

PACIFIC HERRING JUVENILE WINTER SURVIVAL AND RECRUITMENT
IN PRINCE WILLIAM SOUND

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Abstract

Small pelagic fish abundances can vary widely over space and time making them difficult to forecast, partially due to large changes in the number of individuals that annually recruit to the spawning population. Recruitment fluctuations are largely driven by variable early life stage survival, particularly through the first winter for cold temperate fishes. Winter survival may be influenced by juvenile fish size, energy stores, and other factors that are often poorly documented, which may hamper understanding recruitment processes for economically and ecologically important marine species. The goal of this research was to improve understanding of recruitment of Pacific herring (*Clupea pallasii*) within Prince William Sound (PWS) through recruitment modeling and by identifying factors influencing winter survival of young-of-the-year (YOY) herring. Towards this end, my dissertation addresses three specific objectives: 1) incorporate oceanographic and biological variables into a herring recruitment model, 2) describe patterns in growth and condition of PWS YOY herring and their relationship to winter mortality risks, and 3) compare the growth, condition, swimming performance, and mortality of YOY herring that experience different winter feeding levels.

In the recruitment modeling study, annual mean numbers of PWS herring recruits-per-spawner were positively correlated with YOY walleye pollock (*Gadus chalcogrammus*) abundance in the Gulf of Alaska, hence including a YOY pollock index within a standard Ricker model improved herring recruitment estimates. Synchrony of juvenile herring and pollock survival persisted through the three-decade study period, including the herring stock collapse in the early 1990s. While the specific mechanism determining survival is speculative, size-based tradeoffs in growth and energy storage in PWS YOY herring indicated herring must reach a critical size before winter, presumably to reduce size-dependent predation. Large herring

switched from growth to storing energy, and ate more high-quality euphausiid prey, which would delay the depletion of lipid stores that compelled lean herring to forage. Lipid stores were highest in the coldest year of the seven-year field study, rather than the year with the best diets. With diets controlled in a laboratory setting, spring re-feeding following restricted winter diets promoted maintenance of size and swimming ability, but had little effect on mortality rates compared to fish continued on restricted rations. Declines in gut mass, even among fully fed herring, and low growth potential suggest limited benefits to winter feeding. Mortalities due to food restriction compounded by disease were highest among herring that fasted through winter months, and among small herring regardless of feeding level. Taken together, these findings illustrate the importance of achieving a critical size and high lipid stores in the critical period before winter to promote YOY herring winter survival and ultimately recruitment.

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General Introduction

Pacific herring (*Clupea pallasii*; hereafter herring) is a useful model species for investigating recruitment mechanisms in a small pelagic fish species. Herring supported a commercial fishery within Prince William Sound (PWS) before the population crashed in the early 1990s (Thomas and Thorne 2003, Hulson et al. 2008). Additionally, as a lipid-rich forage fish prey for marine fish (Bishop and Powers 2013), seabirds (Willson and Womble 2006, Bishop et al. 2015), and mammals (Iverson et al. 1997), it is an ecologically important link between zooplankton and higher-level predators. The PWS herring population size has varied widely since 1980, the start of the modern stock assessment period, driven in part by variation in annual numbers of fish that mature at age three and recruit to the spawning stock (Quinn et al. 2001, Hulson et al. 2008). Recruitment strength for cold temperate zone fishes can largely depend on first winter mortality (Hurst 2007), which may approach 95 % for PWS herring (Norcross and Brown 2001, Norcross et al. 2001). An understanding of winter mortality mechanisms for young-of-the-year (YOY) herring is thus essential for improving recruitment predictions and understanding the functioning of northern marine ecosystems.

Ecosystem effects on survival and recruitment of herring and other short-lived clupeoid fishes can be important drivers of variation in abundance (Blaxter and Hunter 1982). When these ecosystem forcing factors are shared across species in a region, synchrony in year-class strength or recruitment can occur among species with similar life histories (Hollowed et al. 1987, Mueter et al. 2007). Identifying common abundance or survival trends among fishes in PWS or the broader Gulf of Alaska could thus offer insight into herring recruitment mechanisms.

As a consequence of ecosystem effects, herring recruitment often bears little or no relationship to spawning stock size (Zheng 1996). However, there are few examples of stock

assessment models used in management that incorporate ecosystem variables (Skern-Mauritzen et al. 2016). For PWS herring, stock size has traditionally been estimated using an age-structured-assessment (ASA) model that includes a Ricker stock-recruitment model function to estimate age-three recruits (Hulson et al. 2008). For stock size forecasting, the next year's recruits are predicted using the 10-year median recruitment estimates. The standard Ricker model (Ricker 1975) is commonly used and can account for density-dependent mortality at early life stages, but PWS herring stock size exerts little influence on subsequent numbers of recruits that can vary substantially from the median. Variability in the stock-recruit relationship for cold temperate fishes can be driven by YOY winter mortality (Hurst 2007). Incorporating factors that influence winter survival may therefore improve herring recruitment models, however, winter mortality of PWS herring and other juvenile fish in cold temperate marine ecosystems is not well studied.

Like other fishes in cold temperate coastal areas, juvenile herring in PWS have a short feeding and growing season to prepare for their first winter. Zooplankton prey biomass within PWS typically peaks in May–June, following the spring phytoplankton bloom in April (McRoy et al. 1997, Eslinger et al. 2001). High zooplankton availability with high temperatures in summer can support high growth and survival to the summer's end (Schweigert et al. 2009). Autumn feeding and growth can also boost survival likelihood (Huss et al. 2008, Post and Parkinson 2001) before zooplankton decline to winter lows (McKinstry and Campbell 2018), accompanied by more empty herring stomachs, during October–April (Foy and Norcross 2001).

Winter food scarcity may increase both starvation and predation risk. Starvation risk increases if winter food intake and stored energy cannot meet metabolic demands. Metabolizing stored energy can cause declining condition and ultimately lead to starvation (Paul and Paul

1998). Hunger and zooplankton prey scarcity compel herring to increase search activity (Sogard and Olla 1996), compromising anti-predator schooling behaviors and increasing predation risk (Sogard and Olla 1997).

Winter mortality risk may depend on both fish size and energy stores. Among Pacific salmon (*Oncorhynchus* spp.), attaining a critical size in autumn increases survival likelihood, while size-dependent winter mortality is linked to greater energy stores among larger fish (Beamish and Mahnken 2001, Farley et al. 2011). Similarly, autumn total energy content (the product of weight and energy density) of juvenile walleye pollock (*Gadus chalcogrammus*) can strongly predict survival to recruitment at age one (Heintz et al. 2013). Lower survival among smaller versus larger herring is likely due in part to decreased ability to avoid predation (Christensen 1996). In addition, smaller herring have higher mass-specific metabolic rates that cause them to consume stored energy more quickly than larger individuals (Slotte 1999), further increasing starvation risk. These effects may be synergistic if, for example, starvation impairs the swimming ability of small herring and thus their ability to evade predators. Performance may also suffer following resumption of feeding in spring if compensatory growth, accelerated growth to recover mass lost during winter fasting, exacts a physiological cost (Ali et al. 2003).

Fish responses to low winter food availability can be complex, reflecting tradeoffs in body maintenance, growth, lipid storage, and behavior. These responses have been measured using a variety of morphometric and biochemical indices. The sensitivity of these indices to poor feeding conditions varies by species and life stage (Weber et al. 2003), with the specific responses of juvenile herring being poorly documented.

This dissertation aims to demonstrate how oceanographic and biological factors may affect PWS herring recruitment primarily through influencing winter survival of young-of-the-

year (YOY) herring. The goal of the first chapter is to evaluate the usefulness of generalized Ricker stock-recruitment models that incorporate oceanographic and biological variables as predictors of PWS herring recruitment. Recruitment is likely determined in part by multiple ecosystem factors influencing the survival of juvenile herring, yet few studies show that including ecosystem effects improves models of fish recruitment. The work reported here demonstrates how monitoring ecosystem components, including co-occurring fish stocks, can help understand and model herring recruitment.

A major source of recruitment variability for PWS herring and other cold temperate fishes is first winter survival. The goal of the second chapter is to identify juvenile herring traits and environmental factors useful for understanding herring survival during their first winter. To this end, I investigated relationships among size, growth, energy storage, and diet for YOY herring collected from PWS at the beginning and end of seven winters. Specifically, I sought to determine how protein-based growth and lipid stores relate to YOY herring size at the beginning and end of winter, and how lipid stores influence foraging at the end of winter. I also examined how herring lipid stores at the beginning of winter differed by location and year, and if this could be attributed to differences in diets or annual ocean temperatures. This information allowed me to assess the evidence for a critical size that YOY herring must achieve for winter survival and thereby provide insight into mortality processes for a cold temperate small pelagic fish.

The goal of the third chapter is to investigate how YOY herring condition, growth, swimming performance, and mortality respond to different feeding conditions they may experience during and immediately after winter. Captive juvenile herring were fed at different ration levels in a controlled laboratory environment and their responses observed on a variety of morphometric, biochemical, and behavioral indices: length, wet mass, gut mass, recent growth

(RNA/DNA content), body composition (moisture, lipid, and protein content), and prolonged swim speed. I sought to describe differences in these measures among ration levels, and to identify which indices most clearly distinguished well-fed from fasted herring. Herring that died during the study were enumerated, measured for length, and a subsample chemically analyzed to assess differences in mortality among ration levels and traits of fish that died. This research provides a framework to assess the likelihood of first winter survival of wild juvenile herring and consequently improve the ability to predict their year-class strength.

Chapter 1. Empirically based models of oceanographic and biological influences on Pacific Herring recruitment in Prince William Sound ¹

Abstract

Abundances of small pelagic fish can change dramatically over time and are difficult to forecast, partially due to variable numbers of fish that annually mature and recruit to the spawning population. Recruitment strength of age-3 Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska, is estimated in an age-structured model framework as a function of spawning stock biomass via a Ricker stock-recruitment model, and forecasted using the 10-year median recruitment estimates. However, stock size has little influence on subsequent numbers of recruits. This study evaluated the usefulness of herring recruitment models that incorporate oceanographic and biological variables. Results indicated herring recruitment estimates were significantly improved by modifying the standard Ricker model to include an index of young-of-the-year (YOY) walleye pollock (*Gadus chalcogrammus*) abundance. The positive relationship between herring recruits-per-spawner and YOY pollock abundance has persisted through three decades, including the herring stock crash of the early 1990s. Including sea surface temperature, primary productivity, and additional predator or competitor abundances singly or in combination did not improve model performance. We suggest that synchrony of juvenile herring and pollock survival may be caused by increased abundance of their zooplankton prey, or high juvenile pollock abundance may promote prey switching and satiation of predators. Regardless of the

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mechanism, the relationship has practical application to herring recruitment forecasting, and serves as an example of incorporating ecosystem components into a stock assessment model.

Introduction

Single-species population models commonly used in management of fished stocks have mixed success in predicting future stock size based on past stock size alone. One reason for the difficulty is unaccounted-for ecosystem effects on stock size, yet few examples exist of assessment models incorporating ecosystem variables (Skern-Mauritzen et al., 2016). Ecosystem effects on recruitment are of special interest for herring and other short-lived clupeoid fishes because changes in abundance can be driven largely by variability in the annual number of fish that recruit to the spawning stock (Blaxter and Hunter, 1982).

Pacific herring (*Clupea pallasii*; hereafter herring) is a vital trophic link between plankton and upper-level predatory fish (Bishop and Powers, 2013), seabirds (Willson and Womble, 2006; Bishop et al., 2015), and mammals (Iverson et al., 1997). In addition to its ecological role, herring in Prince William Sound (PWS) supported an important commercial fishery prior to its population collapse in the early 1990s. The population size has fluctuated widely over time since 1980, when the modern stock assessment time series began (Quinn et al., 2001; Hulson et al., 2008). According to age-structured-assessment (ASA) model estimates, pre-fishery stock biomass has ranged from a peak of 139,298 tons (126,369 metric tons [mt]) in 1989, to a low of 10,375 tons (9,412 mt) in 2001 (Wiese et al., 2015). Identifying the main factors controlling PWS herring recruitment is essential for modeling herring population dynamics and understanding the functioning of this ecosystem.

Recruitment strength for PWS herring, conventionally defined as the annual number of age-3 individuals joining the spawning population (Funk, 1994; Williams and Quinn, 2000), may be determined by multiple factors. Of particular importance are seasonal environmental and biological variables that affect herring survival during their first year (Norcross and Brown, 2001), which begins with spawning in April followed by a three- to four-week egg incubation period (Brown et al., 1996). Survival at the egg stage can be affected by predation pressure from seabirds (Bishop and Green, 2001), invertebrates (Haegele and Schweigert, 1991), other fish (Rooper and Haldorson, 2000), and physical factors such as wave and air exposure (Rooper, 1996). Larvae may be susceptible to high predation mortality (Purcell and Grover 1990), drifting to unsuitable habitat (Norcross et al., 2001), and starvation (McGurk et al., 1992). Favorable feeding and growing conditions for larval and early juvenile herring in PWS are compressed by the seasonal pattern of productivity typical of high latitude coastal areas. A large spring phytoplankton bloom in April is generally followed three to four weeks later by increased zooplankton abundance in May through June (McRoy et al., 1997; Eslinger et al., 2001). High spring phytoplankton biomass should support high abundances of summer zooplankton prey for juvenile herring (Eslinger et al., 2001; Ware and Thomson 2005). With sufficient food, herring growth and survival should be promoted by high summer temperatures. Juvenile survival to the end of the first summer can portend relative recruitment strength (e.g., Schweigert et al., 2009), though high variability in the relationship may be due to mortality during the first winter (reviewed in Hurst et al., 2007). Zooplankton abundance declines to winter lows from October or November through March or April, accompanied by a higher proportion of empty stomachs among juvenile herring (Foy and Norcross, 2001). Juvenile herring, like other forage fishes, may experience increased predation risk as hunger and declining condition through winter (Paul and

Paul, 1998) suppress predator avoidance behavior (e.g., Robinson and Pitcher, 1989; Sogard and Olla, 1997). Water temperature (Gay and Vaughan, 2001), food availability (Foy and Norcross, 1999), herring condition (Norcross et al., 2001), and predation pressure (Stokesbury et al., 2002) vary among bays in PWS and over time, and this variability likely contributes to differences in survival to recruitment at age 3. Demonstrations of ecosystem effects on herring recruitment are rare, but recruitment variability has been quantitatively linked to summer (July – August) temperature in the herring hatching year and zooplankton biomass in the following spring (April – May) as herring approach age 1 (Brown and Norcross, 2001). Winter sea surface temperature prior to and including spawning has also been shown to influence recruitment (Zebdi and Collie, 1995; Williams and Quinn, 2000); the mechanism is unclear, but it may involve temperature effects on rates of egg and embryonic development and subsequent timing mismatch to the spring phytoplankton bloom.

Changes in the abundances of the main natural predators of herring, including piscivorous fishes, seabirds, and humpback whales (*Megaptera novaeangliae*), likely cause changes in predation mortality and may impact herring abundance and recruitment. For example, herring recruitment in Hecate Strait, British Columbia tended to be low when Pacific cod (*Gadus macrocephalus*) abundance was high (Walters et al., 1986), though the persistence of that relationship is uncertain (Ahrens et al., 2012). Biomass of predatory Pacific hake (*Merluccius productus*) during the first year for herring negatively affects recruitment of West Coast Vancouver Island herring (Tanasichuk, 2017). Pacific cod and walleye pollock (*G. chalcogrammus*; hereafter pollock) are likely the primary fish consumers of juvenile herring in PWS, as indicated by their abundance and diet composition (Bishop and Powers, 2013). Predation effects may differ with fish predator age, but their relative importance is often unclear.

For example, predation pressure or competition may be greater from juvenile than adult pollock (Sturdevant et al., 2001; Bishop and Powers, 2013) due to greater spatial overlap among juvenile pollock and herring, but adult pollock diets can contain higher proportions of herring (Willette et al., 1999). Hatchery-reared pink salmon (*Oncorhynchus gorbuscha*) fry, released in the hundreds of millions annually since the late 1980s, may negatively influence herring recruitment through competition for zooplankton prey or predation (Deriso et al., 2008; Pearson et al., 2012). Adult Pink Salmon returning to PWS to spawn have also been suggested as important herring predators (Deriso et al., 2008). Seabird predation, predominantly by murre (*Uria* spp.), can remove as much as 10% of the adult herring biomass and even greater biomass of juveniles (Bishop et al., 2015). The abundance of another major herring predator, humpback whales, has increased five-fold since 1978 in PWS (Teerlink et al., 2015), and bioenergetic models indicate they may remove large portions of the herring stock biomass annually (11–77%, Rice et al., 2011; 26%, Pearson et al., 2012). It is unclear how much these sources of predation and competition influence herring stock size through reductions in juvenile survival and recruitment.

Some ecosystem factors influencing herring recruitment may also affect other species with similar early life history traits in the same region. Regional synchrony of strong year classes (Hollowed et al., 1987; Hollowed and Wooster, 1995) or recruitment (Mueter et al., 2007) can occur among some North Pacific fish stocks, especially within species groups that are subject to shared forcing factors. Associations between different species have recently been described for the Bering Sea, where age-4 Chum Salmon (*Oncorhynchus keta*) growth, a proxy for ocean conditions, predicts age-1 pollock recruitment the following year (Yasumiishi et al., 2015). Such connectivity has led to expectations that strong herring year classes in PWS may be portended by high juvenile survival of other species, for example, age-0 gadids in PWS (S. Moffitt, ADFG,

USA, pers. comm.), PWS pink salmon in their first ocean year (Pegau, 2014), and juvenile pollock in Shelikof Strait (Pegau, 2014). Quantifying linkages among species for PWS or the broader Gulf of Alaska (GOA) could aid in understanding and predicting herring recruitment.

