

ASSESSING THE LONG-TERM GROWTH RESPONSE AND AGE ESTIMATION
PRECISION FOR ARCTIC WHITEFISHES IN A RAPIDLY CHANGING NEARSHORE
ENVIRONMENT

By:

Kyle P. Gatt, B.S.

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APPROVED BY:

Dr. Trent M. Sutton, Committee Chair

Dr. Vanessa R. von Biela, Committee Member

Dr. Megan V. McPhee, Committee Member

Dr. Andrew C. Seitz, Chair

Department of Fisheries

Dr. S. Bradley Moran, Dean

College of Fisheries and Ocean Sciences

Dr. Richard L. Collins,

Director of the Graduate School

Abstract

Accurate monitoring of population-level health and productivity is essential for assessing the status and availability of subsistence harvested species at the forefront of climate change. This study used otolith biochronology to assess the long-term growth response of Arctic Cisco *Coregonus autumnalis* during a period of rapid environmental change in the Beaufort Sea region and to identify drivers of growth. A biochronology spanning 22 years (1996–2018) revealed significant interannual variation, with faster growth rates in years with warmer ($R^2 = 0.31$) and more saline ($R^2 = 0.47$) waters during the ice-free summer feeding period (July–September). These results suggested that warming may benefit Arctic Cisco. This study also compared age estimates made using fin rays, scales, and otoliths of four subsistence whitefishes (Arctic Cisco, Least Cisco *Coregonus sardinella*, Broad Whitefish *Coregonus nasus*, and Humpback Whitefish *Coregonus pidschian*) from the Beaufort Sea to compare the aging precision of non-lethal structures (fin rays and scales) to otoliths. Fin rays and scales provided similar age estimates as otoliths until the age of sexual maturity and underestimated otolith age for mature individuals. Scales underestimated age more often and were more difficult to which to assign age than the other two structures. Among Arctic Cisco in Alaska, fin rays and scales provided similar age estimates as otoliths for all age and size classes examined because most individuals in the study area were immature fish. These results suggested that dorsal fin rays may be used to estimate age in Least Cisco <300 mm, Broad Whitefish <450 mm, and Humpback Whitefish <350 mm, and that otoliths should remain the primary aging structure for the largest whitefishes. Overall, this research complements existing monitoring by providing evidence of an Arctic subsistence species that may benefit in part from warming and highlights non-lethal alternatives for monitoring the age structure of juvenile whitefishes.

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General Introduction

The effects of a warming climate are anticipated to be widespread across both terrestrial and aquatic landscapes (Häder and Barnes 2019). Ecosystem response in high latitude regions will be most dramatic as feedback processes increase rates of warming to more than double the global average (Wood et al. 2013; Post et al. 2019). In the recent decade alone, Arctic annual air temperatures have warmed by 0.75°C (Post et al. 2019), bringing rapid change across aquatic and terrestrial landscapes in higher latitudes. Recent warming has led to sea-ice decline and sea-surface warming in the Arctic Ocean (Wood et al. 2013; Stroeve and Notz 2018), which have accelerated erosional processes on the terrestrial landscape and increased transport of inorganic and organic nutrients to the Arctic Ocean (McClelland et al. 2006; Frey and McClelland 2009; Overduin et al. 2014). These cumulative factors have led to shifts in the growth rates and condition of aquatic organisms in the Arctic marine environment (von Biela et al. 2011; Harwood et al. 2015; George et al. 2015; Bonsell and Dunton 2018). The magnitude and direction of change in growth rates and body condition vary by species, population, and life stage, and range from positive to negative based on individual species biology (Reist et al. 2006). Understanding abiotic and biotic factors that have influenced growth and condition is essential to accurately predict the future status of aquatic species at the forefront of climate change (Reist et al. 2006; Morrongiello et al. 2012). Such an understanding is particularly relevant for high-latitude regions because the subsistence harvest of fish is woven into the social and cultural fabric of Indigenous peoples of the Arctic (Wishart 2014).

Somatic growth rate in fishes is an important component of population dynamics and a metric commonly used to assess population-level health and productivity (Hilborn and Walters 1992). Faster growth rates are often associated with greater survival and reproductive output in

many fish species, especially for salmonids (Healey and Nicol 1975; Henderson and Cass 1991; Clark and Bernard 1992). Fish somatic growth is heavily influenced by intrinsic (e.g., age) and extrinsic (e.g., temperature and food availability) factors (Morrongiello and Thresher 2015). Identifying and understanding extrinsic influences on somatic growth is critical to anticipating the effects of future climate warming on Arctic fishes. Despite the importance of climate-growth relationships, such assessments are rare due to the dearth of long-term datasets. The Arctic marine environment is no exception, as limited accessibility, harsh weather conditions, and a short open-water season make monitoring fish populations challenging.

Hard structures collected for aging offer a cost-effective and efficient means to obtain long-term growth rate data in the Arctic marine environment. Fin rays, otoliths, scales, vertebrae, and cleithra have long been used to estimate fish age, which is necessary to estimate growth rate, survival, and age-specific recruitment (Quist and Isermann 2017). Otoliths are the most widely used hard structures for fish aging because they retain both chemical and physical signatures in inert daily and annual increments (Stevenson and Campana 1992; Morrongiello et al. 2012). These signatures may be linked to abiotic and biotic events over the lifespan of a fish by combining methodology borrowed from dendrology (tree-ring science) with linear mixed-effects fish growth models to generate an otolith biochronology (Campana 1990; Campana and Thorrold 2001; Morrongiello et al. 2012). A biochronology represents a fish's biological history (e.g., life-history and demographic data, environmental and physiological records) stored in fish across time and may be used to assess how populations have responded to past natural and anthropogenic disturbances (Morrongiello et al. 2012). Otolith biochronologies have expanded our understanding of not only fish growth, but also ecological function in freshwater (Morrongiello et al. 2011), estuarine (Morrongiello et al. 2014; Doubleday et al. 2015; Barrow et

al. 2018), and marine environments (von Biela et al. 2015; Smoliński and Mirny 2017; Smoliński 2019). Thus, otolith biochronologies offer an ideal approach for exploring the complex relationships driving unique growth patterns in Arctic fishes and for assessing the current status and future availability of species at the forefront of climate change.

Despite the wealth of information stored in hard structures, many Arctic fishes lack any formal assessments into the precision of age estimates using hard structures. In the absence of true age validation methods, precision analyses are used to measure the repeatability of assigning age to a structure and for identifying potential biases (in both structure and reader) that may lead to inaccurate age estimates (Campana et al. 1995). These types of assessments are relevant due to the need to accurately monitor fish stocks. Age-specific biological data obtained from inaccurate age estimates can undermine management of a particular stock by underestimating or overestimating rate-dynamic parameters (e.g., growth, age-specific mortality, and maturation) that are used to assess overall stock health and productivity (Mills and Beamish 1980; Yule et al. 2008). Inaccurate age estimates may also obscure ecological and biological relationships that govern fish growth, inhibiting our ability to accurately assess a species' resilience to further climate change.

The need for climate-growth assessments and identifying the most reliable aging structure for accurate monitoring of fishes in the Arctic has been amplified in recent decades due to rapid environmental and biologic change occurring in the Beaufort Sea. The Pacific Arctic reached a turning point in 2007 with the first in a series of shifts in ice phenology and extent (Wood et al. 2013; Overland et al. 2018). The timing of ice freeze up has occurred consistently later than the 1981–2010 mean ice-up date and may influence marine productivity in the Beaufort Sea (Overland et al. 2018; Bonsell and Dunton 2018). This was particularly the case for

autumn of 2012 when ice-up began five weeks later than the 29-year average (Wood et al. 2013). In addition to a later ice-up date, ice cover in the southern Beaufort Sea has begun to break up 5-7 days earlier per decade since 1979 (Johnson and Eicken 2016). The September sea-ice extent has also continued to decline at a rapid rate. Of the 10 lowest sea-ice extents in recorded satellite history, nine have occurred in the past 13 years (“NSIDC 2019”). Recent rapid reductions in sea-ice extent have been largely due to sea-surface warming and thinning of sea-ice combined with the increased presence of east winds across the Arctic Coastal Plain (Wood et al. 2013). East winds advect thin sea ice out of the Alaska region, which allows for increased stratification of surface waters due to favorable transport of the Mackenzie River discharge plume to offshore waters (Wood et al. 2013; Nghiem et al. 2014). Increased discharge of Arctic rivers has also been noted and related to an amplified hydrological cycle (Bintanja and Selten 2014; Bintanja 2018). Increases in river discharge could result in higher levels of terrestrial organic matter transported to the Beaufort Sea and Arctic Ocean, with the potential to alter primary productivity in coastal and marine food webs that use a combination of terrestrial and marine organic matter (Dunton et al. 2006; Doxaran et al. 2015; Bell et al. 2016; Terhaar et al. 2021). Because alterations would occur at the base of coastal and marine food webs, the impact on higher trophic levels would likely be considerable and could reshape food-web structure and dynamics in the nearshore region.

Coastal waters of the Beaufort Sea are home to several coregonid whitefishes targeted for subsistence fishing including Arctic Cisco *Coregonus autumnalis*, Least Cisco *Coregonus sardinella*, Humpback Whitefish *Coregonus pidschian*, and Broad Whitefish *Coregonus nasus* (Moulton et al. 2010; Brown et al. 2012; Brase and Baker 2014). Prior studies have identified several factors that influence the growth of Arctic Cisco while in Alaskan waters; however, prior

analyses were limited to the age-0 life stage and questions remain about environmental conditions that influence growth in other life stages. Despite wide-spread harvest and their high value in the Arctic regions, coregonid whitefishes lack any formal assessments into the precision of age estimates using hard structures (e.g., otoliths, scales, fin rays, etc.).

This research aimed to address gaps in our knowledge of Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish in the Alaskan Beaufort Sea to better understand the impacts of climate change on high-latitude nearshore ecosystems and to improve monitoring of coregonid whitefishes in the Arctic. Chapter one of this thesis uses an otolith biochronology and mixed-effects models to assess the long-term growth response of sub-adult Arctic Cisco to recent environmental change occurring in the Beaufort Sea and identifies primary drivers of growth in the species. Chapter two assesses whether the precision and readability of age estimates made using dorsal fin rays and scales are similar to those of otoliths in Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish. Results from this research will provide information necessary for properly assessing the current and future status of coregonid whitefishes in the nearshore Beaufort Sea region.

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Chapter 1: Reading Between the Lines: Using an Otolith Biochronology to Assess Interannual Growth Rate Variation and Identify Drivers of Growth in an Arctic Fish¹

Abstract

Arctic ecosystems are undergoing rapid, climate-induced environmental changes, including warming and the loss of sea ice that often negatively affect the production of or access to subsistence foods. To understand the effects of climate change on a key subsistence fish, otolith sclerochronology and linear mixed-effects models were used to reconstruct the growth history of Arctic Cisco *Coregonus autumnnalis*. A biochronology spanning 22 years (1996–2018) revealed significant interannual growth rate variation that was associated to abiotic environmental conditions (salinity and water temperature) and Arctic Cod *Boreogadus saida* abundance during the ice-free summer feeding period (June to late August). Growth rates were faster in years when higher salinity waters were more prevalent ($R^2 = 0.47$), in agreement with a benefit from the onshore movement of productive marine waters via upwelling. Water temperature was also positively associated with growth ($R^2 = 0.31$) and likely mediated through metabolic influences or bottom-up trophic effects. Arctic Cod abundance showed a weak, negative association with growth ($R^2 = 0.22$) that was attributable to differences in habitat selection between species. Our results suggest Arctic Cisco have benefitted from the recent warming of water temperatures. Uncertainty remains if this trend will continue given the rapid pace of climate change and warrants continued monitoring.

¹ Gatt, K. P., V. R. von Biela, T. M. Sutton and M. V. McPhee. 2021. Reading between the lines: using an otolith biochronology to assess interannual growth rate variation and identify drivers of growth in an Arctic fish. In preparation for submission to *Polar Biology*.

Introduction

Ecosystem response to a warming climate will be more dramatic in high-latitude regions as rates of warming continue to occur at more than double the global average (Wood et al. 2013). Over the past decade, annual air temperatures in the Arctic have warmed by 0.75°C (Post et al. 2019), bringing rapid environmental and biological changes across aquatic and terrestrial landscapes. Recent warming has led to sea-ice declines and sea surface warming in the Arctic Ocean (Wood et al. 2013; Stroeve and Notz 2018) and has accelerated erosion in coastal margins (Overduin et al. 2014). Increased terrestrial inputs, coupled with a longer ice-free season, appear to have shifted important biologic parameters such as growth rate and body condition of aquatic organisms in the Arctic marine environment (von Biela et al. 2011; George et al. 2015; Harwood et al. 2015; Bonsell and Dunton 2018). Further shifts in biological parameters are expected given that mean Arctic air temperature is predicted to rise 3 to 10°C over the next 80 years (IPCC 2014) and the ice-free season to increase by five months by 2040 (Wang and Overland 2015). For diadromous fishes in the Arctic, the consequences of increased temperatures will be substantial as their productivity is tied to freshwater, estuarine, and marine habitats which are all undergoing rapid and uncertain change (Reist et al. 2006).

Somatic growth rate in fishes is an important component of population dynamics and a metric commonly used to assess population-level health and productivity (Hilborn and Walters 1992). Faster growth is often associated with greater survival and reproductive output in many fish species (Healey and Nicol 1975; Henderson and Cass 1991; Clark and Bernard 1992). Fish somatic growth is influenced by extrinsic factors (e.g., environmental- or competition; Morrongiello and Thresher 2015), either directly by the influence of temperature on metabolic rate of ectotherms (Pörtner et al. 2001) or the indirect influence of physical conditions on food

availability and quality (Hunt et al. 2011). Understanding past climate-growth relationships may aid in better monitoring and assessing the future status of species at the forefront of climate change. Because subsistence harvest is an essential part of life for Indigenous communities in the Arctic, any shift in the population status of harvested species could have direct impacts on food security for these communities (Brinkman et al. 2014). However, limited access from a short open-water season and harsh weather conditions even in summer make monitoring fish populations in the Arctic difficult.

Hard structures collected for aging offer a cost-effective and efficient means to obtain long-term growth rate data in the Arctic. Otoliths collected for aging retain both chemical and physical signatures at daily and annual increments (Stevenson and Campana 1992; Morrongiello et al. 2012). These signatures may be linked to extrinsic conditions or events over the life span of a fish (Campana 1990; Campana and Thorrold 2001; Morrongiello et al. 2012). By measuring the distances between consecutive translucent zones recorded on an otolith, a growth history is created that reflects annual somatic growth (Stevenson and Campana 1992). This is possible due to the linear relationship often observed between otolith radius and length in many fish species (Francis 1990). Growth histories generated from otolith increment data may be averaged across individuals of a population using tree-ring (dendrology) techniques or mixed-effects modeling for the development of biochronologies (Morrongiello et al. 2012). Population-specific biochronologies represent average year-to-year variability in somatic growth rates (Black et al. 2013b), and therefore an index of production, that may be linked to environmental and biological drivers (e.g., trophic interactions; see Matta et al. 2020). Such analyses have been successfully applied to a wide range of species and regions to assess the impacts of climate change on fish populations (Morrongiello et al. 2011, 2014; Ong et al. 2015; Barrow et al. 2018).

Biochronologies may be correlated among organisms (Black 2009) and across regions (Doubleday et al. 2015; Martino et al. 2019) and species (Izzo et al. 2016), allowing for ecosystem-level assessments into the impacts of climate change. Although biochronologies have been generated in the Alaskan high-Arctic (Black et al. 2013a), few have been developed to assess long-term climate-growth relationships in nearshore ecosystems of the Beaufort Sea.

The Beaufort Sea is arguably one of the best-studied Arctic nearshore ecosystems, with well-documented changes in both aquatic and terrestrial landscapes, as well as strong connectivity between these habitats. On the aquatic landscape, recent warming has resulted in sea-ice loss (Wang and Overland 2015), warmer water temperatures (Priest 2020; Wood et al. 2013) and intensified storm surge activity during the ice-free period (Vermaire et al. 2013). Warmer waters and greater wave action have accelerated erosion processes in the coastal margins (Jones et al. 2009; Sankar et al. 2019). Increased rates of coastal erosion, river discharge (Doxaran et al. 2015), and permafrost degradation (Jorgenson et al. 2006) have increased the transport of terrestrial biomass to the Beaufort Sea (Doxaran et al. 2015), which influences the productivity of coastal and marine food webs (Dunton et al. 2006; Bell et al. 2016). Fish community structure of the nearshore Beaufort Sea has also responded to recent warming with shifts towards an increasing presence of generalist species and with entirely new species to the region (Priest 2020).

Within the nearshore Beaufort Sea, Arctic Cisco *Coregonus autumnalis* is a key species with subsistence value in a region without commercial fishing (Fechhelm et al. 2007; Moulton et al. 2010). Annual harvest of Arctic Cisco averages 26,000 individuals, which often accounts for 85% of harvested fish in the fall under-ice gillnet fishery (Seigle et al. 2019). Because of its value and the potential for oil-and-gas extraction activities across the North Slope of Alaska to

negatively impact harvest, Arctic Cisco have been closely monitored in the Sagavanirktok and Colville River deltas since the late 1970s (Gatt et al. 2019; Seigle et al. 2019). Monitoring coupled with genetic analyses has led to the conclusion that all Arctic Cisco originate from spawning populations in the Mackenzie River and use coastal waters for feeding each summer (Gallaway et al. 1983; Dillinger et al. 1992; Fechhelm et al. 2007; Zimmerman et al. 2013). Arctic Cisco leave their natal streams during spring break up and age-0 individuals spend their first summer in the Beaufort Sea either being retained in Canadian waters or undergo a wind-mediated migration west to rear in the Alaskan Beaufort Sea, ultimately overwintering in deep river channels in the North Slope of Alaska (Craig 1984; Fechhelm and Griffiths 1990). Monitoring has also shown that the species experiences significant interannual variability in its overall size and condition, as well as abundance in Alaskan waters (Fechhelm et al. 1996; Moulton et al. 2010). Previous studies have identified factors that influence the abundance of Arctic Cisco in Alaskan waters (Murphy et al. 2007; Moulton et al. 2010); however, abundance data do not provide an accurate metric of productivity for this species because of the confounding effects that wind has on recruitment to Alaskan waters. Questions remain about the influence of environmental conditions on growth of other life stages when individuals are wholly in the Alaskan Beaufort Sea and whether environmental relationships have changed with recent acceleration of warming and sea-ice loss (Wang and Overland 2015; Priest 2020). Arctic Cisco otoliths have clear annual growth rings and are well suited for growth chronology development. Previous research confirmed that otolith growth is a proxy for somatic growth and provided a >20 year chronology (1978–2004) of age-0 growth during the wind-mediated migration (von Biela et al. 2011).

