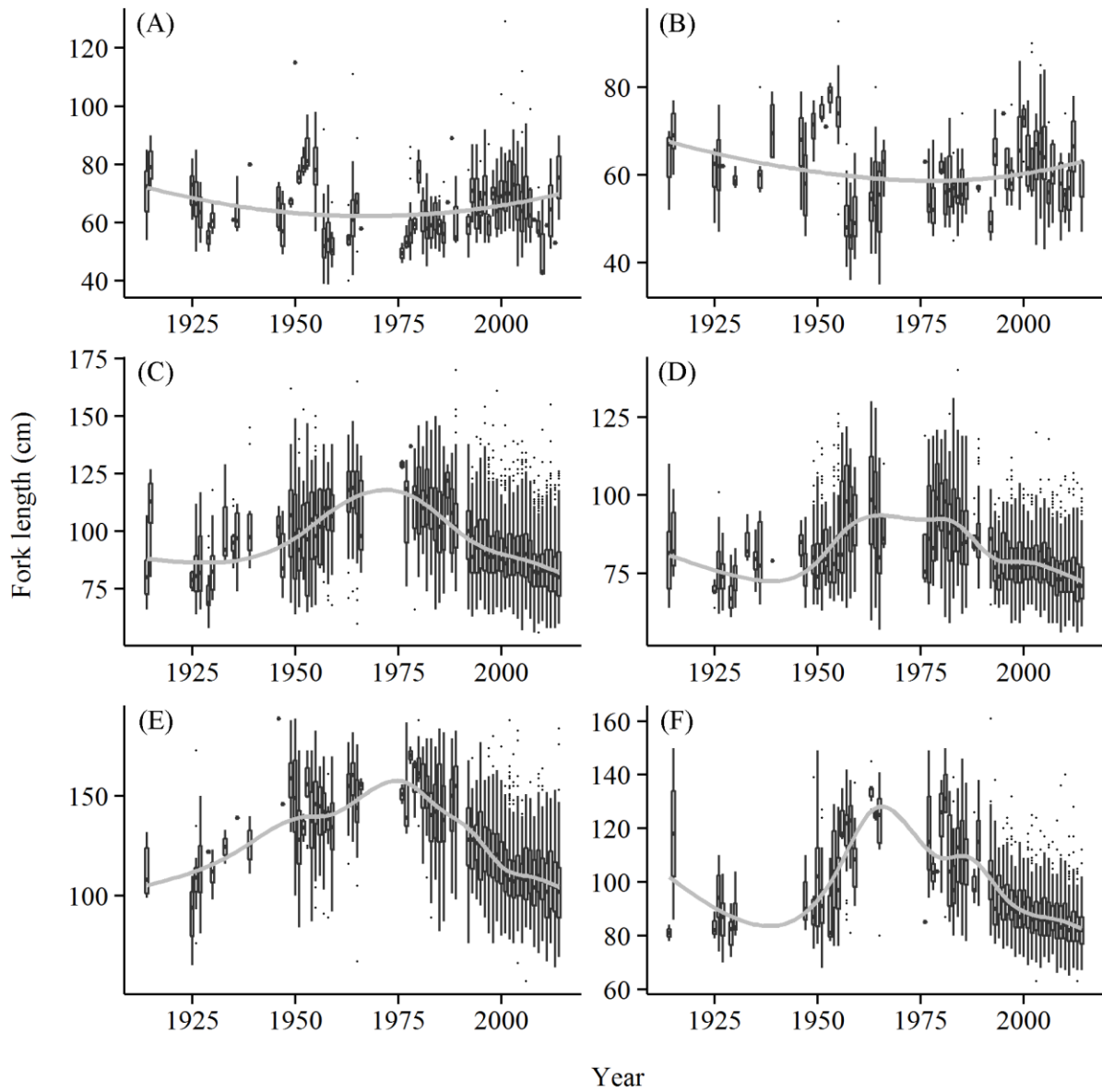
Figure 1.3. Boxplots of coastwide Pacific Halibut fork length-at-age (cm) from 1914 to 2014 for (A) age-5 females, (B) age-5 males, (C) age-10 females, (D) age-10 males, (E) age-15 females, and (F) age-15 males with a generalized additive model smoother (grey line) to aid in visualization. Boxplots show the mean length (black stripe in the box) and the 25th and 75th percentiles (upper and lower hinges of the dark box). The whiskers show 1.5 times the inter-quartile range, and observations beyond the whiskers are plotted as outliers (points).
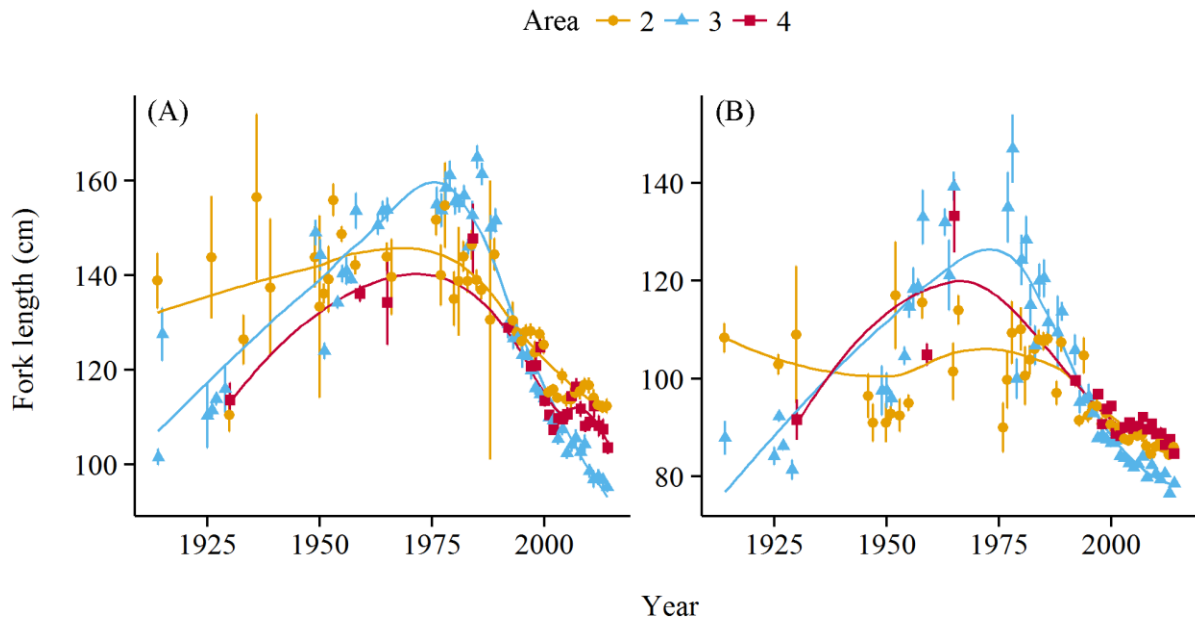
Figure 1.4. Mean fork length (cm) ± SE of age-15 Pacific Halibut (A) females and (B) males in areas 2 (orange circles), 3 (blue triangles), and 4 (red squares) with LOESS smoothers fit to annual means to aid in visualization.
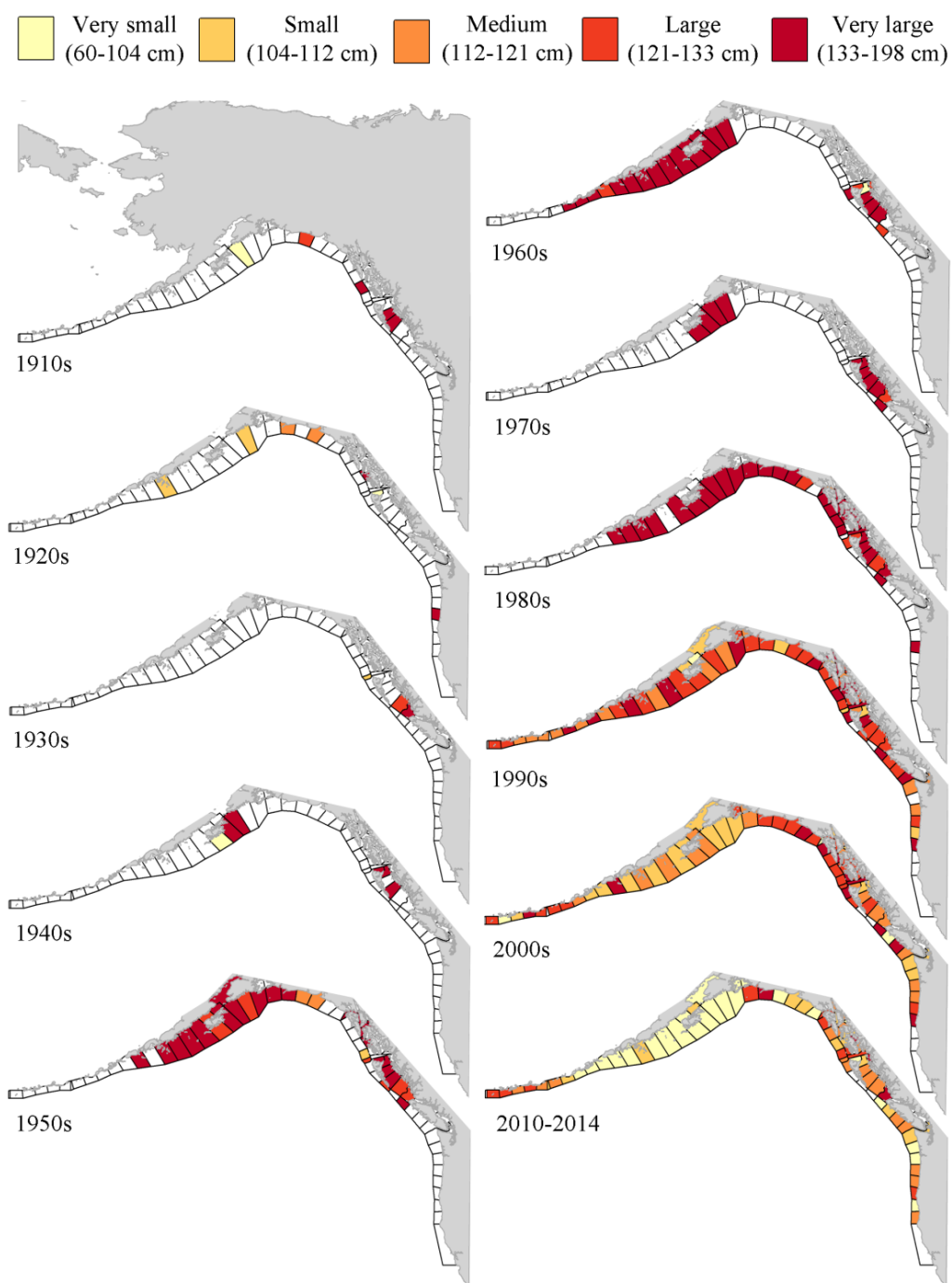
Figure 1.5. Quintiles of mean fork length (cm) of age-15 female Pacific Halibut by IPHC statistical area (polygons) and decade (1910s to 2010s), ranging from very small (pale yellow) to very large (dark red). Note that spatial coverage prior to the 1980s was sparse and inconsistent (white areas indicate that no data were collected during that decade).