The numbers of age-3 recruits and other year classes of PWS herring are estimated by managers using an ASA model (described in Hulson et al., 2008). Herring year-class sizes are estimated using a weighted least squares approach that minimizes differences between model estimates and observations of egg densities, mile-days of milt, age composition from commercial seine catches, age composition from fisheries-independent sampling of spawners, hydroacoustic survey biomass, and Ricker stock-recruitment model estimates of age-3 recruits. The Ricker model (Ricker, 1975) is commonly used to estimate recruitment based on stock size and has a number of desirable model attributes: relative simplicity, ease of linearization for parameter estimation, and the ability to account for productivity and density-dependent effects of stock size on recruitment. Density-dependent effects on recruitment may occur in herring through cannibalism on early life stages (Holst, 1992) or mortality of eggs under high density spawning conditions (Taylor, 1971; Hourston et al., 1984). Including stock size in the recruitment models sets boundaries on recruitment at high or low spawning stock sizes (Quinn and Deriso, 1999); for the PWS herring model, it prevents the ASA model from estimating zero or negative recruits (Hulson et al., 2008). Although a Ricker-type relationship is often used in analyses of herring stocks (e.g., Zheng, 1996; Williams and Quinn, 2000), previous work has shown no obvious stock-recruitment relationship for PWS herring over the observed range of stock sizes (Zheng, 1996). Ricker model estimates of recruitment and the observed abundances of age-3 herring in PWS differ widely. The discrepancy reflects the weak relationship between spawning stock biomass and recruitment for PWS herring (Fig. 1.1), and limits the usefulness of stock size for

projecting recruitment. Therefore, median recruitment for the previous 10-year period is used by managers to estimate recruitment for the following year in PWS herring stock size forecasts. If the weak stock-recruitment relationship is caused by variable survival to recruitment age, models that incorporate factors that influence survival may improve recruitment estimates.

The objective of this study is to evaluate the usefulness of generalized Ricker stock-recruitment models that incorporate oceanographic and biological variables as predictors of PWS herring recruitment. This is motivated by the premise that ecosystem variability affects juvenile fish survival, especially through their first year, and modifies the relationship between the size of the adult spawning population and the number of their offspring that reach maturity.

Methods

Recruitment data

Time series data for recruitment, defined as the annual number of age-3 herring in millions of individuals entering the PWS population, were available for 30 years from 1980 to 2009 (Table 1.A). Recruitment observations were lagged back by three years to match oceanographic and biological conditions in the brood year that herring hatched. That is, the number of age-3 recruits observed in 2012 was used as the 2009 recruitment data point for analysis. Recruitment estimates were generated by the 2012 Alaska Department of Fish and Game (ADFG) ASA model for the PWS herring stock (S. Moffitt, ADFG, USA, unpubl. data).

Stock size

To predict PWS herring recruitment, the biomass of herring that spawned a given year class was included as a variable in the analyses. Annual spawning stock size for 1980–2009, defined as biomass in metric tons of herring age three and older (3+), came from the ASA model that generated the recruitment estimates.

Oceanographic influences

To test whether growing conditions for herring in their first year influenced survival to recruitment, indices of sea surface temperature (SST) and chlorophyll-*a* (Chl) levels during their first spring and summer were included in the analysis. Sea surface temperature for PWS from 1982 to 2009 came from NOAA satellite advanced very high resolution radiometer (AVHRR) data, captured monthly at 4-kilometer resolution (Jet Propulsion Laboratory POET data selection tool, <http://poet.jpl.nasa.gov>, accessed 4/9/2011). To obtain a single data point representing PWS summer SST in one year, temperature readings from 229 pixels across PWS (60.42–60.95°N, 146.10–148.00°W) were spatially averaged by month, and the mean of the monthly averages was computed from June to September. A winter SST index for the same region was computed as the monthly averages from January to April, for comparability with previous studies showing recruitment was affected by SST in the first third of the spawning year (Zebdi and Collie, 1995; Williams and Quinn, 2000). The precise choice of months used would have little effect on model results due to high autocorrelation in SST among adjacent months.

As an index of phytoplankton biomass, Chl measurements for PWS from 1998 to 2009 were obtained from SeaWiFS and MODIS/Aqua satellite data, captured in 8-day successive intervals at 0.25° resolution (NASA Giovanni ocean color radiometry data portal,

http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day, accessed 3/16/2012). To obtain a single data point representing spring Chl, readings from 23 pixels across

PWS (60.1–61.3°N, 145.8–148.5°W) were averaged by month, and the mean of the monthly averages taken from April to June to capture peak Chl from April bloom to initial decline in July.

Biological influences

To address whether adult or YOY Pacific cod and pollock affect juvenile herring survival, adult biomass and YOY abundance estimates of those species were used in herring recruitment models. Annual stock assessment biomass and abundance estimates for Pacific cod and pollock in the Gulf of Alaska (GOA) were used as proxies for the PWS stocks, which are not typically assessed as separate stocks by management agencies (Wessel et al., 2014). Adult (age-3+) Pacific cod stock biomass (1000 mt) from 1980 to 2009 was from the North Pacific Fishery Management Council (NPFMC) GOA Pacific cod stock assessment model estimates (A'mar, Alaska Fisheries Science Center, unpubl. data), and YOY Pacific cod abundance (millions) was from the 2014 stock assessment report (A'mar and Palsson, 2014). Adult (age-3+) pollock biomass (1000 mt) from 1980 to 2009 was from the NPFMC GOA pollock stock assessment report (Dorn et al., 2014). Based on a trawl survey of PWS conducted by the state of Alaska in 1999, managers estimate the PWS pollock biomass represents approximately 1% of the total GOA stock (Dorn et al., 2014; Wessel et al., 2014), but the correlation strength between the overall GOA and the PWS stock sizes is unknown. YOY pollock were not directly estimated in the stock assessment, so the reported abundance of age-1 pollock lagged back by one year to the herring brood year served as a proxy for YOY abundance. Age-1 pollock lagged one year are hereafter referred to as “YOY” pollock.

To evaluate the effect of hatchery-reared pink salmon fry predation or competition on herring recruitment, PWS hatchery fry releases (millions) in the herring brood year from 1980 to 2009 were included in the analysis

(<http://mtalab.adfg.alaska.gov/CWT/reports/hatcheryrelease.asp>, accessed 12/11/14). Total returns of wild and hatchery pink salmon (millions) in the herring brood year from 1980 to 2009 were used as an index of predation by adult pink salmon (R. Brenner, ADFG, USA, unpublished data).

To address the potential impact of humpback whale predation on herring recruitment, this study used mark-resight model estimates of summer PWS whale abundance in the herring brood year from 1983 to 2009 (Teerlink et al., 2015).

Data from surveys conducted by the U.S. Fish and Wildlife Service from 1990 to 2007 (McKnight et al., 2008) were used to assess effects of PWS murre predation on herring recruitment. Surveys were conducted in 10 non-contiguous years: 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2004, 2005, and 2007. Murre abundance data were lagged back by one year to the herring brood year because abundances are from March following the brood year, when the murre population has a late winter peak (McKnight et al., 2008; Bishop and Kuletz, 2013) and the herring cohort spawned the previous year approaches age 1.

Analytical approach

To assess predictors of herring recruitment, generalized Ricker stock-recruitment models that included oceanographic and biological variables were compared using a multiple linear regression approach. Multiple regression models were evaluated in sets with common time frames with no missing data (Table 1.1). For a group of variables within a time frame, a set of

model variants was developed that consisted of a full model containing all variables and simpler models with different variable combinations. All possible variable combinations were generated using the “dredge” function in R (“MuMIn” multimodel inference package, K. Barton, 2011) for the two longest time frames, model sets A (30 years) and B (27 years). For the two shortest time frames, model sets C (12 years) and D (10 years), the number of available variables (12) approached or exceeded the number of annual recruitment observations over those periods (12, 10, respectively), so the number of variables included was reduced. For those model sets, some variables were excluded if they were not significant in the full model or in models derived from longer data sets (F-tests), and failed to improve standard Ricker model performance.

It is important to note that stock size and other variables used in the models were assumed to be known without error. Measurement error in stock and recruitment data can obscure underlying stock-recruitment relationships (Walters and Ludwig, 1981). Unaccounted for imprecision in the estimates for all variables adds uncertainty to the predictions of herring recruitment. This is true for both the standard Ricker model, which relies solely on spawning stock biomass estimates, and for the more complex models explored here.

Recruitment models

To model age-3 herring recruitment, this study used a log-transformed version of the Ricker stock-recruitment model:

$$R = \alpha * S * e^{-\beta * S} ,$$

where R is recruit abundance in millions, α indicates productivity, S is spawning stock biomass in metric tons, and β indicates the level of density dependence (Quinn and Deriso, 1999). The Ricker model was used because it can account for density-dependent influences of stock size on recruitment, and it has often been used in PWS herring stock assessments (Zheng, 1996; Williams and Quinn, 2000; Hulson et al., 2008). The following natural-log transformation is commonly used to normalize recruitment data, linearize the stock-recruitment relationship, and reduce the influence of extreme year classes (e.g., Stocker et al., 1985; Williams and Quinn 2000):

$$\ln(R/S) = \ln(\alpha) - \beta * S.$$

The ratio R/S can be regarded as an index of early life stage survival, assuming that egg production is proportional to spawning stock biomass. The Ricker model can be generalized to include other variables that may affect juvenile fish survival to recruitment age (Quinn and Deriso, 1999). The full multiple linear regression model with all oceanographic and biological variables included in this study is

$$\ln(R/S) = \ln(\alpha) - \beta_1 S + \beta_2 SST_{Summer} + \beta_3 SST_{Winter} + \beta_4 Chl + \beta_5 P_{cod} + \beta_6 P_{cod}YOY + \beta_7 Pollock + \beta_8 PollockYOY + \beta_9 PinkFry + \beta_{10} Pinks + \beta_{11} Murre + \beta_{12} Whales + \epsilon.$$

To assess the effects of these variables without using the assumed Ricker stock-recruit relationship, alternative models were fit using $\ln(R)$ instead of $\ln(R/S)$ as the response variable, and tested with and without herring stock size as a variable:

$$\ln(R) = -a + b_1S + b_2SST + \dots + b_{12}Whales + \varepsilon.$$

For comparison with the 10-year rolling median recruitment used in stock forecasting, annual recruitment using the generalized Ricker model was estimated as

$$\hat{R} = \hat{\alpha} * S * e^{-\hat{\beta}_1 S + \hat{\beta}_2 SST + \dots + \hat{\beta}_{12} Whales}$$

For a given brood year, the generalized Ricker model was fit to data from the start of the time series through the year prior to the brood year. The resulting fitted model was then used to forecast recruitment for the brood year using the values of predictor variables in the brood year. Recruitment for the brood year was also forecast as the median observed recruitment over the 10 prior years. The mean absolute percent differences were then calculated between the Ricker recruitment estimates and observed recruitments, and between the 10-year rolling median and observed recruitments, for brood years 1990–2009.

Bayesian assessment estimates

Stock assessment methods for PWS herring may be modified in coming years by adopting a Bayesian framework for estimating uncertainty in stock biomass and recruitment, weighting data sets according to likelihoods rather than subjectively weighting sums of squares (Pegau, 2014; Muradian, 2017). To test whether the findings would be similar to those based on current ASA model estimates of stock size and recruitment, models were also fit using stock and recruitment estimates from a Bayesian assessment for 1980–2009 (Muradian, 2017).

Model selection

Models were evaluated based on their hindcast fits to ASA model estimates of historically observed recruits per spawner, $\ln(R/S)$. To determine which model in a given time frame was best, all model variants within a set (A–D) were ranked using the small-sample corrected form of the Akaike Information Criterion (AICc):

$$\text{AICc} = -2\ln(L) + 2K + 2K(K + 1)/(n - K - 1),$$

where L is the likelihood, K is the number of parameters in the model, and n is the number of observations. Within each set of models being ranked, the model yielding the lowest AICc score was considered best; models scoring 0–2 points higher than the best model had “substantial support,” those scoring 4–7 higher had “considerably less support,” and those scoring more than 10 higher had “essentially no support” (Burnham and Anderson, 2004).

Model diagnostics

To check for collinearity among explanatory variables, Spearman rank-order correlations were calculated for pairwise comparisons of all variables within each time frame. Correlations among explanatory variables should not affect the significance of a multiple regression model, but can obscure which variables are most influential (Graham, 2003). Alternative models were constructed with and without correlated variables to assess their influence individually and in combination.

Linear regression assumptions of normality and homogeneity of variance were verified with Shapiro-Wilk's tests, quantile-quantile (Q-Q) probability plots, and plots of residuals versus fitted values (Shapiro and Wilk, 1965; Zuur et al., 2007). Independence among time series data points was verified by checking for autocorrelation using correlograms, Durbin-Watson tests, and partial correlograms for the full and best models (Durbin and Watson, 1950; Zuur et al., 2007).

High variability in the herring stock and recruitment data created the potential for unusual observations to influence the regression relationships. To check for influential observations, Cook's distances (Cook and Weisberg, 1982) were calculated for each point in the regressions. This study used the convention that a Cook's distance value > 1 or subjectively much larger than all other values indicated an influential point (Zuur et al., 2007) that should be examined further – for example, by repeating the analysis without that data point.

Results

Overview

Survival of Pacific herring in Prince William Sound to recruitment age showed a strong positive relationship to the abundance of YOY pollock in the Gulf of Alaska (Fig. 1.2). Accounting for YOY pollock abundance in a Ricker stock-recruitment model increased the explained variability in herring recruitment over the longest time series by more than 50% (Table 1.2). The association between pollock and herring persisted across three decades, and encompassed the period of high herring biomasses (50,000–120,000 mt) in the 1980s and low biomasses ($< 20,000$ mt) following the population decline in the early 1990s. Over the four time

frames examined, incorporating YOY pollock abundance alone or in combination with any other oceanographic or biological variables, typically yielded the best model fits. For the longest time series, herring stock size appeared to show density-dependent influence on recruits-per-spawner, but results were mixed. Survival was not significantly influenced by SST in summer or winter of the herring brood year, Chl concentrations in spring, or the abundances or biomasses of seven other potential herring predators and competitors, including YOY and adult Pacific cod, adult pollock, pink salmon hatchery fry and total returning adults, murre, and humpback whales. Recruitment estimates from a generalized Ricker model with YOY pollock abundance also matched observed recruitment more closely than the 10-year rolling median used in forecasting, reducing error by half. The YOY pollock-herring association persisted whether using recruitment as a response without stock size, using current ASA model or Bayesian estimates of herring stock size and recruitment, or using pollock recruits-per-spawner as a predictor.

Model set A – fish populations, 1980–2009

For model set A, containing the longest time series (Table 1.1), 1980–2009, the strongest influence on PWS herring recruits-per-spawner was GOA YOY pollock abundance. The correlation between herring $\ln(R/S)$ and YOY pollock abundance was positive and significant (Spearman's $\rho = 0.557$, $p = 0.001$). For regression analysis, linear regression model assumptions were met, and no influential outliers were identified. In the full model, the only significant terms at the 95% confidence level were herring spawning stock size and YOY pollock abundance (t-test, $p < 0.001$). Herring stock size negatively influenced recruits-per-spawner in the full model, consistent with a density-dependent effect of S on R, but the effect was confounded by correlations with other predictors. Stock size and YOY pollock abundance were

present in all five of the best, lowest-scoring models (Table 1.2; $\Delta\text{AICc} \leq 2.58$) out of 128 possible variable combinations. Stock size alone in the standard Ricker model explained less than 8% of the variability in $\ln(R/S)$, and was not significant. By comparison, the model with S and YOY pollock terms was highly significant and accounted for 61% of recruitment variability.

Other fish population variables did not appear to influence herring recruitment, though some model variants had similar AICc scores and slightly higher R^2 values than the model with S and YOY pollock. The influence of the other variables was confounded by strong correlations among them and with herring stock size. Herring stock size was positively correlated with Pacific cod biomass and pollock biomass (Spearman's rho, $p < 0.001$), and negatively correlated with pink salmon fry ($p = 0.003$) and pink salmon, marginally ($p = 0.058$). These non-herring variables were not significant in the full model, and yielded non-significant model fits when each variable was added to the Ricker model individually.

Model set B – including SST and whales, 1983–2009

For model set B, which included SST (winter and summer) and whales in addition to the fish population variables, the strongest influence on herring recruitment was YOY pollock abundance. In the full regression model spanning 1983–2009, the only significant terms were S ($p = 0.013$) and YOY pollock ($p < 0.001$). Stock size and YOY pollock abundance were present in all five of the best, lowest-scoring model variants ($\Delta\text{AICc} \leq 3.51$) out of 1024 possible variable combinations. The model with S and YOY pollock yielded the second lowest AICc score ($\Delta\text{AICc} \leq 2.81$); the lowest score was obtained for the model that included adult Pacific cod and pollock biomasses in addition to S and YOY pollock. Comparisons of the simplest model variants that contained only each term individually showed that YOY pollock was the

only term significantly related to recruitment. S was marginally non-significant to significant when tested in combination with other terms. The most parsimonious low-scoring model included only herring S and YOY pollock abundance. This model outperformed ($R^2 = 0.612$, $p < 0.001$) the standard Ricker model ($R^2 = 0.111$, $p = 0.090$) in predicting herring recruits-per-spawner.

Model set C – including primary production, 1998–2009

For model set C, which included Chl data as a primary production index for 1998–2009, none of the variables examined significantly influenced herring recruitment. GOA YOY pollock was still the best, though not significant, predictor of herring recruitment over this time frame. The lack of significance was likely due to small sample size rather than a weakening of the pollock-herring relationship over time. The divergence in data points at the end of the time series plot of YOY pollock abundance and herring recruits-per-spawner was not unusual compared to prior years (Fig. 1.2). For this time frame, the number of potential explanatory variables equaled the number of data points, so a reduction in model terms was necessary. Several variables were excluded based on results with model sets A and B: winter SST, YOY Pacific cod abundance, Pink Salmon hatchery fry releases, abundance of adult pink salmon, and abundance of whales. Spring Chl and summer SST also did not interact, despite the expectation that increased food and temperatures are both needed to promote growth and survival, so no interaction term was included. For all 64 resulting variable combinations, the lowest-scoring model contained only the YOY pollock term. Among models with S, the standard Ricker model yielded the lowest AICc score, but explained only 6% of recruitment variability and was not significant ($p = 0.455$). Adding YOY pollock to the Ricker model increased explained variability to 34%, with a

similarly low AICc score ($\Delta\text{AICc} = 0.49$), but also was not significant ($p = 0.157$). Adding Chl to the model with S and YOY pollock increased explained variability by only 8%, increased overall model p to 0.205, and yielded a substantially higher AICc score ($\Delta\text{AICc} = 5.20$).