In light of recent changes occurring in the Arctic and the increasing need to understand how nearshore fish communities will respond to a further changing climate, we developed a growth chronology using otoliths collected during annual monitoring of the nearshore fish community in the Beaufort Sea to assess the response of Arctic Cisco to recent environmental changes and to identify the primary drivers of somatic growth. Our objectives were to (1) assess long-term trends in growth; and (2) identify the primary extrinsic drivers of growth patterns in sub-adult and adult life stages. Given the variability in the Arctic marine environment from year to year, we expected interannual growth rate variation in sub-adult and adults to be evident. Growth rate variation was expected to be most heavily influenced by water temperature and salinity in the nearshore zone, and to a lesser degree the prevailing winds and river discharge across the region. Further, we hypothesized that growth rate variation would be linked to fish abundance in the nearshore zone due to putative density-dependent effects. The information collected during this study will allow for a better assessment of how Arctic Cisco, and potentially other Arctic fishes, may respond to changing climate conditions in the future.

Materials and Methods

Study Site

Arctic Cisco were captured in nearshore waters of the Beaufort Sea near Prudhoe Bay, Alaska (Figure 1). Nearshore waters in this region are relatively shallow (< 2-m deep) and are characteristically estuarine (Dunton et al. 2012). Land-fast ice typically persists until mid-June before giving way to open water and eventually reforming in late September. Spring freshets from rivers deposit large amounts of turbid freshwater into nearshore areas and facilitate melting of land-fast ice (Nghiem et al. 2014). As turbid freshwater mixes with marine water, it forms a band of relatively warm (temperature range = 0.3 to 17.3°C) brackish (salinity range = 0.1 to

32.7 psu) water that extends 750 km along the Beaufort Sea coast during the summer growing period (Gatt et al. 2019). Nearshore waters are minimally influenced by tides, with winds being the predominant driver of currents, mixing patterns, and the extent of the brackish band along the coastline (Dunton et al. 2006). The summer period is dominated by relatively strong (average wind speed = 12.8 km/hr) east-west winds and abrupt shifts in wind directions that cause water levels to fluctuate as much as 0.9 m daily in the Prudhoe Bay region (Gatt et al. 2019). Easterly winds are upwelling favorable, push brackish waters offshore, and lower nearshore water levels. Westerly winds retain brackish waters along the coastline and cause higher nearshore water levels (Ross 1988; Dunton et al. 2006). As a result, environmental conditions are highly dynamic, showing large fluctuations on a spatiotemporal scale.

Nearshore waters of the Beaufort Sea are oligotrophic yet support a relatively high degree of productivity during the short growing season (Dunton et al. 2006). Shortly after land-fast ice begins to retreat, amphidromous and anadromous fishes begin to migrate out of rivers and deltas to nearshore waters to feed (Craig 1984). Fish can reside in these feeding areas until the onset of ice up in late September or October (Craig 1984). The nearshore fish community is dominated by several coregonid whitefishes (e.g., Arctic Cisco, Least Cisco *Coregonus sardinella*, Broad Whitefish *Coregonus nasus*, and Humpback Whitefish *Coregonus pidschian*), Fourhorn Sculpin *Myoxocephalus quadricornis*, and Arctic Cod *Boreogadus saida* during the summer (Craig 1984; Green et al. 2018; Gatt et al. 2019). While in nearshore waters, fish feed on an abundant supply of amphipods, copepods, and mysids that are transported to nearshore areas from offshore waters during periods of intense upwelling (Craig and Dillinger 1981; Craig et al. 1982; Craig 1984; von Biela et al. 2013). It is thought that nearshore consumers could quickly deplete prey resources, such that persistent and substantial upwelling might be a requirement to support the

dietary needs of fish, bird, and marine mammal consumers (Craig 1989). Marine invertebrates are supported by relatively short periods of intense primary production by ice-associated and planktonic algae (Horner and Schrader 1982). Land-fast ice in nearshore waters typically delays peak water column productivity by one month (June to late July) relative to the outer Beaufort Sea shelf (Carmack et al. 2004). As a result of the short period of rapid production, fish here typically attain a majority of their total annual growth from late June to August (Craig 1984).

Fish Capture, Otolith Samples and Preparation

Arctic Cisco were collected during annual monitoring efforts for the Beaufort Sea Long-Term Nearshore Fish Monitoring program between 2003 and 2019 (excluding 2014, when no samples were collected). This monitoring program was initiated in 1981 in response to concerns that recently constructed gravel-filled causeways along the Beaufort Sea coast in the vicinity of Prudhoe Bay had adverse effects on estuarine fishes across the Arctic coast (Gatt et al. 2019). As a result of continued oil and gas development across the North Slope of Alaska, the monitoring program was expanded through the 1990s following standardized procedures that were established in 1985.

During each summer open-water period, paired fyke nets were deployed along the Prudhoe Bay coastline at four consistent sample sites (Figure 1.1). Nets were fished continuously from late June to September and checked daily unless sampling was precluded by unsafe weather conditions. Fish were removed from nets, identified to species, enumerated, measured for fork length (nearest mm), and released live. Each year, a random subset of Arctic Cisco were collected for otolith growth chronology based on fork length using 20-mm length groups (spanning < 120 to > 400 mm). Fish satisfying length-group requirements were assigned a unique identification number, and their otoliths were removed and stored dry in centrifuge vials.

Otoliths were dried, placed in molding trays, and embedded in epoxy resin (West System Epoxy, Gougeon Brothers Inc., Bay City, Michigan). Once embedded, a single transverse cut was made through the nucleus using a low-speed Isomet saw (Buehler, Lake Bluff, Illinois). Sections were lightly polished using 2,000-grit sandpaper to increase clarity of annuli borders. Otoliths images were captured using a high-resolution digital camera (Leica DFC 450, Leica Microsystems Inc., Buffalo Grove Illinois) mounted on a stereomicroscope (Leica M165C) at 40X magnification. Growth increments were measured from the nucleus to the outer margin edge along the longest ventral axis (Figure 1.2) using the ImagePro Plus v.5.1 image processing software (Media Cybernetics, Rockville Maryland). Growth increments were measured (in mm) between the outer edges of adjacent translucent zones (narrow dark bands under reflected light; Figure 1.2). Growth increments were assigned to a growth year (*Year*) by assigning the incomplete increment on the otolith edge to the year of capture and assigning previous years to each successive growth increment moving toward the nucleus. In some cases, this procedure followed the “break-and-burn” aging technique (Christensen 1964) for otoliths collected prior to 2017 if an intact otolith was not available.

As demonstrated by Smoliński et al. (2020), reader error can significantly inhibit the precision of climate-growth relationships. To minimize aging error, a second read was conducted on a subset of individuals, and precision was estimated between consecutive reads using the coefficient of variation (CV) and averaged among fish ($n= 300$, $CV= 0.66$). However, precision is not a proxy for accuracy. Age validation measures were not possible across all age classes in this study and the short life span of Arctic cisco prevented robust cross-dating techniques from being applied to growth increment data (Black et al. 2016). However, the first growth zone was validated using a variation of the modal progression validation method outlined by Campana

(2001; Appendix A). Moreover, growth patterns in older ages were noted among individuals and used to resolve residual reader error, similar to the methods of Matta et al. (2020). Despite these efforts, some unknown dating error likely persisted. Growth data used in analyses were restricted to (a) calendar years that possessed minimum representation of at least seven growth increments (b) from individuals ranging ages 2 to 9. The age-0 growth zone (from the nucleus to the outer edge of the first translucent zone) was removed from analyses because age-0 Arctic Cisco do not occupy the Prudhoe Bay region for the full duration of the open water-period and have different food habits relative to older conspecifics (Fechhelm and Griffiths 1990; Kline et al. 1998; von Biela et al. 2011). The marginal annulus also was removed because it does not represent a full calendar year of growth. Only otoliths possessing clear and readily identifiable annuli borders were selected for analyses.

Growth Models

We used a series of linear mixed-effects models following Morrongiello and Thresher (2015) to investigate sources of growth variation, while also considering the hierarchical structure of growth-increment data. Mixed-effects models allow for climate-growth relationships to be assessed in short-lived species (Martino et al. 2019; Smoliński 2019; Matta et al. 2020), making them apt for analyzing growth increment data in Arctic Cisco. All statistical analyses were conducted in the “lme4” (Bates et al. 2014), “effects” (Fox 2003), and “AICcmodavg” (Mazerolle 2019) packages in the statistical program R version 3.5.1 (R Core Team 2018).

The mixed-effects models account for intrinsic (within individual fish) effects and extrinsic effects simultaneously. Four models with slight differences in parameterizations were considered and a growth chronology of year-specific effects capturing the extrinsic environmental signal was extracted from the best model. Intrinsic sources of growth variation

were assessed using fixed *Age* and random *Sample.ID* terms in all models considered (Table 1.1). The fixed *Age* term accounted for ontogenetic differences in growth among life-stages including the strong tendency for an individual to grow faster at younger ages. The random-intercept term for *Sample.ID* accounted for non-independence of the response by allowing for correlation of growth increments within individuals (Table 1.2). The extrinsic effects of the interannual environmental conditions were captured using a random effect for the calendar year (*Year*). Extrinsic factors were not fit to the intrinsic growth model as fixed effects because of missing data for some time series that complicates the direct comparison of models.

In the simplest model, increment width for individual s at age j for calendar year y was y_{sjy} and was modeled as (Model A; Table 1.2):

$$y_{sjy} = (a_o + \alpha_s + a_y) + \beta_1 x_{sjy} + \varepsilon_{sjy},$$

where a_o and β_1 are the fixed intercept and slope describing the population-wide allometric decline in growth at age (x_{sjy}), α_s and a_y are random intercepts describing growth trajectories of individuals and years, and ε is the residual error. Three additional models were also considered that determined if model fit was improved by the addition of random slopes that modified the fixed slope for age for each individual (β_s , Model B) or *Year* (β_y , Model C) terms to allow for individuals and years to have unique age-related growth trajectories (Rountrey et al. 2014). The most complex model, Model D, adds both of these adjustments (β_s, β_y) to the overall slope of the model with increment width for individual s at age j for calendar year y as:

$$y_{sjy} = (a_o + \alpha_s + a_y) + (\beta_1 + \beta_s + \beta_y)x_{sjy} + \varepsilon_{sjy}.$$

The inclusion of *Age* as a fixed effect allowed for global detrending of ontogenetic-effects, similar to the detrending process used in the dendrology program COFECHA for master

chronology development (Black et al. 2005, 2013). The additional random effect β_s , allows the detrending process to occur on an individualized basis. Two assumptions about chronology development were confirmed prior to fitting growth models. The assumption that a relationship between otolith growth and somatic growth exists was previously supported in Arctic Cisco and this assumption was further verified in our study ($n = 300$, $R^2 = 0.93$; Appendix A). Temporal-growth synchrony among individuals is an important measure for determining the relative strength of a common growth signal in a species or population. For traditional dendrological-based approaches, this measure has typically been reported as an interseries correlation (Mayer-Grissino 2001). We assessed growth synchrony among Arctic Cisco within a given year by calculating the intraclass-correlation coefficient (ICC_{year}) from the best (based on AICc) *Year* intercept-only model (models A, B; Morrongiello and Thresher 2015; Lüdecke 2019).

Prior to model fitting, increment width and *Age* were natural log-transformed to ensure linearity between variables and ensure homogeneity of variance. The *Age* term was mean-centered to assist in model convergence and to aid in coefficient interpretation (Morrongiello and Thresher 2015). Model comparisons were conducted using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004). The model with the lowest AICc of those comparable ($\Delta > 2$ AICc) was considered the optimal growth model for the available data. All models were fit with restricted maximum-likelihood estimation (REML) for unbiased parameter estimates (Zuur et al. 2009). The variance explained by the fixed-and-random-effects structures was assessed using conditional (R^2_C) and marginal (R^2_M) residual sum-of-squares metrics (Nakagawa and Schielzeth 2017). Marginal R^2 measures the variance accounted for by the fixed-effects structures, and conditional R^2 measures the amount of variance accounted for by both the fixed and random effect structures (Nakagawa and Schielzeth 2017).

Extrinsic Growth Predictors

The growth chronology (*Year* effects) was regressed against several extrinsic factors hypothesized to influence Arctic Cisco growth using simple linear models ($\alpha < 0.05$). Extrinsic variables were natural-log transformed to normalize distributions and ensure linearity between terms. Regression of extrinsic variables against year revealed no significant temporal trends ($p > 0.05$).

Environmental predictors of growth rate variation included *water temperature* ($^{\circ}\text{C}$), *salinity* (psu), *wind direction* (km/hr), and *Sagavanirktok River discharge* (referred to as *Discharge* hereafter; recorded as ft^3/s and converted to m^3/s ; Figure 1.3). Each variable was calculated for the year by averaging daily conditions across the growing season (01 July–25 August). Water temperature and salinity data were obtained from annual monitoring efforts of the Beaufort Sea Long-Term Nearshore Fish Monitoring Program. Wind data were used as a relative measure of upwelling along the coast and were obtained from the NOAA National Weather Service at the Deadhorse Airport (hourly wind speed and direction; www.ndbc.noaa.gov/station_history). Because east winds were anticipated to be the primary influence of growth relative to other wind directions, cardinal direction was filtered to only contain values ranging between 45 and 135° . Discharge data were acquired from the U.S. Geological Survey (USGS Station 15908000, Sagavanirktok River, waterdata.usgs.gov) as daily averages. To ensure comparability across results, only environmental data from the years where all variables were collected were used (1996, 1998, and 2001-2018).

The effect of fish abundance on annual growth rates was examined using catch-per-unit-effort (CPUE; number of fish/hr) data obtained from the Beaufort Sea Nearshore Fish Monitoring Project. Abundance metrics were calculated following Green et al. (2019) using

catch data specific to multispecies and length groups that shared similar dietary needs as the sub-adult and adult life stages of Arctic Cisco (see Knutzen et al. 1990) and a metric specific to Arctic Cod. The multispecies abundance metric (referred to as *Whitefishes*) included the CPUE of Arctic Cisco (≥ 120 mm), Broad Whitefish, Least Cisco, and Humpback Whitefish combined. Small Arctic Cisco (< 120 mm) were not included as this size range generally corresponds to age-0 fish that have only recently completed a migration from the Mackenzie River delta with little opportunity for influencing food availability in the Prudhoe Bay region (Kline et al. 1998; von Biela et al. 2013). Arctic Cod CPUE (*ArcticCod*) was examined separately because large schools (up to 400,000 individuals) of this species have been noted to quickly deplete food resources (e.g., zooplankton) in nearshore areas (Craig et al. 1982b). Abundance metrics in the current study were assumed to provide an index for putative density-dependent effects mediated through prey availability in the nearshore zone and thus, having a negative influence on growth. Once extrinsic indices were filtered, and biological metrics were calculated (CPUE), broad measures of environmental conditions within a given year were generated by averaging daily conditions across the growing season (01 July–25 August).

Results

A total of 721 Arctic Cisco and 2,659 growth increments spanning 1996–2018 were used in analyses (Figure 1.4). Individuals ranged from ages 2 to 9 and fork lengths from 112 to 399 mm. The number of growth increments represented in each calendar year ranged from seven in 1996 to 220 in 2002 (Figure 1.4).

Intrinsic Growth Model

Initial model comparisons (based on $\Delta AICc$) supported the inclusion of random *Age* slopes to *Sample.ID* and *Year* and accounted for a high degree of growth variance in Arctic

Cisco ($R^2_C = 0.76$; Table 1.3, Model D). The inclusion of *Year* with random *Age* slopes improved model fit and was the best predictor of growth in the random effects structure. High support for random *Age* slope to both *Sample.ID* and *Year* suggests that the effect of age varied among individuals and to a greater degree, years. Temporal growth synchrony among individuals within a given growth year was estimated with ICC_{Year} as 0.17.

Temporal Growth Patterns

A 22-year Arctic Cisco otolith biochronology spanning 1996 to 2018 was generated using *Year* random intercepts from the optimal growth model identified above (Model D; Figure 1.5). Significant interannual growth rate variability was apparent in the biochronology, showing several years of notably higher and lower average growth. Years of favorable growth occurred in 1998, 2007, 2010, and 2012, whereas years of poor growth occurred in 2001 and 2014.

Extrinsic Predictors

Interannual growth-rate variability in Arctic Cisco was significantly related to several environmental and biotic drivers. Growth was faster in years with high salinity (Table 1.4; $R^2 = 0.47$, $p < 0.001$) and warmer water temperatures (Table 1.4; $R^2 = 0.31$, $p = 0.01$), whereas wind direction and Sagavanirktok River discharge showed no relationship with growth (Table 1.4). Arctic Cod abundance possessed a weak and negative relationship with growth (Table 1.4; $R^2 = 0.22$, $p = 0.04$), with high catches of Arctic Cod in 2002 having a strong influence on this relationship. Whitefish abundance showed no relationship with growth (Table 1.4).

Discussion

In this study, we reconstructed 22 years of growth for Arctic Cisco, an anadromous whitefish species of subsistence value in the Arctic, during a period of rapid environmental and biological change in nearshore waters of the Beaufort Sea. Study results revealed temporal

growth synchrony and significant interannual growth rate variation among the sub-adult and adult life stages. Biochronology suggested that poor growing conditions for Arctic Cisco persisted in the Beaufort Sea from the late 1990s through the early 2000s before switching to more favorable growing conditions from 2006 to 2012. Growth rate variation was most strongly and positively associated with average salinity and water temperature during the ice-free summer growing period. Arctic Cod abundance also showed a weak, negative relationship with growth and showed no evidence of density-dependent effects. Our results support prior observations that favorable growth, beyond the age-0 life stage, is often associated with the presence of warmer, more saline waters in the nearshore zone during the ice-free summer growing period (see Fechhelm et al. 1995, 1996). Results from this study suggest continued environmental changes in the Beaufort Sea region will impact somatic growth rates and potentially, productivity of Arctic Cisco in Alaskan waters of the Beaufort Sea.

Growth declined with age in Arctic Cisco, which is a common feature of fish growth (Barrow et al. 2018; van der Sleen et al. 2018; Martino et al. 2019). Model comparisons suggested the year effect accounted for most of the variation in age-corrected growth, indicating strong influence of extrinsic effects. As a result, it is assumed that climate-related and biological variability (particularly differences in salinity and water temperature) in the nearshore Beaufort Sea are the primary factors influencing growth rate variation for sub-adult and adult life stages of this species. Strong year effects on growth have also been reported to occur in a variety of fish species in different regions (Ong et al. 2015; Smoliński and Mirny 2017; van der Sleen et al. 2018; Smoliński 2019).

Temporal growth synchrony for Arctic Cisco was 0.17 and on the upper end of the range of those reported in the literature using a similar approach (mixed-effects models with ICC):

Snapper *Chrysophrys auratus* (range, 0.039 to 0.103; Martino et al. 2019), Baltic Herring *Clupea harengus* (0.03; Smoliński 2019), European Flounder *Platichthys flesus* (0.02; Smoliński and Mirny 2017), Black Bream *Acanthopagrus butcheri* (range, 0.03 to 0.135; Doubleday et al. 2015), and Tiger Flathead *Platycephalus richardsoni* (range, 0.002 to 0.216; Morrongiello and Thresher 2015). High aging precision in Arctic Cisco (Chapter 2) and large sample sizes in this study should have limited some sources of error in this growth chronology and help explain the high temporal growth synchrony.