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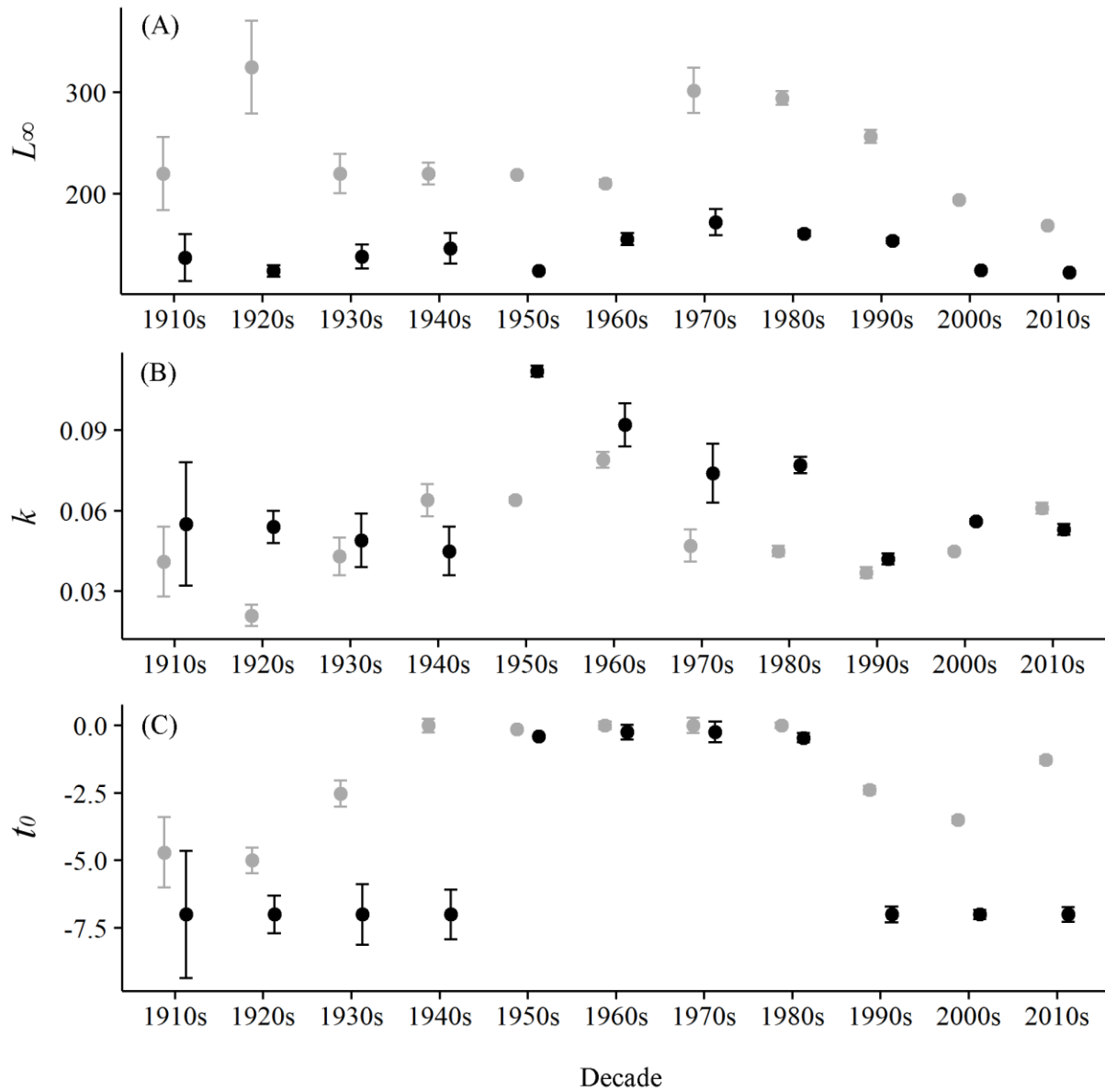
Figure 1.6. Parameter estimates (±SE) of von Bertalanffy growth parameters (A) L_∞, (B) k, and (C) t_0 for females (grey) and males (black) estimated by decade. Parameter estimates are well estimated in recent decades, and consequently the SE bars are difficult to see on this scale.
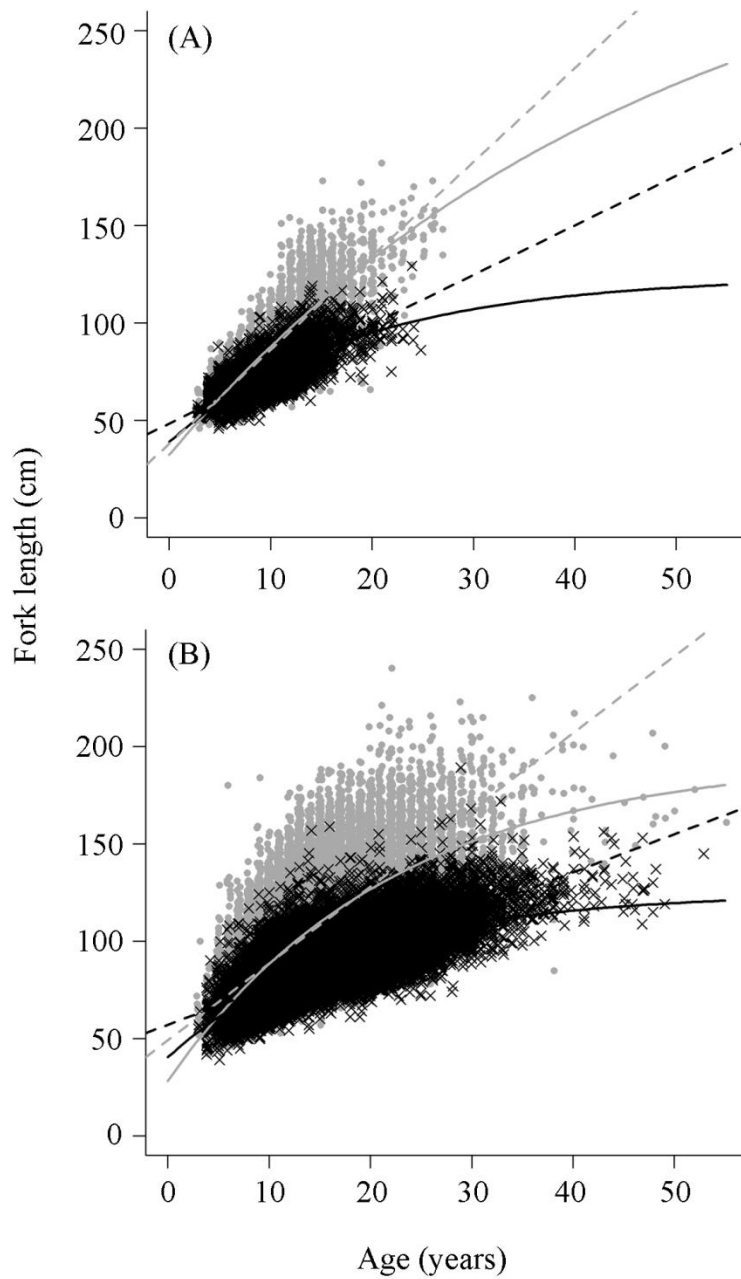
Figure 1.7. Fork length (cm) at age (years) and von Bertalanffy growth model (solid lines) and linear model fits (dashed lines) for females (grey circles) and males (black x's) for (A) 1920s and (B) 2000s.
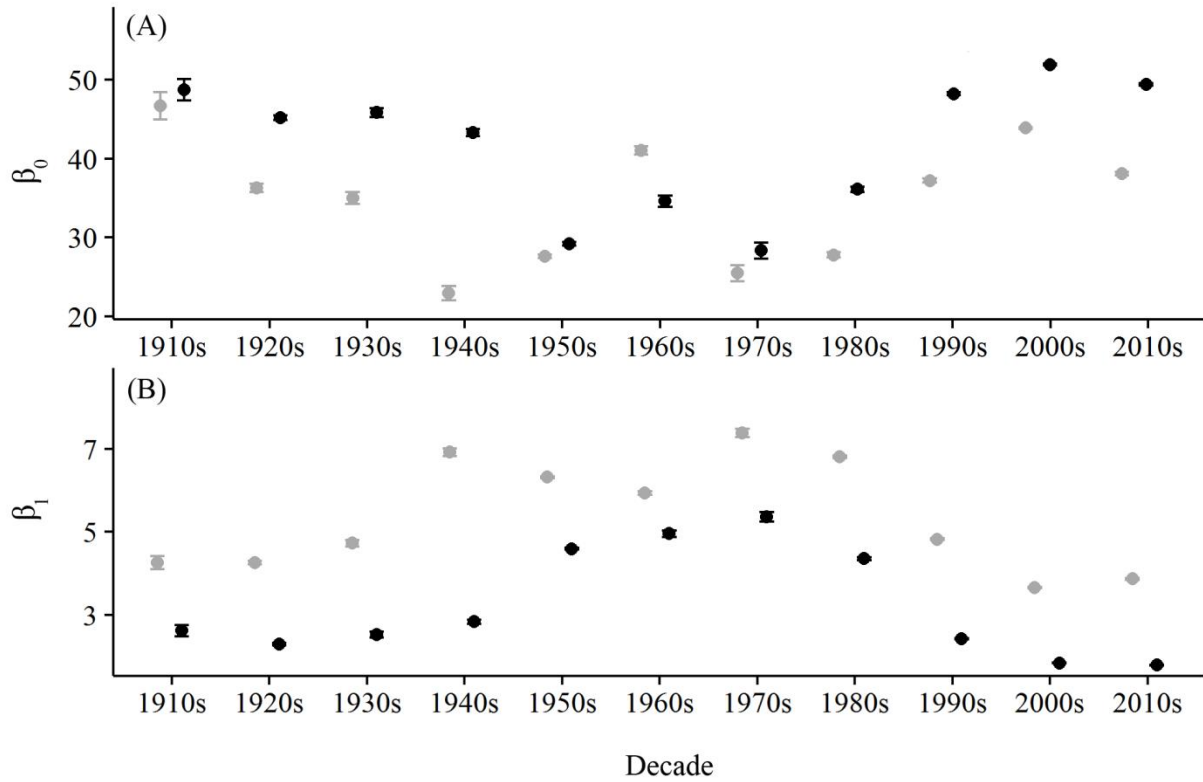
Figure 1.8. Parameter estimates (±SE) of linear model parameters (A) intercept, β_0, and (B) slope, β_0, for females (grey) and males (black) by decade. Data was truncated at age ≤ 25, because growth is well described with a linear trend up to this age. Parameter estimates are well estimated in most decades, and consequently the SE bars are difficult to see on this scale.
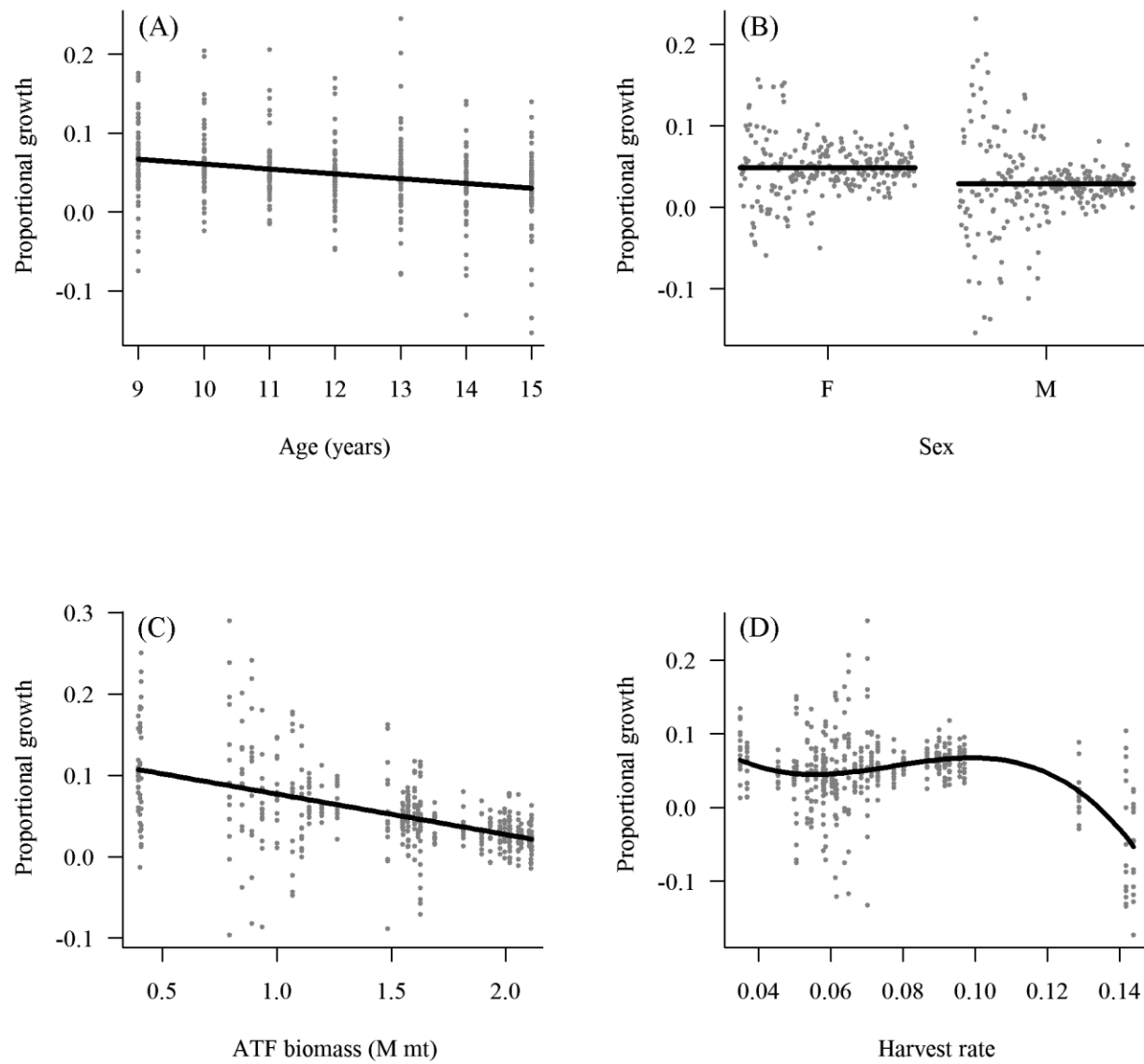
Figure 1.9. Partial residuals (grey points) and fitted values (black lines) for covariates in the best

fit regression model, showing the relationship between proportional growth of Pacific Halibut

(defined as the median annual increase in length conditioned on initial length) and (A) age

(years), (B) sex, (C) Arrowtooth Flounder biomass (ATF) (M mt), and (D) annual harvest rate of

Pacific Halibut.
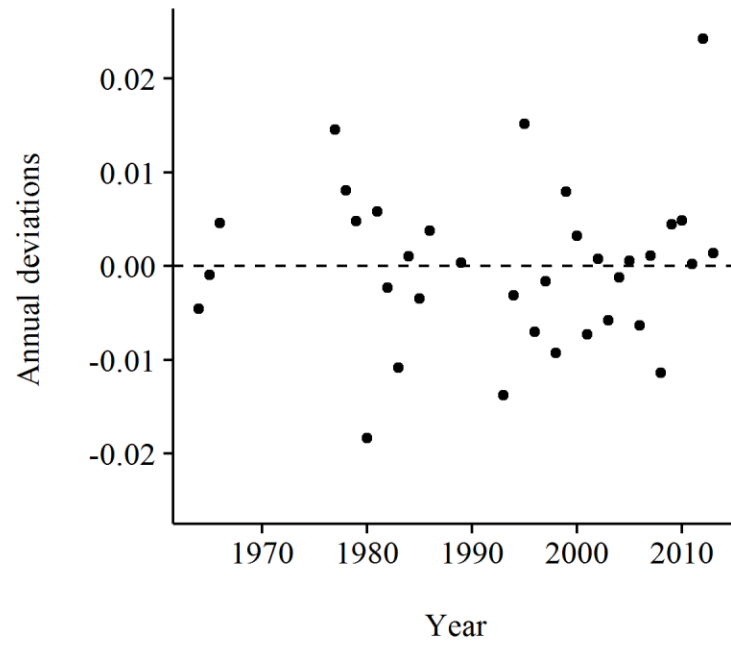
Figure 1.10. Predicted annual deviations (random effects) from the mean intercept of the best fit regression model.

1.9 Tables

Table 1.1. Sample sizes of Pacific Halibut length-at-age data by sex and decade, including years and regulatory areas sampled and maximum age (years) observed in each sample.

Decade	Years sampled	Areas sampled	Sex	n	Maximum age
1910 – 1919	1914, 1915	2B, 3A	F	661	30
			M	515	25
1920 – 1929	1925 – 1927, 1929	2A, 2B, 2C, 3A, 3B	F	4 476	27
			M	4 476	25
1930 – 1939	1930, 1933, 1935, 1936, 1939	2B, 4A	F	1 656	29
			M	1 430	30
1940 – 1949	1946, 1947, 1949	2B, 3A	F	2 097	29
			M	3 070	23
1950 – 1959	all years	2B, 2C, 3A, 3B	F	26 557	32
			M	19 423	30
1960 – 1969	1963 – 1966	2B, 3A, 3B, 4A	F	7 057	29
			M	3 558	26
1970 – 1979	1976 – 1979	2B, 3A	F	1 581	25
			M	1 388	21
1980 – 1989	1981 – 1986, 1988, 1989	2A, 2B, 2C, 3A, 3B, 4C	F	19 640	30
			M	13 085	28
1990 – 1999	1992 – 1999	2A, 2B, 2C, 3A, 3B, 4A, 4B, 4C, 4D	F	37 227	46
			M	24 939	55
2000 – 2009	all years	2A, 2B, 2C, 3A, 3B, 4A, 4B, 4C, 4D, CLS	F	76 518	55
			M	66 701	53
2010 – 2014	all years	2A, 2B, 2C, 3A, 3B, 4A, 4B, 4C, 4D	F	43 425	51
			M	30 747	50

Table 1.2. Correlation coefficients among variables used in regression analysis. Variables include (ATF=Arrowtooth Flounder biomass, HAL=Pacific Halibut biomass, SST=summer sea surface temperatures, SST_1=SST a lag of -1 years, PDO=Pacific Decadal Oscillation, PDO_1=PDO at a lag of -1 years, HR=Pacific Halibut annual harvest rate). The lower half of the diagonal mirrors the top and is omitted to aid in visualization. Values are shown to demonstrate strength of association among covariates and not statistical significance.

	ATF	HAL	SST	SST_1	PDO	PDO_1	HR
ATF	1	0.61	0.36	0.34	0.16	0.16	-0.63
HAL	--	1	0.38	0.38	0.29	0.35	-0.72
SST	--	--	1	0.34	0.40	0.15	-0.36
SST_1	--	--	--	1	0.25	0.40	-0.28
PDO	--	--	--	--	1	0.27	-0.41
PDO_1	--	--	--	--	--	1	-0.35
HR	--	--	--	--	--	--	1

Table 1.3. Model selection results for the top five models used in regression analyses. Results include terms used in each model (ATF=Arrowtooth Flounder biomass, HAL=Pacific Halibut biomass, HR=Pacific Halibut annual harvest rate, PDO=Pacific Decadal Oscillation, *year*=random intercept for sampling year), Δ AIC where "0" indicates the best model by AIC, the number of parameters in the model (k), the marginal R^2, and the conditional R^2.

Model	Δ AIC	k	Marginal R^2	Conditional R^2
Age + Sex + ATF + HR + HR^2 + HR^3 + *year*	0	9	0.23	0.28
Age + Sex + ATF + HAL + HR + HR^2 + HR^3 + *year*	5	10	0.23	0.28
Age + Sex + ATF + HAL + HAL^2 + HR + HR^2 + HR^3 + *year*	7	11	0.24	0.28
Age + Sex + ATF + ATF^2 + HAL + HAL^2 + HR + HR^2 + HR^3 + *year*	12	12	0.24	0.28
Age + Sex + PDO + ATF + HAL + HAL^2 + HR + HR^2 + HR^3 + *year*	16	12	0.25	0.28

Table 1.4. Best fit model parameter estimates (±SE), t-value, and p-value (related significance level) for the fixed effects and standard deviations (SD) for random effects.

Parameter	Estimate (±SE)	t-value	p-value
Intercept	0.40 (0.080)	5.1	< 0.01
Age	-0.0061 (0.0010)	-6.1	< 0.01
Sex (male)*	-0.020 (0.0040)	-4.8	< 0.01
ATF	-0.050 (0.0083)	-6.0	< 0.01
HR	-9.0 (2.9)	-3.1	< 0.01
HR^2	126 (37.2)	3.4	< 0.01
HR^3	-544 (145)	-3.7	< 0.01
Random effects	SD		
Year (intercept)	0.012		
Residual	0.044		

1.10   Appendix

Appendix 1.A Parameter estimates (±SE) for all von Bertalanffy (VB) growth models (L_∞ = asymptotic length in cm, k = proportional to the rate at which L_∞ is reached in years^{-1}, t_0 = the theoretical age at zero length in years) and linear models (LM) (β_0 = y-intercept in cm, β_1 = slope in cm*year^{-1}) by decade, sex, and regulatory area. Akaike Information Criterion (AIC) is shown for both VB and LM, and "Best fit" indicates best model fit by AIC, where the best model has the lowest AIC by 2 (if ≤ 2, LM is selected because it has fewer parameters).