Model set D – including murre, 1990 –/– 2007

For model set D, which included 10 years of murre abundance data, no variables significantly influenced herring recruitment. Variables in this set included all from model set C except Chl, which was replaced with murre. No terms were significant in the full model, and no model variants explained significant variation in herring recruitment, likely due to small sample size. The standard Ricker model yielded the lowest AICc score and accounted for 35.3% of the variability in herring $\ln(R/S)$, though was not significant ($p = 0.070$). Adding murre to the Ricker model explained similar variability (35.6%; $p = 0.214$; $\Delta\text{AICc} = 5.96$). Adding YOY pollock to the Ricker model produced an AICc score similarly low to the Ricker model ($\Delta\text{AICc} = 3.39$), and increased explained variance by $\sim 15\%$, but the fit was also not significant ($p = 0.087$). Murre abundance was highly variable, so analyses were also conducted on log-transformed abundances without one influential year of anomalously high abundance, 1992. The results were similar; no model explained significant variability in herring recruitment, and the standard Ricker model yielded the lowest AICc score.

Using $\ln(R)$ as response

Using $\ln(R)$ as the response variable, independent of stock size, yielded similar overall results: the strongest influence on herring recruitment was clearly YOY pollock abundance. Results differed slightly in that the model with the lowest AICc score included both adult and

YOY pollock without S. While this model explained 69% of the variability in recruitment, most of that explanatory power came from the YOY pollock term; the model with only YOY pollock accounted for 60% of recruitment variability.

Forecasting comparison with 10-year rolling median

The generalized Ricker model with S and YOY pollock abundance estimated recruitment more accurately than the 10-year rolling median recruitment used for forecasting (Fig. 1.3). For this comparison, the coefficients and intercept values were taken from the fitted linearized Ricker model with herring stock size and YOY pollock abundance from model set A.

For the 1990–2009 brood years, the 10-year rolling median recruitment was unrelated to recruitment ($R^2 < 0.01\%$, $p = 0.984$), and deviated from observed recruitment by an average of 131%. In contrast, recruitment modeled using S and YOY pollock abundance was significantly correlated with observed recruitment ($R^2 = 35.9\%$, $p = 0.005$), and deviated by an average of 63%.

Bayesian assessment estimates

The association between herring recruitment and GOA YOY pollock abundance was present whether based on stock and recruitment estimates from the current ASA model or Bayesian estimates. Bayesian assessment estimates (Muradian, 2017) for 1980–2009 were similar to current ASA model values for stock biomass (Bayes $S = 1.15 \cdot S + 445$; $R^2 = 0.975$; mean absolute percent difference = 19.3%) and recruitment (Bayes $R = 1.10 \cdot R - 21.5$; $R^2 = 0.981$; mean absolute percent difference = 30.0%). For model set A, the only significant terms in the full regression model were S ($p = 0.003$) and YOY pollock ($p < 0.001$), and these terms were

included in the 10 best models ($\Delta AICc < 3.50$). The lowest-scoring model contained only S and YOY pollock, accounted for 53% of the variability in herring $\ln(R/S)$, and was highly significant ($p < 0.001$). These findings closely matched the results using the ASA model estimates, as reported above for model set A. Using either approach, S and YOY pollock were the only significant terms in the full model, were present in the best-scoring models, and explained over half of the variability in herring $\ln(R/S)$.

Juvenile pollock survival versus abundance

Using juvenile pollock survival instead of abundance to predict herring recruitment yielded similar results. Juvenile pollock survival to age 1, defined as the number of age-1 “recruits” relative to female spawner biomass (data from Dorn et al., 2014), or $\ln(R/S)$, was more strongly correlated with herring $\ln(R/S)$ ($R^2 = 0.409$, $p < 0.001$) than was YOY pollock abundance ($R^2 = 0.282$, $p = 0.002$). The model including pollock $\ln(R/S)$ and herring S was a weaker predictor of herring $\ln(R/S)$ ($R^2 = 55\%$, $p < 0.001$) than the model using YOY pollock abundance ($R^2 = 61\%$, $p < 0.001$). For model set A, juvenile pollock survival and herring S were the only significant terms in the full regression model, yielded the second-lowest AICc score ($\Delta AICc = 0.88$), and were present in the 10 best models ($\Delta AICc < 3.02$). The agreement between model results based on either pollock survival or abundance follows from the strong positive correlation between YOY pollock abundance and juvenile pollock survival ($R^2 = 0.668$, $p < 0.001$).

Discussion

Pollock-herring association

The positive relationship found between PWS herring recruitment and concurrent GOA YOY pollock abundance may reflect their common responses to variation in abundance or quality of zooplankton prey. Young-of-the-year pollock and herring co-occurring in nearshore habitats of PWS have a high degree of dietary overlap and show similar seasonal changes in diet composition (Sturdevant et al., 1999). In contrast, diets of YOY pollock and Pacific cod differ in PWS (Sturdevant et al., 1999) and the southeastern Bering Sea (Strasburger et al., 2014), as reflected in diverging gill raker morphology as they grow (Lee, 1985). These observations, and the lack of relationship between YOY Pacific cod and herring, could support the hypothesis that the pollock-herring relationship is driven by diet effects. Zooplankton abundance has been shown to influence recruitment for some stocks, e.g., Atlantic Cod in the North Sea (*Gadus morhua*; Beaugrand et al., 2003) and Baltic Sea herring (*Clupea harengus*; Cardinale et al., 2009), and reduced zooplankton abundance may have contributed to the herring population decline in the early 1990s (Cooney et al., 2001; Pearson et al., 2012). Zooplankton may also influence predation pressure on herring if, for example, greater euphausiid abundance promotes prey switching by predators such as adult pollock and whales. Though zooplankton abundance and quality may help explain herring survival to recruitment age, zooplankton data for PWS have not been consistently available since the late 1990s. Continuous plankton recorder data has been collected since 2000 in the GOA (Batten et al., 2016), but limited years overlap with this study and the opportunistic sampling can miss peak zooplankton abundances in some years. Zooplankton sampling may not reflect diets due to selective feeding by herring (Purcell and

Sturdevant, 2001), so diet monitoring would also be needed to describe prey-based links to recruitment.

Diet influence on YOY herring and pollock does not rule out predator influence. While herring are generally minor prey items for Pacific cod or pollock captured in GOA shelf surveys (A'mar and Palsson, 2014; Dorn et al., 2014), predation may be higher in the nearshore PWS habitats that juvenile herring occupy. Pollock and herring in PWS tend to occupy different depths in the water column (Stokesbury et al., 2000; Thomas and Thorne, 2001), which should limit predation opportunities. However, observations of significant herring consumption by Pacific cod and pollock in PWS indicate predation by both gadids may be important (Willette et al., 1999; Bishop and Powers, 2013). High YOY pollock abundance may promote prey switching from juvenile herring to pollock and satiation of predatory adult pollock and Pacific cod (Bishop and Powers, 2013). Cannibalism on juvenile pollock is well documented and a significant factor in pollock population dynamics in the Bering Sea (e.g., Bailey and Dunn, 1979; Mueter et al 2011), though less so in the GOA (Dorn et al., 2014). In the GOA, predator consumption of juvenile pollock tends to level off rather than increase linearly when the juveniles are highly abundant, suggesting predator swamping may occur (Dorn et al., 2014). Predators may be overwhelmed when oceanographic conditions promote high abundances of juvenile pollock, resulting in higher survival rates for both juvenile pollock and herring. Evidence for reduced predation mortality in response to high juvenile fish abundance is limited (Liermann and Hilborn, 2001), but has been shown for some species (e.g., Yellow Perch, *Perca flavescens*, Forney, 1971; Sockeye Salmon, *Oncorhynchus nerka*, Ruggerone and Rogers, 1984). Bottom-up and top-down mechanisms are thus both potentially contributing to the association between

pollock and herring. Evaluating the role of gadid predators in controlling herring recruitment requires abundance and diet data specific to PWS.

Oceanographic influences

The lack of influence of SST on PWS herring recruitment was unexpected, given previous findings positively linking SST to pre-recruit survival of North Pacific herring (Zebdi and Collie, 1995; Williams and Quinn, 2000). SST in the winter before spawning affected recruitment for 12 GOA and British Columbia herring stocks by potentially influencing the timing of larval hatching with respect to favorable spring conditions (Williams and Quinn, 2000). Temperature is often cited as a factor influencing herring recruitment, with high temperatures generally promoting stronger recruitment at higher latitudes (Myers, 1998; Williams and Quinn, 2000), but the effects may be indirect and depend on local conditions. High temperature needs to be accompanied by high food consumption to promote herring growth and survival, but high temperature may not aid growth if it exceeds the optimal range for PWS herring (Batten et al., 2016). High temperatures can also be associated with lower zooplankton abundance in autumn and winter, which could negatively affect herring condition (Foy and Norcross, 2001). Such interactions among variables at a local and seasonal scale likely confound any clear relationship of temperature to recruitment. This is not to say that ocean temperature or climate have no effect on herring recruitment, especially given previous work showing mean herring recruitment in some populations responds to multi-year temperature shifts (Hollowed et al., 1995), but it is difficult to ascertain the relationship on a year-to-year basis.

Chlorophyll-*a* may have shown no effect on recruitment because it is too indirect as an indicator of juvenile herring diet quantity and quality. Using chlorophyll as a proxy for herring

food assumes that higher chlorophyll concentration reflects higher phytoplankton biomass, which then promotes higher abundance of zooplankton prey. These relationships may not hold if the ratio of chlorophyll to phytoplankton biomass changes or grazing by abundant zooplankton suppresses phytoplankton biomass. High overall phytoplankton biomass also may not benefit herring survival if food quality is low. For example, larval fish growth can be sensitive to dietary changes in relative levels of essential fatty acids (Copeman and Laurel, 2010), which differ among phytoplankton taxa and may be transferred up the food chain (Dalsgaard et al., 2003). Food quality for first-feeding herring larvae may drive the positive relationship observed between GOA diatom abundance and PWS juvenile herring first year growth, which should promote herring survival (Batten et al., 2016). Still, it is unclear how well diatom abundance or first year growth reflect herring survival to recruitment age.

Other biological influences

PWS pink salmon fry and adult abundances were expected to affect herring survival through predation or competition with juvenile herring (Deriso et al., 2008; Pearson et al., 2012), but neither was significantly related to recruitment in this study. The Deriso et al. (2008) study modeled herring spawning stock size, via effects of covariates on recruitment and other parameters in the stock model, whereas this work modeled recruitment. Chinook (*O. tshawytscha*), Coho (*O. kisutch*), and to a lesser degree, pink salmon are known consumers of herring (Sturdevant et al., 2012), but predation rates on juvenile herring in PWS are unknown. Though Chinook and Coho Salmon biomasses in PWS are relatively low, high pink salmon abundance, including hatchery releases of several hundred million juveniles annually, may constrain herring abundance and recruitment (Deriso et al., 2008). Adult pink salmon returning

to spawning areas may be important predators of YOY herring (e.g., Stokesbury et al., 2002), but supporting evidence is scant. Stomach contents of PWS pink salmon in the summers of 2009–2011 indicated they consumed juvenile herring only in 2010 (Sturdevant et al., 2013). The estimated 6.41 million juvenile herring consumed sound-wide that year (Sturdevant et al., 2013) represented 5% of the age-3 cohort that recruited two years later (based on 2009 brood year cohort size of 125.5 million), but this figure assumes all were from the same cohort. Predation by juvenile pink salmon on larval or early juvenile herring in summer seems plausible, due to spatial overlap with juvenile herring (Willette et al., 1997) and piscivorous diet (Sturdevant et al., 1999), but has not been documented. Competition for food between juvenile pink salmon and herring may be important, as feeding in both species is reduced in shoals with both present (Sturdevant et al., 1999). But the extent of their co-occurrence and zooplankton prey limitation is unclear, and the present study found fry abundance was unrelated to herring recruitment.

The lack of a relationship between murre and herring recruitment is based on only 10 years of available murre abundance data. Murres are the dominant seabird consumer of adult and juvenile herring, and their widely fluctuating abundances could contribute to variable juvenile herring survival (Bishop and Kuletz, 2013; Bishop et al., 2015). The age composition of juvenile PWS herring in murre diets is not well known, but if murres feed across all juvenile age classes (ages 0–2), the effects of a year of high murre abundance may be spread across several herring recruiting classes and thus difficult to detect. The strong biological plausibility of murre predation influencing juvenile herring abundance suggests that further monitoring of murre populations and age composition of herring consumed is needed to better evaluate the effects on herring recruitment.

The finding of no relationship between PWS humpback whale abundance and herring recruitment may be primarily due to whales targeting adult herring aggregations rather than juveniles (Brown, 2003; Rice et al., 2011), which have lower energy content (Paul et al., 1998). The lack of a relationship between summer whale abundance and herring recruitment could also be in part due to seasonality in whale migration and feeding patterns. Recent estimates of whale abundance in PWS indicate that late autumn and winter abundances may exceed those in summer (Rice et al., 2011; Teerlink et al., 2015; J. Moran, Auke Bay Laboratories, USA, unpubl. data). Whales may consume more herring in winter, when euphausiid prey abundance declines in PWS (Foy and Norcross, 2001) and whale energetic needs increase prior to migration and breeding (Rice et al., 2011). If whales are limiting the size of recruiting year classes, annual estimates of the proportion of juvenile herring removed by whales would be required to inform recruitment predictions.

Other predators not included in this analysis may affect juvenile herring and pollock survival. For example, Arrowtooth Flounder (ATF; *Atheresthes stomias*) was identified as the main groundfish predator of herring in triennial GOA surveys in the early to mid-1990s (Yang and Nelson, 2000). The size range of herring consumed (standard length 127–263 mm) indicates that these were mainly age-1 and age-2 juveniles. ATF is also the dominant predator on juvenile pollock in the GOA (Dorn et al., 2014). However, further GOA surveys in 1999 and 2001 found negligible levels of herring predation by ATF (Yang et al., 2006). Recent winter research surveys also indicate ATF represent less than 1% of the demersal fish assemblage in PWS (Bishop and Powers, 2013). ATF in PWS thus seem unlikely to significantly influence herring recruitment.

Additional factors affecting herring mortality at early life stages were not included in this analysis, mainly due to lack of sufficient time series data on appropriate variables. For example,

jellyfish competition and predation can reduce larval Atlantic Herring (*Clupea harengus*) abundance (Möller, 1984; Lynam et al., 2005). In PWS, dietary overlap between jellyfish and juvenile herring occurs (Purcell and Sturdevant, 2001), and jellyfish abundance may vary widely (Purcell et al., 2000). However, jellyfish abundance time series data are lacking, and the effect of jellyfish on herring recruitment remains unclear.

High mortality may also occur through egg predation by seabirds, which consumed nearly one-third of herring spawn in PWS in spring 1994, mainly by gulls (Bishop and Green, 2001). Gull abundance in PWS is limited to 10 years of intermittent survey data (McKnight et al., 2008), similar to the dataset for murre. Total March gull abundance showed non-significant positive trends with herring recruits ($R^2 = 0.087$, $p = 0.409$) or recruits-per-spawner ($R^2 = 0.362$, $p = 0.066$); given the limited data, it is difficult to draw any conclusions regarding the effect of gull abundances on herring recruitment.

There is debate regarding the role of disease mortality due to viral hemorrhagic septicemia virus (VHSV) and *Ichthyophonus hoferi* in regulating PWS herring stock size and recruitment strength (Marty et al., 2003; Pearson et al., 2012). Previous work showed PWS herring stock biomass estimates were improved by adjusting adult mortality rates to account for disease prevalence, and a disease index was negatively correlated with recruitment in the following year (Marty et al., 2003). Adult herring mortality rates have been subsequently modified in the PWS herring ASA model according to indices of VHSV and *I. hoferi* incidence in spawners. Other analyses do not support a significant effect of either disease on herring recruitment (Deriso et al., 2008; Elston and Meyers, 2009; Pearson et al., 2012). VHSV can infect and kill high proportions of YOY herring in lab studies (Kocan et al., 1997), and clearly has the potential to influence the survival of pre-recruit herring, but effectively monitoring

disease incidence and inferring mortality is problematic (Hershberger et al., 2007, 2010). Lack of appropriate time series data on disease in larval or juvenile herring in PWS precluded analysis of disease in this study.

Future directions

The pollock-herring association reported here may be of practical use for PWS herring management by aiding stock size forecasts, because the GOA pollock stock assessment model provides age-1 pollock abundance estimates two years before age-3 herring recruit to the spawning stock. Adopting the proposed Bayesian method for PWS herring stock assessments should not substantially affect the utility of YOY pollock abundance in forecasting herring recruitment.

The positive association between GOA YOY pollock abundance and PWS herring recruitment should prompt further investigation into the mechanism responsible. The link between herring in PWS and pollock in the GOA suggests large-scale processes are key drivers of herring recruitment. A gulf-wide mechanism is supported by this study and by concordance in high abundances of Shelikof Strait age-1 pollock and high proportions of age-3 herring in PWS spawning biomass (Pegau, 2014).

The pollock-herring association, while relevant to herring recruitment, does not directly address the herring population decline in the early 1990s. The herring stock crash appeared to involve high mortality across age classes, rather than simply a weak recruitment event (Deriso et al., 2008). Herring recruits-per-spawner fluctuated in tandem with pollock before and after the crash, instead of dropping independently as expected if recruitment failure caused the crash. While the specific cause of the crash is debated (Thorne and Thomas, 2008; Pearson et al.,

2012), it is clear that factors unrelated to recruitment may exert a large influence on herring stock size.

PWS herring recruitment predictions may be improved by incorporating time series data on YOY herring size and energy stores in autumn. Large body size and high energy stores would reduce predation risk associated with winter foraging and starvation risk associated with low food availability (reviewed in Sogard, 1997 and Hurst, 2007). Herring size and energy data could indicate survival likelihood more directly than environmental data, because they reflect the integrated environmental conditions herring experienced and the relative risks of predation and starvation mortality. This approach has been demonstrated with survival of age-0 Bering Sea pollock in autumn: total energy, the product of body mass and energy density, is a strong predictor of survival to age 1 the following summer (Heintz et al., 2013).

Conclusions

The GOA pollock-PWS herring association reported here demonstrates how monitoring ecosystem components, including co-occurring stocks, can help understand and model recruitment. Large-scale factors such as food availability or predator abundances may drive similar trends among species with similar habitats and foraging patterns during their early life history (e.g., herring and pollock), but not others (e.g., herring and Pacific cod). While it is difficult to ascertain the relative strength of bottom-up versus top-down mechanisms causing the pollock-herring relationship, they appear to operate over a large, gulf-wide spatial scale. Research into recruitment drivers for either stock is likely to pay dividends for understanding both.