Still, the ICC value reported here and those in other studies using a similar statistical approach is low relative to long-lived species whose synchronicity was estimated with traditional dendrological techniques and interseries correlation from program COFECHA. For example, the interseries correlations reported are 0.40 to 0.57 for Lake Trout *Salvelinus namaycush* (Black et al. 2013; Biela et al. 2021), 0.55 for Yellowfin Sole *Limanda aspera* (Black et al. 2013), 0.53 to 0.55 for Splitnose Rockfish *Sebastes diploproa* (Black et al. 2005; Black 2009), and 0.59 to 0.66 for Bering Sea flatfishes (Matta et al. 2010). The ICC values and interseries correlation values from program COFECHA are likely not directly comparable. The ICC provides a measure of how similar individuals are to each other in a given year (Morrongiello and Thresher 2015), while the interseries correlation measures how similar individuals are to a mean or master chronology that is thought to have a higher signal to noise ratio than the chronology of any one individual (Black et al. 2005). Therefore, it is not surprising that ICC values are consistently lower than interseries correlations. No chronology studies have provided both synchrony metrics for the same data set to assess comparability nor could that be accomplished here given that Arctic cisco are too young to calculate the interseries correlation.

Arctic Cisco grew faster in years with higher than average salinities, a proxy for marine influence. This result differed from those reported for younger age classes for this species, which suggested that salinity negatively impacted growth for age-0 fish but showed no discernable effects for older ages (Griffiths et al. 1992; Priest 2020). Higher salinities in nearshore waters are indicative of a strong marine influence from coastal upwelling events where coastal brackish water is pushed offshore and replaced by more marine waters that often have higher concentrations of nutrients and zooplankton (Ross 1988; Moulton et al. 2010; Schulze and Pickart 2012). Higher zooplankton densities have been previously reported to occur in the transition layer between onshore moving marine water masses and nearshore brackish waters (Craig and Dillinger 1981; Craig et al. 1982b). Isotopic analyses of Arctic Cisco indicated a strong dependence on marine-derived resources by age-3 (Craig 1894; Kline et al. 1998; von Biela et al. 2013). Thus, the observation that Arctic Cisco grow faster in years with higher salinities agrees with the pattern common to upwelling systems worldwide where upwelling increased foraging opportunities near the coast (Black et al. 2011). It is also possible that higher salinities allowed Arctic Cisco to feed more favorably by excluding other whitefishes with lower salinity tolerances (Griffiths et al. 1992; Fechhelm et al. 1996). Analysis of long-term catch data in the nearshore zone has shown that catches of Broad Whitefish, Humpback Whitefish, and Least Cisco were lower at higher salinities, while the presence of Arctic Cisco was greater at higher salinities (Moulton et al. 2010; Priest 2020).

Years of warmer than average water temperatures corresponded with years of increased growth rates, which was expected given the well-established relationship between water temperature and otolith growth for other fishes (Morrongiello et al. 2011; Rountrey et al. 2014; van der Sleen et al. 2018; Vieira et al. 2019; Tanner et al. 2019) and understanding that Arctic

Cisco prefer the warmer range of temperatures available in the Beaufort Sea (Fechhelm et al. 1982; Craig 1984). Relative to prior *in-situ* growth analyses for younger ages, water temperature showed a much weaker relationship with growth rate variation than did other extrinsic factors (Griffiths et al. 1992; Priest 2020). Differential responses to water temperature can be attributed to allometry, specifically that mass-specific storage of energy reserves increases with body size (Shuter et al. 2012). As a result, larger individuals require a lower net energy expenditure to maintain growth during less optimal growing conditions (e.g., colder waters), which may weaken the relationship between water temperature and somatic growth. In addition to direct effects, warmer waters could have indirectly affected growth through lower trophic-level influences. For example, warmer, ice-free waters in the Arctic Ocean promote higher primary productivity in photosynthetic producers (Lewis et al. 2020), which should result in greater productivity at higher trophic levels (Lavoie et al. 2010; Zhixuan et al. 2016). Water temperature has also been identified as a primary factor shaping nearshore fish community structure (Priest 2020) and could have influenced foraging interactions among species. In conclusion, warmer waters likely favored increased growth rates in Arctic Cisco through a combination of direct metabolic and indirect effects.

Arctic Cod abundance showed a weak, negative association with biochronology relative to salinity and water temperature. Years of lower than average Arctic Cod catches typically corresponded to years of increased growth rates in Arctic Cisco. However, there was no evidence of putative density dependence influencing annual growth rates because the highest catch years for Arctic Cod were not associated with the lowest growth years in Arctic Cisco. Alternatively, differences in habitat selection between species driven by thermal preference could have mediated this relationship. Fish distribution in the nearshore zone is not independent of

environmental conditions (Priest 2020) because individuals seek out conditions that optimize growth and survival (Hansen and Closs 2009). As previously mentioned, Arctic Cisco prefer and grow more rapidly at the warmer end of the range of water temperatures available in the Beaufort Sea during the ice-free summer period (11-16°C; Fechhelm and Gallaway 1982; Griffiths et al. 1992; Priest 2020). Conversely, Arctic Cod prefer and grow more rapidly at lower water temperatures below 7°C (Laurel et al. 2016; Marsh and Mueter 2019). It is also possible that Arctic Cod's association with Arctic Cisco growth rate variation was spurious, as suggested by the low-predictive power and significance of this association. This was further supported by examination of the regression diagnostic plots which indicated the presence of highly influential points (e.g., Arctic Cod catches in 2002 and 2016) and a slight non-random distribution in the residuals.

East wind speed and Sagavanirktok River discharge showed no association with the biochronology. Prior research has suggested that growth rate variability in Arctic Cisco is influenced by prevailing winds during the summer ice-free growing period (see Fechhelm et al. 1996; von Biela et al. 2011). Prevailing winds are a driver of mixing patterns along the Beaufort Sea coast (Ross 1988; Dunton 2006) and may provide an index for the onshore movement of marine invertebrates to the nearshore zone. However, the presence of sea ice can influence the strength of upwelling and circulation patterns on the Beaufort Sea shelf by weakening the effects of wind forcing (weaker upwelling) or imposing more stress on the water column (stronger upwelling), which may contribute to the low predictive power of wind in the current study (Pickart et al. 2009; Schulze and Pickart 2012). River discharge was suspected to be linked to growth rates through influencing foraging success and behavior, prey availability in the nearshore zone, and osmoregulatory efficiency (De Robertis et al. 2003; Lowe et al. 2015). Such

influences were not likely detected by the biochronology due to the short temporal extent of high-discharge events into the Sagavanirktok River delta and the fact that Arctic Cisco are a mobile species able to move out of the river delta in search of more optimal growing conditions. Although river discharge was a significant factor influencing growth rates at the age 0 life stage of the species (von Biela et al. 2011), discharge data were not lagged to account for biological processes in the current study.

This study has several important caveats that limit interpretations. The extensive summer range of Arctic Cisco along the Beaufort Sea coast likely influenced the strength of a common growth signal shared among individuals (Erickson and Bond 1989). Low site fidelity would generally limit the detection of climate-growth relationships to broader scale growth synchronizers (Black et al. 2009). Thus, it is possible that the low spatial coverage of extrinsic measurements (e.g., water temperature and salinity) in this study, relative to Arctic Cisco's summer range, weakened the strength of extrinsic-growth relationships. Future studies should investigate the spatial connectivity of environmental and biologic conditions along the Beaufort Sea. Such information will be essential for understanding future climate-growth relationships in the nearshore Beaufort Sea.

Although sea ice extent and timing were not assessed in this study, we suspect it to be a significant factor influencing growth rate variation at the sub-adult and adult life stages of Arctic Cisco. A growth response would be anticipated because biological productivity and oceanographic processes in the Beaufort Sea region are linked to the presence of sea ice (Craig et al. 1982a; Craig 1984; Vermaire et al. 2013; Ji et al. 2013; Hunt et al. 2014). As noted by Priest (2020), there is a lack of high-resolution sea-ice data for the nearshore Beaufort Sea. Preliminary analyses attempted to estimate growing season length using satellite imagery data from the

NASA Worldview application (<https://worldview.earthdata.nasa.gov/>), part of the NASA Earth Observing System Data and Information System (EOSDIS). However, this approach yielded nothing conclusive given the high subjectivity in determining the beginning and end of the growing season. Future studies should assess the linkage between sea ice and growth rate variability of Arctic Cisco, as well as other nearshore Beaufort Sea fishes.

As previously noted, there is a current lack of long-term prey data in the nearshore Beaufort Sea. Future studies should assess the link between the abundance, composition, and quality of prey resources in nearshore areas of the Beaufort Sea. Such information would increase the understanding of links between offshore processes and secondary productivity in the nearshore zone, as well as, trophic interactions in this environment. In conjunction with prey resource data, isotopic analyses will be required to further understand trophic dependencies of nearshore fishes.

In this study, otolith biochronology identified significant interannual growth rate variation in the subsistence fish species, Arctic Cisco. In recent decades, the nearshore Beaufort Sea has undergone rapid environmental changes. For example, mean annual water temperatures in the nearshore zone have warmed by 1.4°C since 2001 while the length of the ice-free season increased by 58 days from 1979 to 2016 (Bonsell and Dunton 2018; Priest 2020). East winds have also shown an increasing prevalence in the nearshore Beaufort Sea and, in the absence of land-fast ice, have increased the intensity and frequency of shifting water masses along the coast (Reimnitz and Maurer 1979; Vermaire et al. 2013; Wood et al. 2013; Priest 2020). These cumulative factors, coupled with increased terrestrial inputs into the Beaufort Sea, could mean a more productive ice-free feeding period for Arctic Cisco (Doxaran et al. 2015; Wang and Overland 2015). Despite these apparent benefits, there remains uncertainty in the abundance,

composition, and quality of prey items at warmer temperatures (Hunt et al. 2011; Dezutter et al. 2019). Further, it is unclear how productivity in Arctic Cisco will respond to the freshening of the Beaufort Sea and increasing number of species in the nearshore zone (Preist 2020; Proshutinsky et al. 2019). This study further emphasizes the need for continued monitoring of high-latitude nearshore ecosystems at the forefront of climate change, as shifts in productivity will have direct consequences on food security for Indigenous communities in the region.

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Tables

Table 1.1 Description of intrinsic and extrinsic parameters and their data ranges used in linear mixed-effects models for Arctic Cisco incremental-growth analyses for the Prudhoe Bay, region of Alaska.

Parameter	Description	Data Range
<i>Sample.ID</i>	Unique fish identification number	
<i>Age</i>	Age growth increment was formed	2 to 9 years
<i>Year</i>	Calendar year growth increment was formed	1996–2018
<i>SST</i>	Mean annual water temperature (in °C)	1996, 1998, 2001–2018
<i>Salinity</i>	Mean annual salinity (in psu)	1996, 1998, 2001–2018
<i>Wind Direction</i>	Mean annual east wind speed (in km/hr)	1996–2018
<i>Discharge</i>	Mean annual Sagavanirktok River discharge (in m ³ /s)	1996–2018
<i>Whitefishes</i>	Mean annual catch-per-unit effort for whitefish abundance (in n/hr)	2001–2018
<i>Arcticcod</i>	Mean annual catch-per-unit effort for Arctic Cod abundance (in n/hr)	2001–2018

Table 1.2 Mixed-effects model structures used to predict Arctic Cisco growth near Prudhoe Bay, Alaska. Terms are defined as follows: *Age*: age at increment formation; *Sample.ID*: individual fish; *Year*: the calendar year at increment formation. Random effects are written in lmer4 format.

Model	Fixed Effects	Random Effects
A	<i>Age</i>	$(1 Sample.ID) + (1 Year)$
B	<i>Age</i>	$(Age Sample.ID) + (1 Year)$
C	<i>Age</i>	$(1 Sample.ID) + (Age Year)$
D	<i>Age</i>	$(Age Sample.ID) + (Age Year)$

Table 1.3 Parameter and variance estimates of optimal growth model structure describing Arctic Cisco growth near Prudhoe Bay, Alaska. The **bolded** model was identified as the optimal growth model. Column terms are as follows: AICc: Akaike's information criterion corrected for small sample sizes; R^2_M : r-squared marginal; R^2_C : r-squared conditional; $\Delta AICc$: difference in AICc from the optimal growth model. Models are written in lmer4 format, where random-effects are written in parenthesis. The *Age* term, representing age at increment formation, was log-transformed and mean-centered prior to model fitting. The *Sample.ID*, representing individual fish, and *Year*, representing the calendar year at increment formation, were treated as factors in all model comparisons.

Model		AICc	R^2_M	R^2_C	$\Delta AICc$
A	<i>Age</i> + (<i>I</i> <i>Sample.ID</i>) + (<i>I</i> <i>Year</i>)	-537	0.66	0.76	206
B	<i>Age</i> + (<i>Age</i> <i>Sample.ID</i>) + (<i>I</i> <i>Year</i>)	-597	0.66	0.77	146
C	<i>Age</i> + (<i>I</i> <i>Sample.ID</i>) + (<i>Age</i> <i>Year</i>)	-686	0.61	0.75	56
D	<i>Age</i> + (<i>Age</i> <i>Sample.ID</i>) + (<i>Age</i> <i>Year</i>)	-743	0.62	0.76	0

Table 1.4 Coefficient of determination (R^2), intercept, slope and associative p -values for relationships with the Arctic Cisco otolith biochronology near Prudhoe Bay, Alaska. Significant relationships ($p < 0.05$) with the otolith biochronology are **bolded**. Acronyms are defined as annual averages of water temperature (*SST*), salinity (*Salinity*), east wind speed (*Wind Direction*), Sagavanirktok River discharge (*Discharge*), catch-per-unit effort of multiple whitefish species (Arctic Cisco, Least Cisco, Broad Whitefish and Humpback Whitefish; *Whitefishes*), and catch-per-unit effort of Arctic Cod during the ice-free summer feeding period (01 July – 25 August) in the Beaufort Sea, Alaska.

Covariate	R^2	Intercept	Slope	p -value
<i>SST</i>	0.31	0.31	1.76	<0.05
<i>Salinity</i>	0.47	0.56	1.26	<0.001
<i>Wind Direction</i>	0.04	-0.02	0.10	0.72
<i>Discharge</i>	0.08	0.72	-0.15	0.11
<i>Whitefishes</i>	0.11	0.13	-0.00	0.09
<i>ArcticCod</i>	0.22	0.09	-0.03	<0.05

Figures

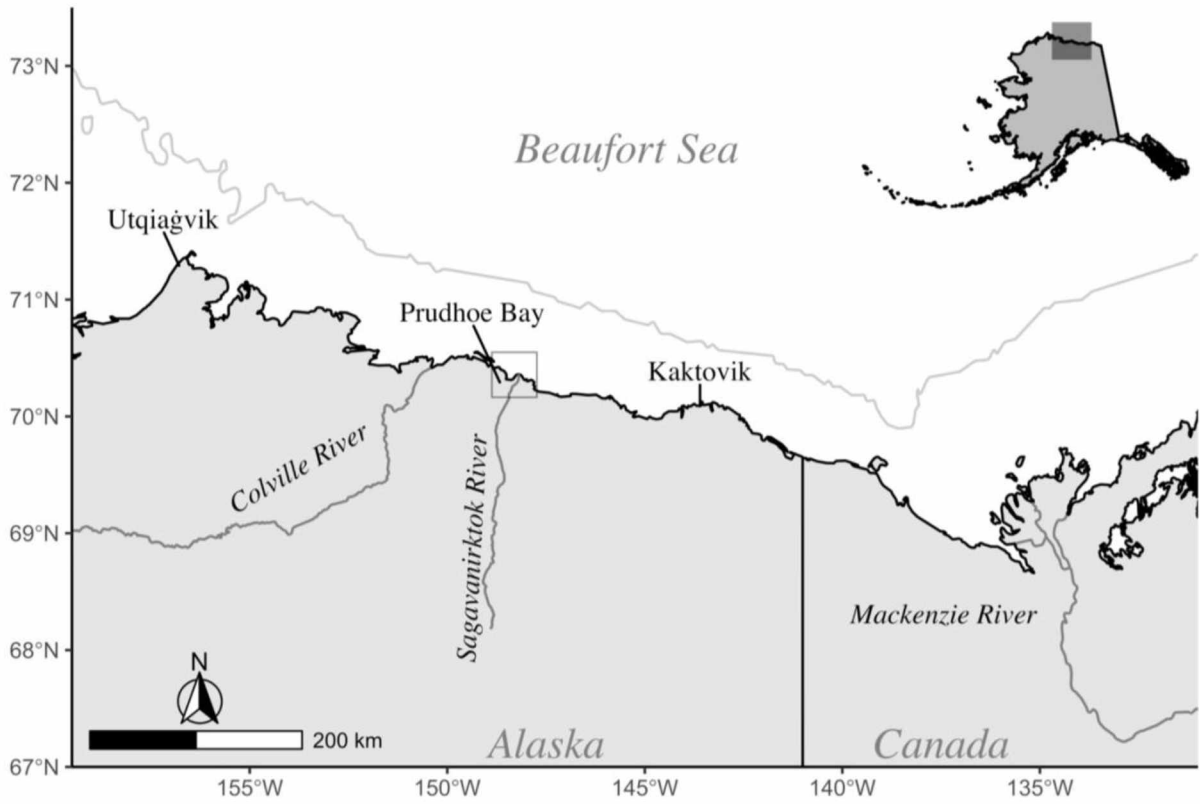


Figure 1.1 The Alaskan Beaufort Sea coast with a 200-m contour showing the geographic distribution and sampling area (indicated by grey box) from which Arctic Cisco were collected outside Prudhoe Bay, Alaska.