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1910s	F	all	220 (36.3)	0.041 (0.013)	-4.7 (1.3)	51.5 (2.0)	4.7 (0.2)	5842.3	5839.7	LM
1910s	M	all	137 (23.1)	0.055 (0.023)	-7.0 (2.4)	52.8 (1.6)	2.9 (0.2)	4101.5	4097.8	LM
1910s	F	2B	253 (40.5)	0.045 (0.013)	-2.5 (0.8)	43.5 (2.2)	6.3 (0.2)	3789.9	3804.1	VB
1910s	F	3A	325 (172.7)	0.021 (0.017)	-4.5 (2.5)	37.8 (3.5)	4.8 (0.3)	1857.9	1847.6	LM
1910s	M	2B	176 (36.7)	0.045 (0.018)	-5.5 (1.6)	47.4 (1.7)	4.0 (0.2)	2599.7	2605.7	VB
1910s	M	3A	128 (44.8)	0.052 (0.048)	-7.0 (6.1)	51.4 (3.2)	2.4 (0.3)	1351.5	1342.2	LM
1920s	F	all	325 (45.6)	0.021 (0.004)	-5.0 (0.5)	38.1 (0.6)	4.8 (0.1)	33491.8	33482.7	LM
1920s	M	all	124 (5.7)	0.054 (0.006)	-7.0 (0.7)	48.6 (0.4)	2.5 (0.0)	31742.7	31654.9	LM
1920s	F	2A	325 (531.7)	0.022 (0.049)	-6.0 (4.8)	43.5 (3.1)	5.2 (0.4)	923.0	918.1	LM
1920s	F	2B	325 (195.6)	0.019 (0.015)	-7.0 (1.5)	43.1 (0.9)	4.5 (0.1)	8036.4	8010.8	LM
1920s	F	2C	325 (420.4)	0.021 (0.036)	-4.0 (2.7)	29.9 (2.6)	5.4 (0.3)	1375.9	1367.8	LM

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Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1920s	F	3A	173 (7.2)	0.071 (0.007)	0.0 (0.4)	39.9 (1.3)	4.8 (0.1)	16915.0	17062.8	VB
1920s	F	3B	325 (142.5)	0.020 (0.012)	-3.2 (1.1)	26.9 (1.5)	4.9 (0.1)	5255.1	5252.2	LM
1920s	M	2A	103 (20.4)	0.093 (0.076)	-7.0 (5.7)	58.5 (1.8)	2.3 (0.2)	933.8	932.4	LM
1920s	M	2B	160 (34.5)	0.040 (0.016)	-7.0 (1.4)	44.5 (0.7)	3.4 (0.1)	10127.4	10072.5	LM
1920s	M	2C	188 (231.3)	0.029 (0.055)	-7.0 (5.4)	38.2 (1.7)	3.5 (0.2)	2120.7	2118.7	LM
1920s	M	3A	140 (13.0)	0.048 (0.010)	-5.4 (1.3)	45.2 (0.8)	2.8 (0.1)	13149.5	13171.8	VB
1920s	M	3B	124 (12.8)	0.059 (0.015)	-3.7 (1.4)	40.6 (1.2)	2.8 (0.1)	4638.4	4654.8	VB
1930s	F	all	220 (19.3)	0.043 (0.007)	-2.5 (0.5)	37.1 (0.9)	5.3 (0.1)	12893.1	12903.0	VB
1930s	M	all	138 (11.9)	0.049 (0.010)	-7.0 (1.1)	49.6 (0.7)	2.8 (0.1)	9948.5	9938.1	LM
1930s	F	2B	325 (70.9)	0.027 (0.008)	-2.8 (0.6)	31.5 (1.0)	6.1 (0.1)	10540.0	10533.0	LM
1930s	F	4A	291 (76.7)	0.026 (0.011)	-2.8 (1.3)	34.1 (2.0)	4.9 (0.2)	2180.5	2185.3	VB
1930s	M	2B	133 (31.9)	0.053 (0.028)	-7.0 (2.4)	47.2 (1.0)	3.1 (0.1)	9032.9	9015.5	LM
1930s	M	4A	154 (38.4)	0.044 (0.025)	-5.2 (3.5)	46.7 (2.8)	2.8 (0.2)	893.0	894.5	LM
1940s	F	all	220 (10.9)	0.064 (0.006)	0.0 (0.3)	22.5 (1.1)	7.9 (0.1)	18030.3	17928.5	LM
1940s	M	all	146 (15.1)	0.045 (0.009)	-7.0 (0.9)	46.3 (0.6)	3.2 (0.1)	22491.6	22463.1	LM
1940s	F	2B	325 (57.4)	0.030 (0.007)	-1.8 (0.4)	25.7 (1.2)	7.1 (0.1)	9490.7	9441.1	LM

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1940s	F	3A	281 (37.8)	0.048 (0.012)	0.0 (0.7)	30.4 (2.3)	7.5 (0.2)	8182.3	8242.7	VB
1940s	M	2B	139 (16.3)	0.049 (0.012)	-7.0 (1.1)	46.2 (0.6)	3.2 (0.1)	18725.8	18701.4	LM
1940s	M	3A	174 (93.3)	0.035 (0.037)	-7.0 (5.3)	30.4 (2.3)	7.5 (0.2)	3674.6	3671.5	LM
1950s	F	all	219 (2.0)	0.064 (0.001)	-0.1 (0.0)	27.9 (0.3)	7.2 (0.0)	224298.2	228204.9	VB
1950s	M	all	124 (0.9)	0.112 (0.002)	-0.4 (0.0)	29.6 (0.3)	5.2 (0.0)	153745.9	157602.0	VB
1950s	F	2B	325 (21.3)	0.032 (0.003)	-2.0 (0.2)	31.8 (0.6)	7.0 (0.1)	44665.2	44472.2	LM
1950s	F	2C	325 (15.3)	0.035 (0.002)	-0.6 (0.1)	19.7 (0.7)	8.0 (0.1)	27837.2	27869.0	VB
1950s	F	3A	194 (1.9)	0.079 (0.002)	0.0 (0.0)	28.3 (0.4)	7.1 (0.0)	98030.1	100987.5	VB
1950s	F	3B	247 (9.8)	0.055 (0.004)	0.0 (0.2)	27.5 (1.1)	7.4 (0.1)	24606.3	24824.2	VB
1950s	F	4A	163 (3.2)	0.099 (0.005)	0.0 (0.2)	49.0 (1.1)	5.0 (0.1)	16954.4	17604.1	VB
1950s	F	CLS	325 (21.8)	0.041 (0.004)	0.0 (0.1)	5.2 (0.8)	10.3 (0.1)	10276.3	10652.2	VB
1950s	M	2B	129 (4.9)	0.061 (0.006)	-7.0 (0.6)	53.6 (0.4)	2.9 (0.0)	45983.1	46023.8	VB
1950s	M	2C	128 (3.3)	0.085 (0.005)	-1.5 (0.1)	28.6 (0.6)	4.9 (0.1)	23837.9	24158.0	VB
1950s	M	3A	144 (2.0)	0.093 (0.003)	-0.2 (0.1)	22.0 (0.4)	6.2 (0.0)	52156.0	53534.9	VB
1950s	M	3B	136 (5.6)	0.090 (0.008)	-0.4 (0.2)	28.9 (1.4)	5.2 (0.1)	12274.1	12422.7	VB
1950s	M	4A	117 (1.6)	0.132 (0.006)	0.0 (0.2)	43.6 (1.1)	3.7 (0.1)	8706.9	9373.8	VB

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1960s	F	all	210 (3.6)	0.079 (0.003)	0.0 (0.1)	44.8 (0.6)	6.7 (0.1)	58774.7	60101.3	VB
1960s	M	all	155 (5.8)	0.092 (0.008)	-0.2 (0.3)	36.4 (0.9)	5.6 (0.1)	29056.3	29239.0	VB
1960s	F	2B	176 (4.9)	0.095 (0.008)	-0.1 (0.4)	57.7 (1.6)	4.7 (0.1)	6338.4	6482.7	VB
1960s	F	3A	216 (6.5)	0.077 (0.005)	0.0 (0.2)	43.0 (1.0)	7.0 (0.1)	22012.8	22428.6	VB
1960s	F	3B	243 (8.9)	0.065 (0.005)	0.0 (0.2)	35.4 (0.9)	7.8 (0.1)	27723.4	28134.1	VB
1960s	F	4A	325 (106.2)	0.040 (0.020)	0.0 (1.0)	10.2 (4.1)	9.4 (0.4)	2157.4	2155.6	LM
1960s	M	2B	194 (38.9)	0.034 (0.012)	-7.0 (1.6)	48.6 (1.4)	3.5 (0.1)	4425.5	4431.0	VB
1960s	M	3A	193 (20.8)	0.065 (0.014)	-0.7 (0.6)	31.9 (1.4)	6.4 (0.1)	12339.7	12366.4	VB
1960s	M	3B	183 (16.8)	0.076 (0.014)	0.0 (0.4)	26.4 (1.4)	6.9 (0.2)	11085.9	11115.7	VB
1960s	M	4A	325 (447.5)	0.030 (0.056)	0.0 (2.3)	8.8 (5.6)	7.6 (0.6)	740.0	735.8	LM
1970s	F	all	302 (22.3)	0.047 (0.006)	0.0 (0.3)	24.9 (1.2)	8.5 (0.1)	13175.8	13347.7	VB
1970s	M	all	172 (12.9)	0.074 (0.011)	-0.2 (0.4)	36.4 (0.9)	5.6 (0.1)	11108.5	11160.0	VB
1970s	F	2B	325 (75.8)	0.033 (0.012)	-2.4 (1.1)	41.4 (2.4)	6.6 (0.2)	2685.4	2686.6	LM
1970s	F	3A	325 (31.8)	0.043 (0.007)	0.0 (0.3)	17.9 (1.3)	9.3 (0.1)	10409.2	10526.3	VB
1970s	M	2B	218 (102.4)	0.029 (0.023)	-7.0 (3.0)	47.4 (1.9)	3.7 (0.2)	2252.6	2245.1	LM
1970s	M	3A	267 (45.0)	0.043 (0.011)	-0.2 (0.4)	17.4 (1.4)	7.6 (0.2)	8639.0	8656.2	VB

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1980s	M	all	161 (3.0)	0.077 (0.003)	-0.5 (0.2)	37.8 (0.4)	4.9 (0.0)	103911.9	104472.1	VB
1980s	F	2A	224 (31.2)	0.061 (0.016)	0.0 (0.7)	30.7 (2.6)	6.8 (0.3)	1179.3	1195.1	VB
1980s	F	2B	261 (15.2)	0.047 (0.005)	-0.6 (0.3)	31.7 (0.9)	6.9 (0.1)	26517.8	26640.0	VB
1980s	F	2C	262 (9.9)	0.051 (0.004)	0.0 (0.2)	33.6 (0.8)	7.0 (0.1)	45931.0	46325.7	VB
1980s	F	3A	325 (11.4)	0.042 (0.002)	0.0 (0.1)	25.5 (0.6)	8.3 (0.1)	76014.8	76652.9	VB
1980s	F	3B	325 (44.9)	0.042 (0.009)	0.0 (0.5)	17.8 (2.1)	9.2 (0.2)	10290.3	10323.6	VB
1980s	F	4C	325 (48.7)	0.043 (0.010)	0.0 (0.6)	24.0 (2.3)	8.8 (0.2)	3531.3	3579.8	VB
1980s	M	2A	127 (13.6)	0.117 (0.041)	-0.1 (1.4)	46.6 (3.7)	3.9 (0.4)	536.3	547.9	VB
1980s	M	2B	153 (9.0)	0.057 (0.008)	-3.7 (0.6)	44.5 (0.6)	3.8 (0.1)	19180.1	19236.8	VB
1980s	M	2C	156 (4.1)	0.080 (0.005)	-0.3 (0.3)	40.7 (0.7)	4.6 (0.1)	34785.0	35024.4	VB
1980s	M	3A	202 (9.6)	0.058 (0.005)	-0.4 (0.3)	30.1 (0.7)	6.0 (0.1)	42890.5	43020.6	VB
1980s	M	3B	183 (28.8)	0.062 (0.019)	-0.6 (0.9)	30.0 (2.1)	5.7 (0.2)	4482.7	4492.5	VB
1980s	M	4C	230 (200.3)	0.058 (0.087)	0.0 (3.1)	20.3 (9.6)	8.1 (1.0)	259.6	260.1	LM
1990s	F	all	256 (6.4)	0.037 (0.002)	-2.4 (0.2)	40.8 (0.3)	5.3 (0.0)	310094.1	310817.7	VB
1990s	M	all	154 (2.6)	0.042 (0.002)	-7.0 (0.3)	53.7 (0.2)	2.6 (0.0)	183643.6	183985.7	VB
1990s	F	2A	208 (21.3)	0.052 (0.010)	-2.0 (0.6)	39.7 (1.0)	5.6 (0.1)	17233.2	17262.9	VB

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1990s	F	2B	293 (29.6)	0.028 (0.004)	-4.5 (0.5)	45.1 (0.7)	5.1 (0.1)	55769.7	55822.2	VB
1990s	F	2C	215 (7.3)	0.060 (0.004)	0.0 (0.3)	39.5 (0.9)	5.7 (0.1)	36730.0	37017.2	VB
1990s	F	3A	325 (36.8)	0.027 (0.004)	-2.4 (0.4)	33.1 (0.7)	5.8 (0.1)	68458.1	68485.8	VB
1990s	F	3B	243 (21.0)	0.039 (0.006)	-2.3 (0.5)	39.2 (0.9)	5.3 (0.1)	49429.3	49480.6	VB
1990s	F	4A	226 (10.0)	0.051 (0.004)	0.0 (0.3)	35.0 (0.9)	5.5 (0.1)	30819.7	31001.6	VB
1990s	F	4B	197 (4.4)	0.070 (0.004)	0.0 (0.2)	48.0 (0.8)	5.0 (0.1)	26615.3	27034.6	VB
1990s	F	4C	210 (19.3)	0.062 (0.012)	-0.7 (0.6)	40.0 (1.7)	6.1 (0.2)	10051.8	10085.1	VB
1990s	F	4D	206 (14.5)	0.052 (0.008)	-1.3 (0.7)	43.4 (1.3)	4.8 (0.1)	12413.0	12467.2	VB
1990s	M	2A	123 (5.8)	0.092 (0.015)	-2.4 (1.0)	52.3 (1.0)	3.1 (0.1)	5328.3	5363.5	VB
1990s	M	2B	124 (3.7)	0.061 (0.006)	-7.0 (0.8)	57.4 (0.4)	2.2 (0.0)	32820.9	32825.9	VB
1990s	M	2C	187 (14.1)	0.033 (0.005)	-7.0 (0.9)	50.0 (0.6)	3.0 (0.0)	17971.3	18005.5	VB
1990s	M	3A	163 (12.3)	0.037 (0.006)	-7.0 (0.9)	48.4 (0.5)	2.8 (0.0)	39283.0	39256.8	LM
1990s	M	3B	158 (10.0)	0.039 (0.006)	-7.0 (1.0)	50.9 (0.5)	2.6 (0.0)	34363.0	34392.0	VB
1990s	M	4A	165 (7.4)	0.037 (0.004)	-7.0 (0.8)	52.8 (0.5)	2.5 (0.0)	22856.6	22918.3	VB
1990s	M	4B	134 (2.0)	0.073 (0.004)	-3.4 (0.4)	60.7 (0.5)	2.3 (0.0)	23822.2	24241.0	VB
1990s	M	4C	196 (55.4)	0.030 (0.016)	-7.0 (3.0)	48.0 (2.1)	3.0 (0.2)	1337.9	1338.9	LM