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Figures

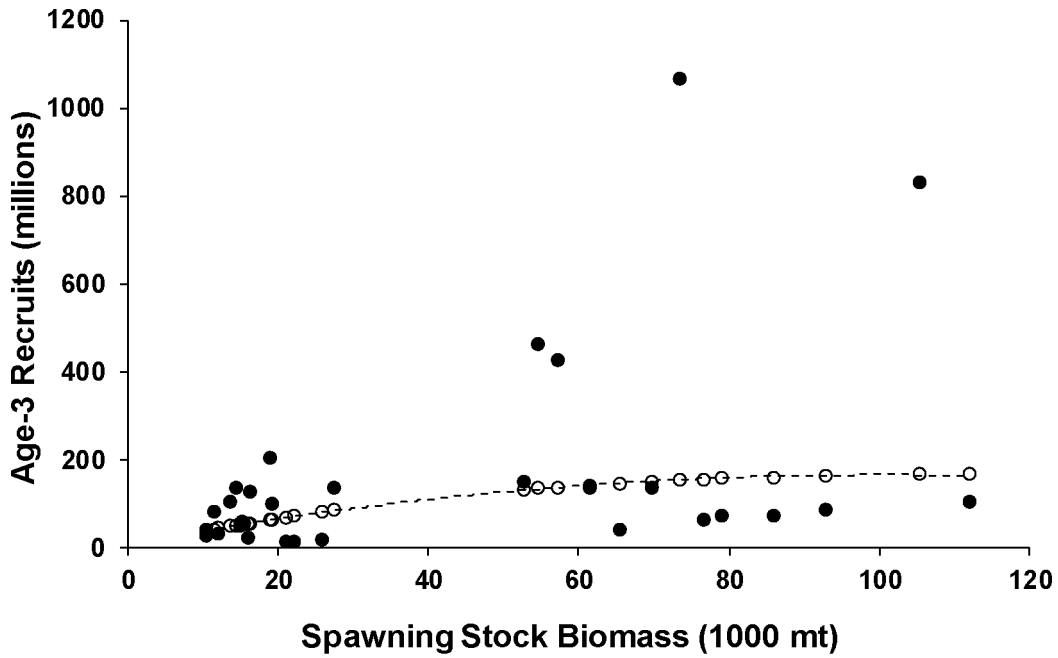


Figure 1.1 PWS Pacific herring age-3 recruits (millions) vs. spawning stock biomass (1000 metric tons), observed (●) and estimated by Ricker stock-recruit model (○, dashed line).

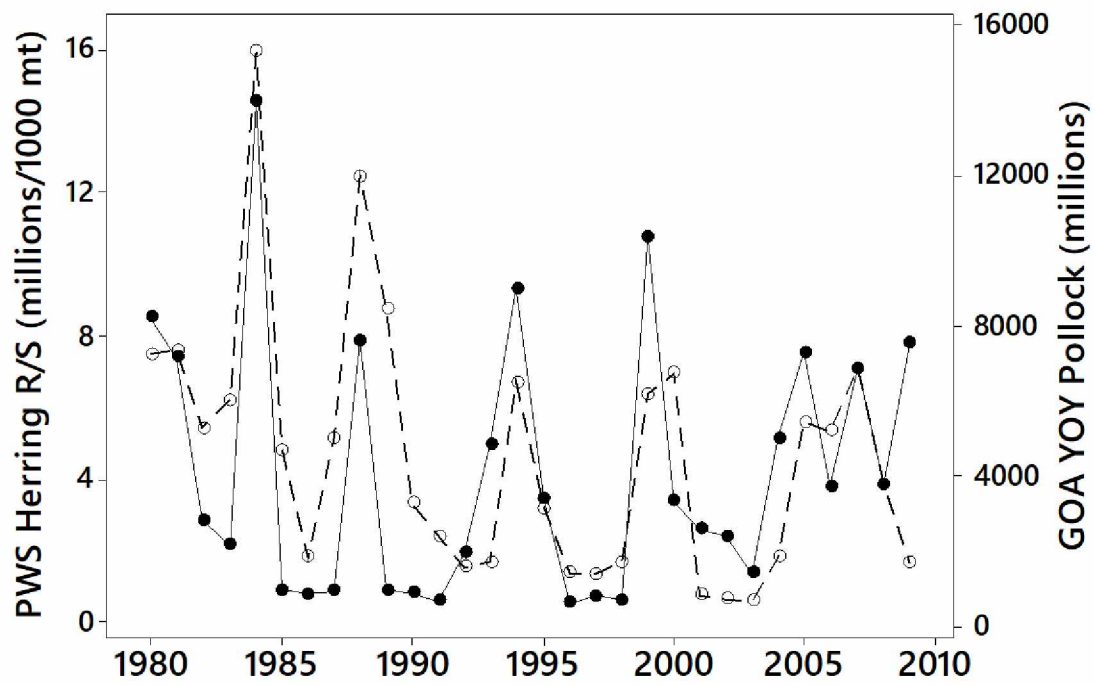


Figure 1.2 PWS Pacific herring age-3 recruits (R; millions) per spawning stock biomass (S; 1000 metric tons) by brood year (●); GOA YOY walleye pollock (millions), estimated as age-1 pollock lagged back 1 year to the herring brood year (○).

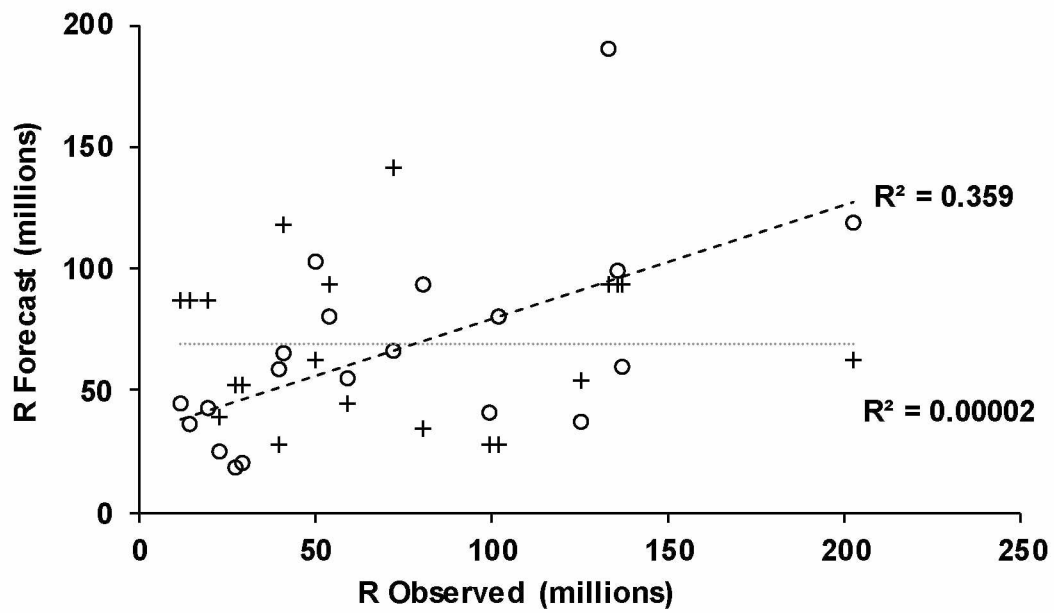


Figure 1.3 PWS Pacific herring age-3 recruits (millions), predicted by Ricker model with GOA YOY walleye pollock (○), and rolling 10-year median recruitment (+), plotted versus observed recruits (millions).

Tables

Table 1.1 Regression model variables with sets of models (A–D) in which they were used indicated by “+.” Time series length for each model set is given in parentheses. Years covered by model sets: A (1980–2009), B (1983–2009), C (1998–2009), D (1990–2007, with gaps). Annual data represent conditions in the same year, except where noted as lagged. PWS = Prince William Sound; GOA = Gulf of Alaska; YOY = young-of-the-year.

Variable	Description	A (30 yr)	B (27 yr)	C (12 yr)	D (10 yr)
R	recruits; abundance of age-3 herring in PWS, lagged three years	+	+	+	+
S	spawning stock biomass of PWS herring	+	+	+	+
$\ln(\alpha)$	intercept in linear regressions	+	+	+	+
$\beta_1 \dots \beta_{12}$	variable coefficients in linear regressions	+	+	+	+
SSTSummer	sea surface temp. in PWS (Jun – Sep)		+	+	+
SSTWinter	sea surface temp. in PWS (Jan – Apr)		+	+	+
Chl	chlorophyll- <i>a</i> concentration in PWS, spring/summer (Apr – Jun)			+	
Pcod	Pacific cod age-3+ biomass in the GOA	+	+	+	+
PcodYOY	Pacific cod YOY abundance in the GOA	+	+		
Pollock	Walleye pollock age-3+ biomass in the GOA	+	+	+	+
PollockYOY	Walleye pollock YOY abundance in the GOA (age-1 lagged one year)	+	+	+	+
PinkFry	Pink salmon hatchery fry releases in PWS	+	+		
Pinks	Pink salmon total adult returns in PWS	+	+		
Murres	murre abundance in PWS in March, lagged one year				+
Whales	humpback whale attendance in PWS, summer (Apr – Sep)		+		

Table 1.2 Multiple linear regression terms and results for select alternative models from model set A (full model, 5 lowest AICc scores, and simplest models with and without herring stock size, S), using data from 1980–2009. F-test statistics (F), coefficients of determination (R^2), and significance values (p) are given for F-tests comparing each model with the null model, and differences relative to the lowest corrected Akaike Information Criterion score ($\Delta AICc$). See Table 1.1 for descriptions of variables.

Model terms: $\ln(R/S) \sim \dots$	F	R^2	p	$\Delta AICc$
<i>Full model:</i>				
S + Pcod + PcodYOY + Pollock + PollockYOY + PinkFry + Pinks	6.09	0.659	<0.001	13.21
<i>Five lowest-scoring models:</i>				
S + PollockYOY	20.97	0.608	<0.001	0
S + PollockYOY + Pinks	15.34	0.639	<0.001	0.46
S + PollockYOY + Pollock	15.01	0.634	<0.001	0.87
S + PollockYOY + Pcod	13.74	0.613	<0.001	2.52
S + PollockYOY + PcodYOY	13.7	0.613	<0.001	2.58
<i>Simplest models, with and without S:</i>				
S + Pcod	2.27	0.144	0.123	23.46
S + PcodYOY	2.53	0.158	0.098	22.96
S + Pollock	2.15	0.138	0.136	23.68
S + PinkFry	2.34	0.148	0.116	23.33
S + Pinks	1.17	0.079	0.327	25.64
S	2.42	0.079	0.131	22.96
Pcod	0.02	0.001	0.881	25.42
PcodYOY	0.97	0.034	0.332	24.42
Pollock	0.01	<0.001	0.912	25.43
PollockYOY	11.02	0.282	0.003	15.49
PinkFry	0.17	0.006	0.684	25.26
Pinks	0.26	0.009	0.612	25.16

Table 1.A All data used in the analyses (continued on next page). See Table 1.1 for variable descriptions. See text for data sources.

Year	R – Lag 3 (10 ⁶)	S (metric tons)	ln (R/S)	SST Summer (°C)	SST Winter (°C)	Chl	Pcod (10 ³ metric tons)	Pcod YOY (10 ⁶)
1980	463.6	54475.11	-4.77				1624.670	320.265
1981	424.2	57285.42	-4.91				1586.070	254.068
1982	150.2	52621.12	-5.86	10.950	4.264		1504.780	295.072
1983	133.1	61500.46	-6.14	12.300	4.620		1401.980	145.211
1984	1065.2	73338.66	-4.23	12.658	4.780		1264.790	390.703
1985	85.4	92928.26	-6.99	10.955	4.488		1157.820	414.097
1986	61.7	76632.56	-7.12	11.370	3.723		1028.890	176.107
1987	69.7	79018.35	-7.03	11.871	4.677		972.643	327.204
1988	831.5	105401.27	-4.84	11.772	4.581		950.770	309.750
1989	101.9	112130.39	-7.00	11.975	3.860		878.232	310.288
1990	72.2	85993.13	-7.08	12.936	3.735		838.127	405.093
1991	40.7	65389.25	-7.38	11.363	3.132		782.279	293.991
1992	136.7	69761.66	-6.23	11.578	4.349		740.946	253.799
1993	135.8	27287.16	-5.30	12.440	4.203		738.720	328.682
1994	133.2	14289.43	-4.68	12.304	4.524		740.281	259.853
1995	53.6	15546.98	-5.67	11.679	4.142		732.112	362.095
1996	11.6	20950.71	-7.50	12.400	4.205		719.517	231.215
1997	19.2	25743.70	-7.20	13.839	3.957		692.044	205.016
1998	14.1	22065.11	-7.35	12.323	5.703	0.5373	686.513	171.738
1999	202.3	18781.91	-4.53	11.583	4.351	0.5385	656.421	241.546
2000	50.2	14856.91	-5.69	12.326	4.226	0.7581	603.097	261.777
2001	27.3	10468.94	-5.95	12.393	4.693	0.5759	550.354	194.512
2002	28.9	11901.59	-6.02	12.195	3.556	0.7479	529.119	124.960
2003	22.5	16091.37	-6.57	13.147	5.708	0.5727	518.736	180.017
2004	99.0	19227.22	-5.27	14.274	4.646	0.5392	498.786	156.678
2005	102.1	13516.19	-4.89	14.112	4.709	0.5717	451.601	236.190
2006	39.5	10392.70	-5.57	11.914	4.370	0.4723	424.851	339.879
2007	80.7	11360.71	-4.95	12.338	3.768	0.4213	395.738	311.125
2008	58.9	15220.43	-5.55	10.779	4.049	0.5054	390.517	439.749
2009	125.5	16122.50	-4.86	11.900	3.464	0.4028	422.309	352.985

(Table 1.A ... continued.)

Year	Pollock (10 ³ metric tons)	Pollock YOY – Age 1, Lag 1 (10 ⁶)	Pink Fry (10 ⁶)	Pinks (10 ⁶)	Murres – Lag 1 (10 ³)	Whales	Bayes R – Lag 3 (10 ⁶)	Bayes S (metric tons)
1980	1743	7251	21.64176	18.71922			447.91	57230
1981	2694	7339	72.53800	25.12905			373.56	66260
1982	2935	5282	78.01800	26.97483			119.70	57700
1983	2771	6032	92.98453	20.40984		52.8	142.15	67500
1984	2425	15278	85.13600	33.97709		73.3	1237.93	79520
1985	1983	4708	154.79410	33.25863		71.1	136.76	96280
1986	1624	1857	200.42330	14.56712		66.9	28.43	84730
1987	1996	5029	251.93330	34.29280		62.7	29.67	95600
1988	1910	11962	532.04450	14.97346		84.3	844.99	122030
1989	1731	8431	507.66970	27.86068	7.439	95.9	62.41	124990
1990	1575	3295	615.12720	48.14768	24.103	96.7	135.11	107570
1991	1757	2416	603.51810	41.09184		91.6	18.25	94970
1992	2118	1594	495.70190	10.31921	220.969	117.0	94.46	93740
1993	1845	1731	567.32050	8.389238	51.727	124.6	76.91	38830
1994	1539	6493	489.22060	36.91824		120.9	142.02	20490
1995	1286	3171	613.15820	20.98541	46.079	125.0	69.83	18710
1996	1077	1440	641.67540	28.11908		156.9	6.08	20520
1997	1108	1405	483.70400	31.14881	87.714	154.1	22.41	27920
1998	982	1726	542.38310	33.51494		147.9	10.27	21890
1999	782	6176	602.12890	56.35720	31.159	148.8	210.28	14930
2000	689	6748	586.60700	44.59996		139.5	39.97	13430
2001	655	871	621.06210	42.39767		141.8	19.03	11910
2002	821	749	603.75470	23.03203		144.2	26.15	14660
2003	1025	699	607.94330	63.20437	70.935	135.2	16.74	19900
2004	835	1880	638.84690	29.82770	92.777	131.7	102.28	20330
2005	687	5441	564.05310	76.42172		124.7	94.69	15890
2006	588	5215	599.49030	26.82117	34.482	118.7	28.11	13700
2007	561	6872	617.60830	69.06474		143.3	53.48	15360
2008	856	3808	610.63990	45.38412		134.3	9.23	21140
2009	1292	1697	640.20260	24.48669		193.9	77.84	20120

Chapter 2. Growth, energy storage, and feeding patterns reveal winter mortality risks for juvenile Pacific herring in Prince William Sound, Alaska, USA²

Abstract

First winter survival of juvenile cold temperate fish can be an important recruitment driver. Winter survival may be influenced by size and energy reserves, with larger, fatter individuals less vulnerable to predation and starvation. However, limited information regarding relationships among size, growth, and energy reserves often hampers understanding recruitment processes for economically and ecologically important marine species. To better understand winter mortality risks, we examined growth and lipid storage patterns in young-of-the-year (YOY) Pacific herring *Clupea pallasii* in Prince William Sound, Alaska, USA, near the onset (November) and end (March) of 7 winters during 2009–2016 that occurred before and during the North Pacific marine heat wave. Herring length in November determined energy allocation, with a shift from protein-based growth to lipid storage occurring at ~76 mm fork length. We suggest that size-selective predation pressure causes small herring below this size to favor growth over storing fat. Low March lipid stores apparently compelled herring to avoid starvation by foraging, behavior that could increase predation risk especially for small herring. Larger herring ate more high-quality euphausiid prey than did small herring during November, reinforcing the advantages of large size. Herring lipid stores were highest in the coldest study year, rather than the year with the best diets, presumably due to low temperature slowing metabolic rates. Our findings suggest

² Sewall, F., Norcross, B., Vollenweider, J., Heintz, R. 2019. Growth, energy storage, and feeding patterns reveal winter mortality risks for juvenile Pacific herring in Prince William Sound, Alaska, USA. Mar. Ecol. Prog. Ser. 623, 195–208.

overwinter survival models could be improved with unbiased estimates of late autumn YOY herring size and energy distributions, seasonal temperature measurements, estimates of food consumption, and knowledge of local predator densities.

Introduction

Survival of juvenile marine fishes prior to recruitment to adult stocks is determined via poorly understood processes that—for many stocks of small pelagic fish—result in weak relationships between stock size and annual recruitment (Zheng 1996). Uncertainty in the stock-recruitment relationship for high-latitude fishes can be driven by variable young-of-the-year (YOY) winter mortality (Hurst 2007). Developing mechanistic models relating winter survival to specific fish traits and environmental factors may improve the ability to predict recruitment (Heintz et al. 2013). However, mortality processes for fish in high-latitude marine environments in winter are generally not well-studied (Hurst 2007).