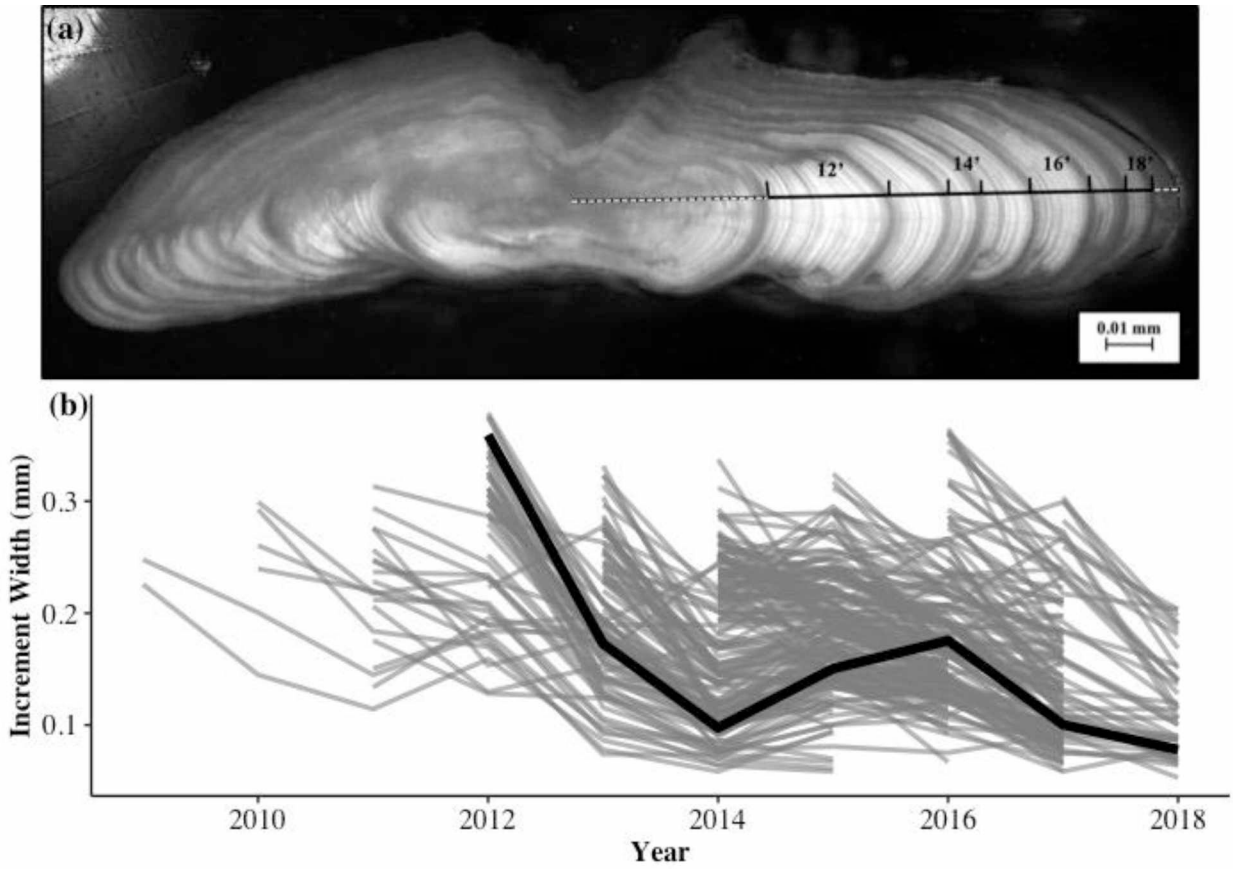


Figure 1.2 (a) A transverse otolith section from an age-8 Arctic Cisco captured in 2019 near Prudhoe Bay, Alaska. The measurement axis (black line) and annuli (tick marks) with corresponding year assignments (in shorthand notation) are shown. The age-0 and marginal measurements (represented as dashed lines here) were excluded from analyses because they do not represent a full year of growth. (b) Raw growth increments (grey lines; measured in mm) of individuals captured between 2016 and 2019 organized by capture year. The bold black line represents the raw growth increments from the eight-year-old Arctic Cisco pictured above (a).

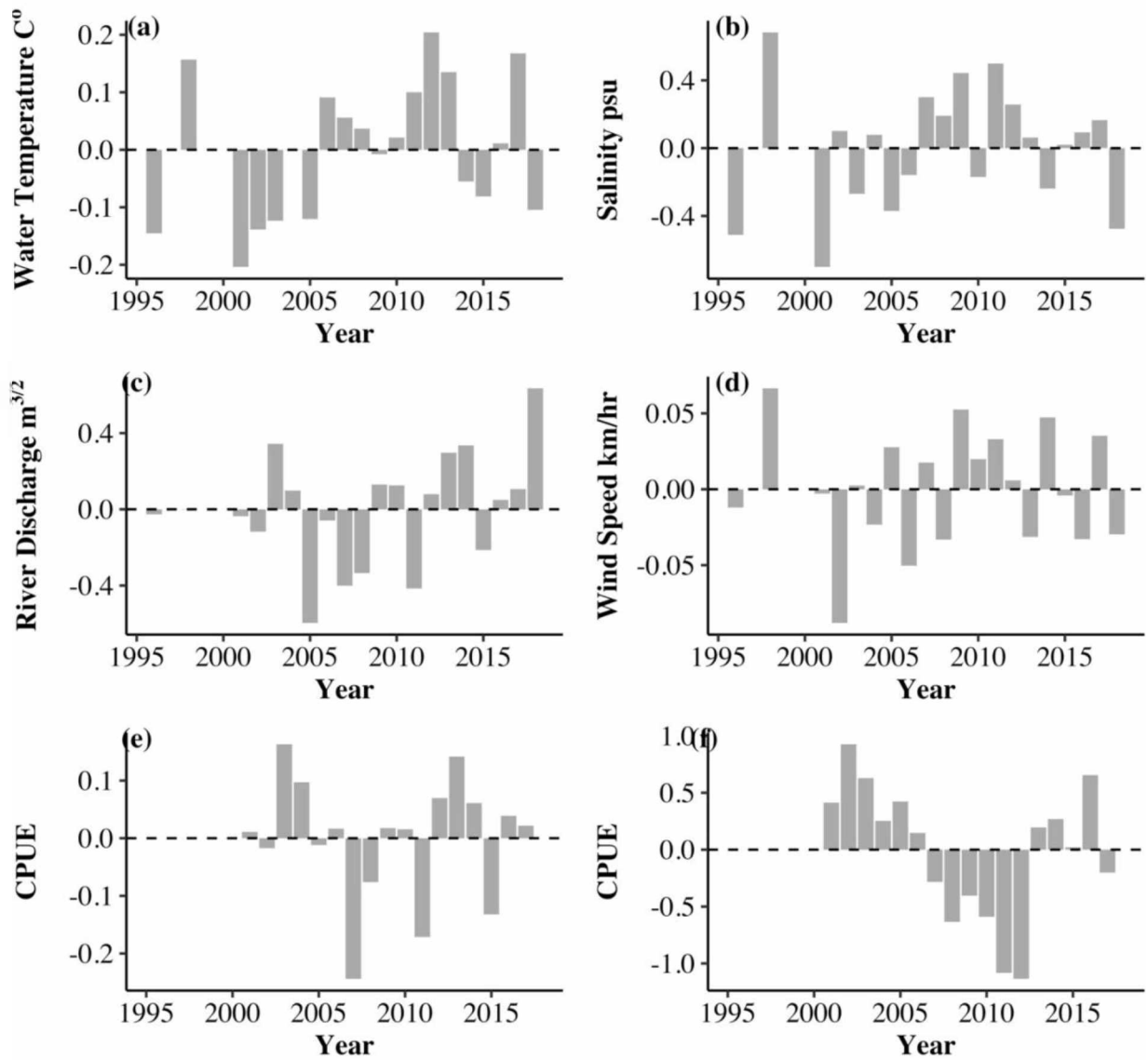


Figure 1.3 Mean annual values for environmental conditions (a, b, c, d), whitefish abundance (panel e), and Arctic Cod abundance (panel f) in the nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska. Environmental and catch data were mean-centered to aid in visualization of interannual variability.

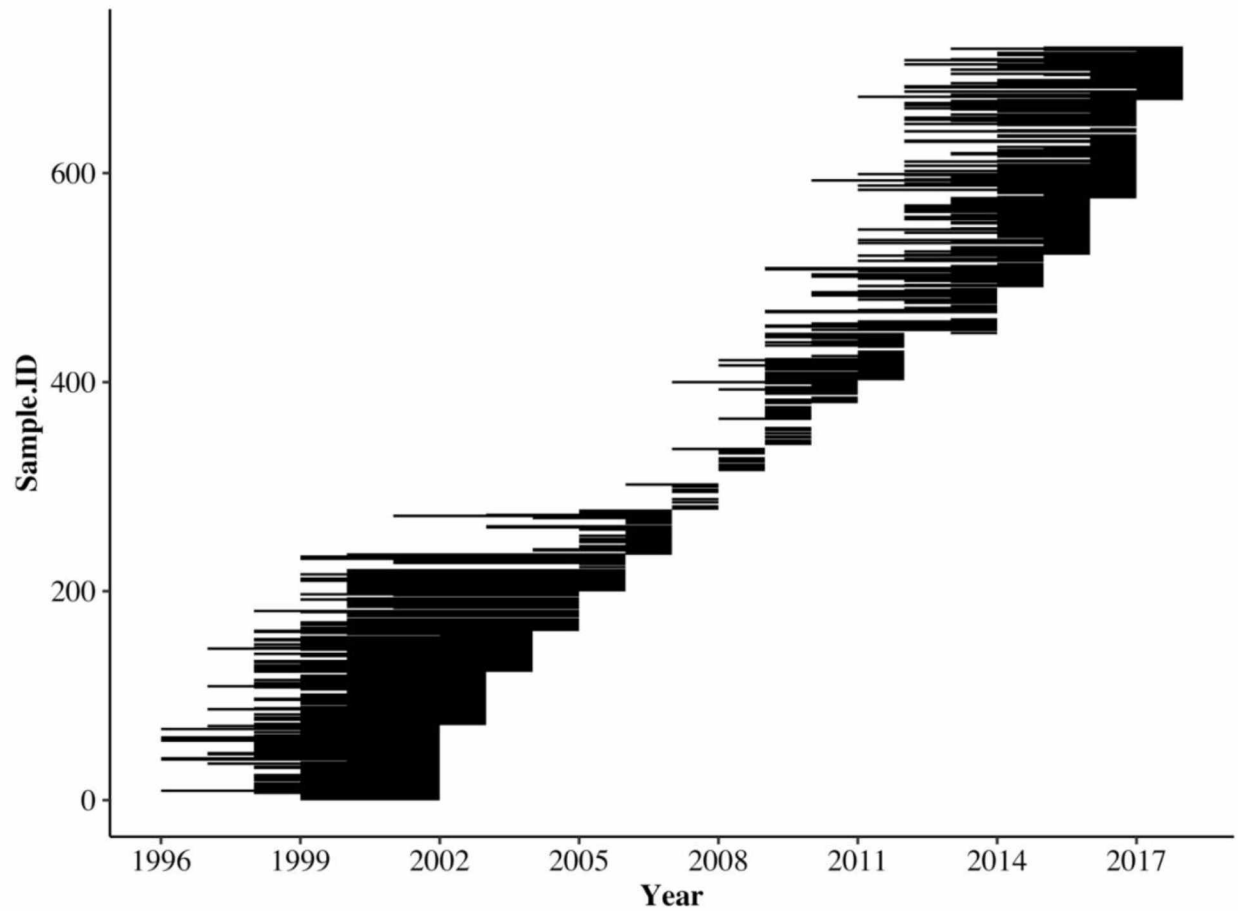


Figure 1.4 Temporal coverage of the 2,696 growth increments from 730 Arctic Cisco captured near Prudhoe Bay, Alaska used in analyses. Each line represents the growth history of an individual (*Sample.ID*) starting at age-1 (left side) to the date of capture (right side). No fish were sampled in 2014 and each growth year was represented with at least seven growth increments.

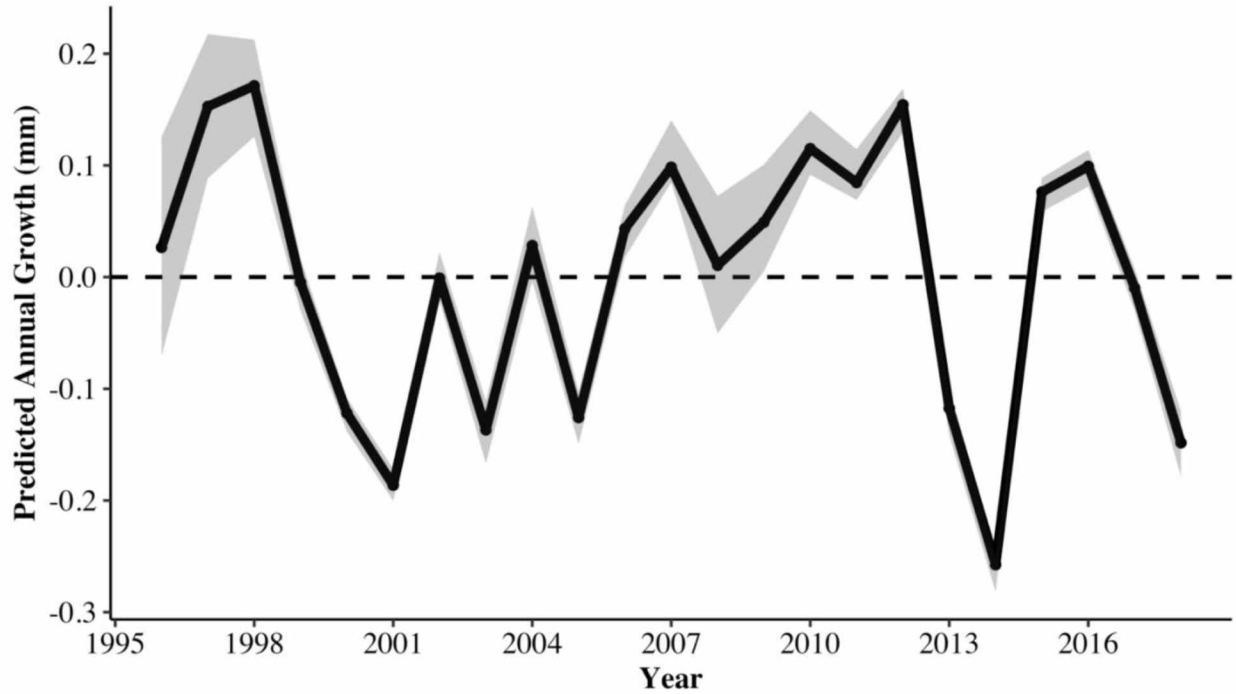


Figure 1.5 The extracted year effect (black line) and associated standard error (grey shaded area) from the intrinsic growth model used to describe Arctic Cisco growth (Table III, model D) near Prudhoe Bay, Alaska. The black line represents the otolith biochronology for the sub-adult and adult life stages of Arctic Cisco. Years of faster growth are those when the solid black line and shaded area are above the dashed line and years of poor growth are those where the line and shaded region are below the dashed line.

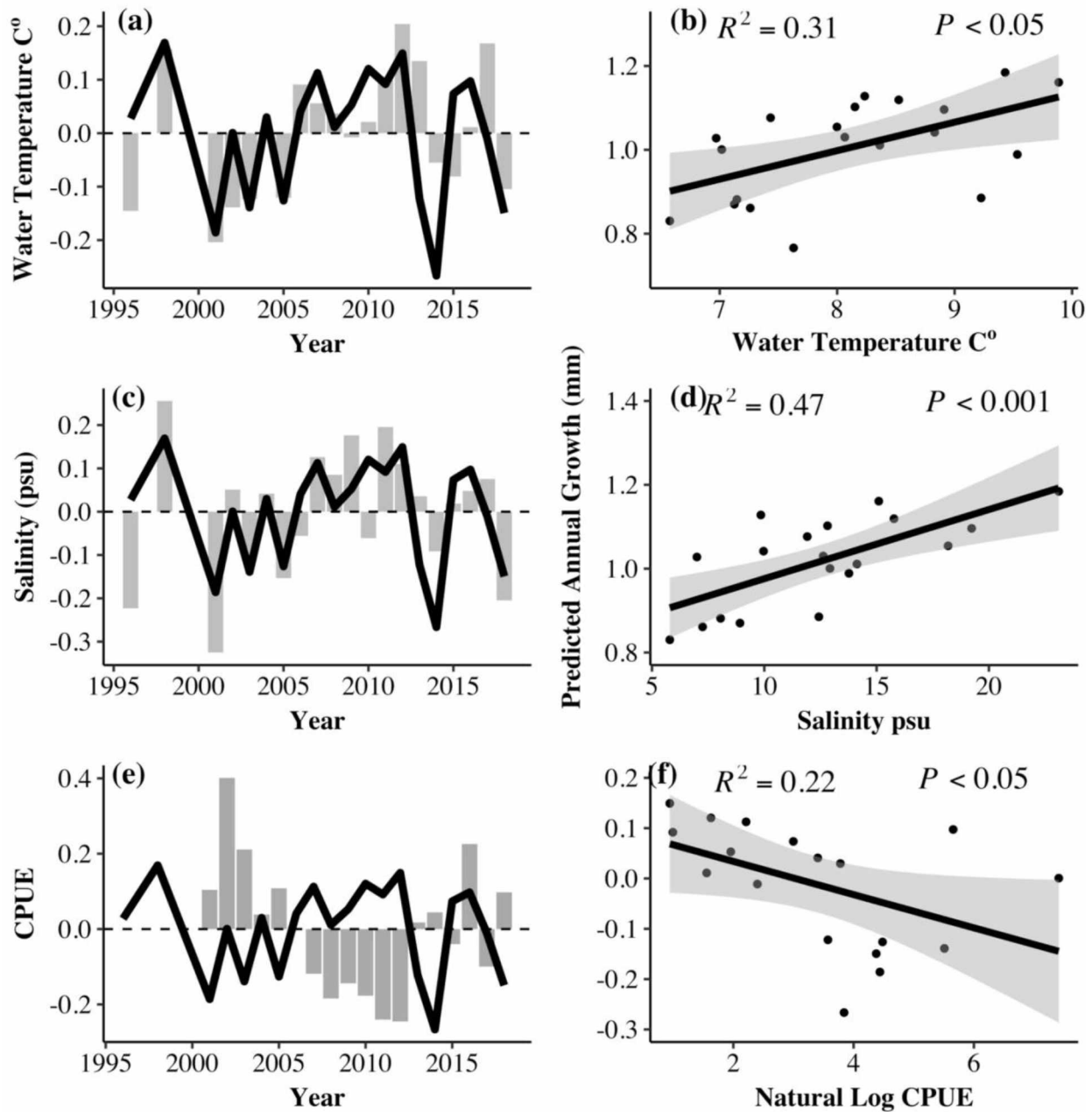


Figure 1.6 Significant correlates (bars in a,c,e; $P < 0.05$) with the Arctic Cisco otolith biochronology (the solid black line in plots a, c, and e) near Prudhoe Bay, Alaska and their associative linear model predictions with 95% confidence interval (shaded area): (a, b) mean annual water temperature, (c, d) mean annual salinity, and (e, f) mean annual Arctic Cod catch per unit effort (CPUE). All extrinsic correlates were natural log-transformed and mean-centered prior to model fitting.