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
1990s	M	4D	136 (6.2)	0.068 (0.010)	-2.5 (1.0)	56.1 (1.3)	2.4 (0.1)	3811.3	3914.7	VB
2000s	F	all	194 (2.1)	0.045 (0.001)	-3.5 (0.1)	49.1 (0.2)	3.9 (0.0)	628102.3	630569.5	VB
2000s	M	all	125 (0.7)	0.056 (0.001)	-7.0 (0.2)	57.2 (0.1)	2.0 (0.0)	484484.8	484803.0	VB
2000s	F	2A	146 (3.7)	0.081 (0.006)	-2.2 (0.4)	53.6 (0.6)	3.7 (0.0)	34354.5	34561.9	VB
2000s	F	2B	234 (11.5)	0.033 (0.003)	-5.1 (0.4)	48.7 (0.4)	4.3 (0.0)	102924.3	103097.8	VB
2000s	F	2C	242 (9.7)	0.036 (0.003)	-3.0 (0.3)	42.0 (0.4)	4.9 (0.0)	102886.2	103134.6	VB
2000s	F	3A	164 (4.7)	0.058 (0.004)	-3.2 (0.4)	51.6 (0.5)	3.6 (0.0)	96042.2	96246.9	VB
2000s	F	3B	155 (5.0)	0.063 (0.005)	-2.4 (0.4)	46.4 (0.5)	3.8 (0.0)	72780.2	72961.9	VB
2000s	F	4A	167 (3.1)	0.069 (0.003)	-0.4 (0.2)	42.0 (0.5)	4.3 (0.0)	69721.9	70342.2	VB
2000s	F	4B	175 (1.8)	0.078 (0.002)	0.0 (0.2)	52.4 (0.5)	4.2 (0.0)	56457.8	58143.7	VB
2000s	F	4C	162 (5.0)	0.082 (0.007)	0.0 (0.3)	41.5 (0.9)	4.7 (0.1)	11811.0	12149.6	VB
2000s	F	4D	226 (7.1)	0.031 (0.002)	-5.3 (0.4)	52.0 (0.4)	3.5 (0.0)	72073.9	72399.2	VB
2000s	F	CLS	170 (49.3)	0.062 (0.041)	-1.7 (2.6)	39.5 (3.6)	4.6 (0.4)	332.0	332.4	LM
2000s	M	2A	115 (2.6)	0.069 (0.006)	-7.0 (0.8)	60.5 (0.4)	1.9 (0.0)	16670.9	16786.6	VB
2000s	M	2B	113 (1.6)	0.068 (0.004)	-7.0 (0.5)	57.8 (0.2)	1.9 (0.0)	60262.0	60083.8	LM
2000s	M	2C	136 (3.3)	0.050 (0.003)	-7.0 (0.5)	54.2 (0.3)	2.4 (0.0)	53494.7	53615.8	VB

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
2000s	M	3A	103 (1.2)	0.075 (0.004)	-7.0 (0.6)	59.9 (0.3)	1.5 (0.0)	62866.5	62996.6	VB
2000s	M	3B	109 (1.6)	0.069 (0.004)	-6.2 (0.6)	56.7 (0.3)	1.7 (0.0)	70462.1	70716.4	VB
2000s	M	4A	120 (1.5)	0.063 (0.003)	-5.2 (0.4)	54.3 (0.3)	2.0 (0.0)	76658.9	77223.4	VB
2000s	M	4B	128 (0.7)	0.072 (0.002)	-4.1 (0.2)	62.5 (0.2)	2.0 (0.0)	84137.0	86126.4	VB
2000s	M	4C	107 (2.7)	0.102 (0.011)	-2.1 (0.7)	51.6 (0.8)	2.2 (0.1)	3229.9	3311.6	VB
2000s	M	4D	138 (3.0)	0.047 (0.003)	-7.0 (0.6)	55.9 (0.4)	2.1 (0.0)	40366.8	40466.0	VB
2000s	M	CLS	109 (4.9)	0.090 (0.020)	-3.7 (1.8)	56.9 (1.5)	1.8 (0.1)	495.4	513.4	VB
2010s	F	all	169 (2.0)	0.061 (0.002)	-1.3 (0.1)	43.9 (0.3)	4.0 (0.0)	354604.2	356434.6	VB
2010s	M	all	123 (1.1)	0.053 (0.002)	-7.0 (0.3)	54.5 (0.1)	1.9 (0.0)	220290.9	220619.1	VB
2010s	F	2A	134 (3.7)	0.113 (0.011)	0.0 (0.5)	52.5 (0.9)	3.8 (0.1)	29839.5	30004.8	VB
2010s	F	2B	191 (7.9)	0.053 (0.005)	-1.8 (0.4)	42.8 (0.7)	4.6 (0.1)	55875.4	56070.6	VB
2010s	F	2C	226 (12.8)	0.041 (0.004)	-2.1 (0.4)	38.3 (0.7)	5.0 (0.1)	61655.7	61778.7	VB
2010s	F	3A	190 (16.6)	0.036 (0.006)	-5.6 (0.9)	47.1 (0.7)	3.4 (0.1)	47862.9	47897.6	VB
2010s	F	3B	165 (14.8)	0.045 (0.008)	-4.2 (0.8)	42.1 (0.8)	3.6 (0.1)	42110.3	42143.9	VB
2010s	F	4A	153 (3.4)	0.072 (0.004)	-0.2 (0.3)	42.4 (0.6)	3.7 (0.1)	41750.6	42157.8	VB
2010s	F	4B	188 (3.8)	0.064 (0.003)	0.0 (0.2)	42.9 (0.7)	4.5 (0.1)	28614.0	29579.0	VB

Appendix 1.A continued

Decade	Sex	Area	L_∞ (±SE)	k (±SE)	t_0 (±SE)	β_0 (±SE)	β_1 (±SE)	AIC (VB)	AIC (LM)	Best fit
2010s	F	4C	197 (11.6)	0.053 (0.006)	0.0 (0.4)	27.1 (1.1)	5.3 (0.1)	17287.0	17540.7	VB
2010s	F	4D	152 (3.3)	0.067 (0.004)	-1.1 (0.4)	48.6 (0.6)	3.2 (0.0)	21409.8	21674.4	VB
2010s	M	2A	107 (5.0)	0.077 (0.016)	-6.6 (1.9)	60.2 (0.8)	1.7 (0.1)	9560.9	9586.9	VB
2010s	M	2B	109 (3.0)	0.069 (0.008)	-7.0 (1.0)	57.4 (0.4)	1.8 (0.0)	26720.4	26762.9	VB
2010s	M	2C	126 (5.4)	0.053 (0.007)	-7.0 (1.0)	53.1 (0.5)	2.2 (0.0)	24822.7	24876.7	VB
2010s	M	3A	101 (1.5)	0.070 (0.005)	-7.0 (0.7)	56.4 (0.3)	1.5 (0.0)	31619.1	31771.9	VB
2010s	M	3B	102 (2.0)	0.073 (0.006)	-5.4 (0.7)	52.0 (0.4)	1.7 (0.0)	32619.7	32793.4	VB
2010s	M	4A	117 (2.1)	0.060 (0.004)	-5.1 (0.5)	51.9 (0.3)	1.9 (0.0)	30583.6	30869.7	VB
2010s	M	4B	126 (1.0)	0.079 (0.003)	-1.9 (0.2)	56.1 (0.3)	2.2 (0.0)	38741.1	39883.5	VB
2010s	M	4C	111 (3.4)	0.095 (0.011)	-0.9 (0.7)	46.3 (1.0)	2.4 (0.1)	4299.5	4393.2	VB
2010s	M	4D	122 (3.3)	0.052 (0.005)	-7.0 (0.9)	54.9 (0.5)	1.8 (0.0)	11794.6	11875.2	VB

Chapter 2. Cumulative effects of size-selective fishing on size-at-age of Pacific halibut (*Hippoglossus stenolepis*)[1]

2.1   Abstract

The biomass of Pacific halibut (*Hippoglossus stenolepis*) has been declining since the late 1990s, and reductions in size-at-age since the 1980s explain more than half of the observed decline in halibut biomass. For example, on average an age-20 female halibut weighed 55 kg in 1988 but weighed 20 kg in 2014. We hypothesize that declines in size-at-age are, in part, the result of size-selective fishing. An age- and size-structured equilibrium model was developed to examine the long-term relationship between fishing mortality and size-at-age. Historical estimates of fishing mortality for Pacific halibut ranged between 0.18 and 0.60, with a mean of 0.40 over 2000-2014; fishing mortality was significantly higher in the eastern Gulf of Alaska than in the central or western Gulf of Alaska. Results suggest that fishing can explain between 30% to nearly 100% of the observed declines in size-at-age since the 1980s, depending on sex, age, and region. Given that length-at-age for any given cohort is highly variable, Pacific halibut are vulnerable to the cumulative effects of size-selective fishing. The most effective management action to potentially reverse trends in size-at-age would be to reduce harvest rates to diminish the intensity of size selection. Additional research is needed to better understand the potential for other mechanisms to the observed variability in size-at-age of Pacific halibut.

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[1] Sullivan, J.Y., Martell, S.J.D., Kruse, G.H. 2016. Cumulative effects of size-selective fishing on size-at-age of Pacific halibut (*Hippoglossus stenolepis*). Prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences.

2.2   Introduction

Fisheries have been called large-scale experiments in life history evolution (Rijnsdorp 1993).

Size-selective fishing occurs when the large individuals of a particular species are preferentially

harvested (Fenberg and Roy 2008) and can result from minimum legal size limits, gear

selectivity (Millar 1992), and fisher or processor preference (Reddy et al. 2013). Such selective

removals mean that smaller, younger fish play a larger role in reproduction, thus contributing

disproportionately to subsequent generations (Law and Grey 1989). Fisheries-induced evolution

is a process whereby fishing acts as an agent of genetic selection in a population under the

condition that growth and other linked life history attributes (e.g., size- or age-at maturity) are

heritable traits (Law 2000). Large declines in size- or age-at-maturity in many commercially

exploited fish stocks have been offered as evidence of fisheries-induced evolution (Heino and

Dieckmann 2008, Sharpe and Hendry 2009).

However, some purported instances of fisheries-induced evolution have been challenged, in part

due to difficulties to conclusively demonstrate this phenomenon in wild populations (e.g.,

Hilborn and Minte-Vera 2008). The primary challenge associated with fisheries-induced

evolution is reconciling estimates of a trait's heritability and the selection differential imposed by

a fishery with observed changes in a phenotypic trait over a given period of time (Law 2007).

Especially in long-lived fish species with long generation times, quantitative genetic models fail

to predict the changes in traits observed across numerous marine stocks, even under high

exploitation rates (Hendry and Kinnison 1999). A secondary challenge is clearly demonstrating

that changes in life history traits are due to fishery-induced evolution and not due to other

factors, such as variations in fish density and environmental conditions (Dieckmann and Heino

2007).

Relatively absent from this debate has been the fact that size-selective fishing can alter phenotypic traits, such as size-at-age, even *without* a genetic effect (Walters and Martell 2004, Martell et al. 2015). For instance, consider a fish population in which each cohort is composed of groups of fish, each with their unique growth curves. Under size-selective fishing, fishing mortality imposes differential total mortality whereby groups of fish with faster growth suffer higher mortality than those with slower growth. Removal of these faster growth types leads to a surviving population composed of groups of fish with slower mean growth resulting in changes in estimates of biological reference points, such as F_{MSY}, the fishing mortality associated with maximum sustainable yield (Martell et al. 2015).

Our overall goal is to assess the potential for fisheries to cause phenotypic changes in a population in the absence of genetic selection. To do so, we developed an age- and size-structured equilibrium model to examine the relationship between the cumulative effects of size-selective fishing and fishery removals on size-at-age. We focused on size-selective fishing caused by minimum size limits and gear selectivity because they are most readily controlled by managers. For fishing mortality, we included all mortality of a given species associated with fishing activity, including directed harvest, bycatch in non-directed fisheries, and discard mortality of sub-legal fish or fish that die as a result of lost gear. We hypothesized that fast-growing individuals are subjected to higher total mortality relative to slow growing individuals because they recruit to the minimum size limits at a younger age. Over time, the result is a truncated population, comprised of smaller, slower growing individuals. A similar model was used to examine post-release survival and the efficacy of size limits in blue, white, and striped marlin fisheries (Pine et al. 2008). Parametrization of these types of models relies heavily on pre-existing knowledge or published values of somatic growth, survivorship, natural mortality,

maturity, and fishery selectivity. The growth curve, which defines mean size-at-age and variability in size-at-age, is used to generate a series of "growth-type groups," or groups within a cohort that differ in growth and relative abundance (Walters and Martell 2004). Model results are evaluated in terms of changes in mean size-at-age with fishing mortality under equilibrium conditions. As model results are sensitive to the level of variability in size-at-age (as measured by the coefficient of variation in mean length-at-age), fishery selectivity, and discard mortality rates, we explored interactions among these parameters on the estimates of optimal fishing mortality, and the resulting changes in size-at-age.

We applied this model to Pacific halibut (*Hippoglossus stenolepis*), which support a culturally and economically valuable fishery in the northeast Pacific Ocean spanning waters off the U.S. west coast, British Columbia, and Alaska (Keith et al. 2014). Pacific halibut are a large, long-lived pleuronectid, attaining maximum ages over 50 years, lengths up to 2.5 m, and weights to 230 kg. On average, females and males mature at ages 12 and 8 years, respectively (Stewart 2014). A commercial longline fishery for halibut has been managed by the International Pacific Halibut Commission (IPHC) since 1923. Fishery management has been aided by extensive biological research and fishery monitoring efforts, including an impressive time series of length-at-age data from fisheries-independent surveys since 1914.

Pacific halibut are an excellent case study for our approach, because there is a high degree of spatial variability in both size-at-age and exploitation rates in the North Pacific Ocean, which allows us to test the efficacy and utility of this model at multiple spatial scales (Martell et al. 2013). Pacific halibut experienced extreme variability in size-at-age since at least the 1920s. Their size-at-age was low in the 1920s, increased steadily until it peaked in the 1980s, and declined precipitously from 1990 to 2014 (Figure 2.1) (Keith et al. 2014). Geographic variability

is evidenced by recent sharp declines in size-at-age in the central and western Gulf of Alaska, while declines in the eastern Gulf of Alaska have been less severe. Causes of variability in size-at-age are poorly understood, although there is some evidence that growth is density-dependent and may be influenced by environmental factors linked to the Pacific Decadal Oscillation (PDO), a long-lived El Niño-like pattern of Pacific climate variability (Clark et al. 1999, Clark and Hare 2002). The possibility that declines in Pacific halibut size-at-age are the result of cumulative effects of size-selective fishing and high exploitation rates in the 1990s and 2000s has yet to be investigated. Other potential approaches to investigate fishing as a cause of evolution in size-at-age are not practical for Pacific halibut. For example, probabilistic maturation reaction norms (PMRNs), a tool used to attempt to disentangle genetic from plastic adaptation of maturation schedules in many other marine species (Dieckmann and Heino 2007), cannot be applied to halibut, because age-at-maturity for female halibut appears to have remained constant despite large variability in halibut size-at-age (Clark et al. 1999, Stewart 2014). Ongoing histological studies at the IPHC have confirmed limitations to the maturity data obtained during surveys, namely misspecification of mature, resting females as "immature" and difficulties determining age at first maturity (B.M. Leaman, IPHC, Seattle, Washington, personal communication, 2016). Quantitative genetic modeling is not currently possible, as genetic studies have focused on stock structure (Grant et al. 1984, Nielsen et al. 2009) and estimates of heritability of growth are unavailable for this species.

2.3 Materials and methods

2.3.1 Data

We estimated values of somatic growth and maturity using fisheries-independent length-at-age data collected during IPHC setline surveys between 1980 and 1989. All years are well

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represented, with the exception of 1987, when no surveys were conducted. This time period was selected because it corresponds to a peak in halibut size-at-age. During surveys, IPHC scientists collected fork lengths and otoliths and determined sex and maturity status by macroscopic examination of gonads of sampled individuals. These data were collected in the Gulf of Alaska along the continental shelf in four IPHC regulatory areas: 2B (British Columbia), 2C (Southeast Alaska), 3A (central Gulf of Alaska), and 3B (western Gulf of Alaska) (Figure 2.2).