For pre-recruit fish, chances of survival may increase for individuals that grow rapidly to large size (Anderson 1988, Miller et al. 1988). Greater body mass and length generally improve survival of juvenile fish by reducing their vulnerability to both starvation and predation (Sogard 1997). For example, size is a key predictor in models of juvenile Pacific salmon *Oncorhynchus* spp. survival, for which failure to reach a minimum critical size by autumn results in higher winter mortality (Beamish & Mahnken 2001, Moss et al. 2005). Size-dependent winter mortality among salmon has been linked to size-related differences in stored energy levels (Beamish & Mahnken 2001, Farley et al. 2011). Stored energy levels are thus often used as an alternative indicator of mortality risk. Winter mortality risk in wild fish populations is inferred to be high if

they approach minimum levels of lipid or energy necessary for survival in laboratory studies (Paul & Paul 1998, Sogard & Olla 2000). Some models relating winter survival to energy reserves rely solely on laboratory-derived energy loss rates, the number of days spent fasting, and the minimum energy density required for survival (Paul & Paul 1998, Patrick 2000). Yet, size or energy data alone may not provide the best survival estimates. For example, survival of juvenile walleye pollock *Gadus chalcogrammus* to age-1 is better predicted when size and energy data are combined (Heintz et al. 2013).

Attaining large size and energy stores for winter survival may be promoted by late autumn growth and food availability. Late season growth has been associated with YOY survival for northern freshwater species (Huss et al. 2008, Post & Parkinson 2001). A fish that is able to eat and sustain growth at the onset of winter is unlikely to be consuming its stored energy. As juvenile fish grow, their capacity for storing energy increases more rapidly than their metabolic costs (e.g. for walleye pollock; Heintz & Vollenweider 2010). Thus, fish that are eating well and growing in late autumn should be less vulnerable to starvation during winter, when zooplankton abundance typically declines (Foy & Norcross 2001, McKinstry & Campbell 2018).

Prey availability strongly influences the response of juvenile fish growth to temperature. When food is more abundant, growth rate increases rapidly with temperature and peaks at a higher temperature (Beauchamp et al. 2007). However, growth may be inhibited when temperature exceeds the optimal range for a given species (Laurel et al. 2016). High temperatures can also be associated with lower abundance of zooplankton prey in autumn and winter (Foy & Norcross 2001).

Zooplankton scarcity in winter likely increases the predation risk associated with visual foraging (Scheuerell & Schindler 2003), especially for smaller fish (Sogard & Olla 1997). When

food is limited, fish appear to increase their searching activity (Sogard & Olla 1996). Small fish use their energy stores at higher rates than larger fish (Schultz & Conover 1999) and are consequently more reliant on foraging to survive winter (Heintz & Vollenweider 2010). Greater predation vulnerability of small fish is thus likely a major driver of size-dependent mortality in winter (Sogard 1997).

Pacific herring *Clupea pallasii* (hereafter herring) serves as an instructive model organism for investigating winter mortality mechanisms in a small pelagic fish species due to its life history, ecology, behavior, and social value. Herring in Prince William Sound (PWS), Alaska supported a commercial fishery before the population crashed in the early 1990s (Thomas & Thorne 2003, Hulson et al. 2008). Additionally, it is an ecologically important forage fish prey for piscivorous fish, seabirds, and marine mammals in part due to its schooling behavior and high lipid stores (Iverson et al. 1997, Thomas & Thorne 2001). Storing lipids depends on seasonally variable zooplankton prey that becomes scarce in winter (Foy & Norcross 2001). Consequently, winter feeding and growth for YOY herring are limited and mortality risk is high. Mortality of YOY herring overwintering in dense schools nearshore exceeds that of older herring offshore, and varies among years and bays in PWS (Stokesbury et al. 2002). Model mortality estimates can be as high as 95%, suggesting that first year winter mortality is a primary driver of year-class strength (Norcross & Brown 2001, Norcross et al. 2001). Thus, understanding the mechanisms of YOY herring winter mortality would improve predictive models of survival and ultimately recruitment.

The goal of this study was to identify juvenile herring traits and environmental factors useful for understanding mechanisms driving first-winter herring survival. To this end, we investigated relationships among size, growth, energy storage, and diet for YOY herring

collected from PWS at the beginning and end of 7 winters. Specifically, we sought to determine how protein-based growth and lipid stores relate to YOY herring size at the beginning and end of winter, and how lipid stores influence foraging at the end of winter. We also examined how herring lipid stores at the beginning of winter differed by location and year, and if this could be attributed to differences in diets. This information allowed us to assess the evidence for a critical size that YOY herring must achieve for winter survival and thereby provide insight into mortality processes for a high-latitude small pelagic fish.

Methods

Field sampling

Juvenile herring were collected from multiple sites in Prince William Sound, Alaska (Fig. 2.1) during November and March across 7 winters (November 2009 through March 2016), to investigate spatial and interannual variability in growth, energy storage, and diets. Sampling effort (Table 2.A.1, labeled Table S1 in the Supplement at www.int-res.com/articles/suppl/m623p195_supp.pdf) focused on Eaglek Bay, Lower Herring Bay, Simpson Bay, Whale Bay, and Zaikof Bay, due to their coverage across regions of PWS and for continuity with previous herring research (Norcross et al. 2001), while additional bays (Port Fidalgo, Port Gravina, and Windy Bay) were sampled opportunistically. Collection gear included cast nets (4.8 mm, 6.4 mm, and 9.5 mm square mesh), single- and variable-mesh gillnets (9.5, 12.7, and 19.1 mm square mesh through 2012; 6.4, 7.9, and 9.5 mm square mesh after 2012), and mid-water trawls (38 mm square mesh at opening decreasing to 12 mm at codend). Collected herring were randomly subsampled, frozen, and transported by air to the Alaska Fisheries Science Center's

Auke Bay Laboratories (Juneau, AK), for measurements of fork length (FL, to nearest 1 mm) and wet weight (to nearest 0.001 g) along with chemical analysis. Growth and energy stores were typically measured on a target sample size of 20 individuals per site within a bay (Table 2.A.2), chosen in 5-mm size bins to proportionally represent the length–frequency distributions of the field-collection subsamples. Catches were generally smaller in March than the preceding November. Sample sizes for analysis across PWS ranged from 139 for November 2013 to 28 for March 2016.

Growth

The recent growth of individual herring was assessed using RNA/DNA ratios. Higher RNA/DNA indicates greater protein synthesis rates over the preceding few days (Buckley 1984, Buckley et al. 1999). The RNA and DNA contents of 10–15 mg plugs of dorsal white muscle tissue representing less than 1% of fish body mass were determined with a fluorometric dye-binding assay using the methodology of Caldarone et al. (2001) as modified by Sreenivasan (2011). Muscle tissues were sonicated in buffered detergent, sequentially treated with fluorescing dye, RNase, and DNase enzymes, and fluorescence was read by spectrophotometer at each step. Fluorescence readings were calibrated according to the RNA/DNA ratios in known quantities of standard materials, consisting of calf liver 18S + 28S ribosomal RNA and calf thymus DNA (Sigma), that were run with each batch of 20 samples. Sample RNA/DNA ratios across multiple processing batches were standardized to an average standard slope ratio of 3.84 to ensure comparability among batches and to facilitate comparisons with other studies (Caldarone et al. 2006). Method blanks were processed concurrently with samples to check for contaminants introduced at any step in the procedure.

Energy storage

The lipid content of herring was used as a measure of stored energy. Prior to lipid analysis of herring, stomachs were excised, stomach contents removed and stored individually for diet analysis, and stomachs returned to carcasses. Following removal of muscle plugs and stomach contents, individual herring were homogenized with mortar and pestle to minimize tissue loss. Homogenates were analyzed for lipid mass as a percentage of wet tissue mass (% lipid) following procedures described in Vollenweider et al. (2011b). Briefly, lipid extraction was performed following a modified Folch method (Folch et al. 1957) using a Dionex 200 Accelerated Solvent Extractor, followed by drying and weighing lipid extracts. NIST reference materials were used for quality control to verify lipid analysis. Each sample batch was also processed concurrently with in-house reference materials to check accuracy, a sample replicate to check precision, and a method blank to check for contaminants.

The minimum lipid level needed for survival was estimated using data from a previous laboratory study of captive juvenile herring (Vollenweider et al. 2011a). For that study, YOY herring were collected in Puget Sound, WA, held at 3 temperatures in replicated tanks, and fed until a 10-wk winter fasting period. Fish that died while fasting were sampled ($n = 45$) for lipid analysis. Log-transformed lipid data were pooled from starvation mortalities across treatment groups to establish the average survival threshold level of lipid cited in the present study.

Feeding and diet

To assess influences of diet mass and composition on herring growth and energy stores, and as an indicator of foraging activity, stomach contents were weighed throughout the study

period. For the last 5 winters of the study, November 2011 through March 2016, individual prey items were then enumerated and identified to the lowest taxon practical. Due to degradation from digestion and handling, total mass of prey by taxon was estimated by multiplying counts of individuals for each taxon by values for their undigested mass from literature (Coyle et al. 1990, Foy & Norcross 1999). Thus all prey of a given taxon were assumed to have the same mass, given the impracticality of accurately measuring all prey items.

Statistical analysis

Size-based trade-offs between growth and energy storage

To evaluate the relationship between YOY herring growth and energy storage, RNA/DNA and % lipid data pooled across years were fit to length for November and March using piecewise linear regressions (Muggeo 2003). Relationships to size were reported on a length basis rather than mass basis because % lipid is a mass-based index and therefore % lipid and mass would not be independent measures. RNA/DNA and lipid data were transformed (natural log and square root, respectively) to meet regression assumptions of normally distributed residuals and equal variances. A piecewise regression approach was used because we expected the energy allocation strategy could shift at a fixed length for juvenile herring, as has been observed for other juvenile fishes in seasonal environments (Post & Parkinson 2001, Stallings et al. 2010). In addition, exploratory analysis of November data using generalized additive models (GAMs; Wood 2006) suggested that the slopes of the relationships between RNA/DNA or % lipid and length were not linear and changed abruptly at intermediate lengths. The RNA/DNA–length relationship had up to 2 plausible breakpoints: one at which RNA/DNA decreased rapidly with length, and a second at which RNA/DNA reached a minimum metabolic threshold and

remained constant with length. The lipid–length relationship had 1 plausible breakpoint at which lipid increased rapidly with length, with no upper limit observed. Given that the relationships of RNA/DNA and % lipid to length could follow piecewise linear patterns, statistical software (R package ‘Segmented’; Muggeo 2014) employing least-squares regression was used to identify the line breakpoints where the relationships changed. To compare use of plausible alternative models, piecewise (1 or 2 breakpoints for RNA/DNA, 1 breakpoint for lipid), simple linear, quadratic, and GAM (limited to ≤ 4 knots) candidate models were ranked using Akaike Information Criterion (AIC):

$$AIC = -2\ln(L) + 2K$$

where L is the likelihood, and K is the number of parameters in the model. The model with the lowest AIC score was deemed the best; models scoring 0–2 points higher had ‘substantial support,’ those scoring 4–7 higher had ‘considerably less support,’ and those scoring >10 higher had ‘essentially no support’ (Burnham & Anderson 2004).

Growth and energy storage across years and bays

To assess the influence of year and location on growth and energy stores, a 2-way ANOVA was performed using the best regression model residuals for RNA/DNA and %lipid as the response variables. Residuals from the best regression models were used to remove the effects of herring size. Size bias in the herring sampling gear prohibited direct comparisons of growth or energy storage among years and bays, with cast nets capturing smaller fish during November (mean FL \pm SE: 72.8 ± 0.8 mm, $n = 290$) than trawls (85.4 ± 1.1 mm, $n = 145$) or

gillnets (88.7 ± 0.7 mm, $n = 309$) (Fig. S1). ANOVA was performed only using the 5 primary bays with data from November and March for at least 2 of the 7 years (Table 2.A.2), and year–bay interactions were not tested due to missing data. Post-hoc Tukey pairwise comparisons were used to identify specific years and bays that differed.

To investigate the role of temperature in driving yearly differences in growth or energy stores, water temperature data was obtained from the NOAA Cordova tide station ($60^{\circ}33.5'N$, $145^{\circ}45.3'W$). Annual mean temperatures were obtained by averaging hourly, daily, and then monthly values. Mean annual residuals from lipid and RNA/DNA piecewise regressions were fit to annual average water temperatures in simple linear regression models.

Feeding and diet

To investigate diet as a driver of differences in herring growth and energy stores, we compared YOY herring diets among years and bays using several metrics. Stomach fullness, expressed as stomach contents mass as a percentage of herring body mass, was used as an indicator of feeding success. To assess whether depletion of energy stores influenced feeding, stomach fullness as a function of lipid level in November versus March was compared using rank-based robust regression employing a Wald test and reduction in dispersion test (Kloke & McKean 2012) using the R ‘Rfit’ rank-based estimation package (Kloke & McKean 2016). Note that for a given fish, percent stomach fullness and percent lipid are independent measures of stomach contents mass and lipid mass, respectively, normalized to body mass. Frequency of occurrence of prey by taxa during November was calculated to assess differences in prey selection across years. To simplify analysis, prey were aggregated into groups of large copepod species, small copepod species, euphausiids, and other taxa. Large versus small copepods were

categorized based on adult body length greater or less than 2.5 mm, following the convention of Foy & Norcross (1999). Euphausiids included primarily adults and few furcilia. To evaluate the relative importance of different prey, the average contribution by mass for each prey group (%) was determined for all samples pooled at the level being compared (year or bay). Diet composition differences by year, bay, and herring length were assessed by non-parametric permutational multivariate ANOVA (PERMANOVA) based on Bray-Curtis dissimilarities in taxa proportions by mass (Anderson 2001), using the R ‘Vegan’ community ecology package (Oksanen et al. 2018). Opportunistically sampled bays such as Port Fidalgo were excluded from that analysis due to limited years of data. Variation in the probability of eating individual prey taxa as a function of herring length was evaluated using logistic regression on prey presence/absence data. Simpson Bay and opportunistic bays were excluded from that analysis due to absence of euphausiids. Diet types were assigned according to the category of prey that made up at least 50% of the diet mass they consumed. High variability and skew in the diet data required log transformation and use of non-parametric Mann-Whitney tests, and Welch’s ANOVA (Welch 1951, Day & Quinn 1989) using weighted least squares to compare years and bays due to unequal variances. Games-Howell pairwise comparisons (Games & Howell 1976, Day & Quinn 1989) were used to identify specific years and bays that differed.

Results

Size-based trade-offs between growth and energy storage

Energy allocation to protein-based growth versus lipid storage varied with YOY herring length. For November, the relationship of RNA/DNA to length was best described by a

piecewise regression model with 2 breakpoints (Fig. 2.2; Table 2.A.3) that identified lengths where the relationship shifted. Herring smaller than 74 mm FL (95% CI: 70–78 mm) in November typically had the highest RNA/DNA, while RNA/DNA decreased rapidly with length for individuals larger than 74 mm FL (piecewise regression, $R^2 = 0.36$, $p < 0.001$). RNA/DNA for herring larger than 85 mm FL (95% CI: 82–88 mm) approached a minimum level for routine metabolism and no growth, as previously determined in herring starved under laboratory conditions (RNA/DNA ratio ~4–5; Sreenivasan 2011). In contrast, YOY herring lipid content for November increased with body size. Herring larger than 76 mm FL (95% CI: 65–87 mm) stored lipid at a higher rate than smaller herring. Percent lipid and FL were weakly related (piecewise regression, adj. $R^2 = 0.15$, $p < 0.001$).

For March, relationships of RNA/DNA and % lipid to length were similar to those for November, with RNA/DNA decreasing with size and lipid increasing with size (Fig. 2.3), though the best-fitting model forms differed from November (Table 2.A.4). The inverse linear relationship between RNA/DNA and FL was weak but statistically significant ($R^2 = 0.21$, $p < 0.001$, $n = 446$), and showed no evidence of nonlinearity. RNA/DNA values were generally slightly higher in March than November. Lipid levels were generally lower in March than in November, with especially large decreases in % lipid among herring larger than the November lipid accumulation breakpoint (>76 mm FL). The piecewise model differed negligibly from the best-scoring quadratic model, so it was used to identify the breakpoint at which lipid increased with length. Percent lipid was uniformly low across lengths for herring smaller than 89 mm FL in March, while lipid levels for larger herring were variable and increased with length, resulting in a significant but weak overall relationship to length (piecewise regression, $R^2 = 0.08$, $p < 0.001$, $n = 461$).

Growth and energy storage across years and bays

Growth and condition of YOY herring before winter varied across years and bays in PWS. Year and bay significantly influenced November growth (2-way ANOVA, $R^2 = 37.1\%$; $F_{\text{Year } 6, 639} = 39.58$, $p < 0.001$; $F_{\text{Bay } 4, 639} = 26.65$, $p < 0.001$) and lipid levels (2-way ANOVA, $R^2 = 17.8\%$; $F_{\text{Year } 6, 628} = 17.65$, $p < 0.001$; $F_{\text{Bay } 4, 628} = 5.63$, $p < 0.001$). Herring in 2012 had the highest RNA/DNA ratio (Table 2.1) and % lipid (Table 2.2) over the 7-yr period studied. The 2012 cohort continued to have high lipid levels in March 2013 (2-way ANOVA, $R^2 = 23.2\%$; $F_{\text{Year } 6, 373} = 16.17$, $p < 0.001$; $F_{\text{Bay } 4, 373} = 1.13$, $p = 0.341$; Table 2.3). The 2012 cohort experienced the lowest annual average water temperature of the study period (Fig. 2.4), suggesting that cooler temperature promoted YOY herring condition and growth. However, given the short time series, the effects of water temperature on RNA/DNA ($F = 3.09$, $p = 0.139$) and lipid ($F = 2.85$, $p = 0.152$) were not statistically significant, and the apparent relationships were largely driven by the low 2012 temperature.

The lipid stores and growth of juvenile herring in November varied widely among bays across years, such that no specific bay consistently produced herring in the best condition (Fig. 2.A.2). Simpson Bay herring tended to be below average in growth (Table 2.A.5) and lipid (Table 2.A.6) across years, while Whale Bay herring tended to be above average across years.