Chapter 2: Precision of Three Hard Structures in Four Whitefishes²

Abstract

Inaccuracies in aging data can impact sustainable management practices and hinder the ability to monitor stocks. We sought to determine if dorsal fin rays and scales of Arctic Cisco *Coregonus autumnalis*, Least Cisco *Coregonus sardinella*, Broad Whitefish *Coregonus nasus*, and Humpback Whitefish *Coregonus pidschian* collected from the Beaufort Sea, Alaska were reliable predictors of age relative to otoliths. Coefficient of variation (CV) and reader confidence scores of age estimates made from three independent readers were used to assess precision and readability of structures within each species. Age-bias plots were used to detect systematic biases as a function of age. Among-reader precision was highest in otoliths for Arctic Cisco and Least Cisco (both CV= 10.40%) and in dorsal fin rays for Broad Whitefish (CV= 6.87%) and Humpback Whitefish (CV= 6.79%). Scales had the lowest among-reader precision for all species and only were statistically different from that of otoliths in Broad Whitefish and Humpback Whitefish. Within-reader, among-structure bias plots showed that fin rays and scales provided similar age estimates as otoliths only up to the age of maturity, which was specific to each species. Structure comparisons and age-bias plots suggested that fin rays underestimated age less than scales. Further, reader confidence was lowest in scales for all species. These results suggest that dorsal fin rays may be conservatively used to estimate age in Least Cisco < 300 mm, Broad Whitefish < 450 mm, and Humpback Whitefish < 350 mm, and that otoliths should remain the primary aging structure for larger individuals. For Arctic Cisco, fin rays and scales provide

²Gatt, K. P., T. M. Sutton, L. M. Hynes, V. R. von Biela, M. V. McPhee. 2021. Precision of four hard structures in four Arctic whitefishes. In preparation for submission to *North American Journal of Fisheries Management*.

similar age estimates as otoliths for all age and size classes. Overall, this study demonstrates that non-lethal structures may be used to conservatively estimate age in immature Arctic whitefishes.

Introduction

Accurate aging information retained in hard structures of fishes (e.g., otoliths, fin rays, scales, etc.) is fundamental to the development of sound management decisions that sustain commercial, recreational, and subsistence harvest of fish stocks (Ricker 1969; Beamish and McFarlane 1995). Age-specific biological data obtained from inaccurate age estimates can have negative impacts on the management of a particular stock by under- or over-estimating rate-dynamic parameters (e.g., growth, age-specific mortality, maturation), which are used to assess stock health and productivity (Mills and Beamish 1980; Bertignac and de Pontual 2007; Yule et al. 2008). Inaccuracies in age estimates may also impact the characterization of physical (e.g., water chemistry) and biological (e.g., species interactions, prey availability) relationships that regulate fish population dynamics. Misidentifying these relationships inhibits the ability to make accurate assessments of a species' resilience to environmental change, which is occurring in Arctic regions at more than double the rate of the global average (Wood et al. 2013).

In the subarctic and Arctic regions of Alaska and Canada, Arctic Cisco *Coregonus autumnalis*, Least Cisco *Coregonus sardinella*, Humpback Whitefish *Coregonus pidschian*, and Broad Whitefish *Coregonus nasus* are prominent members of the fish community (Scott and Crossman 1973; Mecklenburg et al. 2002; Gatt et al. 2019). The complex, and in some cases, variable life history of these whitefishes, allows them to exploit a variety of freshwater and marine habits (Craig 1984; Harris et al. 2012). Similar to other whitefishes, the four aforementioned species are commonly harvested for subsistence and commercial purposes throughout their geographic range (Moulton et al. 2010; Brown et al. 2012; Brase and Baker 2014). In addition to their consumptive value, multi-generational harvest of these species has

also earned them cultural and social prominence among Indigenous peoples in the Arctic (Harper et al. 2007; Moulton et al. 2010).

Despite wide-spread harvest and high value in the Arctic, many whitefishes lack formal assessment of the precision of age estimates using hard structures. In the absence of true age validation methods, precision analyses are used to measure the repeatability of assigning age to a structure and for identifying potential biases (in both structure and reader) that may lead to inaccurate age estimates (Campana et al. 1995). Historically, whitefishes have been assigned age estimates using otoliths, fin rays, and scales (Watkins et al. 2015b; Stewart et al. 2016; Lepak et al. 2017). For slow-growing, high-latitude whitefishes, otoliths are generally regarded as the most reliable structure for estimating age based on precision analyses (Howland et al. 2004; Zhu et al. 2015). Despite the reliability of otoliths, these structures can be time-consuming to remove and require euthanizing fish, which may limit the number of individuals that can be efficiently and sustainably removed from a population. Further, the time and cost of processing otoliths may be greater than for alternative structures (Muir et al. 2008b). There has been success in reliably assigning age estimates to whitefishes using alternate, non-lethal structures (Howland et al. 2004; Muir et al. 2008b; Watkins et al. 2015b). Conflicting results, however, suggest that aging structure and precision analyses need to be species, and in some cases, population-specific (see Zhu et al. 2015).

No prior study has attempted to statistically quantify the reproducibility of age estimates in Arctic Cisco, Least Cisco, Humpback Whitefish, and Broad Whitefish. Precision analyses for high-latitude populations of Lake Whitefish *Coregonus clupeaformis* found fin rays and scales to be suitable nonlethal alternatives for estimating ages in individuals less than age 10 (Zhu et al. 2015b). Identifying age-estimate biases along a gradient of length are directly applicable to those

studies that sample a subset of the population, where alternative structures have the potential to provide precise age estimates without sacrificing the fish. For instance, 90% of all Arctic Cisco and Broad Whitefish captured during annual monitoring of nearshore fish assemblages in the Beaufort Sea, Alaska, are less than 249 mm fork length and are younger than four years old based on cohorts distinguishable in length-frequency plots (Green et al. 2018; Gatt et al. 2019; K. Gatt, University of Alaska Fairbanks, unpublished data). Based on precision analyses for closely related species (Howland et al. 2004; Mills and Chalanchuk 2004; Muir et al. 2008b; Zhu et al. 2015b), we anticipate scales and fin rays to be as precise as otoliths for estimating ages up to the age of maturation for whitefishes in the Arctic.

To assess the aforementioned hypothesis, age estimates of Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish were compared using dorsal fin rays and scales to those made using otoliths. We sought to determine whether the age estimates and readability of non-lethal structures were similar to otoliths. Specifically, we evaluated between-reader precision, assessed age-estimation biases, and compared reader confidence among structures for each of the four species. Information gained from this study will aid fisheries professionals in selecting the most appropriate hard structure for assigning whitefish age. This will, in turn, allow more accurate estimation of rate-dynamic parameters and better monitor stocks at the forefront of climate change.

Methods

Field Collection

Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish were collected using paired fyke nets deployed in nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska (Green et al. 2018; Gatt et al. 2019). Fish sampling occurred over a ten-day period from

21 July to 01 August during the 2019 Beaufort Sea Long-Term Nearshore Fish Monitoring Project field season. The short duration of the sampling period provided consistency in the edge interpretation by standardizing the “plus growth” in the margins of each individual fish. Plus growth refers to the incomplete annual increment in the process of being formed when the fish is captured. Fyke nets measured 1.8 m x 1.7 m with 1.27-cm stretch mesh. A net lead of 2.5-cm stretch mesh that was 60-m long and 1.8-m height extended from the attachment point between the fyke nets to the shore. Attached to the opening of each fyke net frame was a 15-m wing block net (1.8-m high, 2.5-cm stretch mesh) that was placed at a 45° angle toward the shore to funnel fish into each net. Each day, captured fish were enumerated, identified to species, and measured to the nearest 1-mm fork length (FL). Individuals for this study were collected based on fork length using 25-mm length groups spanning length ranges specific to each species (Appendix B). When numbers permitted, a minimum of five individuals were randomly selected from each length group following age-based sampling protocols of Miranda and Colvin (2017).

Once FL was measured, aging structures were removed from each fish. Sagittal otoliths were extracted following protocols detailed in Secor et al. (1992). Dorsal fin rays were removed by cutting the first four spines at the point of insertion using scissors, similar to procedures reported by Borkholder and Edwards (2001). A minimum of 10 scales were collected from the left side of each fish in the region posterior to the dorsal fin and above the lateral line. This region was chosen because a large portion of individuals retained scales in this region relative to other locations on the body (e.g., behind the pectoral fin) and larger scales from this region allowed for greater ease in interpreting crowded annuli for older fish (McInerny 2017). All sagittal otoliths were cleaned of excess tissue and fluid, and stored in pre-labeled centrifuge

vials, while dorsal rays and scales were stored in separate, pre-labeled coin envelopes. Prior to processing, all structures were placed in a fume hood and allowed to dry for up to two weeks.

Structure Preparation

Aging structures included: (1) transverse cut sagittal otoliths; (2) whole dorsal fin rays; and (3) scales pressed between two microscope slides (hereafter referred to as “mounted scales”). For preparation, otoliths were embedded in epoxy (West System Epoxy, Gougeon Brothers Inc., Bay City, Michigan) using silicone multi-well embedding molds (Electron Microscopy Sciences, Hatfield, Pennsylvania). A single cut was made through the nucleus along the transverse plane separating the structure into posterior and anterior sections. Cuts were made with an Isomet low-speed saw (Buehler, Lake Bluff, Illinois) equipped with a single diamond wafering saw blade (blade thickness = 0.23 mm). Posterior and anterior sections were lightly hand-polished using wetted, 2,000-grit waterproof sandpaper, and placed in black molding clay. Mineral oil was applied on the polished surface to increase the clarity of zonation. Only whole otoliths absent of vaterite replacement were considered for aging analyses.

The first four dorsal fin rays were cut at their base just behind the point of inflection to separate the rough edge from the rest of the ray. Individual fin rays were separated from tissue and hand-polished using 2,000-grit wetted sandpaper. For individuals less than 150 mm in length, we mounted fin rays in epoxy to prevent fracturing of the fin ray shaft during the polishing process. All cutting was conducted using a rotary Dremel tool (Dremel, Racine, Wisconsin) fixed to a cutting platform and equipped with a diamond-tipped cutting wheel. Care was taken not to cut or polish too far from the point of insertion because the precision of dorsal fin rays for aging has been shown to diminish with increased distance from the proximal end of the spine (Koch et al. 2008; Watkins et al. 2015a). Fin rays were imaged by placing individual

rays in black molding clay, proximal end up, and a thin layer of mineral oil was added to increase clarity of zonation for imaging under reflected light. The proximal end of each fin ray was placed 90° to the scope lens and light was applied directly to the polished surface.

Scales containing residue that reduced annuli clarity were cleaned with hot water prior to being mounted on microscope slides. A minimum of six scales were mounted for each individual and imaged using transmitted light. Only scales void of reabsorption and eroded edges were considered for analyses.

Age Determination

Age determinations from otoliths, fin rays, and scales were made from three independent readers using images captured using a high-resolution Leica DFC 450 digital camera (Leica DFC 450, Leica Microsystems Inc., Buffalo Grove Illinois) mounted on a Leica M165C stereomicroscope (10-60X magnification) under 20-60X magnification (Figure 2.1). Leica Application Suite software was used to view and enhance images. Two of the three readers had prior fish aging experience using otoliths, fin rays, and scales; reader 1 had prior knowledge in assigning age estimates to the species in this study, whereas reader 2 had not previously aged the four whitefishes examined in this study. Reader 3 had no prior experience in annuli identification, which provided a relative measure of the amount of experience needed to assign precise age estimates using these structures. To avoid reader bias, each reader independently assigned age estimates using all three structures without knowledge of fish length and age estimates from other readers. Images were organized into separate libraries by species and structure. At no point were readers allowed to assign age estimates to multiple structures and species in the same day to avoid bias. Before age estimation, readers were provided sample images with annuli marked to refresh individuals of annulus patterns on each structure similar to

the methods of Watkins et al. (2015) and Branigan et al. (2019). Scale annuli were identified as areas of high circuli density and cutting over of successive circuli. Dorsal fin ray and otolith annuli were identified as translucent bands separated by opaque areas (Schill et al. 2010; Fischer and Koch 2017).

Immediately after counting annuli on each structure, each reader assigned a confidence score to their age estimate following the 0 (no confidence) to 3 (complete confidence) rating criteria used by Spiegel et al. (2010). Confidence-rating criteria score provided an additional measure of the readability of a given structure (Fitzgerald et al. 1997; Koch and Quist 2007; Spiegel et al. 2010). Any fish with an individual structure where a confidence rating among readers averaged <1 was removed from analyses due to poor quality.

Data Analyses

To compare precision among-readers, within-structure and within-reader, among-structures, coefficients of variation (CV) were calculated as:

$$CV_j = 100X \frac{\sqrt{\frac{\sum_{i=1}^R (x_{ij} - X_j)^2}{R-1}}}{X_j},$$

where x_{ij} was the i th age estimate for the j th fish, X_j was the average age of the j th fish, and R was the number of times the fish was aged (Campana et al. 1995). The CV was calculated for each fish and aging structure and averaged to estimate among-reader precision by structure. Because fin ray and scale age were anticipated to deviate from otolith age (referred to as inflection point hereafter), CV was averaged across all fish and structures (e.g., otoliths versus fin rays) pre- and post-inflection point for within-reader, among-structure comparisons. A coefficient of variation score < 5% has been used as the reference point for aging analysis, where lower CV scores

indicate higher precision (Campana 2001). A Kruskal-Wallis test was used to test for differences in precision among otoliths, fin rays, and scales for each species. This test was chosen over a one-way analysis of variance (ANOVA) test to account for unequal variances. When a significant difference was detected, a Dunn's test (Dunn 1964) was used to identify the location of the significant differences.

Age-bias plots were constructed to evaluate precision and identify bias in age estimates following Campana et al. (1995). Reader bias (among-readers, within-structure) was visually checked by plotting the mean ages of fish estimated by reader 1 for a given structure against those made by reader 2 and reader 3. Reader-1 age estimates were used as the "reference ages" and plotted on the x-axis of age-bias plots while reader-2 and reader-3 age estimates were plotted on the y axis. If there was complete agreement between readers, age estimates followed a 1:1 line of equivalence. If reader 2 overestimated ages compared to reader 1, then the mean age for that cohort fell above the equivalence line. The dispersion of age estimates and number of age classes deviating from the line of equivalence described reader bias; for example, mean ages surrounded by 95% confidence intervals deviating from a line of equivalence for more than two consecutive years were identified as reader bias in this study. Age estimates made within-reader, among-structures for each fish were averaged and plotted to assess age structure bias. Structure bias was detected if age estimates among-structures deviated from the line of equivalence. The dispersion and number of cohorts deviating from the line equivalence were used to describe structure bias.

To assess confidence ratings by structure, a Kruskal-Wallis test by ranks was conducted for each species to account for unequal variances. When a significant difference was detected, a Dunn test (Dunn 1964) was used to determine which combinations were different. All statistical

analyses used a type-I error rate at $\alpha = 0.05$ using program R studio (R development Core Team 2012, Version 1.1.383).

Results

Of the 224 whitefish collected for precision analyses, 203 individuals (53 Arctic Cisco, 44 Least Cisco, 58 Broad Whitefish, and 48 Humpback Whitefish) were assigned age estimates using otoliths, fin rays, and scales. Fork lengths ranged from 124 to 401 mm in Arctic Cisco, 115 to 370 mm in Least Cisco, 184 to 521 mm in Broad Whitefish, and 167 to 415 mm in Humpback Whitefish (Figure 2.2). Age distributions by FL differed among species and structures (Figure 2.2). Mean ages were highest for otoliths in all species, followed by fin rays and scales (Figure 2.2). For Arctic Cisco, fin rays included the most age classes (ages 1 to 9), followed by otoliths and scales (ages 2 to 9). For Least Cisco, Broad Whitefish, and Humpback Whitefish, otoliths provided a wider range of ages and more age classes (ages 2 to 26, 3 to 22, and 3 to 28, respectively) followed by fin rays (ages 2 to 16, 3 to 18, and 3 to 17, respectively) and scales (ages 2 to 14, 2 to 15, and 2 to 15, respectively).

Among-reader, within-structure age-bias plots showed few consistent deviations (more than two years) from the 1:1 line of equivalence (Appendices E-H). The most notable deviation from this line occurred between scale age estimates for Humpback Whitefish between readers 1 and 2 (Appendix H). Reader 2 appeared to consistently under-age individuals relative to reader 1 between ages 7 and 12. Across all species and structures, reader 2 deviated from reader 1 ages more often than reader 3. Reader 1 had the highest precision of age estimates across all species, followed by reader 3 and reader 2 (Appendix I). Among-reader, within-structure CV of age estimates were generally high in all species, but not all structures (Table 2.1). Broad Whitefish had the lowest mean CV among readers and structures (CV = 8.39%), followed by Humpback

Whitefish (CV = 10.44%), Arctic Cisco (CV = 11.56%), and Least Cisco (CV = 12.01%). Among-reader, within-structure mean CV was lowest in otoliths for Arctic Cisco and Least Cisco (both CV = 10.40%) and fin rays for Broad Whitefish (CV = 6.87%) and Humpback Whitefish (CV = 6.79%; Table 2.1). However, similar among most species, scales had the highest mean CV among readers, but were only statistically higher than otoliths for Broad Whitefish ($H = 11.41$, $df = 2$, $P < 0.05$) and Humpback Whitefish ($H = 17.11$, $df = 2$, $P < 0.001$; Table 2.1).

Within-reader, among-structure bias plots showed fin rays and scales provided similar age estimates as otoliths up to the age of inflection, after which non-lethal structures underestimated otolith age (Figure 2.3; Appendices I-J). Underestimation of fish age was less for Arctic Cisco than for the other species; however, both fin rays and scales began to underestimate fish age at age 8 (Figure 2.3). Arctic Cisco scales had higher concordance with otolith age estimates prior to the age of inflection (CV scale-otolith = 8.66%) than fin rays (CV fin ray-otolith = 10.11%), and underestimated fish age more at older ages (CV scale-otolith = 10.43%, CV fin ray-otolith = 10.08%; Table 2.2; Figure 2.3). Underestimation of fish age began in Least Cisco at age 6 for fin rays and age 8 for scales, and was most pronounced after age 8 for both structures. Least Cisco scales had higher concordance with otolith age estimates prior to the age of inflection (CV fin ray-otolith = 11.91%, CV scale-otolith = 10.92%), and more severely underestimated fish age than fin rays at older ages (CV scale-otolith = 33.24%, CV fin ray-otolith = 28.85%; Table 2.2; Figure 2.3). Despite these general trends, no significant differences in CV fin ray-otolith and scale-otolith comparisons were detected pre- and post-inflection point for Arctic Cisco and Least Cisco. Underestimation of fish age in Broad Whitefish began at age 12 for fin rays and scales. Broad Whitefish fin rays had higher concordance with otolith age

estimates prior to the inflection point (CV fin ray-otolith = 6.57%, CV scale-otolith = 7.72%), and underestimated fish age less than scales for older ages (CV fin ray-otolith = 20.36%, CV scale-otolith = 29.40%; $H = 13.62$, $df = 1$, $P < 0.001$; Table 2.2; Figure 2.3). Underestimation of fish age was most apparent in Humpback Whitefish, with fin rays and scales showing minimal bias starting at age 6 and increasing significantly by age 10 for both structures (Figure 2.3). Humpback Whitefish fin rays had significantly higher concordance with otolith age estimates prior to the age of inflection (CV fin ray-otolith = 7.38%, CV scale-otolith = 11.99%; $H = 8.29$, $df = 1$, $P < 0.05$), and underestimated fish age less than scales at older ages (CV fin ray-otolith = 25.46%, CV scale-otolith = 44.81%; $H = 22.11$, $df = 1$, $P < 0.001$; Table 2.2; Figure 2.3).