2.3.2   Estimation of growth and maturity

We fit a standard three-parameter von Bertalanffy growth model by sex to length-at-age data to characterize growth in the 1980s. Regional models were fit by regulatory area and a coastwide model was fit to all areas combined, allowing us to compare model results over two spatial scales. Mean fork length L (cm) at age a (year) was modeled as:

$$(2.1) \qquad L_a = L_\infty (1 - \exp(-k(a - t_0))) + \varepsilon ,$$

where L_∞ (cm) is the asymptotic mean fork length, k (year^{-1}) is the rate at which individuals reach maximum lengths, and t_0 is the theoretical age at zero length (year). We assumed a normal error structure for deviations around the mean length-at-age, and used maximum likelihood methods to estimate model parameters using the following negative log-likelihood:

$$(2.2) \qquad -\log L(\mathbf{y} \mid L_a, \sigma_a^2) = n \log(\sigma_a) + \frac{n}{2} \log(2\pi) + \frac{1}{2\sigma_a^2} \sum_{i=1}^{n} (y_i - L_a)^2 ,$$

where y_i represents observed length-at-age. The standard deviation in length-at-age for a given age is given by:

$$(2.3) \qquad \sigma_a = L_a CV_L ,$$

where CV_L is the coefficient of variation which is estimated by fitting the model to the observed length-at-age data.

Sex-specific growth parameters and CVs were used as inputs in the equilibrium model. In the equilibrium model, each cohort is segregated into sub-groups, or growth-type groups, that differ in growth rates (Walters and Martell 2004). To initialize each cohort, we first partition the total abundance into each group, where we assume the distribution of slow and fast growing halibut is normally distributed. We use the variance in length-at-age and the normal distribution to partition for each growth-type group (g) as a fraction of the total variance in the population:

(2.4)
$$\sigma_{a,g}{}^2 = \frac{1}{G}(L_a CV_L)^2 = \frac{1}{G}\sigma_a{}^2 .$$

where G is the number of growth-type groups (G=11). The proportion of individuals recruiting into each growth-type group, p_g, follows a normal distribution, where:

(2.5)
$$p_g = \int_{g=-1.96}^{g=1.96} (2\pi\sigma^2)^{-1/2} \exp(-g^2) \, dg .$$

We assumed that no genetic selection occurs; i.e., there is no heritability of growth-type group from one generation to the next, and each new cohort has the same normal distribution of growth type groups in the initial year of recruitment. All fork lengths are converted to net weights (kg) using the following allometric equation:

(2.6)
$$w = \alpha L^\beta ,$$

with $\alpha=3.139\times10^{-6}$ and $\beta=3.24$ for both sexes (Clark 1992). This length-weight relationship represents the net weight of halibut (head and viscera removed) and is roughly 75% of the round weight.

We estimated maturation schedules for females during the 1980s using a generalized linear model approach for logistic regression, where the probability of being mature is defined as a function of age:

$$(2.7) \qquad \log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 a .$$

We derived the age-at-50% maturity (a_{50}) and the instantaneous rate of maturation (k_{mat}) as:

$$(2.8) \qquad a_{50} = \frac{-\beta_0}{\beta_1} ,$$

and

$$(2.9) \qquad k_{mat} = \frac{\beta_0 + \beta_1 a}{a - a_{50}} .$$

2.3.3 Equilibrium Model

The age- and size-structured equilibrium model employs methods similar to those used to evaluate various spawner- or recruit-based metrics in fisheries management (e.g., Goodyear 1993), as well as approaches to examine effects of discard mortality in fisheries managed with minimum size limits (Coggins et al. 2007, Pine et al. 2008, Martell et al. 2015). The steps for model development are described below.

We assumed an underlying stock-recruitment relationship using a Beverton-Holt stock-recruitment model, which can be expressed under equilibrium conditions as a function of the compensation ratio (Goodyear 1977) and the relative spawning potential ratio:

$$(2.10) \qquad R = R_0 \frac{CR - (\phi_e / \phi_f)}{CR - 1} ,$$

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where R_0 is the average recruitment under unfished conditions and the compensation ratio CR is defined as the maximum possible relative increase in juvenile survival rates (from egg to age-1) as a population is decreased from an unfished state to near zero (Walters and Martell 2004). The spawning biomass per recruit under unfished and fished conditions, ϕ_e and ϕ_f, was calculated as a function of survivorship and fecundity, and fecundity was assumed to be proportional to mature female body weight. The compensation ratio can be defined as a function of the steepness parameter h (Mace and Doonan 1988):

$$(2.11) \qquad\qquad CR = \frac{4h}{(1-h)} \ .$$

A summary of the parameters used as input values for equilibrium model initialization can be found in Table 2.1.

We estimated the survivorship ι to age in a given growth-type group using the following recursive equation:

$$(2.12) \qquad \begin{aligned} \iota_{a,g} &= 1 & \text{for } a{=}1 \\ \iota_{a,g} &= \iota_{a-1.g}\exp(-Z_{a,g}) & \text{for } a{>}1. \end{aligned}$$

The total instantaneous mortality $Z_{a,g}$ is the sum of the instantaneous natural mortality M, which was constant and instantaneous fishing mortality rate $F_{a,g}$. We included post-release mortality associated with discarding fish below the minimum size limit by modeling the vulnerability-at-age v_a as a joint probability of both capture and retention (Martell et al. 2015):

$$(2.13) \qquad\qquad v_a = v_c[v_r + d(1-v_r)],$$

such that the probability of a fish dying is the product of the probability of being caught and retained (v_c) and then either retained (v_r) or released (1- v_r) and subsequently dying with probability d. We fixed the discard mortality rate d to 0.16, the assumed rate in the commercial halibut fishery (Gilroy and Stewart 2013). We examined the influence of discard mortality rate on size-at-age over a range of potential discard mortality rates.

The selectivity curves used in the Pacific halibut assessment have been revised on numerous occasions since the 1970s, and there has been much debate and uncertainty over the efficacy of length- versus age-based selectivity curves (Stewart and Martell 2014a). We used sex- and length-based selectivity curves from the 2011 assessment for fishery selectivity and shifted the curves to the left and right by 20% to evaluate the sensitivity of model results to selectivity (Figure 2.3) (Stewart et al. 2013). The fishery selectivity represents all fish handled in the commercial longline fishery, retained and discarded.

2.3.4 Estimating historical fishing mortality

We compared observed declines in size-at-age with predicted declines in size-at-age given estimates of historical fishing mortality from the 1980s to 2014. Obtaining estimates of fishing mortality on a coastwide or regulatory area scale proved very challenging due to limitations associated with how halibut biomass is assessed and apportioned between regulatory areas. The 2015 assessment provides estimates of the coastwide exploitable biomass (Ebio), or the fraction of the total biomass available to the directed fishery (> 82 cm) (Table 2.2) (Stewart et al. 2016). The Ebio is apportioned between regulatory areas based on the weight-per-unit-effort of legal-sized halibut in the IPHC survey (Table 2.2) (Webster and Stewart 2016). The Ebio is then divided by area using the IPHC harvest policy, which is 19.6% coastwide, 21.5% for areas 2B, 2C, and 3A, and 16.1% for area 3B (Stewart et al. 2016). We estimated the realized harvest rates

for coastwide and regulatory areas as the ratio of total removals to total Ebio and apportioned

Ebio accordingly (Table 2.3). We estimated historical mean fishing mortality rate F from the

mean harvest rate (or exploitation rate, u) over 2000-2014 using the following equation:

(2.14) $u = F(1-\exp(-Z))/Z$,

with an assumed constant M of 0.2.

We treat such estimates of historical fishing mortality rate as approximations and interpret results

as an index of fishing mortality for several reasons: (1) there is uncertainty (CV = ~ 20%) in the

Ebio estimates, (2) Ebio only includes legal-sized fish, so actual coastwide exploitation rates are

likely to be lower, and (3) errors in spatial apportionment of Ebio estimates by regulatory area

are likely, as the procedure does not account for the geographic distribution of small fish. We

also could not include any information about harvest rates in the 1990s because the modern

survey began in 1997 and apportioned Ebio estimates were not available before 2000. Despite

these potential caveats, the fact that realized harvest rates exceeded the target harvest rates

defined by the harvest policy in most years between 2000 and 2014 in all areas leads us to

surmise that fishing mortality rates were likely very high throughout the study area over this time

period (Figure 2.4).

2.4   Results

2.4.1   Estimation of growth and fishing mortality

We found large differences in von Bertalanffy growth parameters between sexes and regulatory

areas (Table 2.4). Females exhibited much higher L_∞ than males, and males exhibited a higher k,

indicating that males reach asymptotic length at a younger age. Areas 3A and 3B in the western

Gulf of Alaska exhibited much higher L_∞ than areas 2B and 2C in the eastern Gulf of Alaska.

Overall, the CV_L was high for both sexes (CV_L=0.14) and ranged between 0.11 and 0.17 among regulatory areas. We estimated female A_{50} and k_{mat} to be 12.8 years and 0.72 years^{-1}, which is close to maturity estimates from the 2013 IPHC setline survey (A_{50}=11.6 years) (Stewart 2014). Estimates of mean fishing mortality ranged between 0.18 and 0.60, with a mean of 0.40 over 2000-2014 (Table 2.5). Estimates of fishing mortality in areas 2B and 2C were significantly higher than in areas 3A and 3B. For example, the mean F in area 2B was 0.79 but was only 0.29 in area 3B.

2.4.1   Equilibrium model

Even moderate levels of fishing mortality resulted in large reductions in size-at-age under equilibrium conditions. The coastwide model predictions of weight-at-age under increasing fishing effort exhibited the same general shape of the observed reductions in weight-at-age from the 1980s to 2014, which indicates that size-selective fishing is likely a contributing factor to declines in size-at-age (Figure 2.5). There was little to no change in size-at-age predicted for younger ages (< 8 years) because they are not recruited to the minimum legal size limit, and therefore are not subject to the cumulative effects of size-selective fishing. Differences in size-at-age became more pronounced with age, as fishing effects compound with each subsequent year of selective removals. Using estimated mean F (Table 2.5), fishing explained approximately one half to one third of the observed declines in coastwide weight-at-age from the 1980s to 2014 for age-15 females and males, respectively (Figure 2.5).

Due to large differences in growth and fishing mortality between areas in the Gulf of Alaska, we found regional models to be quite informative. For example, in areas 2B and 2C, where F was very high over this time period, fishing could explain nearly all of the observed declines in weight-at-age for age-15 females, and more than one of half for age-15 males (Figure 2.6).

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Conversely, in areas 3A and 3B, where F was comparatively low and observed declines in weight-at-age were very large, fishing explained less than one third of observed declines in weight-at-age for both sexes since the 1980s (Figure 2.7).

Model results were weakly sensitive to shifting the fishery selectivity curve to the left and right by 20% at the age of entry for the halibut fishery (Figure 2.8). Age of entry corresponds to ages 8 to 10 and 10 to 14 for female and male halibut, respectively. Interestingly, shifting the fishery selectivity curve by ±20% does not change the ultimate weight-at-age trajectories predicted by the model. Males appear to be slightly more sensitive to changes in fishery selectivity than females. We found that increases in F do not influence the shape or magnitude of the effect of selectivity on weight-at-age (Figure 2.8). Simply put, predicted changes in weight-at-age are the result of high fishing mortality rates and cannot be explained by shifts in the selectivity curve.

Changes in the minimum legal size limit and discard mortality resulted in minimal changes to predicted weight-at-age under equilibrium conditions (Figure 2.9). Instead, increases in fishing mortality appear to have the strongest influence on predicted weight-at-age. For example, the predicted mean weight of age-15 females was the same for all size limits between 50 and 125 cm under a wide range of discard mortality rates for $F<0.25$. If the size limit was increased to >125 cm then our results indicate that weight-at-age would remain relatively constant even at high levels of F. At a discard mortality rate of 0.5, an unrealistically high rate for the directed Pacific halibut fishery, we found that discard mortality counteracts the effects of size-selective fishing because most discarded sub-legal fish do not survive. Under current fishery selectivity, we found no evidence that reducing the size limit would result in changes in predicted size-at-age.

We found a strong interaction between CV_L and fishing mortality rate (Figure 2.10). If CV_L is low (e.g. CV_L =0.01), there is no relationship between fishing and size-at-age. However, as CV_L increases, the effect of fishing on size-at-age is multiplicative. If CV_L was actually higher than estimated, fishing could easily explain 100% of the observed declines in size-at-age.

2.5   Discussion

Using an age- and size-structured equilibrium model, we demonstrated the capacity for size-selective fisheries to cause a large shift in the population size-at-age, even in the absence of genetic selection or heritability of growth. The steep declines in size-at-age predicted by our model simulations suggest that size-selective fishing could be a major factor in observed declines in size-at-age of Pacific halibut since the 1980s. Based on calculations using estimated mean F, fishing explained approximately one half to one third of the observed declines in coastwide weight-at-age from the 1980s to 2014 for age-15 females and males, respectively. Even more striking, fishing was able to explain nearly 100% of the observed declines in size-at-age in areas 2B and 2C in the eastern Gulf of Alaska, where fishing mortality has been historically high from the 1980s to 2014. Observed effects of size-selective fishing on size-at-age are primarily driven by variability in growth, with faster growing individuals experiencing a higher total F.

Pacific halibut appear to be particularly vulnerable to size-selective fishing effects, because they have a notably high coefficient of variation in length-at-age and the minimum size limit regulation further intensifies this selection. The underlying mechanism generating this large variability in size-at-age is unknown, but it may be attributed to a high diversity of ecological conditions throughout the Gulf of Alaska to eastern Bering Sea to which Pacific halibut are exposed during their 6-mo larval drift and extensive counternatant migration with ontogeny (Skud 1977). The conceptual model of ontogenetic migration for halibut suggests buoyant larvae

are advected counterclockwise in the Gulf of Alaska by the Alaska Current, and juveniles and adults undergo long return migrations in order to reach broadly distributed feeding grounds along the continental shelf (Skud 1977, Webster et al. 2013, Keith et al. 2014). Mature halibut migrate to deep waters beyond the continental slope to spawn during November to March and return shoreward to feeding grounds in summer (St-Pierre 1984). Given this highly migratory life history, halibut are likely to experience a wide range of thermal regimes, competitor densities, and prey fields seasonally over their lifetimes. These are all factors that could contribute to the high coefficient of variation observed in halibut growth. Recent tagging studies have yielded estimates of migratory rates between regulatory areas as a function of size (Webster et al. 2013). Results elucidate complex migratory patterns in adult Pacific halibut, in which fish from areas 3B are more likely to emigrate at smaller sizes, while fish in areas 3A, 2B, and 2C are more likely to emigrate from these areas at larger sizes. It remains unclear how persistent these trends are over time, but such apparent size-dependent migrations, coupled with different conditions encountered along divergent migratory pathways, likely contribute to individual variability as well as spatial patterns in length-at-age. It may also help explain why declines in size-at-age in the western and central Gulf of Alaska have been much more severe than in the east.

Our results rely on a range of assumptions about the underlying biology of Pacific halibut and the fishery. First, we assumed that the basic growth curve in the population has been stable over the time period of our study. If growth is a temperature- or density-dependent process, we cannot easily incorporate the effects of variability or trends in environmental conditions or population dynamics into an equilibrium model. Second, we assumed a constant allometric equation in the model, which could influence our predictions of changes in size-at-age. For instance, if the condition factor in the allometric equation β was smaller, as was estimated in Courcelles (2012),

it would magnify the resulting predicted declines in size-at-age. Third, we fixed natural mortality and discard mortality rates in our model, an assumption that may influence the accuracy of our results if these are size-dependent processes. For example, if smaller individuals experienced significantly higher natural or discard morality than larger fish, it may dampen the observed effects of size-selective fishing. Fourth, although size-at-age was relatively insensitive to shifts in fishery selectivity, we did not consider selectivity curves with different structural forms or selectivity curves resulting from different minimum size limits. We also assumed that fishery selectivity curves were constant for all areas, but there is some evidence that selectivity may vary between regulatory areas (Clark and Kaimmer 2006, Webster et al. 2013). A cogent next step would be to examine the influence of area-specific selectivity curves and varying structural forms (e.g., dome-shaped) on model results. We also did not incorporate the potential effects of bycatch of halibut in other fisheries on size-at-age, primarily due to the challenge associated with identifying a common selectivity curve for the numerous fisheries that intercept halibut as bycatch. It is possible that bycatch fisheries could act as a "normalizing force" to size-selective fishing, because the majority of halibut caught as bycatch are sublegal fish (Martell et al. 2015). However, if discard mortality rates in bycatch fisheries like the Pacific cod longline fishery are wrong, it could result in a much higher F than currently estimated. This is especially true in areas such as 3B, where bycatch constitutes a large portion of the total mortality of halibut. Finally, underpinning this analysis are strong assumptions related to the IPHC apportionment process, namely that catchability is constant across the range of the halibut stock. Violations of the catchability assumption could strongly affect our understanding of the stock size, geographic distribution of Pacific halibut, and resulting estimates of F.