Feeding and diet

Herring nearing exhaustion of their stored fat by late winter were compelled to feed (Fig. 2.5). Herring stomach fullness was inversely related to lipid level with November and March pooled (Table 2.4). However, a model with separate slopes by month performed significantly

better (reduction in dispersion test, $F = 5.5$, $p = 0.004$). Using the 2-slope model, comparison of intercepts and slopes showed that stomach fullness for March was higher initially and declined more rapidly with lipid level than for November, indicating a stronger effect and greater need to feed during March. Though herring approaching the minimum survival threshold lipid level of $1.28 \pm 0.10\%$ tended to be small, and stomach fullness was negatively related to herring length (Table 2.A.7), feeding in March also occurred among large herring (Fig. 2.A.3).

Juvenile herring in November 2011 generally ate more than during other years, as shown by higher stomach content mass relative to body mass (Fig. 2.A.4), though log-transformed stomach fullness values in 2011 did not statistically differ from 2010 and 2012 (Table 2.A.8). Diet composition differed by year, bay, and herring length, in order of effect size, though the effects of each were only moderate (Table 2.5). Relative to other years, diets in 2011 showed a high proportion by mass and frequency of occurrence of euphausiids (Fig. 2.A.5), an especially energy-rich prey item (Foy & Norcross 1999). Euphausiids did not exceed 2% occurrence in PWS herring stomachs for any of the other 4 years examined.

Across years, the probability of eating euphausiids increased with herring length (logistic regression, $p < 0.001$), and the relationship was evident in bays with high proportions of euphausiids eaten (e.g. Whale Bay; Fig. 2.6). Considering only herring larger than 76 mm FL, representing those large enough to store more lipids and eat euphausiids, diets that consisted of primarily euphausiids ($>50\%$ by mass) were associated with the highest RNA/DNA (Welch's ANOVA, $R^2 = 5.00\%$, $F_{5, 359} = 3.54$, $p = 0.010$) and % lipid residuals (Welch's ANOVA, $R^2 = 0.64\%$, $F_{5, 359} = 0.52$, $p = 0.757$), although the lipid differences were not significant. Variation in euphausiid consumption among bays in 2011, the only year with significant euphausiids in diets, may have contributed to differences in herring condition. In 2011, among herring larger than 76

mm FL, those caught in Whale Bay ate the most euphausiids (Fig. 2.A.6) and had higher RNA/DNA and % lipid than other bays (Fig. 2.A.7). Across years however, no bay showed consistently high stomach fullness (Fig. 2.A.8).

Discussion

Size- and energy-dependent mortality risks

YOY herring apparently need to reach a critical size threshold before they begin storing fat for winter. The observed shift from growth at small sizes to energy storage at larger sizes indicates that body size determines the energy allocation strategy of YOY herring near the onset of winter. The shift from growth to energy storage likely reflects tradeoffs in size-dependent winter mortality risks by predation versus starvation. Herring that fail to exceed a critical size by November may continue to allocate energy to growth in an attempt to reduce risk of predation by Pacific cod *Gadus macrocephalus*, walleye pollock and other groundfish (Bishop & Powers 2013). Groundfish predation declines sharply for YOY herring larger than 75–80 mm FL (Bishop et al. 2017). Because that is smaller than the typical (mean, median, or mode) size of herring captured for this study, it suggests that small YOY herring may be eaten disproportionately to their occurrence in the population, though gear selectivity prohibits definitive size comparison. Predation risk may be reduced for larger juvenile herring due to their increased swimming ability (Christensen 1996) or size relative to the gape size of predators (Scharf et al. 2000). With lower predation risk, larger herring may benefit from a shift in strategy from growth to storing fat for winter use.

Depletion of winter fat stores may compel herring to feed and to risk predation to avoid starvation. Lipid stores during November were generally low among small herring, indicating they started winter with high starvation risk. By late winter in March, small, lean herring tended to have fuller stomachs than larger, fatter herring, suggesting that small herring rely on winter feeding to survive. In contrast, large herring, which generally had high lipid stores at the onset of winter in November, and low stomach fullness by late winter in March, can use more fat to survive without significant winter feeding. Winter fasting by high-lipid herring may reflect a survival strategy; feeding may not be worth the associated predation risk if prey scarcity largely precludes growth and the risk of lipid depletion is low. Winter feeding triggered by lipid depletion is also seen in YOY striped bass *Morone saxatilis* (Hurst & Conover 2001), indicating the tradeoff in winter predation and starvation risk occurs among diverse species. Food deprivation in herring (Robinson & Pitcher 1989) and other schooling fishes (Morgan 1988, Sogard & Olla 1997) decreases anti-predator schooling behavior. Predation risk would also be heightened during winter, when the low prey availability (Foy & Paul 1999) requires greater foraging effort. The need to forage would be highest for small herring with low lipid stores that are unlikely to sustain them until food availability increases in spring (Paul & Paul 1998). Additionally, their higher mass-specific metabolic rates (Schultz & Conover 1999) would cause them to exhaust lipid stores more quickly than larger herring. Risk appears lowest for large fish that store the most lipid prior to winter, not only because they would be better at escaping predation attempts, but also because they could endure longer without foraging and increasing exposure to predators.

Energy-dependent mortality risk is not necessarily equivalent to size-dependent risk, as feeding triggered by low stored energy levels was not limited to smaller fish. While lipid

generally increased with size, herring of a given size showed a wide range of lipid levels that could reflect differences in their prior feeding or thermal histories. Regardless of the cause, observations of lipid levels and stomach fullness indicate many large fish deplete their lipid stores by March and must also forage. Although many herring in March exceeded the modal size of YOY herring consumed by groundfish, they were within the range of sizes eaten, thus increased foraging activity could still increase predation risk for larger herring with low energy stores. Consequently, juvenile herring survival may depend on total energy, the product of body mass and energy density, similarly to YOY pollock (Heintz et al. 2013). Winter survival is likely highest among fish larger than the critical size for fat storage in November, due to their reduced risk of both starvation and foraging-induced predation.

Relatively little work has been published about size-dependent winter mortality in Pacific herring. Size-dependent mortality is often inferred from increases in mean size in a population over winter, but evidence distinguishing this effect from growth is limited. Juvenile herring in Resurrection Bay, Alaska and PWS show an increase in average length over winter, which likely reflects loss of smaller herring from the population because the low mean stored energy makes growth unlikely (Paul & Paul 1998, Foy & Paul 1999). Though the present study lacks unbiased mean size estimates, the small herring present in November collections were less common during March. Small herring in this study in November and March allocated available energy to growth rather than fat, but significant winter growth was unlikely because RNA/DNA levels were much lower than in earlier autumn (September 2012 mean RNA/DNA 15.1 ± 0.2 ; Heintz et al. 2017) and approached minimum levels needed for routine metabolism. Building on past efforts, we thus present further evidence that size-dependent winter mortality of YOY is an important factor in northern Pacific herring populations.

Environmental influences on survival

Cool autumn temperatures may promote better pre-winter herring condition, at least over the temperature range and feeding conditions present in this study. One of the important features of this study is that sample collections spanned years before and during the North Pacific Ocean marine heat wave event of 2014–2015 ('The Blob'; Bond 2014, Di Lorenzo & Mantua 2016). This enabled comparisons of herring across a relatively large change in annual average sea temperatures. Over the 7-yr study period, herring had the best condition in 2012, when November water temperature was coldest. Cold temperature may promote higher lipid levels in herring by slowing metabolism and rate of fat loss. Higher fat reserves would not only minimize imminent starvation risk, but also delay the need for foraging activity with its attendant predation risk. Herring were the leanest in 2015, the warmest year of the study. An increase in autumn and winter temperatures of 2°C from 1996 to 1997 was associated with lower zooplankton abundance in PWS (Foy & Norcross 2001). Warm years may thus decrease autumn zooplankton abundance, resulting in poor feeding and low fat stores before winter, both of which were observed in 2015. Even with abundant food, fat storage capacity can decline when temperatures increase beyond a species-dependent optimum (Copeman et al. 2017). Regardless of the mechanism, the contrast in lipid levels we observed matched the pattern in herring energy density between the warm year 2015 and the cold year 2012 (Gorman et al. 2018).

The finding of high RNA/DNA in the coldest year suggests better growth at lower temperatures, at least over the temperature range observed in this study. However, it is unclear to what extent high RNA/DNA in a colder year is due to lower efficiency of translating RNA into protein at colder temperatures. While elevated RNA/DNA indicates growth in mass and length in

larval and juvenile fish (Bulow 1970, Folkvord et al. 1996), the amount of growth represented by a given level of RNA is temperature-sensitive. A temperature increase of 1°C can increase growth 1% per day at a given RNA/DNA level for some marine fish larvae, though RNA/DNA ratios are generally comparable without corrections for temperatures within 2°C (Buckley et al. 1999). For our direct RNA/DNA comparisons among bays, the temperature differences among bays were typically small (<2°C; R. Campbell, Prince William Sound Science Center, pers. comm.). In contrast, lower growth efficiency at colder temperatures likely contributed to the higher RNA/DNA seen in March than November, which typically differed by more than 3°C. Likewise, higher RNA/DNA may be required by YOY herring in a colder year to achieve similar growth as lower RNA/DNA in a warmer year. High temperature may promote growth when food is abundant, but may not if food is limited or temperatures exceed the optimal range for PWS herring. The positive temperature–growth relationship for PWS herring can break down in years when the July–August average temperature exceeds 12.5°C (Batten et al. 2016). August temperatures approached that point in 2014–2015, years marked by persistent unusually warm sea temperatures ('The Blob') in the North Pacific Ocean (Bond 2014, Di Lorenzo & Mantua 2016). More observations, particularly in cold years, would help clarify the response of herring RNA/DNA and growth to temperature. Given recent findings that warm summers and abundant plankton promote first-year herring growth (Batten et al. 2016), and the present finding that herring condition before and after winter was best in a cold year, the best temperature conditions supporting YOY herring survival are likely a warm summer followed by a cold winter. Concurrently, zooplankton prey quantity and quality must be sufficient to promote high growth in summer and forestall starvation in winter.

The effect of diet differences on YOY herring growth and condition was less clear than the effect of temperature, though euphausiids may have played an important role. Herring prey consumption appeared highest during November of 2011 among the 5 years analyzed, but did not lead to greater growth or fat stores relative to other years. Euphausiid consumption by large herring, consistent with previous observations (Foy & Norcross 1999), is presumably enabled by large gape size and swimming ability and further reinforces the survival advantages of large size. Though the effect was weak, large herring with euphausiid-dominated diets had higher growth and possibly greater fat stores than similarly sized herring eating other prey, suggesting a positive feedback loop between herring size and euphausiid consumption. Differences in euphausiid consumption among bays in 2011, when feeding conditions were best, may have contributed to differences in herring condition. Herring growth and lipid levels in 2011 were highest in Whale Bay, where diets were euphausiid-dominated. Availability of euphausiids, with their large size and high energy density relative to copepods and other zooplankton (Foy & Norcross 1999), could maximize return on herring foraging effort. Given that euphausiids may also reduce predation pressure on herring by serving as alternative prey for groundfish and whales (Lang et al. 2005, Schweigert et al. 2010), euphausiids may promote herring survival in years when they are abundant, though not all bays may support euphausiids and benefit herring equally.

Different oceanographic conditions among bays may drive spatial differences in herring condition observed in our study and previous studies (Norcross et al. 2001). For example, the tendency for higher herring growth and energy stores observed in Whale Bay, a deep unsilled fjord, were likely driven by a unique combination of local zooplankton production and seasonal influx of zooplankton from the Gulf of Alaska (Gay & Vaughan 2001, Gorman et al. 2018). This

localized variability in winter habitat quality means that bays likely contribute unequally to recruitment to the PWS herring stock, though no single bay is consistently best at promoting juvenile herring survival. Overwintering in several diverse bays may thus represent a portfolio strategy (Figge 2004, Schindler et al. 2015) in which variation in overall PWS herring abundance is dampened by minimizing the impact of occasionally poor conditions and high mortality in any given bay.

Given the importance of first winter survival in determining eventual recruitment to the adult stock (Hurst 2007, Norcross et al. 2001), our findings suggest biological and ecological variables that should be considered for development of winter survival models. The size-based trade-off in growth versus energy storage we observed at the start of winter, and an energy storage-based tradeoff in winter feeding versus not feeding, suggest that quantitative models of YOY herring winter survival should use unbiased estimates of late autumn size and energy distributions. In addition, challenges to herring winter survival should be characterized by seasonal temperature measurements and estimates of food consumption and local predator densities. While this study focused on the survival of herring during their first winter, mortality at other periods can strongly influence survival until recruitment to the adult stock. High first winter survival appeared to be promoted by good condition of YOY herring in 2012, as indicated by aerial survey observations of schools of age-1 herring an order of magnitude more abundant than usual in summer 2013 (Pegau 2014). The 2012 YOY herring were expected to contribute strongly to the 2015 adult spawning stock at age 3, but low spawner abundance in 2015 made the stock age composition unclear (S. Moffitt, Alaska Department of Fish and Game, pers. comm.). Regardless of the 2012 cohort strength relative to other years, low overall stock size in 2015 suggests high mortality after their first winter and before recruiting at age 3, possibly related to

the extreme warming event in the North Pacific in 2014–2015. High water temperatures in that period are linked to a range of impacts in the North Pacific (Di Lorenzo & Mantua 2016), including Gulf of Alaska fish species and their predators (Zador & Yasumiishi 2017). Effects on fish included record low abundances of larval and age-1 juvenile walleye pollock (Zador & Yasumiishi 2016, Dorn et al. 2017) and declines in abundance of juvenile Pacific cod across age classes (Barbeaux et al. 2017), likely due to increased natural mortality. High juvenile fish mortality was likely driven partly by food limitation, caused by shifts toward smaller, lower energy zooplankton prey during the warming event (McKinstry & Campbell 2018, Batten et al. 2018). The unusual marine heatwave may thus have contributed to high mortality of age-1+ juvenile herring, including the 2012 cohort. In more typical years, a key determinant of recruitment is survival through the first winter, which we have shown can be promoted by large size and high fat stores in autumn.

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Figures

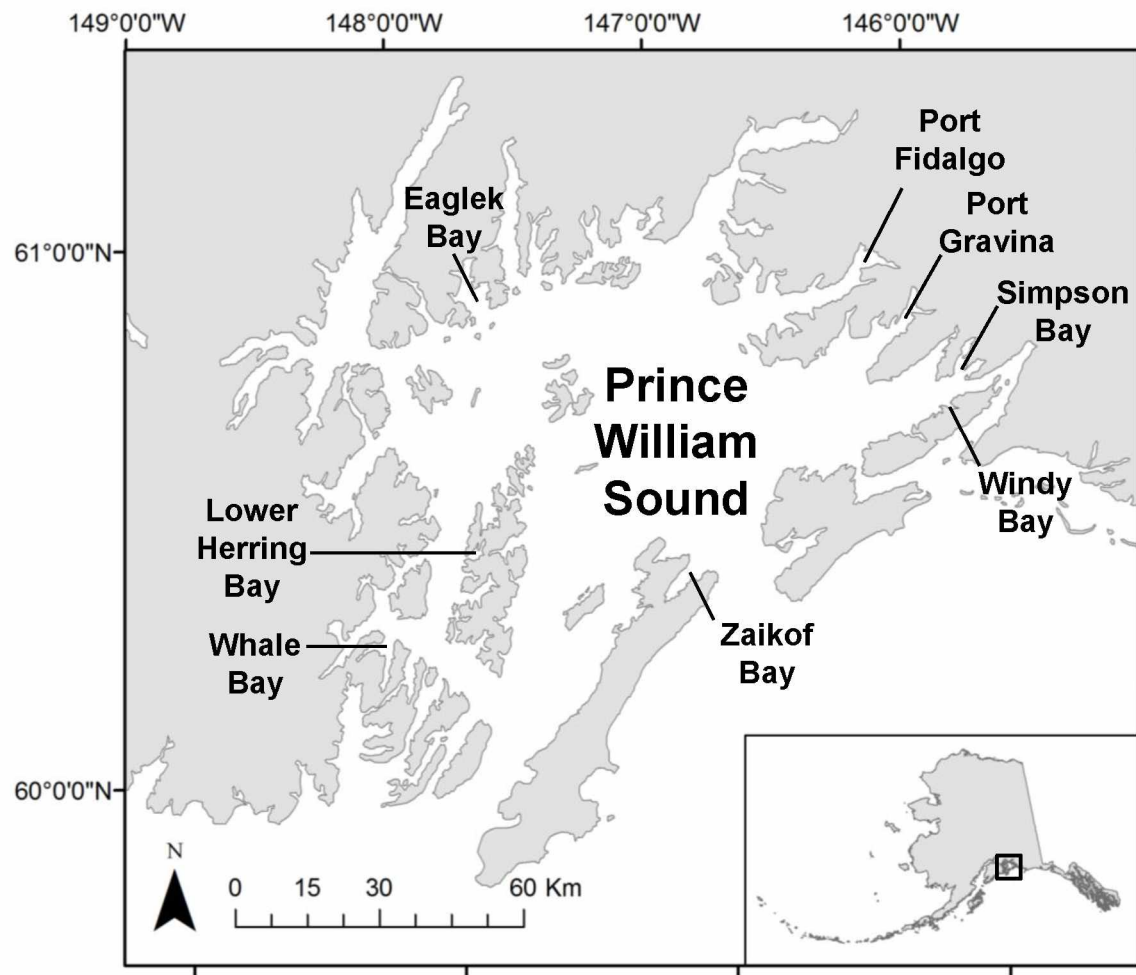


Figure 2.1 Study area indicating primary collection sites for young-of-the-year Pacific herring.