Among-reader confidence showed similar trends as precision. Reader confidence was on average highest for reader 1, followed by reader 3 and reader 2 (Appendix C). Overall, readers were generally less confident in scale age estimates than for otolith and fin ray age estimates in all species (Table 2.2). Confidence in scale age estimates were only significantly lower than otolith age estimates in Broad Whitefish ($H = 30.09$, $df = 2$, $P < 0.001$), and Humpback Whitefish ($H = 30.09$, $df = 2$, $P < 0.001$; Table 1). Confidence among readers for Arctic Cisco structures showed a diverging trend from other species, with readers being less confident in both scale and fin ray age estimates than otolith age estimates ($H = 23.70$, $df = 2$, $P < 0.001$; Table 2.1). No significant differences in mean reader confidence were detected among structures for Least Cisco (Table 2.1).

Discussion

This study provides the first comparative assessment on precision among hard structures used to estimate age in Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish. These results corroborate previous research that showed that the reliability of non-lethal

structures, such as dorsal fin rays, for aging high-latitude whitefishes declines after the onset of reproductive maturity (Brown et al. 2012). Moreover, these results suggest that scales are the least reliable aging structure for older, slower-growing whitefishes and should only be used for individuals prior to reproductive maturity (Mills and Beamish 1980; Barnes and Power 1984; Howland et al. 2004; Mills and Chalanchuk 2004; Zhu et al. 2015).

Structure-bias plots indicated that fin rays and scales provided similar age estimates for younger age classes and identified the presence and location of the inflection point beyond which fin rays and scales underestimate age. The location of the inflection point varied by species and not by the aging structure, suggesting that age bias resulted from a biological change that influenced the growth of all structures. Indeed, the species specific ages of inflection corresponded to the age of maturity (Philo et al. 1993; Moulton et al. 1997; Brown 2008; Bradley et al. 2016). This result supported prior assumptions that slowing growth at maturity causes annuli to narrow, crowd, and underestimate age (Brown et al. 2012). Stolarski and Sutton (2013) reported a similar outcome for Dolly Varden *Salvelinus malma* in northern Alaska, where fin rays and scales deviated from otolith age estimates at the age of reproductive maturity. Annuli formation in fin rays and scales are more susceptible to crowding because they are more closely associated with somatic growth rate than otoliths, a structure in which growth is primarily influenced by metabolic processes (Mosegaard et al. 1988; Casselman 1990). As a result, the crowding of annuli is often more pronounced in fin rays and scales, especially at the margins for older individuals. Severely crowded annuli increase the difficulty in interpreting marginal growth and often lead readers to underestimate age using fin rays and scales (Mills and Beamish 1980; Casselman 1990). The results of the current study differ somewhat from those reported in Lake Whitefish (see Zhu et al. 2015) in that the onset of age underestimation was often similar-among

structures for each whitefish species. The synchronous onset of underestimation further suggests rapid early growth coupled with strong ontogenetic effects likely influenced trends in age underestimation in this study.

After the age of inflection, scales and fin rays underestimated otolith age, but was more pronounced in scales, particularly for older ages. Precision analyses for closely related whitefishes have demonstrated that scales consistently produce lower age estimates than otoliths (Barnes and Power 1984; Muir et al. 2008a; Herbst and Marsden 2011; Stewart et al. 2016; Lepak et al. 2017) and fin rays (Mills and Beamish 1980; Howland et al. 2004; Muir et al. 2008b; Zhu et al. 2015). In addition to whitefishes, similar trends have also been reported for other fish species (Welch et al. 1993; Rude et al. 2013; Oele et al. 2015; Acre et al. 2017). Scale age underestimation has been most pronounced in slow-growing, long-lived species and/or stocks of a species (Mills and Chalanchuk 2004). For example, Howland et al. (2004) reported that scales in a slow-growing population of Inconnu *Stenodus leucichthys* in the Canadian Arctic underestimate otolith age by as much as 13 years in mature individuals. Whitefishes in the current study showed similar trends of underestimation; for example, scales of Least Cisco underestimated otolith age by as much as 17 years. As noted previously, a problem with using scales for aging older individuals is the crowding of circuli in the growth zone after reproductive maturity. Stolarski and Sutton (2013) noted the presence of a “dense edge” in the scales of mature Dolly Varden, which causes age underestimation. Similarly, whitefish scales in the current study also exhibited circuli crowding in the growth zone which increased the difficulty in interpreting patterns of crossing over toward the margins for older fish.

Fin rays underestimated otolith age less than scales based on age-bias plots and within-reader, among-structure age comparisons. Although the fin ray aging method has been validated

for Lake Whitefish (Mills and Chalanchuk 2004), several studies have demonstrated that fin rays underestimate otolith ages for older fish (Herbst and Marsden 2011; Zhu et al. 2015). In contrast, Howland et al. (2004) reported Inconnu fin rays produced similar age estimates as otoliths across all age classes and noted a slight underestimation of age in the oldest age classes. Severe annulus crowding toward the ray margins for older individuals lead to age underestimation using fin rays, largely because fin ray margins were too opaque to recognize annuli borders (Mills and Chalanchuk 2004). However, in the current study, readers noted that annuli clarity was greater than scales. A common aging error cited for using fin rays, aside from annulus crowding in the margins, is the identification of interior annuli (Beamish 1981; Howland et al. 2004). This did not influence aging estimation in the current study. We found that not having to take additional cuts beyond the initial cut (see Koch et al. 2008) and using dorsal fin rays, which have larger radii than pelvic and pectoral fin rays, allowed adequate spacing between early annuli. Several checks, which had thinner borders than true annuli, were noted and were most pronounced in Least Cisco and Arctic Cisco.

Comparisons of among-reader precision suggested that scales were less precise predictors of age than otoliths and fin rays for Beaufort Sea whitefishes. Moreover, readers had greater difficulty in assigning ages to scales than the other two structures. Although otoliths and fin rays have been shown to be more precise than scales in Inconnu (Howland et al. 2004), this is not always the case for other whitefishes. Herbst and Marsden (2011) and Zhu et al. (2015) reported scales to be more precise than fin rays but less precise than otoliths in Lake Whitefish in Lake Champlain and Great Slave Lake. In contrast, Muir et al. (2008b) found fin rays to be more precise than otoliths and scales. For Mountain Whitefish *Prosopium williamsoni*, scales were more precise than fin rays and otoliths (Watkins et al. 2015). Different relationships among

whitefish species may be attributed to differences in precision assessment (between independent readers versus repeated reads from the same reader), processing methodology, variable life-history types, the environment, or a combination of these factors (Branigan et al. 2019). Despite the variability in precision, readers have consistently found difficulty in assigning ages to scales relative to otoliths or fin rays (Herbst and Marsden 2011; Zhu et al. 2015).

Precision in the current study was generally low, with no structure for any of the species achieving an acceptable level of precision (5%, as suggested by Campana 2001). Precise aging is more challenging for Beaufort Sea whitefishes than for closely related species due to their diadromous life histories and extreme climatic and biological variability of the Arctic nearshore environment. For example, Beaufort Sea whitefishes are iteroparous and do not spawn in successive years nor do all individuals undergo marine migrations each summer period (Brown et al. 2012). Further, growth rates of Beaufort Sea whitefishes show a high degree of interannual variability (see Chapter 1 of this study). Variability in life-history characteristics among fish and growth among years likely attributed to noise to aging structures in the form of checks, poorly formed annuli, and conspicuously narrow or wide growth zones. These cumulative factors can increase difficulty in consistently interpreting annuli formation patterns and likely attributed to lower overall precision.

Ages determined from non-lethal structures showed the highest consistency with those from otoliths in Arctic Cisco. This is likely because most Arctic Cisco captured in Prudhoe Bay are not yet reproductively mature (Brown 2008). Once they reach maturation at ages 7 to 8, Arctic Cisco migrate from Prudhoe Bay to spawn in the Mackenzie River, Canada (Dillinger et al. 1992; Brown 2008). Thus, it is likely that ontogenetic effects do not slow growth sufficiently to cause severe annulus crowding in Arctic Cisco captured in Alaskan waters.

Based on the results of this study, dorsal fin rays and scales appear to provide a non-lethal alternative to estimate the age of Beaufort Sea whitefishes prior to reproductive maturity. Because few mature Arctic Cisco are captured in the Alaskan Beaufort Sea, this study was unable to identify the age or size beyond which fin rays and scales did not offer reliable alternatives to otoliths for aging purposes. Due to lower reader confidence (poor readability) and higher rates of reabsorption in scales of Least Cisco, we recommend limiting the use of age estimation with dorsal fin rays for Least Cisco less than age 10 and 300 mm in length. Further, we recommend limiting the use of age estimation with dorsal fin rays for Broad Whitefish less than age 12 and 450 mm in length, and Humpback Whitefish less than age 8 and 350 mm in length. For individuals greater than these ages and lengths, otoliths remain the primary hard structure to estimate age. In cases in which non-lethal structures are required to age mature individuals, dorsal fin rays are preferred to scales. We emphasize that the applicability of these structures be assessed on a population-specific basis because variable life-history types (e.g., dwarf populations of Least Cisco; Mann and McCart 1981) and because latitudinally-dependent maturation schedules (Brown et al. 2012; Harper et al. 2012) could cause divergence from these results.

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Tables

Table 2.1 Precision of age estimates, measured as mean coefficient of variation (CV), and readability, measured as mean confidence score (0 = no confidence to 3 = complete confidence), across readers for each hard structure used to estimate the ages of Arctic Cisco, Least Cisco, Broad Whitefish and Humpback Whitefish captured in the Beaufort Sea outside Prudhoe Bay, Alaska. Values followed by different letters in each column for each species are significant different ($P < 0.05$).

Species	Structure	Mean CV	Mean Confidence
Arctic Cisco	Otolith	10.40 y	2.60 y
	Fin Ray	11.27 y	2.28 z
	Scale	13.00 y	2.27 z
Least Cisco	Otolith	10.40 y	2.28 y
	Fin Ray	11.10 y	2.19 y
	Scale	14.52 y	2.10 y
Broad Whitefish	Otolith	6.92 y	2.49 y
	Fin Ray	6.87 y	2.57 y
	Scale	11.39 z	2.05 z
Humpback Whitefish	Otolith	10.56 y	2.40 y
	Fin Ray	6.79 y	2.29 y
	Scale	13.98 z	1.83 z

Table 2.2 Mean coefficient of variation (CV) of dorsal fin ray and scale age estimates compared to otolith age estimates across-readers in pre- and post-inflection point in Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish captured in the Beaufort Sea, Alaska. Values followed by different letters for each species were significant different ($P < 0.05$).

Species	Comparison	Pre-inflection CV	Post-inflection CV
Arctic Cisco	Otolith - Fin Ray	10.11 y	10.08 y
	Otolith - Scale	8.66 y	10.43 y
Least Cisco	Otolith - Fin Ray	11.91 y	28.85 y
	Otolith - Scale	10.92 y	33.24 y
Broad Whitefish	Otolith - Fin Ray	6.57 y	20.36 y
	Otolith - Scale	7.72 y	29.40 z
Humpback Whitefish	Otolith - Fin Ray	7.38 y	25.46 y
	Otolith - Scale	11.99 z	44.81 z

Figures

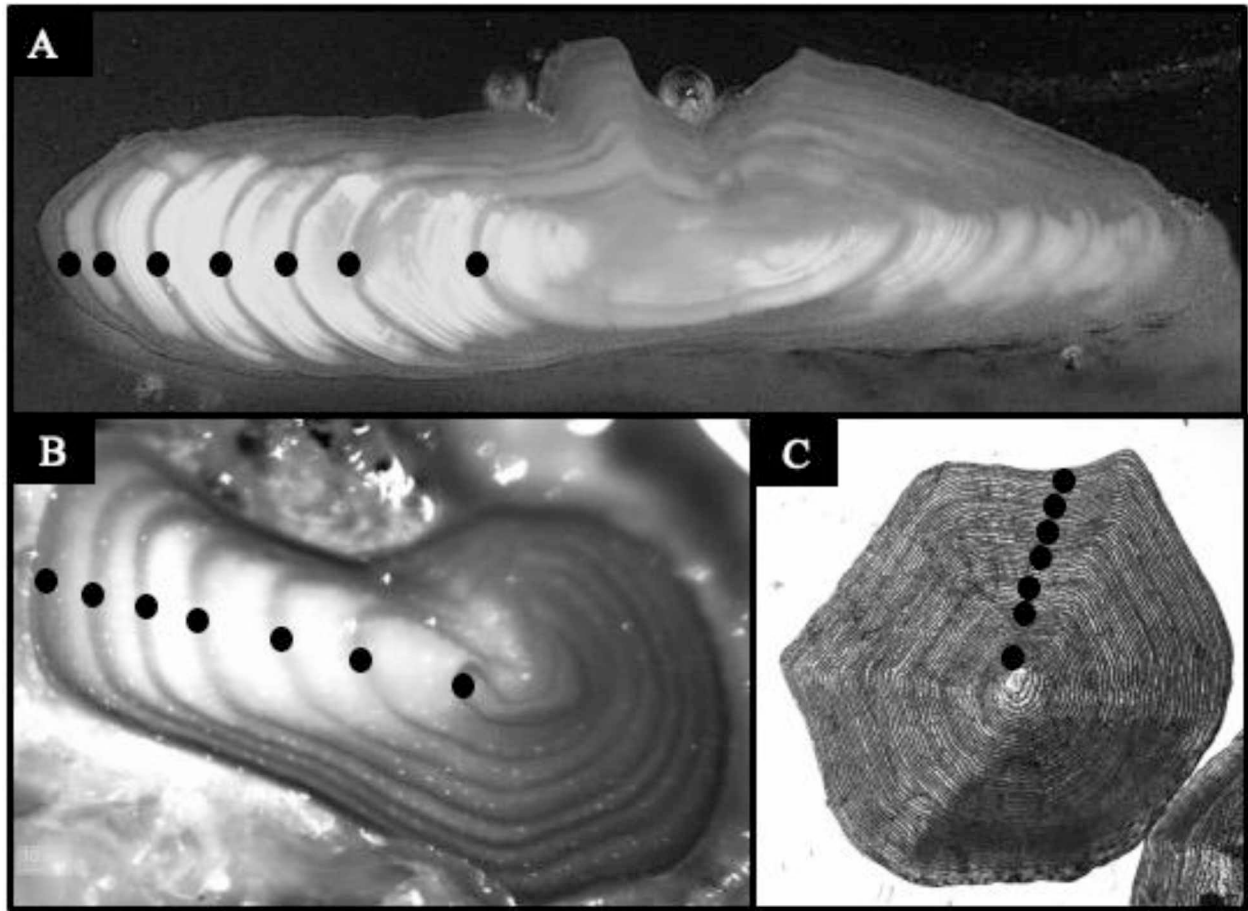


Figure 2.1 Aging structures used in precision analyses for an age-7 Broad Whitefish captured in the nearshore waters of the Beaufort Sea of Alaska: (A) a transverse cut sagittal otolith showing translucent and opaque (annuli) zones; (B) a dorsal fin ray cut transverse showing translucent and opaque (annuli) zones; (C) a scale showing regions of crowded circulli (annuli).

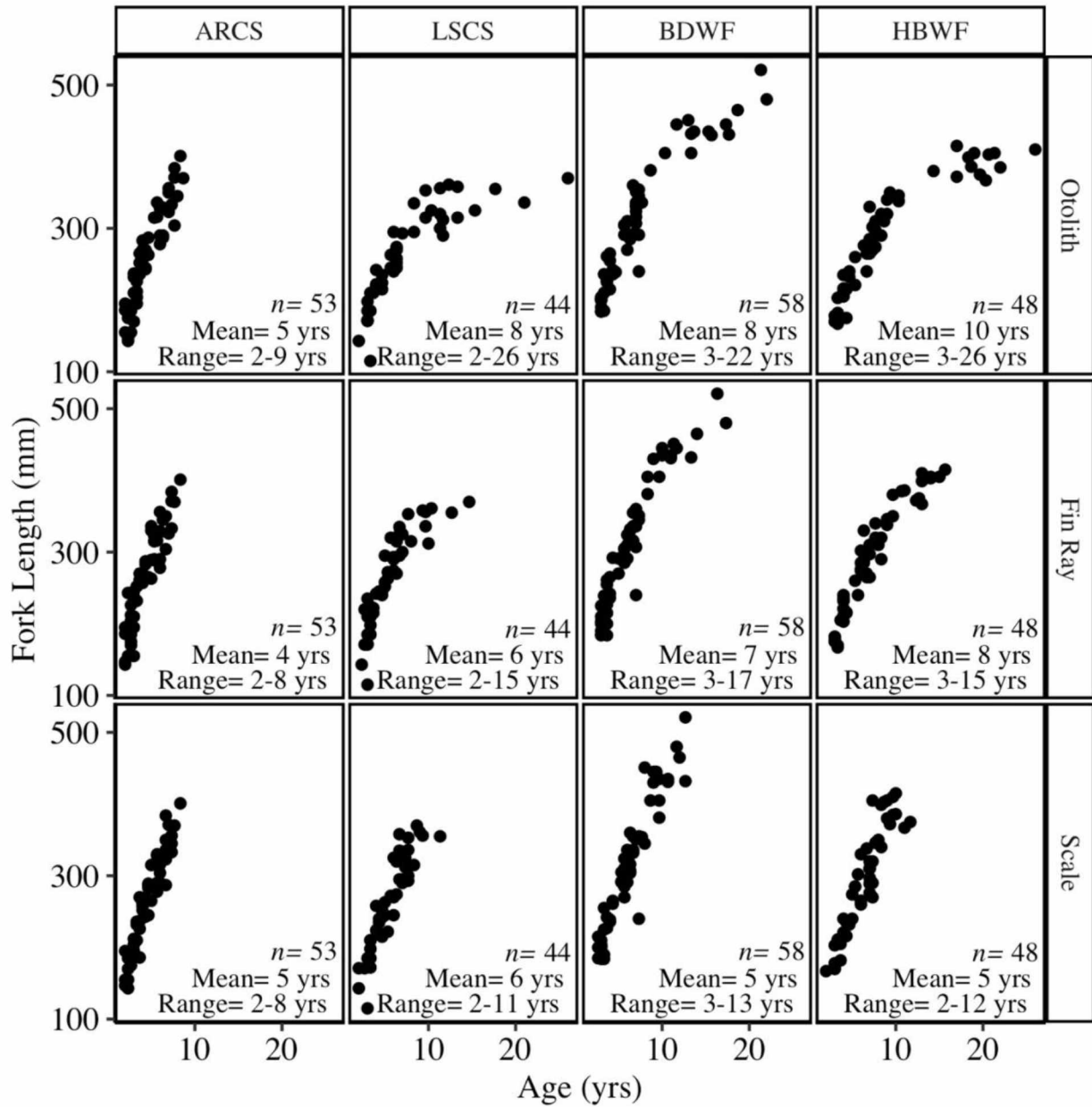


Figure 2.2 Mean ages by fork length estimated from otoliths, dorsal fin rays, and scales for Arctic Cisco (ARCS), Least Cisco (LSCS), Broad Whitefish (BDWF), and Humpback Whitefish (HBWF) captured in the nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska. The number of individuals assigned age estimates, average age and range are also shown.