This modeling approach has numerous applications to fishery management. In particular, it demonstrates the utility of developing harvest policy from a growth type group model, rather than relying on a mean size-at-age approach that implicitly assumes fishing can have no effect on changes in size-at-age. Our study builds off a similar model used to examine the effects of size limits, bycatch, and wastage of Pacific halibut on biological reference points and optimal harvest rates (Martell et al. 2015). That study highlighted the potential tradeoffs of decreasing the minimum size limit in the directed halibut fishery from 82 cm to 66 cm. Under the lower size limit, directed yield increased by 9-13% and wastage due to discard mortality was significantly less; however, the average weight and total value of the catch was much lower because of increased retention of smaller, more abundant halibut that are worth less per pound. A similar model demonstrated that size limits have the potential to decrease fishery efficiency and can contribute to recruitment overfishing over a range of life history types due to negative impacts of discard mortality (Coggins et al. 2007). These consequences were most severe for long-lived, low-productivity life history types, which include species like Pacific halibut. In all cases, a decrease in F was required in order to achieve sustainability and maximize fishery performance. Our approach increases the utility of these pre-existing, highly flexible models and provides managers with another tool to better understand the impacts of selective fishing and the tradeoffs inherent in fisheries management.

For the case of Pacific halibut, we found that fishing has likely contributed to declines in size-at-age owing to the large variability in growth, relatively high harvest rates, and the use of a minimum size limit. As managers cannot control variability in halibut growth, they should consider reductions in harvest rates that would assuage the size-selective fishing effects. While our estimate of exploitation rate has caveats, it suggests that harvest rates during 2000-2014 were

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too high, especially in the eastern Gulf of Alaska. Strong retrospective bias in the stock

assessment models in the 1990s and 2000s contributed to over-harvest during this time period, as

biomass estimates were inflated nearly 40% (Valero 2012). Area apportionments were revised

based on tagging data that suggested biomass was disproportionately allocated to the eastern

Gulf of Alaska due to an assumption that regulatory areas were closed populations (Valero

2012). Of particular interest to managers and stakeholders is the relatedness of the size-at-age

problem to recent declines in exploitable biomass in the Pacific halibut fishery, which has

decreased by 60% from 2002 to 2013 (Stewart and Martell 2014b). Though recent assessments

have addressed the issue of retrospective bias, the problem of an abundant population of slow-

growing individuals with small size-at-age remains, though there is evidence that further declines

in size-at-age may be abating in recent years (Stewart et al. 2016). We found no indication that a

reduced size limit in the directed halibut fishery would ameliorate the size-at-age problem, but a

reduced minimum size limit could reduce discard mortality, thus leading to a more efficient use

of the resource (Martell et al. 2015). Given that a high coefficient of variation in length-at-age

renders Pacific halibut vulnerable to size-selective fishing effects, the most effective

management action would be to reduce harvest rates to diminish the intensity of size selection.

On a broader scale, the selective harvest of larger-bodied individuals at high exploitation rates

may contribute to declines in size-at-age in fisheries around the world (Myers and Worm 2003).

As of 2011, 90% of global fish stocks were characterized as either fully fished or overfished, up

from 60% in 1974 (FAO 2014). To maintain age- and size-structure in fish stocks, it may be

essential to consider the effects of size-selective fishing when developing harvest policies.

Although we found substantial evidence for fishing effects on declines in Pacific halibut size-at-

age, we cannot rule out effects of other contributing factors. For instance, we were unable to

consider the potential for fisheries-induced evolution. Our modeling efforts do not eliminate the need for understanding or quantifying fisheries-induced evolution; instead, we provide a tool to evaluate historical patterns and future regulatory changes. Our model can be extended to incorporate genetic effects, such as heritability of growth or maternal effects, when such data become available. Future work at the IPHC aims to identify growth-related genetic markers in halibut through laboratory experiments, which will greatly increase our understanding of growth as an individual trait versus population-level characteristic. Histological studies confirming the efficacy of maturity determination of halibut in the field may make a PMRN approach possible in the future. Gaining a better understanding of the genetic basis for reductions in size-at-age due to size-selective fishing is essential to future management of the halibut fishery, because there is a potential for maladaptive traits related to mean body size, such as egg size or size at hatch, that can impede recovery of the stock (Walsh et al. 2006).

Trends from small size-at-age in the 1920s and 1930s to large size-at-age in the 1970s and 1980s and back to small size-at-age in the 2000s could be taken to suggest that changes in size-at-age are attributable to multi-decadal processes other than genetics. It has been hypothesized that climate regime shifts in the North Pacific Ocean, best characterized by the PDO, influence population dynamics of a diverse number of taxa (reviewed by Francis et al. 1998). Climate regime shifts, in particular the 1976/1977 shift in PDO from negative to positive, has been proposed to indicate a role of temperature on recruitment of Pacific halibut, which could indirectly influence subsequent growth through density dependence as strong year classes recruit to the population (Clark and Hare 2002). Individual growth may be temperature-mediated, although the positive correlation between halibut otolith growth and sea surface temperatures diminishes after age-2 (Hagen and Quinn 1991). The bioenergetic processes dictating halibut

growth remain poorly understood. A study in Cook Inlet, Alaska (area 3A) using stable isotope analysis found evidence that faster growing halibut may feed at a higher trophic level and exploit a broader prey base (Webster 2014). Ongoing research using otolith increment data aims to evaluate temperature effects on physiology and prey availability using bioenergetics modeling (K. Holsman, NMFS, Alaska Fisheries Science Center, pers. comm.). Also, long-term trends in the biomass of halibut and the potential competitor, arrowtooth flounder (*Atheresthes stomias*), appear to track well with trends in size-at-age, providing evidence of intra- or interspecific competition. We are currently investigating hypotheses related to environmental and ecological variability in the North Pacific Ocean as alternative explanations for long-term variability in size-at-age of Pacific halibut.

2.6   Acknowledgements

2.7 References

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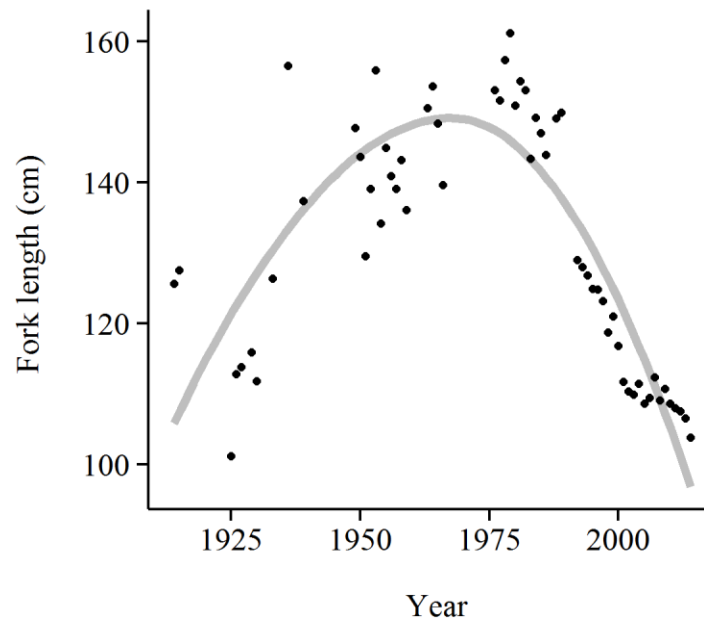
2.8   Figures

Figure 2.1. Annual mean fork lengths (cm) of age-15 females from 1914 to 2014 (points), with a

LOESS smoother (grey line) to aid in visualization. The trend is characteristic of female and

male size-at-age for ages >8 years over this time period. This summary uses fisheries-

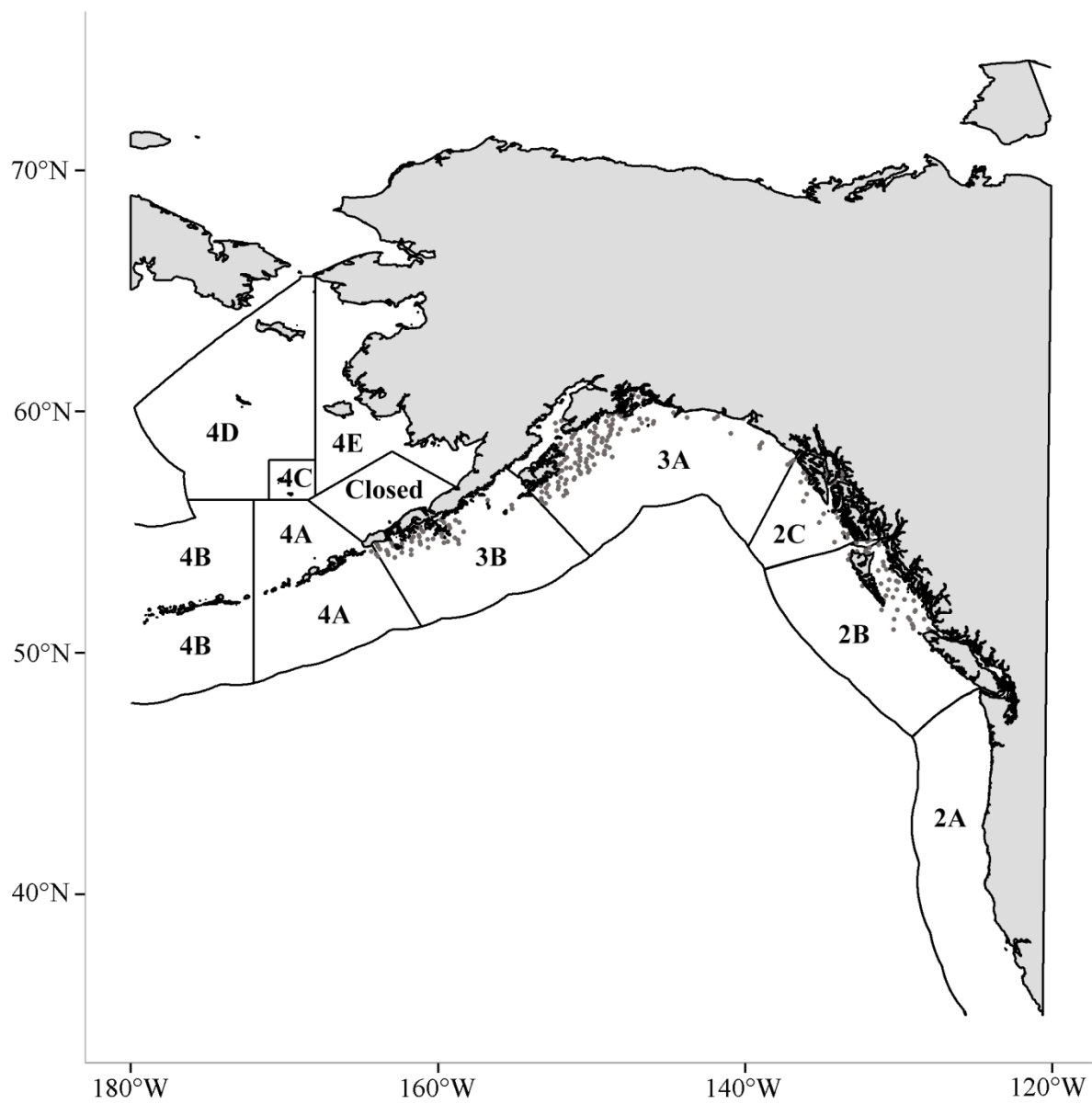independent length-at-age data from the IPHC.

Figure 2.2. Map of IPHC regulatory areas (polygons) and survey stations (grey points) where length-at-age and maturity data were collected. Stations were jittered for visualization.
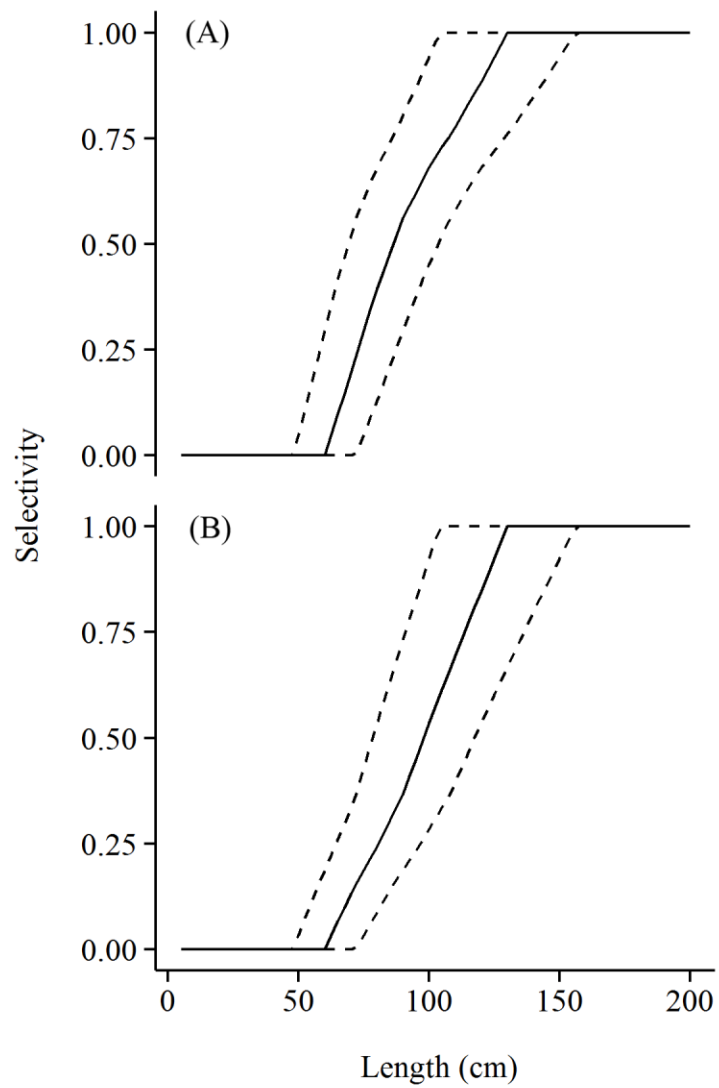
Figure 2.3. Length-based selectivity curves for the commercial halibut fishery for females (A) and males (B). The dashed lines show selectivity curves shifted to the right and left by 20%.
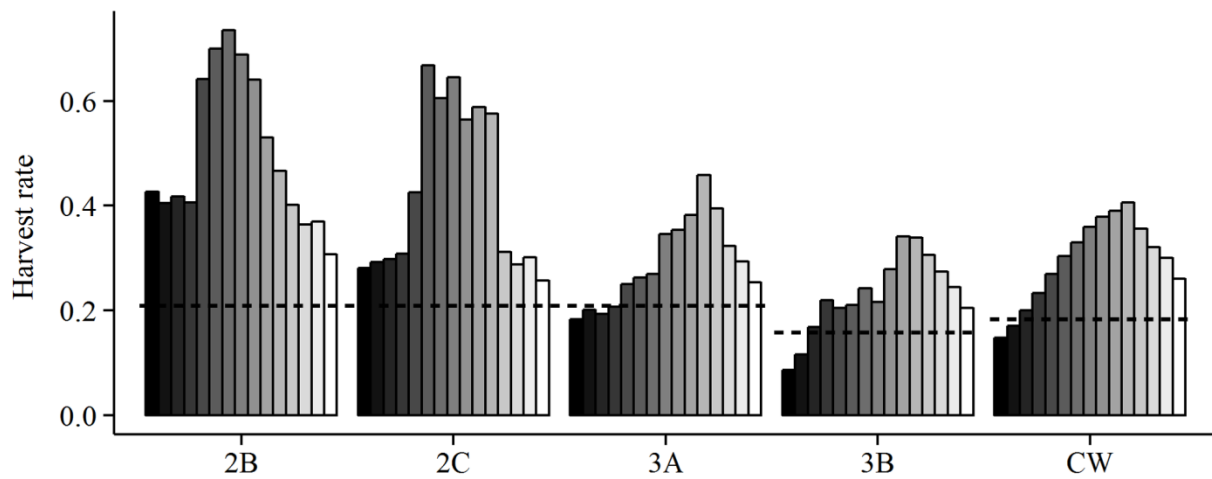
Figure 2.4. Estimated harvest rates from 2000 to 2014 in IPHC regulatory areas 2B, 2C, 2A, 3B, and coastwide (CW). Each bar represents a harvest rate in a given year with earlier years shown in darker bars and later years shown in lighter bars. The dashed lines represent the area-specific target harvest rates defined by IPHC harvest policy (21.5% in 2B, 2C, and 3A, 16.1% in 3B, and 19.6% coastwide).