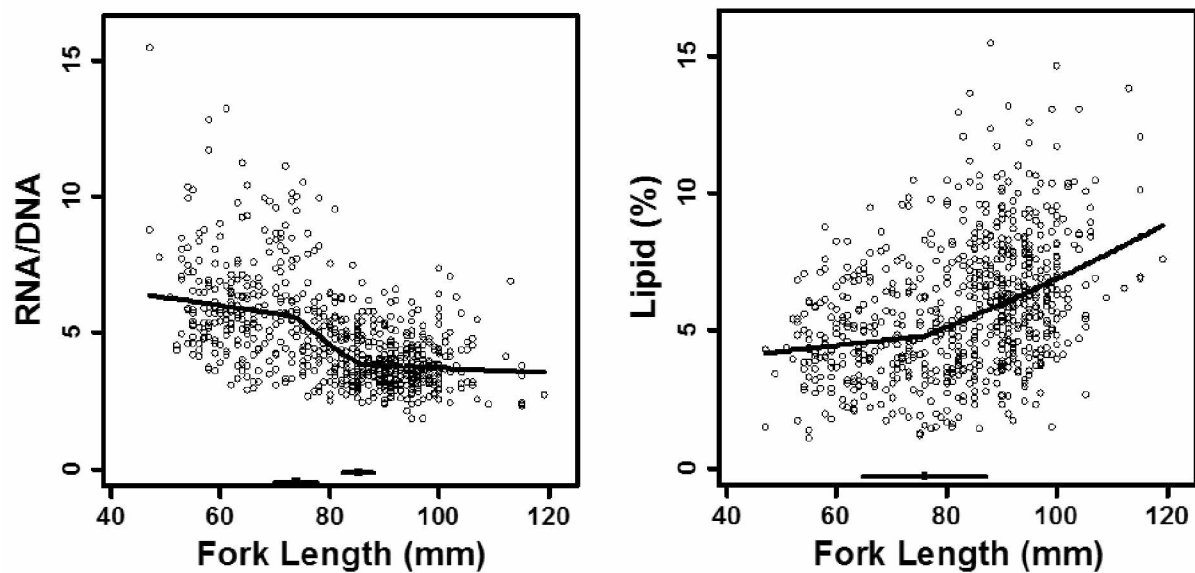


Figure 2.2 RNA/DNA (left panel; $n = 745$) and lipid content (% wet tissue mass) (right panel; $n = 734$) as a function of fork length, for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015. Lines: back-transformed (exponentiated and squared) predicted values from the piecewise regression model fits to log- and square-root transformed data (bars at bottom: breakpoints and 95% CIs).

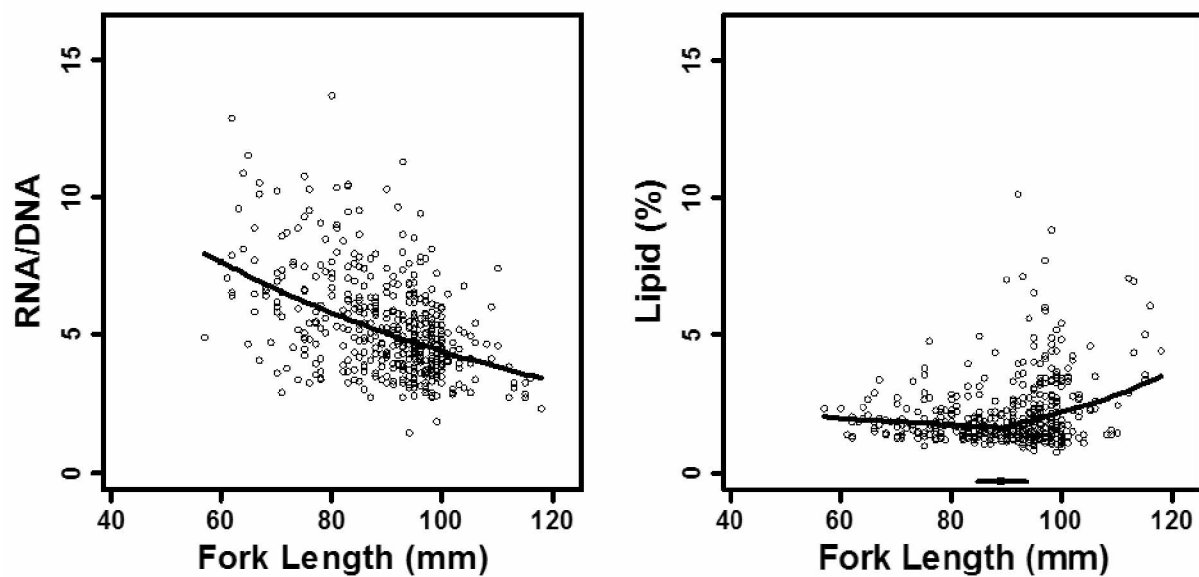


Figure 2.3 RNA/DNA (left panel; $n = 446$) and lipid content (% wet tissue mass) (right panel; $n = 461$) as a function of fork length, for young-of-the-year herring collected in Prince William Sound, AK, in March 2010–2016. Lines: back-transformed (exponentiated) predicted values from the linear and piecewise regression model fits to log-transformed data, respectively (bar at bottom: breakpoint and 95% CI).

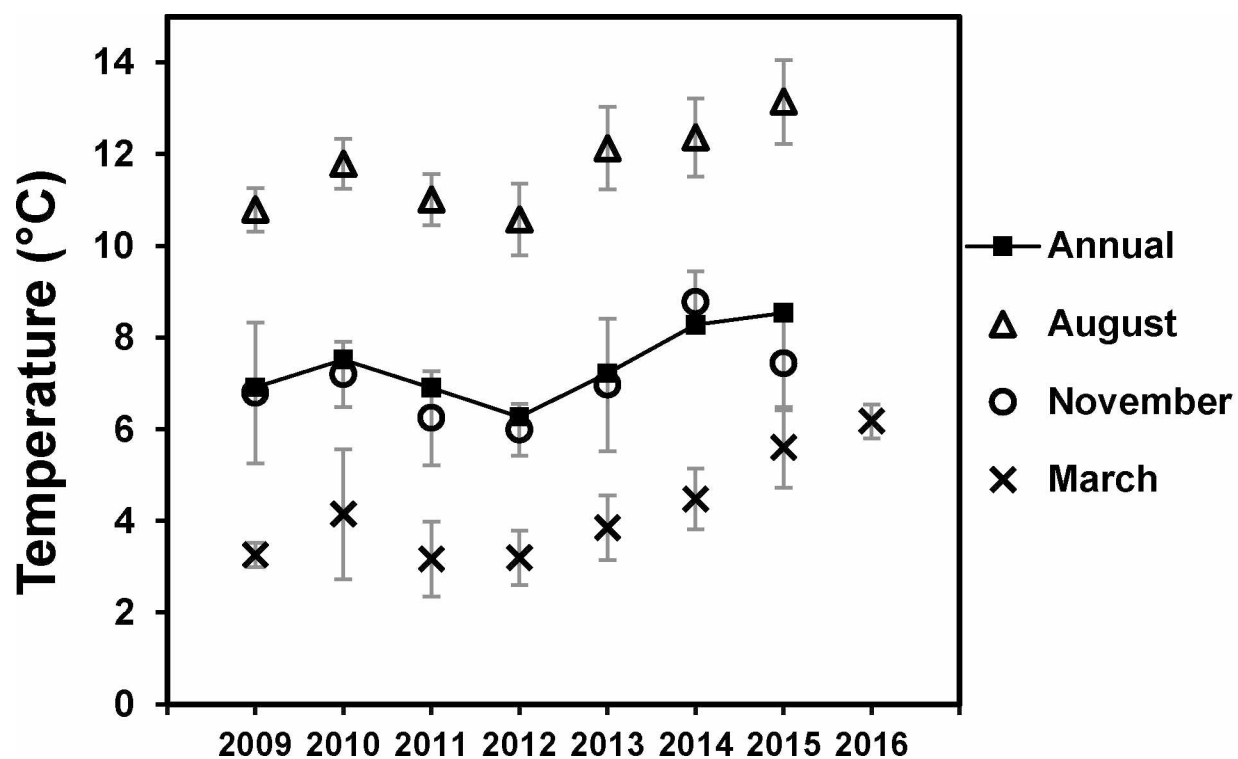


Figure 2.4 March, August, November, and annual mean water temperatures (°C) in Prince William Sound, AK, in 2009–2016, as measured at NOAA Cordova tide station, ~2 m below mean lower low water. Error bars for monthly means are standard deviations of daily means. Annual means are point estimates. November means are partially obscured by annual means. (Data downloaded 8/8/16 from <https://tidesandcurrents.noaa.gov/stationhome.html?id=9454050>)

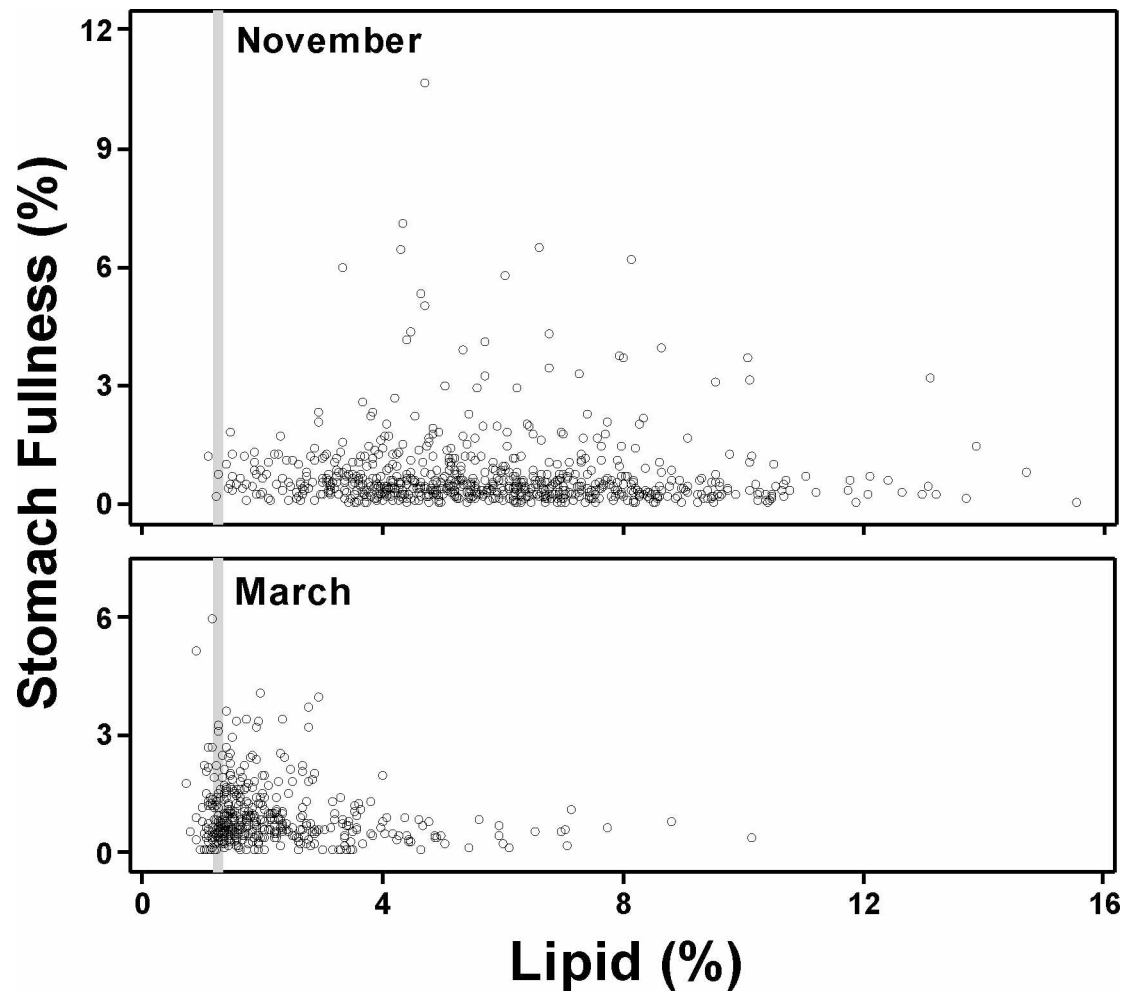


Figure 2.5 Stomach fullness (stomach contents mass as % of body mass) versus lipid content (% wet tissue mass) for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015 (top panel; $n = 710$) and March 2010–2016 (bottom panel; $n = 444$). Gray line: survival threshold level of lipid (1.28 ± 0.10 %) under laboratory conditions.

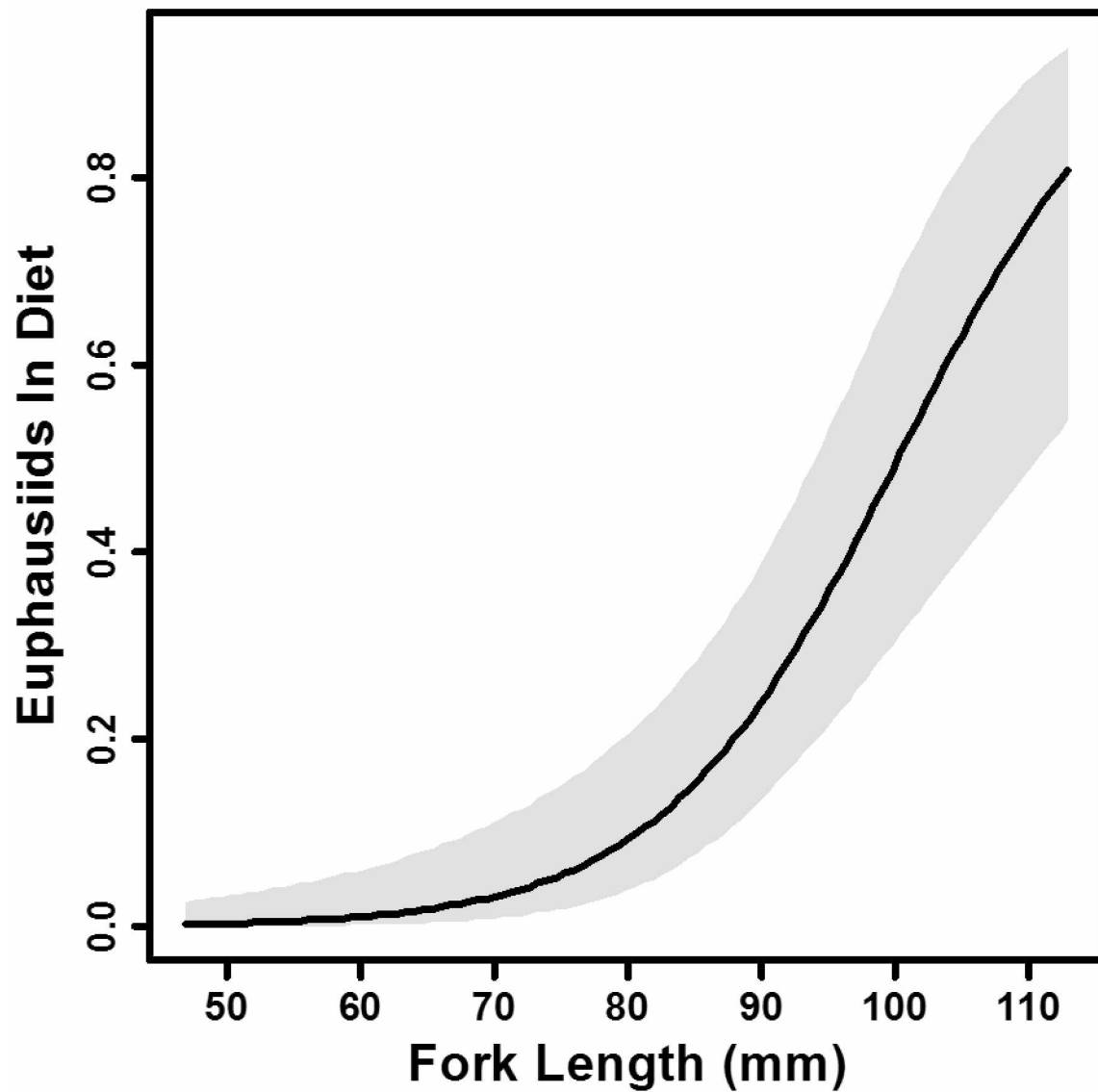


Figure 2.6 Probability of eating euphausiids (95% confidence band) as a function of herring fork length, for young-of-the-year herring with non-empty stomachs collected in Whale Bay, Prince William Sound, AK, in November 2011–2015.

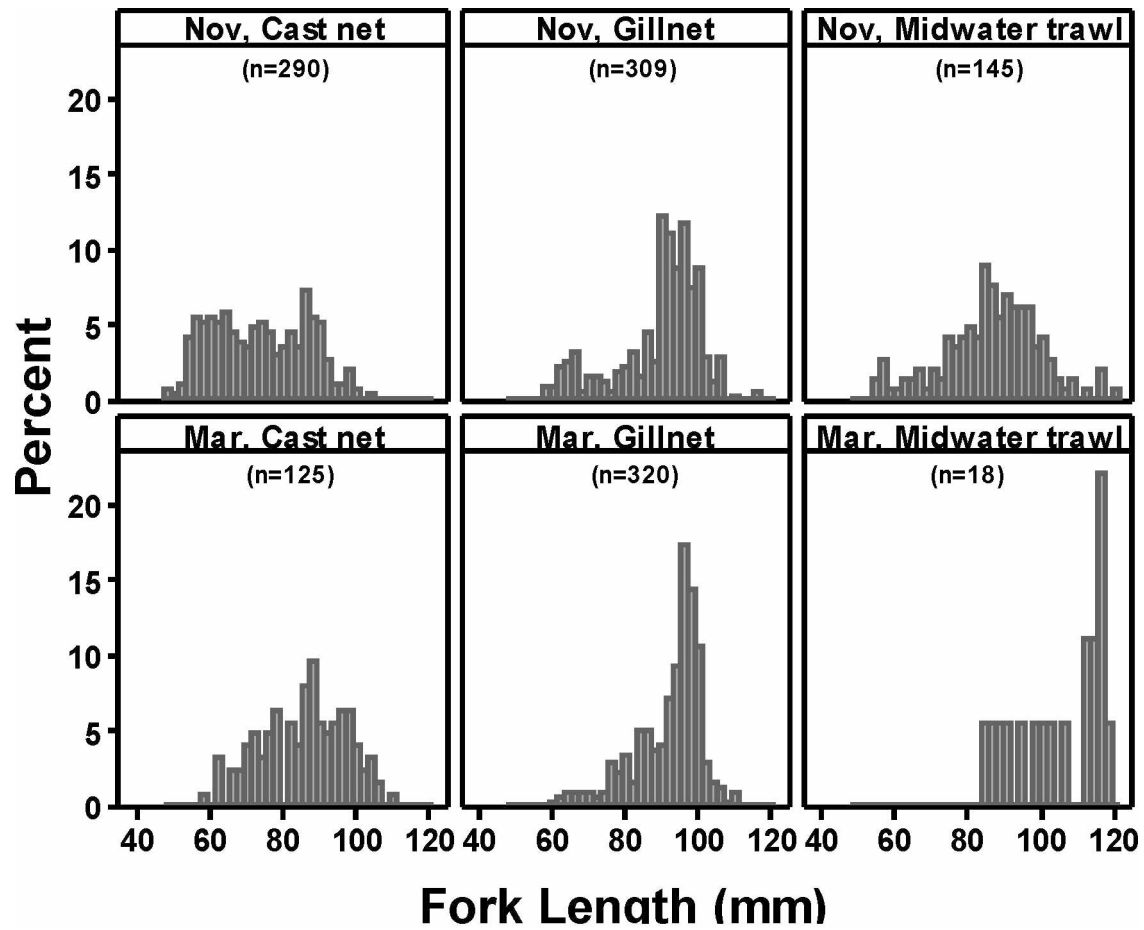


Figure 2.A.1 Fork lengths (mm) for young-of-the-year herring collected in Prince William Sound, AK, by cast net, gillnet, and midwater trawl in November 2009–2015 (top panels) and March 2010–2016 (bottom panels).