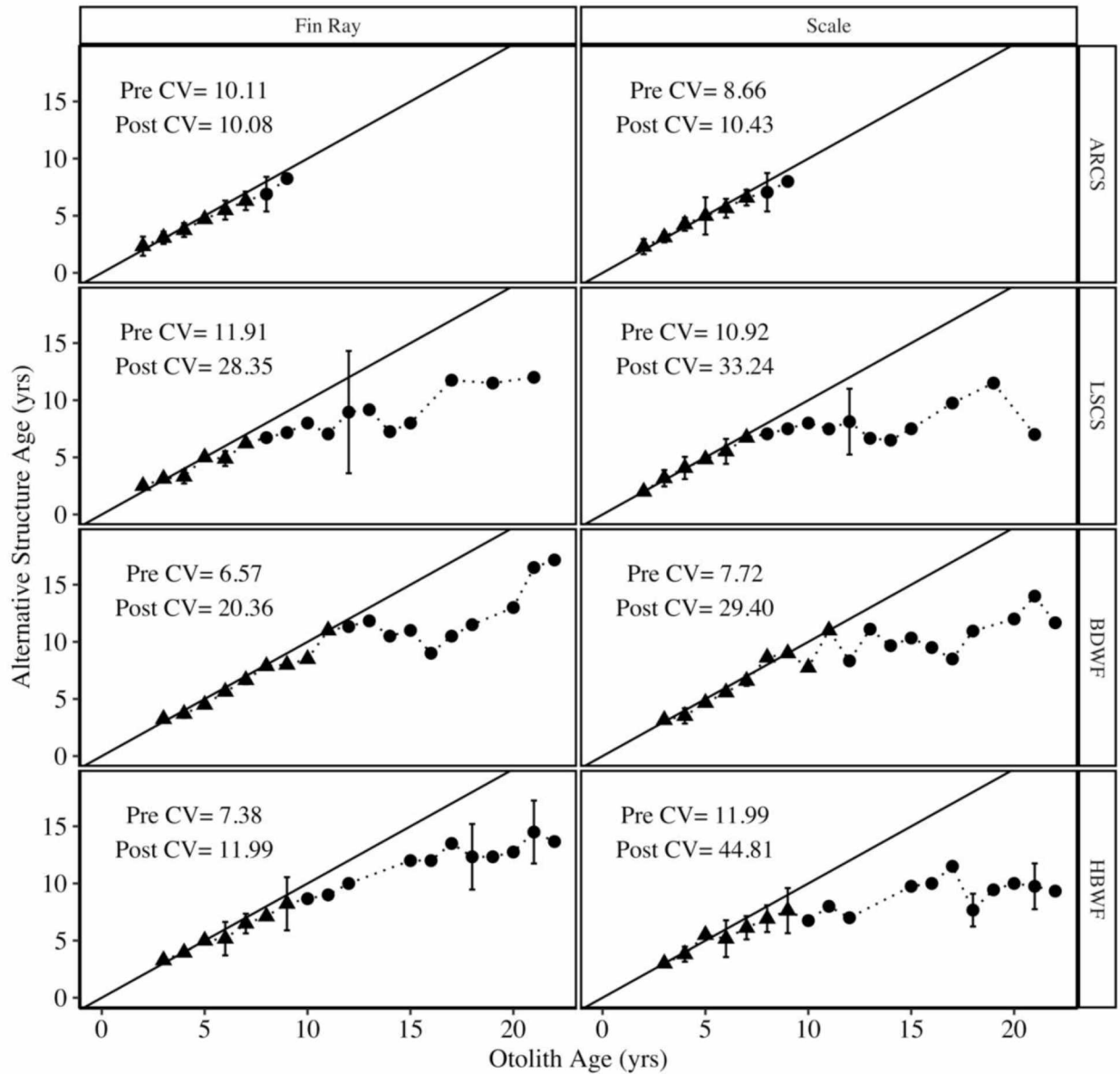


Figure 2.3 Age-bias plots of mean ages estimated among readers from dorsal fin rays and scales relative to otoliths age estimates for Arctic Cisco (ARCS), Least Cisco (LSCS), Broad Whitefish (BDWF), and Humpback Whitefish (HBWF) collected in nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska. Triangles represent ages estimated pre-inflection point and circles represent ages estimated post-inflection point. The solid line represents the line of equivalence and error bars represent 95% confidence intervals. Mean coefficient of variation (CV) of dorsal fin ray and scale age estimates compared to otolith age estimates across-readers for pre- and post-inflection point is represented in the upper left of each panel.

General Conclusion

With warming in the Arctic regions continuing to occur at a faster rate than the global average (Post et al. 2019), there will be an increased need to accurately monitor the health and productivity of Arctic species. Research and monitoring efforts will be most-needed for subsistence species residing in nearshore high-latitude ecosystems at the terrestrial-riverine-marine interface as they will integrate the effects of warming across both terrestrial and aquatic landscapes and are therefore most susceptible to the effects of climate change. This need is even more pronounced for coregonid whitefishes with diadromous life histories in high-latitude nearshore ecosystems, which utilize coastal waters for migration, feeding, and rearing (Reist et al. 2006). As Arctic annual air temperatures rise by 3–10°C over the next 80 years, we anticipate impacts on the productivity of coregonids in high-latitude nearshore ecosystems (IPCC 2014). The study described herein provides key insights for how productivity in Arctic cisco may respond to further warming while also providing information necessary for improving monitoring of coregonid whitefishes in the Beaufort Sea Alaska.

Chapter 1 of this thesis assessed the long-term growth response of Arctic Cisco, a key species of customary and traditional significance on Alaska's Coastal Plain, to recent environmental and biological variability in the Beaufort Sea. Using incremental growth data contained in otoliths of Arctic Cisco collected during annual monitoring efforts of the Beaufort Sea Nearshore Fish Monitoring Project between 2003 and 2018, we provided evidence of substantial inter-annual growth rate variation in recent decades that was synchronous among individuals and suggestive of a shared environmental driver. Indeed, growth rate variability was most closely associated with summer salinity and water temperature. Since 2001, nearshore water temperatures in the Prudhoe Bay region of the Beaufort Sea have increased by 1.4°C

(Priest 2020). Based on these results, Arctic Cisco could potentially benefit in the short-term from warmer water temperatures in the nearshore zone due to increased metabolic efficiency (Fechhelm and Gallaway 1982). However, the primary driver of growth in the species, i.e., salinity, suggests favorable growth is heavily influenced by the onshore movement of more productive marine from offshore areas, and the epibenthic marine invertebrates inhabiting them. No recent prey availability data exists for the nearshore Beaufort Sea and uncertainty remains into how lower trophic-level productivity will respond to increasing temperatures (Dezutter et al. 2019). Further, analysis for long-term catch rate data in the Prudhoe Bay region suggests an increasing presence of new species in the nearshore zone which may result in unforeseen consequences and alter trophic interactions (Priest 2020). Uncertainty into the direction to which productivity will respond to increasing temperatures emphasizes the need for continued research and monitoring of high-latitude nearshore ecosystems in the Beaufort Sea.

Chapter 2 of this thesis assessed the age precision and readability (based on confidence scores assigned to age estimates) of non-lethal fin rays and scales compared to otoliths of Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish. Otoliths are generally regarded as the most reliable structure for estimating age in coregonids. We compared age estimates made from three independent readers ranging in experience and found non-lethal structures (fin rays and scales) provided similar age estimates as otoliths up to the age of sexual maturity. After the age of sexual maturity, both fin rays and scales underestimated fish age relative to otoliths. Underestimation was most pronounced in scales and readers often had greater difficulty in annulus interpretation (reflected with lower confidence scores) than they did in other structures. Reader experience was not a significant factor influencing precision and readability, suggesting minimal training could increase the precision of age estimates in these structures. Overall, we

provided evidence to suggest that fin rays offer a non-lethal alternative means for estimating age and, therefore, monitoring population-level health and productivity in immature Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish in the Beaufort Sea Alaska. Our results supported prior assumptions into the limitations of non-lethal structures for estimating the age of high-latitude coregonid whitefishes (see Brown et al. 2012) and adds to a growing body of literature suggesting scales underestimate age in slow-growing fish populations. This study provides information necessary for improving monitoring and management of Arctic Cisco, Least Cisco, Broad Whitefish, and Humpback Whitefish.

Although this research addressed several gaps in our knowledge of coregonid whitefishes in the Beaufort Sea, several research opportunities were identified. As previously noted, there is a complete lack of recent prey data for the nearshore Beaufort Sea. Further studies should assess the spatiotemporal quality and quantity of prey items in the nearshore zone, especially in relation to environmental (e.g., salinity, water temperature, wind speed) and oceanographic processes (e.g., strength and direction of coastal currents). Further, while attempting to assign age estimates to Least Cisco, Broad Whitefish, and Humpback Whitefish in chapter two of this research, readers often noted the presence of a conspicuously narrow growth zone (poor growth year) that corresponded with the 2014 growth year across all species. Based on the biochronology generated in chapter one of this research, 2014 was the poorest growth year in recent decades for Arctic Cisco. Thus, it is likely that the same extrinsic factors driving productivity in Arctic Cisco also influence productivity in other species in the nearshore environment. Future studies should attempt to apply a biochronology approach to other species in the nearshore zone as this information would provide a greater understanding of ecosystem response to climate change in the Beaufort Sea region. Finally, further studies should attempt to assess how various preparation

methodologies for aging analysis impact the precision and readability of hard structures in high-latitude coregonid whitefishes.

Overall, this research demonstrates the importance of age and growth-based research for monitoring and assessing the impacts of environmental change on fisheries at the forefront of climate change. The otolith biochronology developed in chapter one of this research is one of most northerly developed biochronologies for any North American species thus far. This study provides substantial insight into the response of an Arctic species to further climate change and contributes to a growing body of literature regarding otolith biochronology development and analysis. Chapter two of this research is the first to quantify and describe the precision and readability of hard structures in Arctic whitefishes of the Beaufort Sea region. This study emphasizes the importance of species-specific aging assessments and provides greater awareness towards the precision of hard structure in coregonid whitefishes. Most importantly, this research advances knowledge into the application of age and growth data in fisheries science.

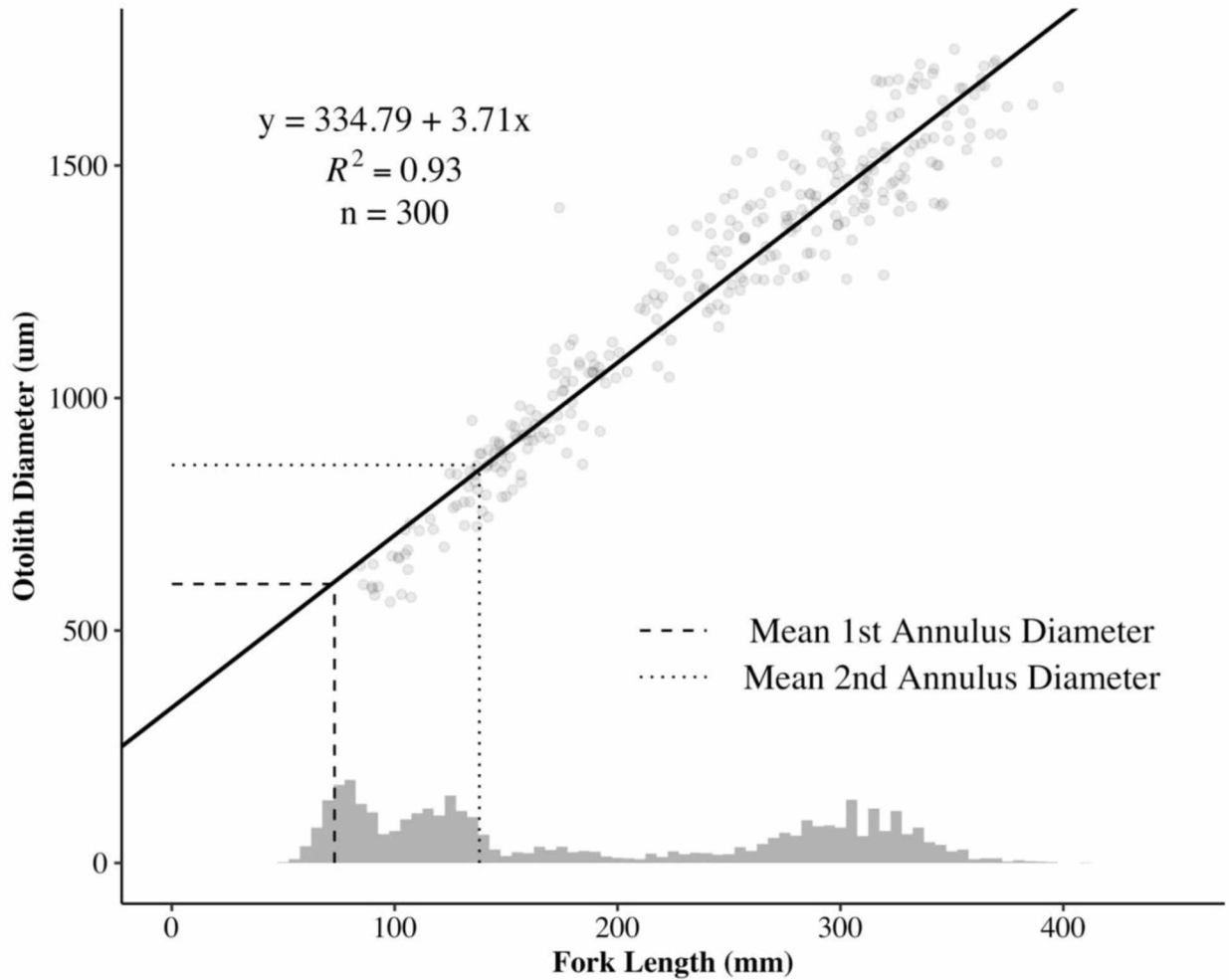
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Appendices

Appendix A. Linear regression fork length and otolith radius for Arctic Cisco captured in the Beaufort Sea outside Prudhoe Bay, Alaska. used in biochronology development overlaid with length frequency of individuals captured shortly after annuli deposition. The first two modes on the length-frequency plot represent the age-0 and age-1 cohorts, respectively. Dashed lines represent mean annular measurements.



Appendix B. The number of whitefishes captured in the Beaufort outside Prudhoe Bay, Alaska collected from 25-mm length groups for precision analyses. Where possible, a minimum of five individuals were collected for each length group. Individual species are represented as four-letter abbreviations in the table (ARCS = Arctic Cisco, LSCS = Least Cisco, BDWF = Broad Whitefish, HBWF = Humpback Whitefish).

Length Group (mm)	ARCS	LSCS	BDWF	HBWF
≤ 149	6	2	0	0
150-174	5	4	0	0
175-199	6	5	5	2
200-224	4	6	7	3
225-249	6	5	6	6
250-274	6	6	4	4
275-299	7	5	4	5
300-324	5	5	6	6
325-349	9	5	5	5
350-374	5	7	5	5
375-399	2	0	2	6
400-424	0	0	4	5
425-449	0	0	6	5
<450	0	0	5	0
Total	62	50	59	53

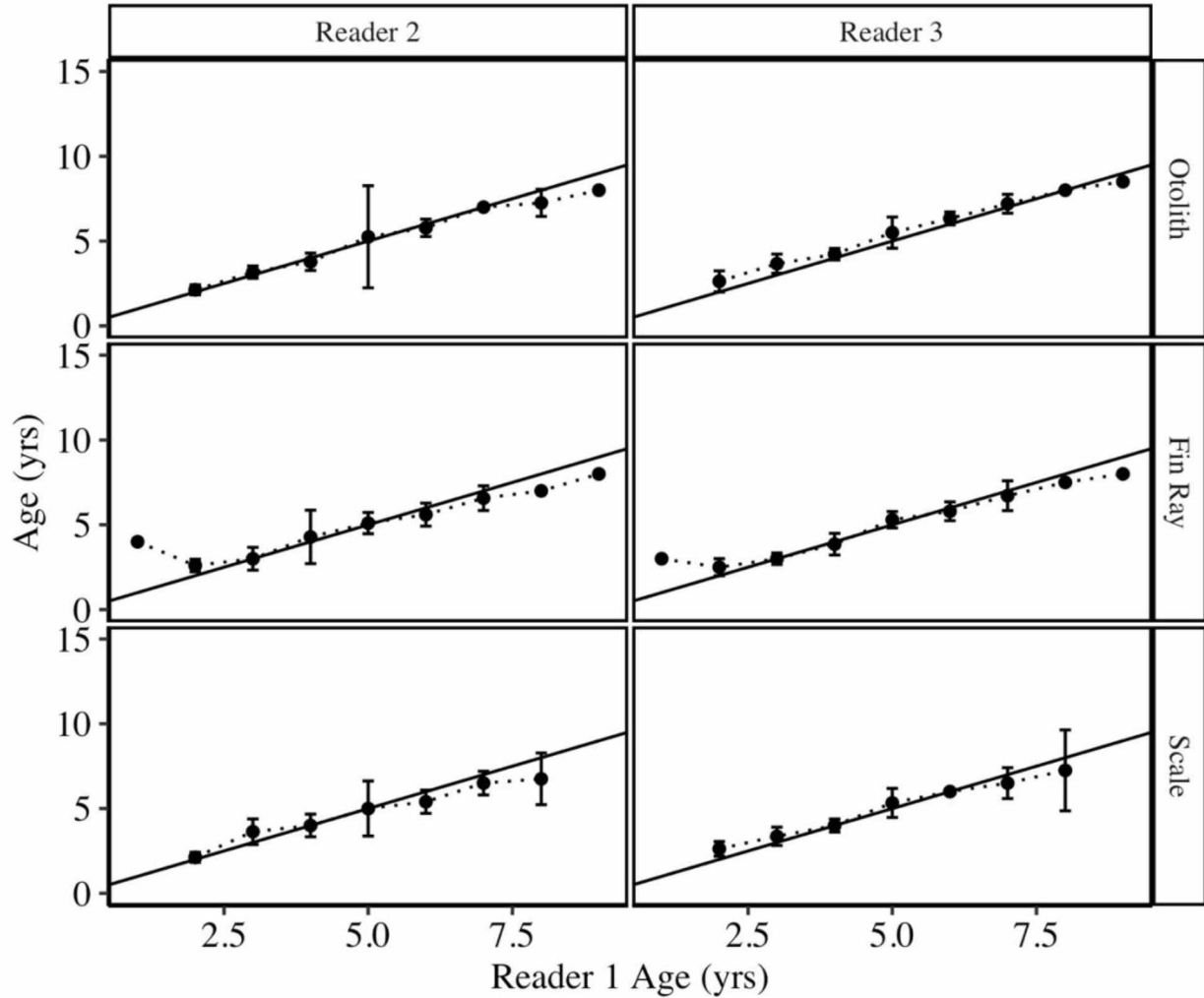
Appendix C. Precision of age estimates, measured as mean coefficient of variation (CV), within-reader, among-structure for Arctic Cisco, Least Cisco, Broad Whitefish and Humpback Whitefish captured in the Beaufort Sea outside Prudhoe Bay, Alaska. All comparisons are made relative to otolith age.