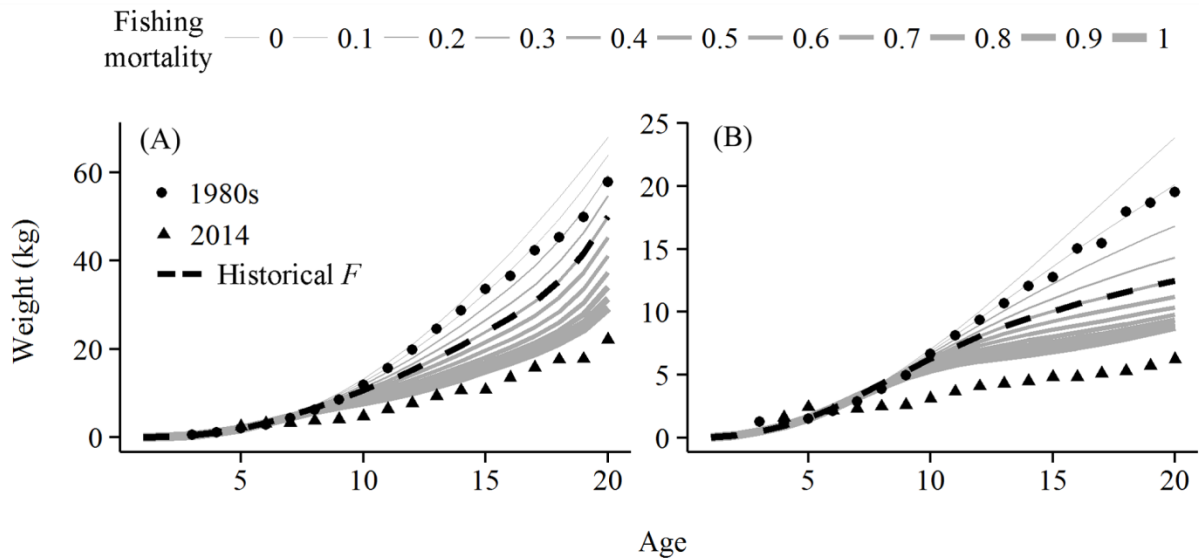Figure 2.5. Coastwide model predictions of weight-at-age under a range of levels of fishing

mortality (thicker grey lines represent higher levels of fishing mortality) compared with observed

weight-at-age in the 1980s (points) and 2014 (triangles) for females (A) and males (B). The

dashed black line shows predicted weight-at-age given our best estimate of historical mean

fishing mortality (F=0.4).

Figure 2.6. Model predictions of weight-at-age for the eastern Gulf of Alaska under a range of levels of fishing mortality (thicker grey lines represent higher levels of fishing mortality) compared with observed weight-at-age in the 1980s (circles) and 2014 (triangles) for females in area 2B (A), males in area 2B (B), females in area 2C (C), and males in area 2C (D). The dashed black line shows predicted weight-at-age given our best estimate of historical mean fishing mortality ($F=0.8$ in area 2B and $F=0.6$ in area 2C).
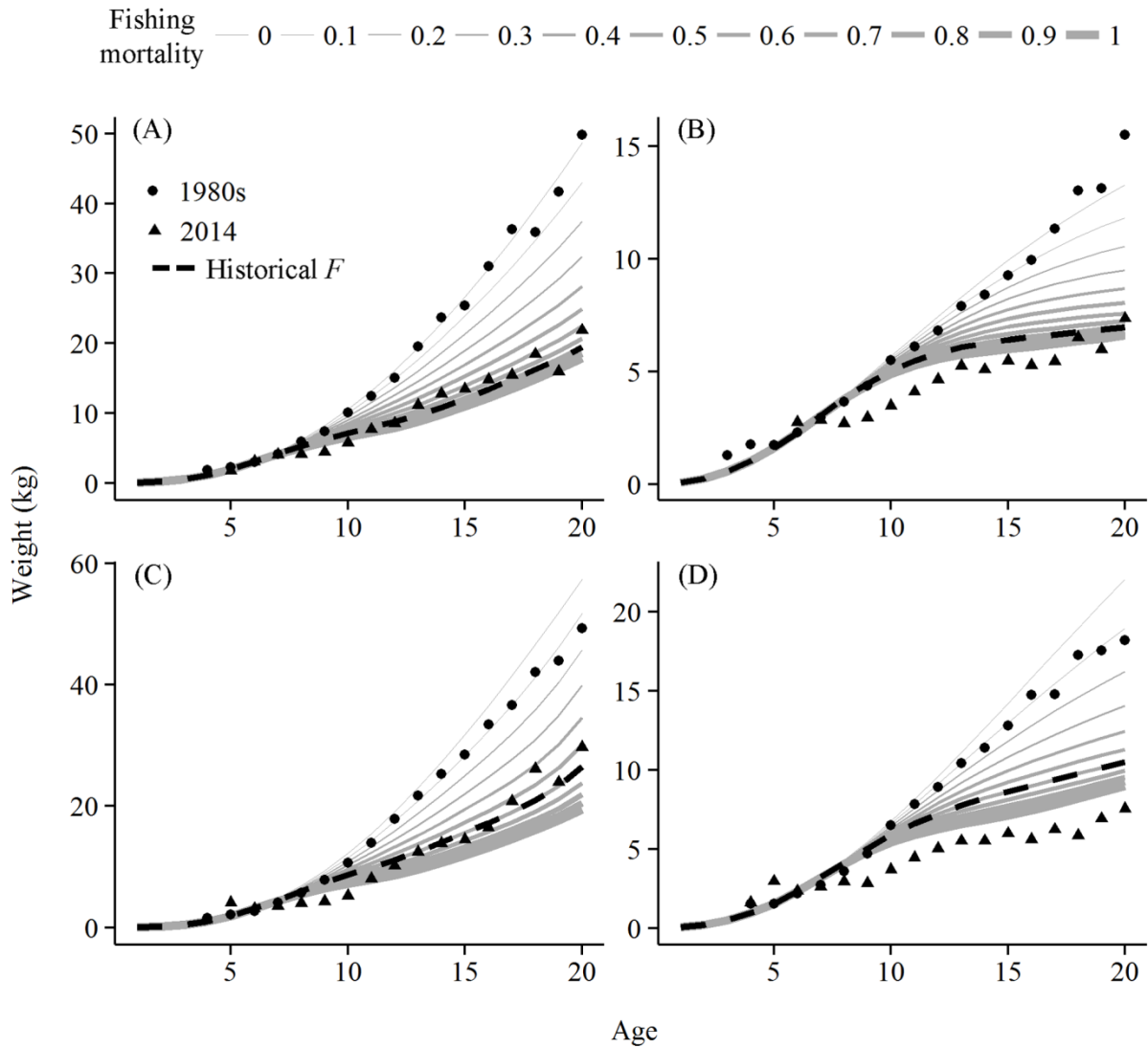
Figure 2.7. Model predictions of weight-at-age for the western Gulf of Alaska under a range of levels of fishing mortality (thicker grey lines represent higher levels of fishing mortality) compared with observed weight-at-age in the 1980s (circles) and 2014 (triangles) for females in area 3A (A), males in area 3A (B), females in area 3B (C), and males in area 3B (D). The dashed black line shows predicted weight-at-age given our best estimate of historical mean fishing mortality (F=0.4 in area 3A and F=0.3 in area 3B).
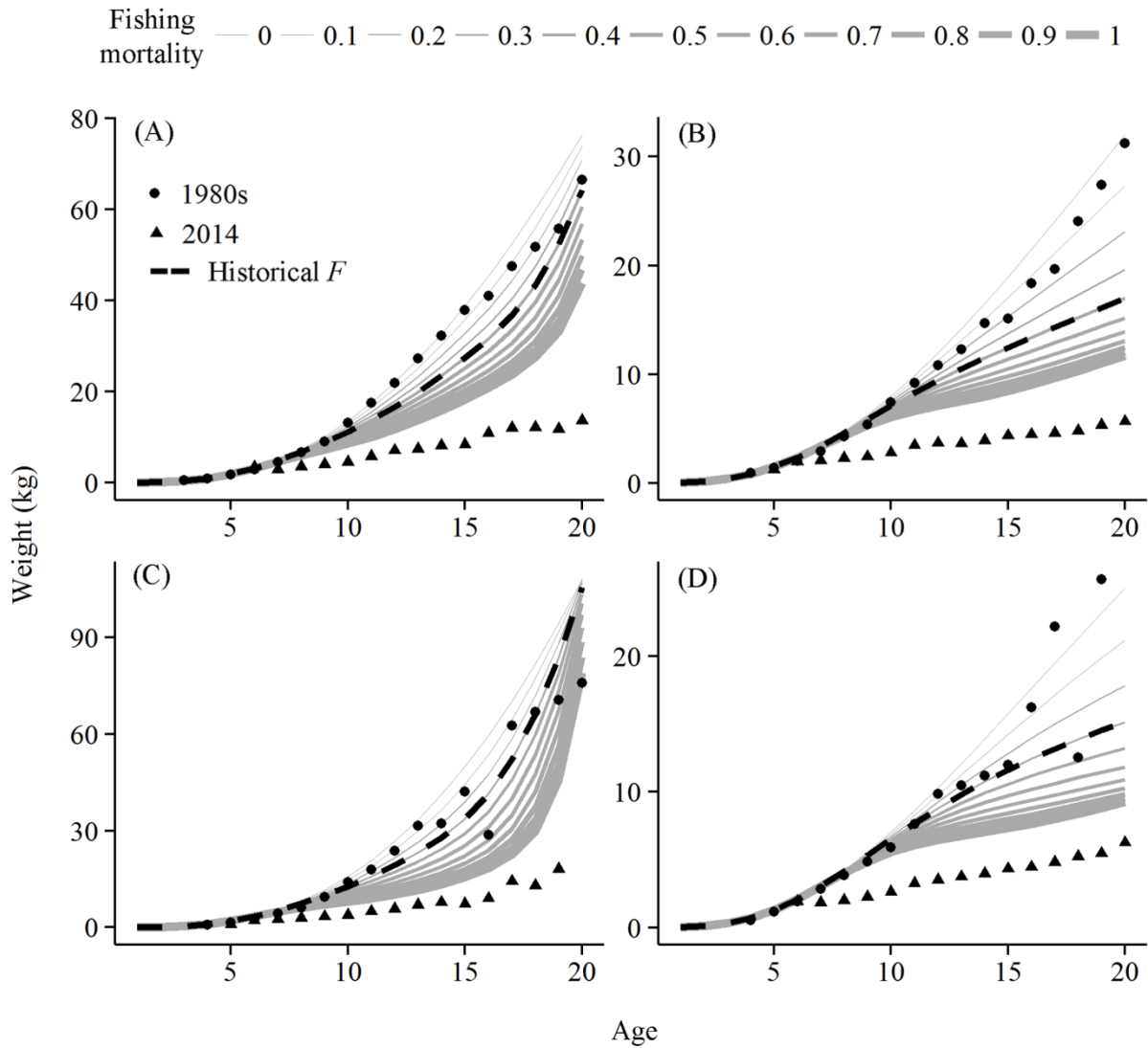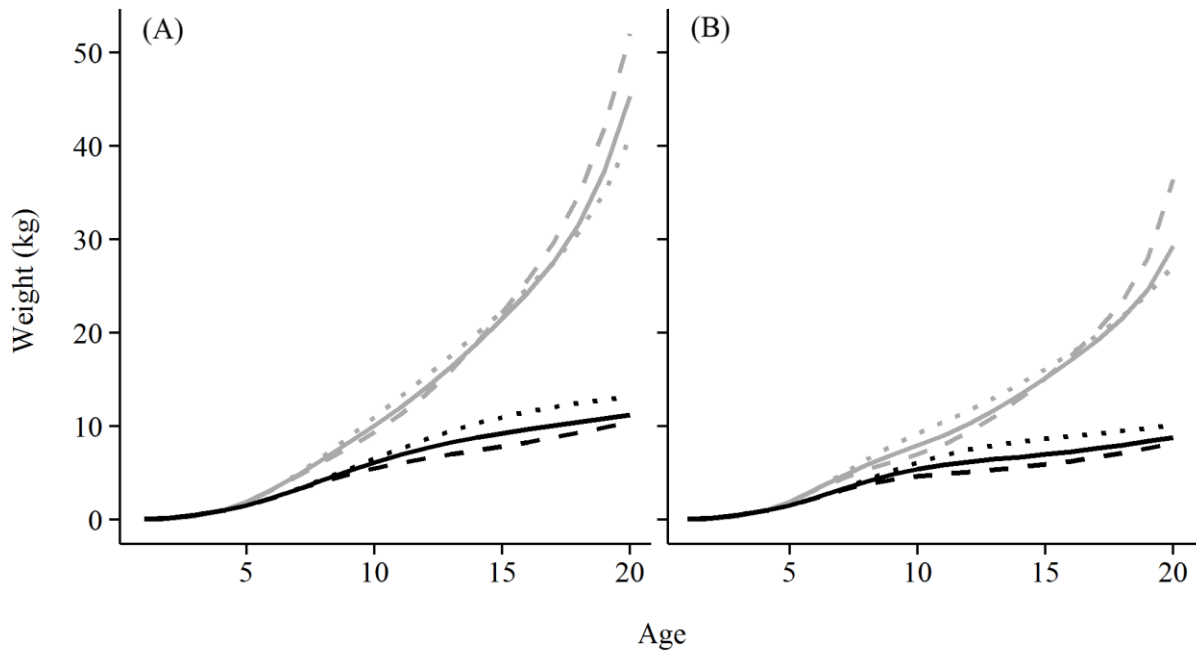
Figure 2.8. Model predictions of weight-at-age using different selectivity curves for *F*=0.5 (A) and *F*=1.0 (B) under equilibrium conditions. The solid lines show results using the selectivity curve from the 2011 assessment (used in this analysis), while the dashed and dotted lines show results when the curve is shifted to the left and right by 20%, respectively. Females are shown in grey and males are shown in black.
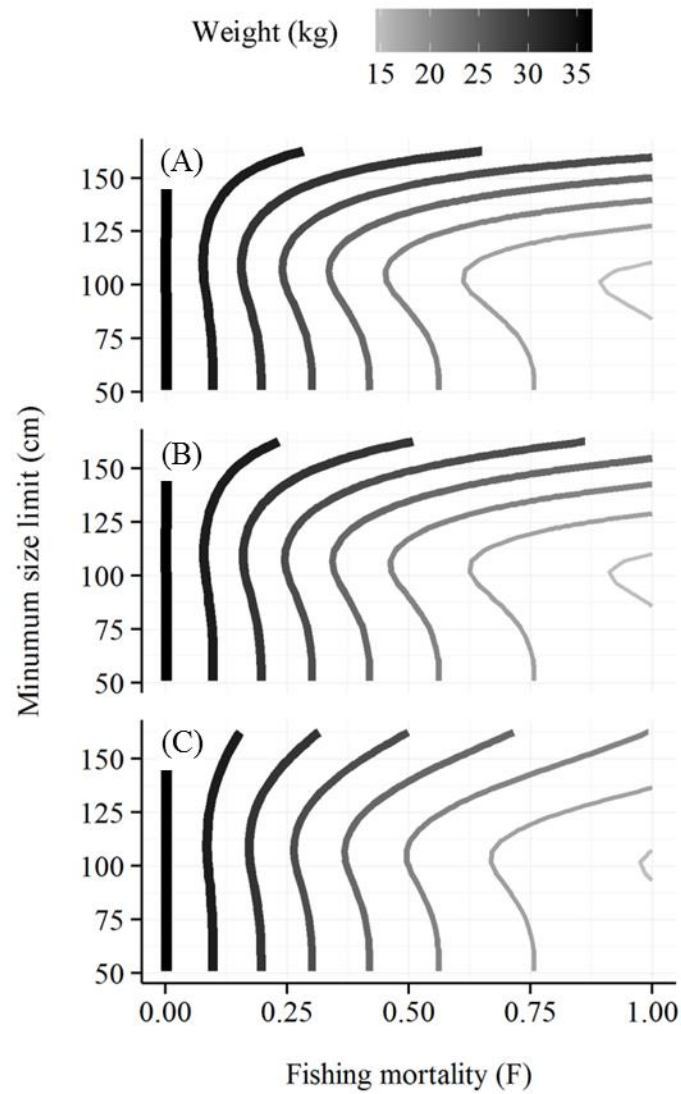
Figure 2.9. Predicted mean weight (kg) of age-15 females by minimum size limit (cm) and fishing mortality rate in the coastwide model for three discard mortality rates (d): $d=0.1$ (A), $d=0.2$ (B), and $d=0.5$ (C). The darker, thicker lines represent conditions resulting in larger mean weights, while the lighter, narrower lines represent conditions resulting in lower mean weights.
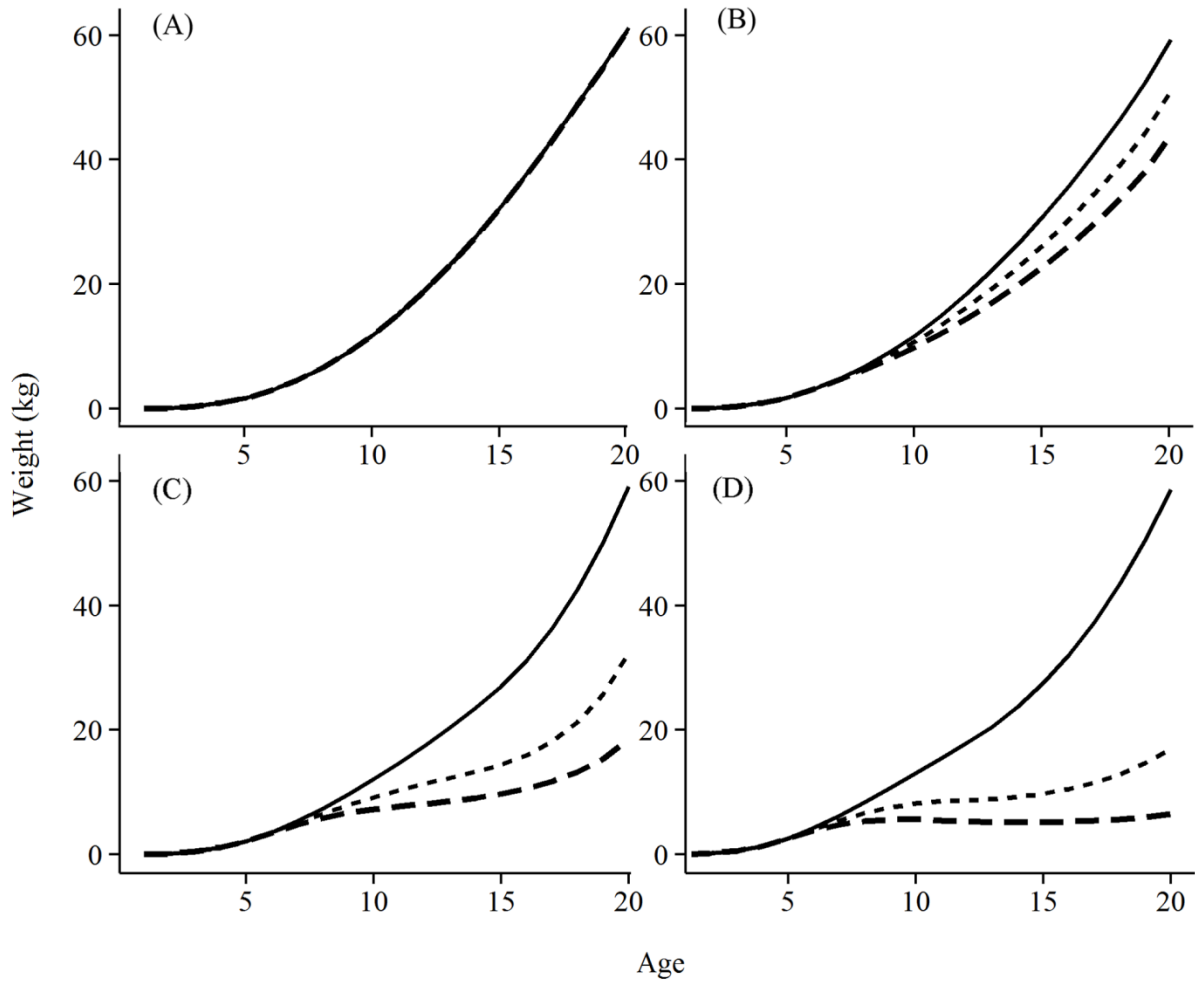
Figure 2.10. Predictions of coastwide female weight-at-age under four assumptions of coefficient of variation in length-at-age (CV_L): CV_L =0.01 (A), 0.10 (B), 0.20 (C), and 0.30 (D). The different line types represent model predictions under F=0.2 (solid line), F=0.5 (dotted line), and F=0.8 (dashed line).