Species	Comparison	Reader 1	Reader 2	Reader 3
Arctic Cisco	Otolith - Fin Ray	5.27	12.94	12.09
	Otolith - Scale	4.22	13.57	8.78
Least Cisco	Otolith - Fin Ray	14.83	24.90	16.00
	Otolith - Scale	18.25	25.86	15.05
Broad Whitefish	Otolith - Fin Ray	7.33	13.71	8.44
	Otolith - Scale	10.91	18.01	9.58
Humpback Whitefish	Otolith - Fin Ray	9.39	17.61	12.11
	Otolith - Scale	17.20	30.99	18.57

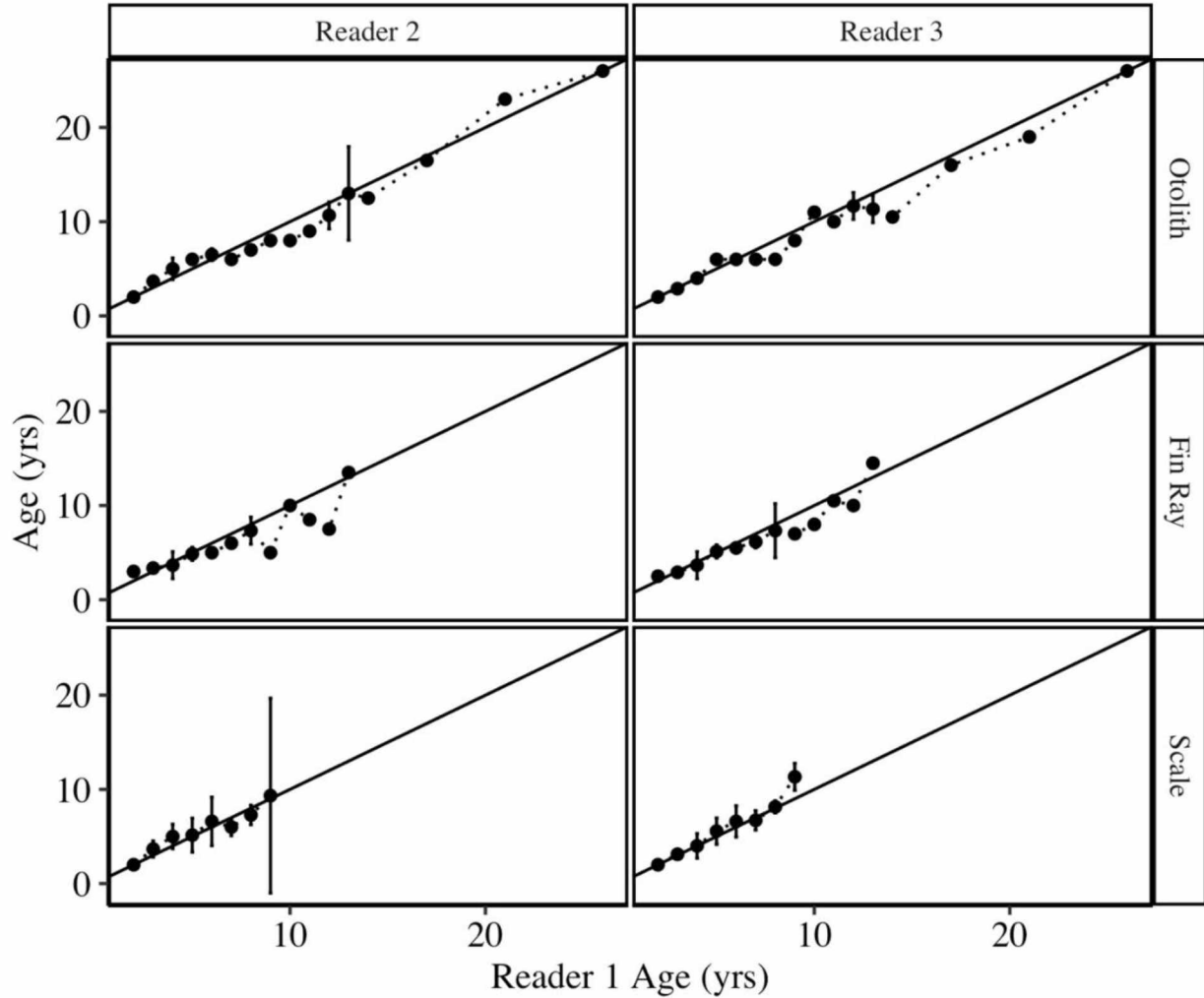
Appendix D. Readability rating, measured as mean confidence score (0 = no confidence to 3 = complete confidence), assigned by each reader for each hard structure used to estimate the ages of Arctic Cisco, Least Cisco, Broad Whitefish and Humpback Whitefish captured in the Beaufort Sea outside Prudhoe Bay, Alaska.

Species	Structure	Reader 1	Reader 2	Reader 3
Arctic Cisco	Otolith	3.00	2.30	2.49
	Fin Ray	2.74	1.42	2.28
	Scale	2.62	1.74	2.45
Least Cisco	Otolith	2.59	1.75	2.50
	Fin Ray	2.45	1.45	2.66
	Scale	2.23	1.70	2.36
Broad Whitefish	Otolith	2.81	2.29	2.36
	Fin Ray	2.79	2.14	2.79
	Scale	2.36	1.41	2.38
Humpback Whitefish	Otolith	2.71	2.17	2.31
	Fin Ray	2.62	1.90	2.35
	Scale	1.94	1.35	2.19

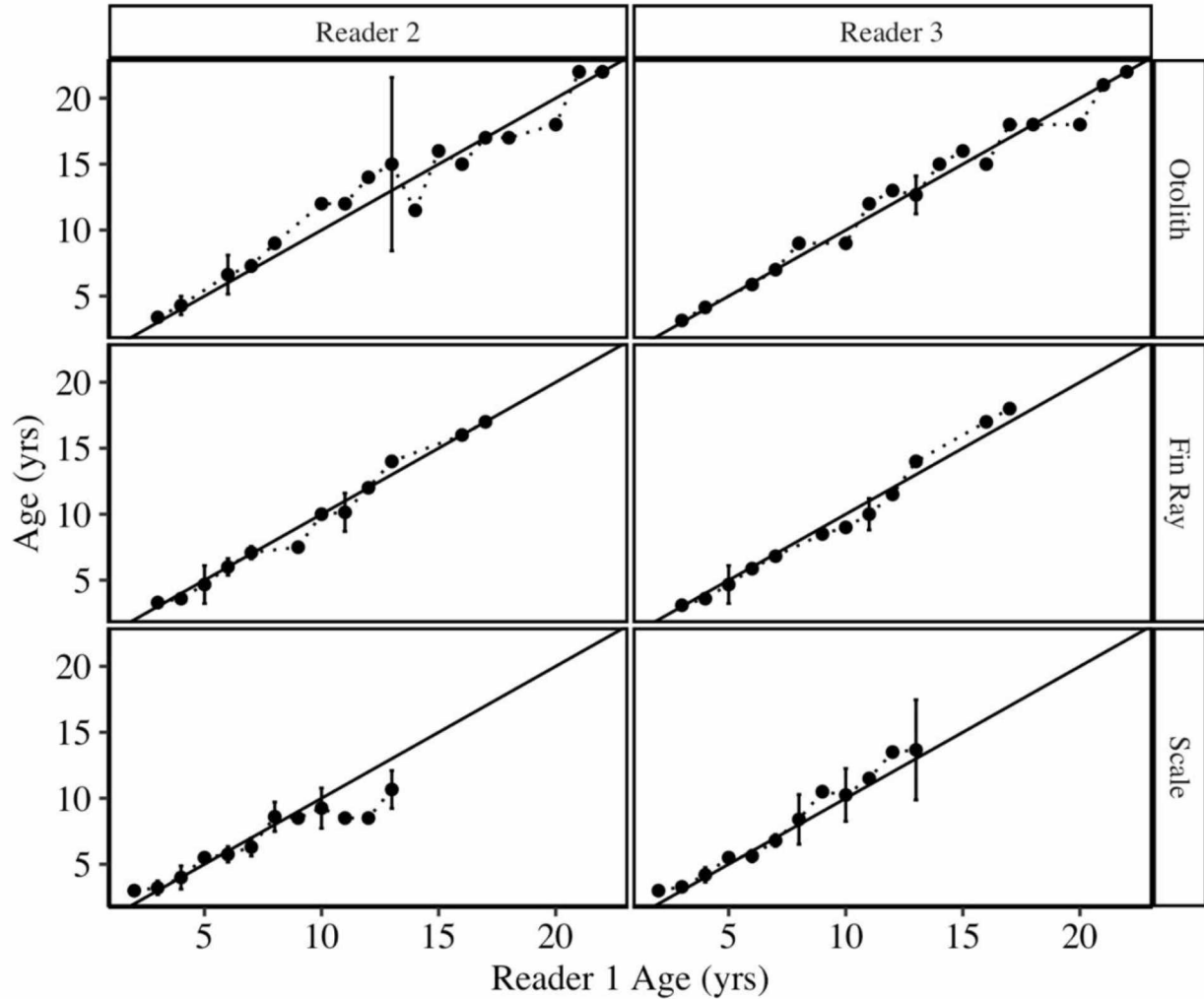
Appendix E. Among-reader, within-structure age-bias plots of age determinations made using otolith, dorsal fin rays, and scales in Arctic Cisco captured in the Beaufort Sea, outside Prudhoe Bay, Alaska. Error bars represent 95% confidence intervals for points with multiple observations around the mean age assigned by reader 1 relative to all other fish assigned an age by other readers (Campana et al. 1995).



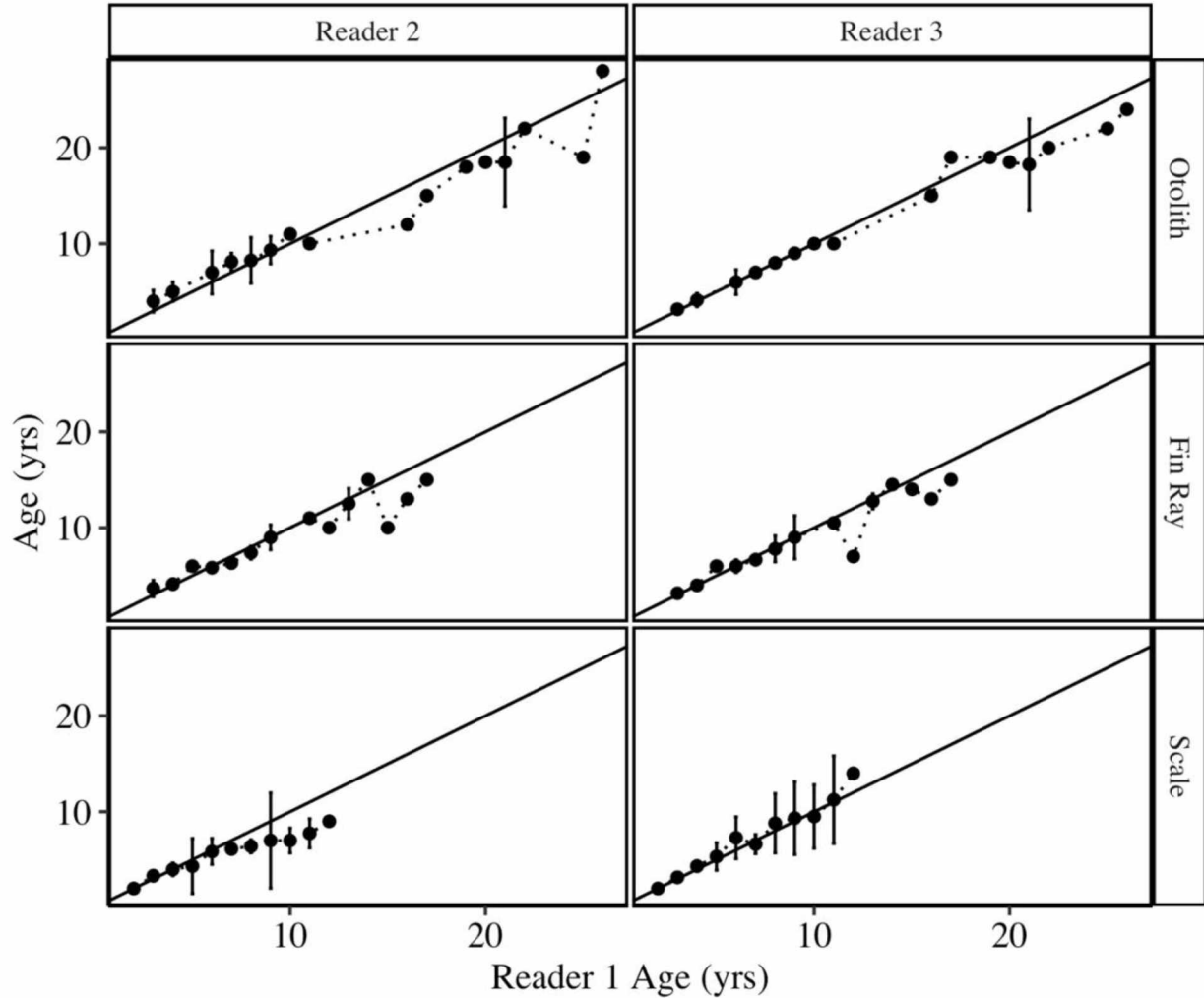
Appendix F. Among-reader, within-structure age-bias plots of age determinations made using otolith, dorsal fin rays, and scales in Least Cisco captured in the Beaufort Sea, outside Prudhoe Bay, Alaska. Error bars represent 95% confidence intervals for points with multiple observations around the mean age assigned by reader 1 relative to all other fish assigned an age by other readers (Campana et al. 1995).



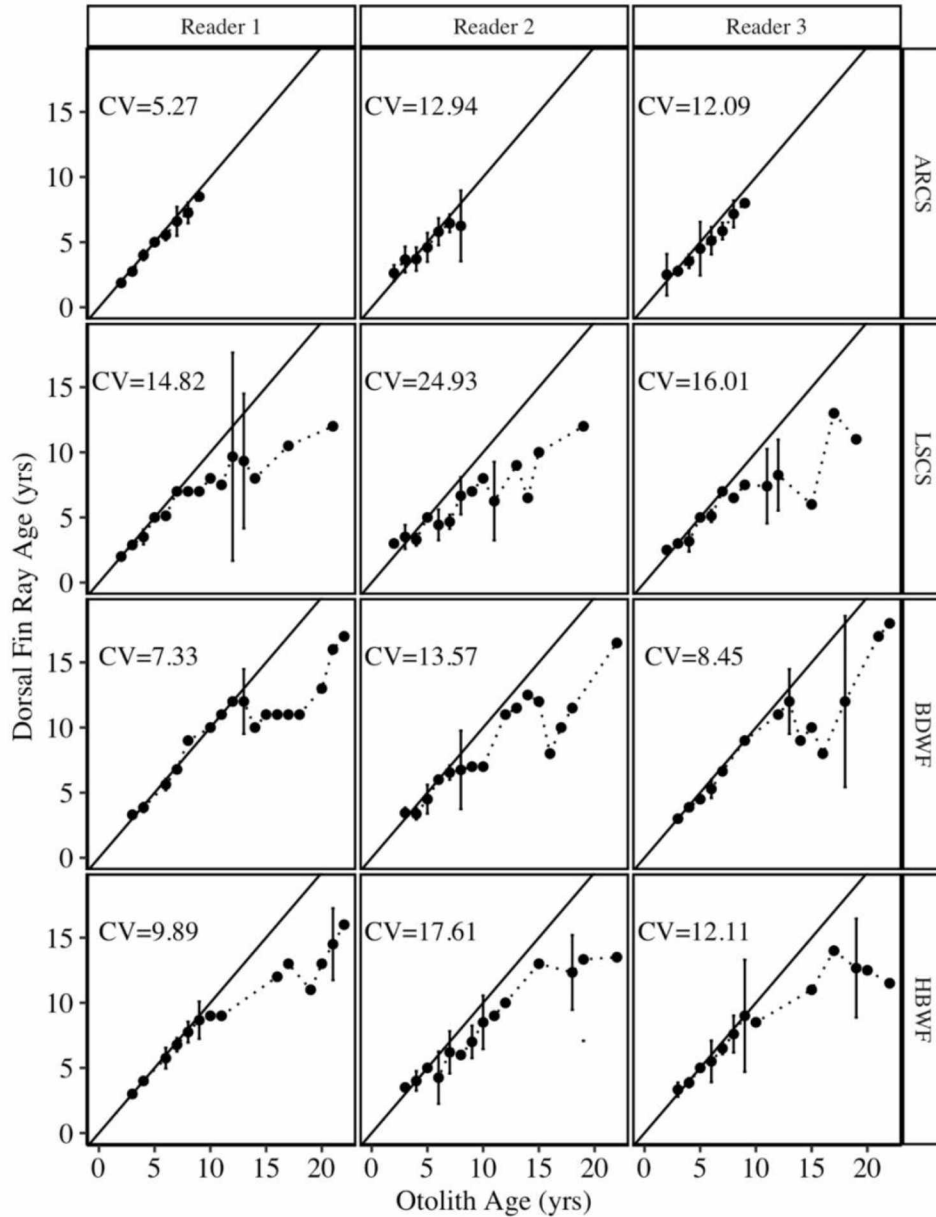
Appendix G. Among-reader, within-structure age-bias plots of age determinations made using otolith, dorsal fin rays, and scales in Broad Whitefish captured in the Beaufort Sea, outside Prudhoe Bay, Alaska. Error bars represent 95% confidence intervals for points with multiple observations around the mean age assigned by reader 1 relative to all other fish assigned an age by other readers (Campana et al. 1995).



Appendix H. Among-reader, within-structure age-bias plots of age determinations made using otolith, dorsal fin rays, and scales in Humpback Whitefish captured in the Beaufort Sea, outside Prudhoe Bay, Alaska. Error bars represent 95% confidence intervals for points with multiple observations around the mean age assigned by reader 1 relative to all other fish assigned an age by other readers (Campana et al. 1995).



Appendix I. Within-reader, among-structure bias plots of age determinations made with dorsal fin rays, and scales compared to otoliths in Arctic Cisco (ARCS), Least Cisco (LSCS), Broad Whitefish (BDWF), and Humpback Whitefish (HBWF) collected in nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska. Solid line represents the line of equivalence and error bars represent 95% confidence intervals. Precision of each structure was measured as mean coefficient of variation (CV) among readers and represented in the top left of each panel.



Appendix J. Age bias plots of determinations made using scales compared to otoliths for Arctic Cisco (ARCS), Least Cisco (LSCS), Broad Whitefish (BDWF), and Humpback Whitefish (HBWF) collected in nearshore waters of the Beaufort Sea outside Prudhoe Bay, Alaska. Solid line represents the line of equivalence and error bars represent 95% confidence intervals. Precision between structures is indicated as mean coefficient of variation (CV). Precision of each structure was measured using mean coefficient of variation (CV) among readers and presented in the top left of each panel.