2.9   Tables

Table 2.1. Parameter values used in coastwide and regional model simulations.

Parameter	Description	Females	Males
M	Instantaneous natural mortality rate	0.20^a	0.17^a
G	Number of growth trajectories	11	11
α	Length-weight constant (cm, kg)	3.139×10^{-6b}	3.139×10^{-6b}
β	Allometric parameter	3.24^b	3.24^b
h	Beverton-Holt steepness parameter	0.75^c	0.75^c

[a]Stewart and Martell (2014b)

[b]Clark (1992)

[c]Martell et al. (2015)

Table 2.2. Estimated coastwide exploitable biomass (Ebio, million tonnes) and the apportioned Ebio by IPHC regulatory area from 2000 to 2014.

Year	Ebio	2B	2C	3A	3B
2000	0.2839	0.0134	0.0181	0.0693	0.0918
2001	0.2499	0.0135	0.0167	0.0671	0.0723
2002	0.2204	0.0153	0.0169	0.0711	0.0535
2003	0.1914	0.0155	0.0170	0.0707	0.0406
2004	0.1685	0.0104	0.0152	0.0647	0.0389
2005	0.1484	0.0098	0.0098	0.0623	0.0323
2006	0.1304	0.0092	0.0105	0.0591	0.0238
2007	0.1142	0.0083	0.0088	0.0485	0.0229
2008	0.1018	0.0073	0.0083	0.0439	0.0209
2009	0.0885	0.0074	0.0063	0.0364	0.0172
2010	0.0808	0.0085	0.0057	0.0288	0.0164
2011	0.0760	0.0100	0.0058	0.0264	0.0138
2012	0.0731	0.0098	0.0076	0.0260	0.0117
2013	0.0724	0.0094	0.0087	0.0270	0.0102
2014	0.0740	0.0114	0.0105	0.0244	0.0100

Table 2.3. Estimated total removals (thousand tonnes) coastwide and by IPHC regulatory area from 2000 to 2014. Total removals include harvest from the directed fishery, estimated discards from the directed fishery, sport harvest, subsistence harvest, and bycatch of halibut in other fisheries.

Year	Coastwide	2B	2C	3A	3B
2000	41.97	5.69	5.08	12.71	7.87
2001	42.70	5.46	4.89	13.49	8.41
2002	44.22	6.39	5.03	13.72	8.98
2003	44.57	6.30	5.24	14.66	8.91
2004	45.34	6.64	6.48	16.15	7.93
2005	45.09	6.87	6.54	16.37	6.77
2006	43.05	6.79	6.39	15.94	5.77
2007	41.00	5.71	5.66	16.76	4.94
2008	38.53	4.67	4.67	15.54	5.83
2009	34.55	3.95	3.70	13.94	5.86
2010	32.82	3.98	3.27	13.19	5.54
2011	27.05	4.01	1.81	10.43	4.22
2012	23.44	3.56	2.18	8.40	3.21
2013	21.79	3.50	2.61	7.92	2.49
2014	19.28	3.51	2.71	6.17	2.05

Table 2.4. Estimated von Bertalanffy growth parameters used in coastwide and regional model simulations. See text for definition of parameters.

Sex	Region	n	L_∞ (cm)	k (year^{-1})	t_0 (year)	CV_L
Female	Coastwide	19 021	313	0.042	-2.60×10^{-8}	0.14
	2B	3 282	287	0.039	-1.00	0.14
	2C	5 433	269	0.049	-1.20×10^{-7}	0.14
	3A	9 124	367	0.035	-2.10×10^{-8}	0.15
	3B	1 182	590	0.021	-1.10×10^{-7}	0.13
Male	Coastwide	12 977	172	0.066	-0.92	0.17
	2B	2 629	122	0.110	-1.00	0.14
	2C	4 430	165	0.069	-1.00	0.11
	3A	5 344	205	0.057	-0.43	0.13
	3B	575	170	0.073	-0.040	0.14

Table 2.5. A summary of historical instantaneous fishing mortality (F) estimated from harvest rates from 2000 to 2014 for all IPHC regulatory areas combined and for areas 2B, 2C, 3A, and 3B.

Region	Minimum	25th quartile	Mean	75th quartile	Maximum
Coastwide	0.18	0.32	0.40	0.50	0.60
2B	0.42	0.58	0.79	1.19	1.60
2C	0.34	0.4	0.64	1.00	1.30
3A	0.22	0.29	0.39	0.49	0.70
3B	0.11	0.25	0.29	0.37	0.47

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General Conclusions

Pacific Halibut size-at-age exhibited dramatic "rollercoaster" trends in the northeastern Pacific Ocean from 1914 to 2014, with low size-at-age in the 1920s, gradually increasing to a maximum in the 1970s and 1980s, followed by steep declines after 1990. These findings are consistent with other studies, though there is some indication that trends in size-at stabilized during 2013 to 2015 (Clark et al. 1999, Clark and Hare 2002, Stewart et al. 2016). We found strong regional trends in Pacific Halibut over this time period. The highest size-at-age and subsequent steepest declines were observed in the central and western Gulf of Alaska. For example, the mean (±SE) fork length of an age-15 female in this area was 110 cm (±6.7) in 1925, 165 cm (±2.5) in 1985, and only 95 cm (±1.1) in 2014. In contrast, length-at-age was more stable in Southeast Alaska, British Columbia, and offshore Oregon and Washington between 1914 and 1980, and low size-at-age was not observed in these areas until after 1980. Relatively few data were available from the Bering Sea and Aleutian Islands prior to 1990, but it appears that temporal trends in size-at-age were similar to trends in the western Gulf of Alaska. Differences in growth and size-at-age between areas could be attributed to size-dependent migration, with larger fish (at age) migrating from the west to the eastern Gulf of Alaska (Webster et al. 2013). Alternatively, regional differences could be driven by habitat quality, prey availability, or temperature differences. For example, preliminary results from bioenergetics modelling suggest that growth rates may be higher for Pacific Halibut in the western Gulf of Alaska due to cooler temperatures and access to more energy rich prey items (e.g. Walleye Pollock) (K. Holsman, NMFS, Alaska Fisheries Science Center, personal communication). These results explain historical patterns in size-at-age, when size-at-age in the central and western Gulf of Alaska was high, but do not explain current trends in size-at-age that show fish are larger at age in the eastern Gulf of Alaska than in the west.

In Chapter 1, we tested hypotheses related to the influence of environmental and ecological factors on Pacific Halibut growth. We found strong support for the hypothesis that Pacific Halibut growth is negatively related to Arrowtooth Flounder owing to interspecific competition for limited shared prey resources. Arrowtooth Flounder biomass increased nearly five-fold from 1960 to 2013 (Spies and Turnock 2013), and there is evidence of resource limitation from 1986 to 2008, when the biomass of Walleye Pollock, a shared dominant prey item of Arrowtooth Flounder and Pacific Halibut, was low (Dorn et al. 2013, Yang 1995). We found some support that Pacific Halibut growth is negatively related to Pacific Halibut biomass owing to intraspecific competition with Pacific Halibut (i.e. density-dependent growth), which is consistent with a previous study that found a strong negative relationship between mean weight at age-8 and abundance of age-8 Pacific Halibut (Clark and Hare 2002). Although we did not use regional indices of biomass for Pacific Halibut or Arrowtooth Flounder, there is strong evidence from NOAA bottom trawl surveys that densities of both of these species are dramatically higher in the western Gulf of Alaska, suggesting that competition may be more prominent in the west than in the east (von Szalay et al. 2010). Finally, we found no evidence of a temperature effect on Pacific Halibut growth, which is consistent with a previous study that found no relationship between the Pacific Decadal Oscillation and growth (Clark and Hare 2002). However, there may be an indirect or lagged response of growth to environmental variability. For example, although the underlying mechanisms remain poorly understood, warm ocean temperatures are related to strong year classes of Pacific Halibut, which could lead to delayed density-dependent growth as cohorts recruit to the fishable stock (Parker et al. 1995, Clark et al. 1999). Future research into environmental or climate effects on Pacific Halibut growth, recruitment, or biomass should focus on low frequency trends or integrated effects (e.g. Di Lorenzo and Ohman 2013). Overall, our model results indicated that a relatively

low percentage of variability in Pacific Halibut growth could be explained by the environmental and ecological variables examined in this study (28%), which suggests that other factors are more influential.

In Chapter 2, we demonstrated the capacity for size-selective fishing to cause a large shift in the size-at-age of Pacific Halibut using an age- and size-structured equilibrium model developed by Martell et al. (2015). The steep declines in size-at-age predicted by our model simulations suggest that size-selective fishing could be a major factor in observed declines in size-at-age of Pacific Halibut since the 1980s. Owing to misspecifications in the previously used stock assessments, realized harvest rates of Pacific Halibut were very high from the 1990s to 2010, exceeding IPHC harvest policy in almost all years during this time period. Based on calculations using estimated mean fishing mortality F, fishing explained approximately 30% and 50% of observed declines in coastwide weight-at-age from the 1980s to 2014 for age-15 females and males, respectively. Even more striking, fishing was able to explain nearly 100% of the observed declines in size-at-age in areas 2B and 2C in the eastern Gulf of Alaska, where F has been highest from the 1980s to 2014. However, in areas 3A and 3B, where the largest declines in size-at-age have been observed, fishing only explained approximately 25% of observed declines for age-15 individuals, which we attribute to relatively low estimates of F in these areas. These findings are compatible with Chapter 1 conclusions, which suggest that inter- and intraspecific competition may play a more prominent role in the western Gulf of Alaska, where densities of both Pacific Halibut and Arrowtooth Flounder are highest.

This study contributes to understanding of environmental, ecological, and fishery effects on growth and size-at-age of Pacific Halibut. It is likely that all factors examined in this study contribute to some degree to temporal and spatial variability observed in Pacific Halibut size-at-

age. Pacific Halibut assessments should consider future climate and ecological variability and could benefit from the inclusion of predator, competitor, and prey dynamics through a multi-species model (e.g. Van Kirk et al. 2010). Additionally, the high degree of migration that occurs throughout the lifetime of Pacific Halibut warrants the development of a spatially explicit stock assessment model (Skud 1977, Loher and Seitz 2006, Webster et al. 2013). Finally, we demonstrated the benefits of using a growth-type group model instead of relying solely on mean size-at-age when setting harvest policy, because the latter assumes that fishing has no effect on size-at-age. Given that a high coefficient of variation in length-at-age renders Pacific Halibut vulnerable to size-selective fishing effects, the most effective management action would be to reduce harvest rates to diminish the intensity of size selection.

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