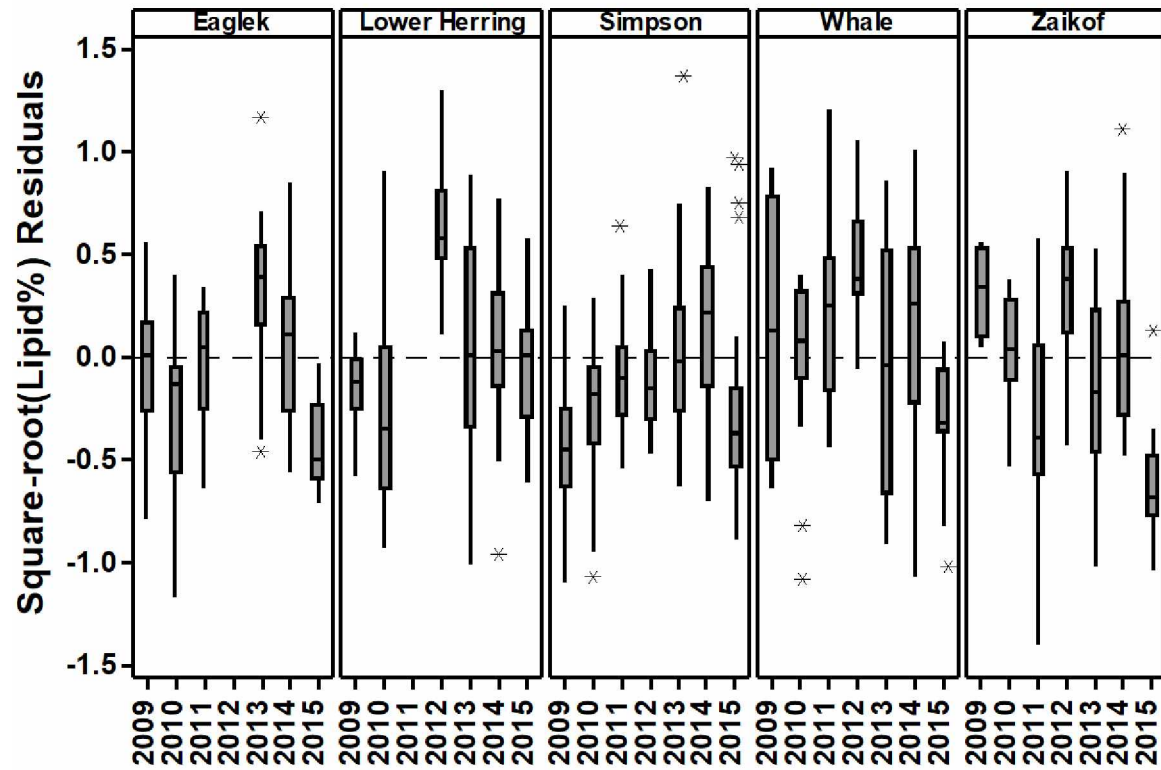


Figure 2.A.2 Residuals from the piecewise regression of square-root transformed lipid versus length of young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015. Medians, interquartile ranges (IQR), whiskers (≤ 1.5 IQR) and outliers (*, > 1.5 IQR) are shown.

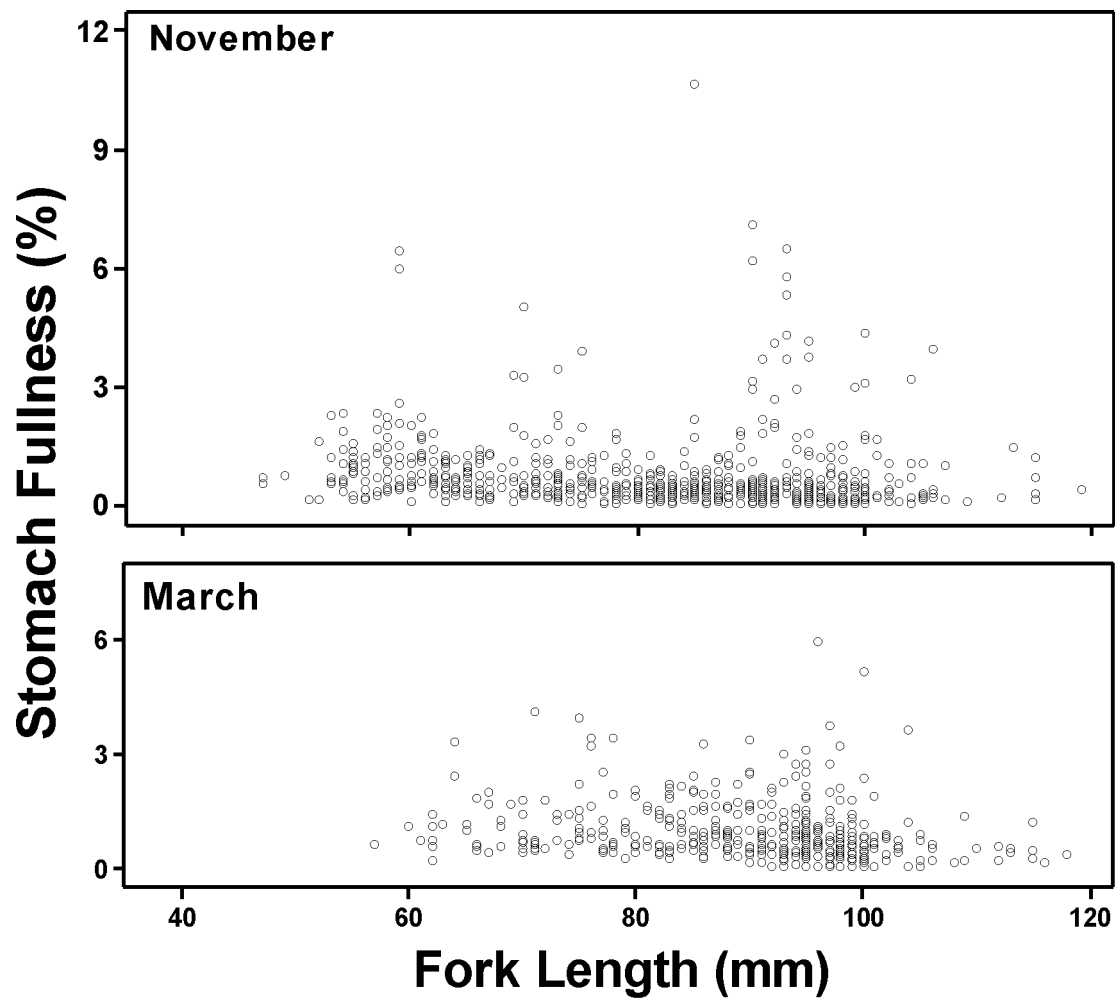


Figure 2.A.3 Stomach fullness versus fork length (mm) for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015 (top panel; $n = 710$) and March 2010–2016 (bottom panel; $n = 444$).

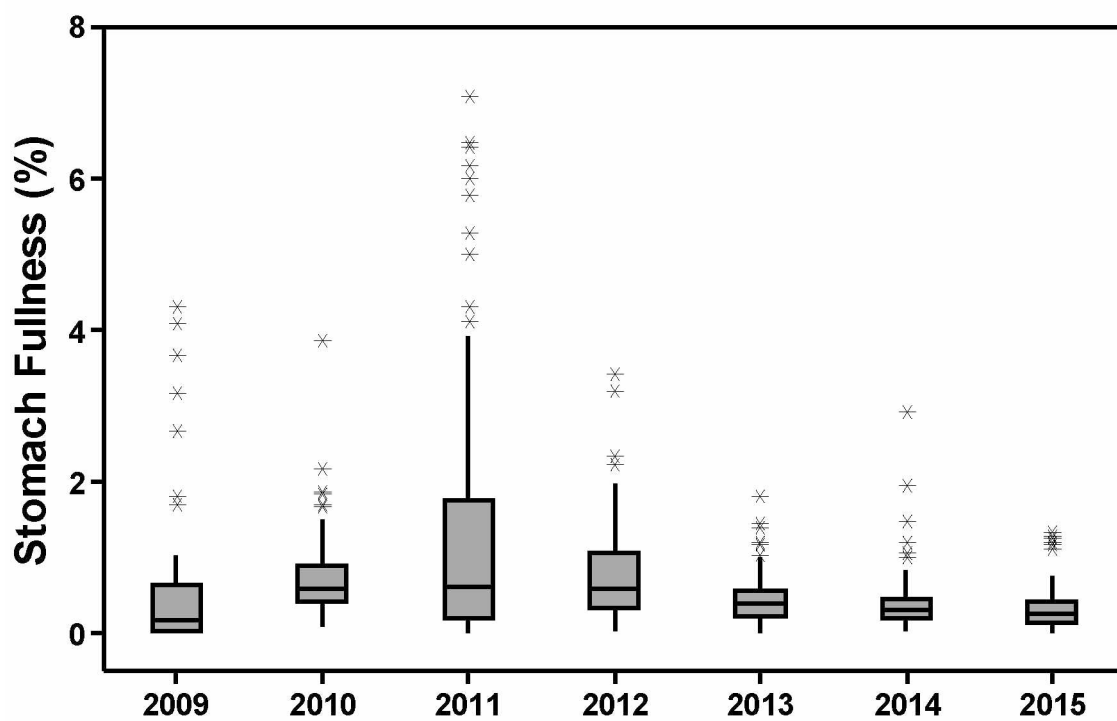


Figure 2.A.4 Stomach content mass as a percentage of body mass for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

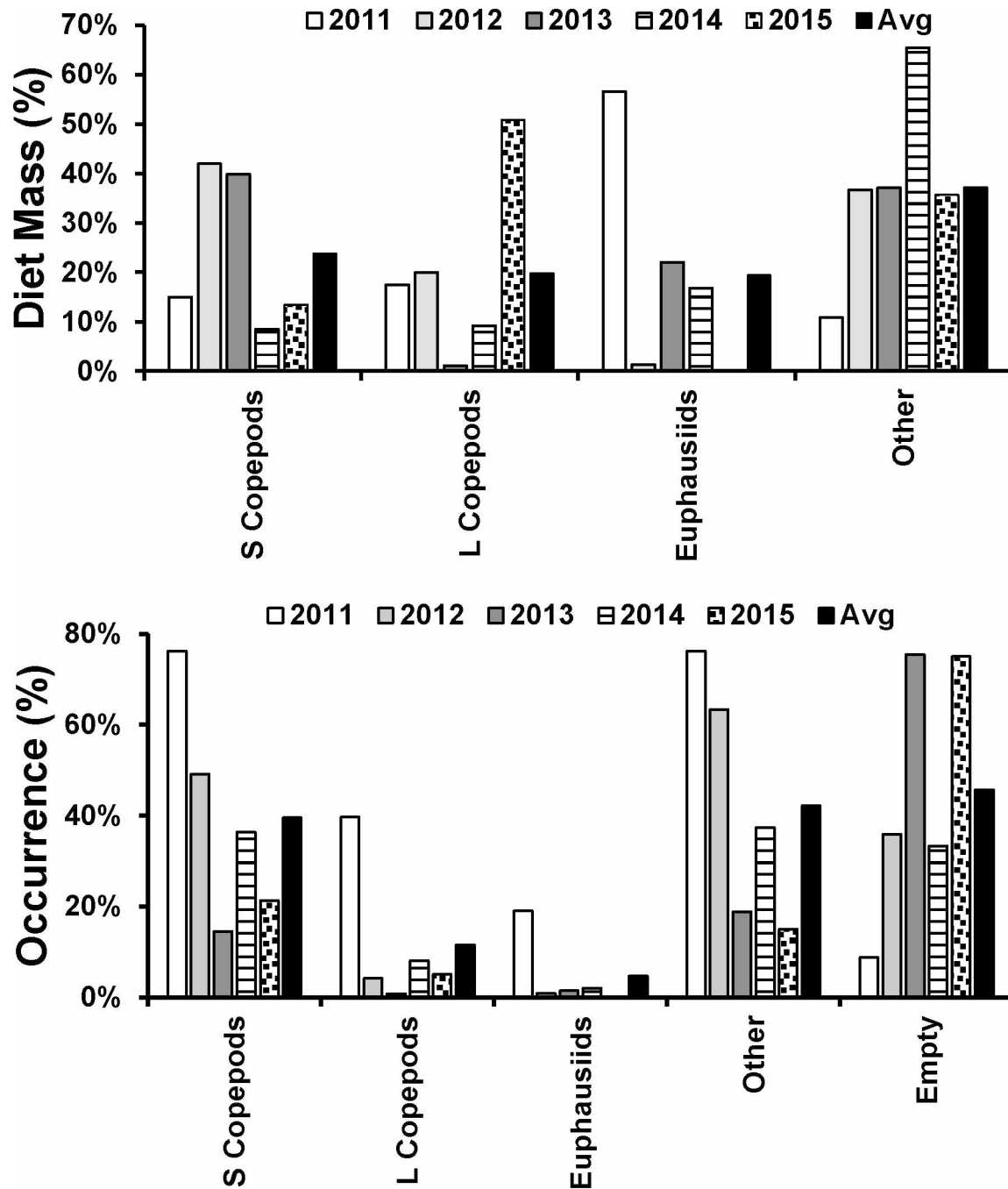


Figure 2.A.5 Mass of prey consumed as percentage of total diet mass consumed, pooled by year (top panel; N = 312 non-empty stomachs), and frequency of occurrence of prey as a percentage of numbers of stomachs examined (bottom panel; N = 563) for young-of-the-year herring collected in Prince William Sound, AK, in November 2011–2015.

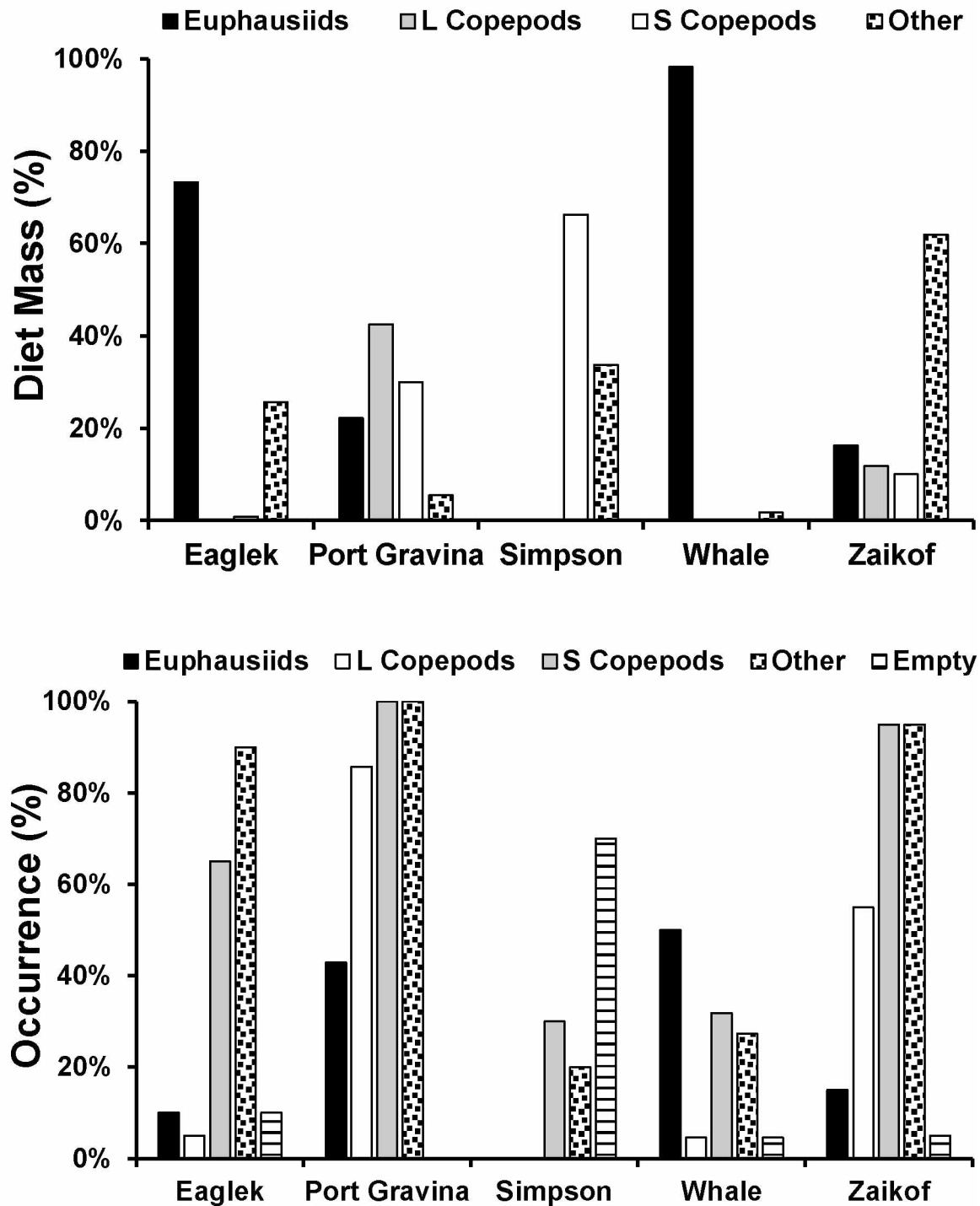


Figure 2.A.6 Mass of prey items consumed as percentage of total mass consumed (top panel; N = 75 non-empty stomachs), pooled by bay, and frequency of occurrence of prey as a percentage of numbers of stomachs examined (bottom panel; N = 86) for young-of-the-year herring > 76 mm FL collected from 5 bays in Prince William Sound, AK, in November 2011.

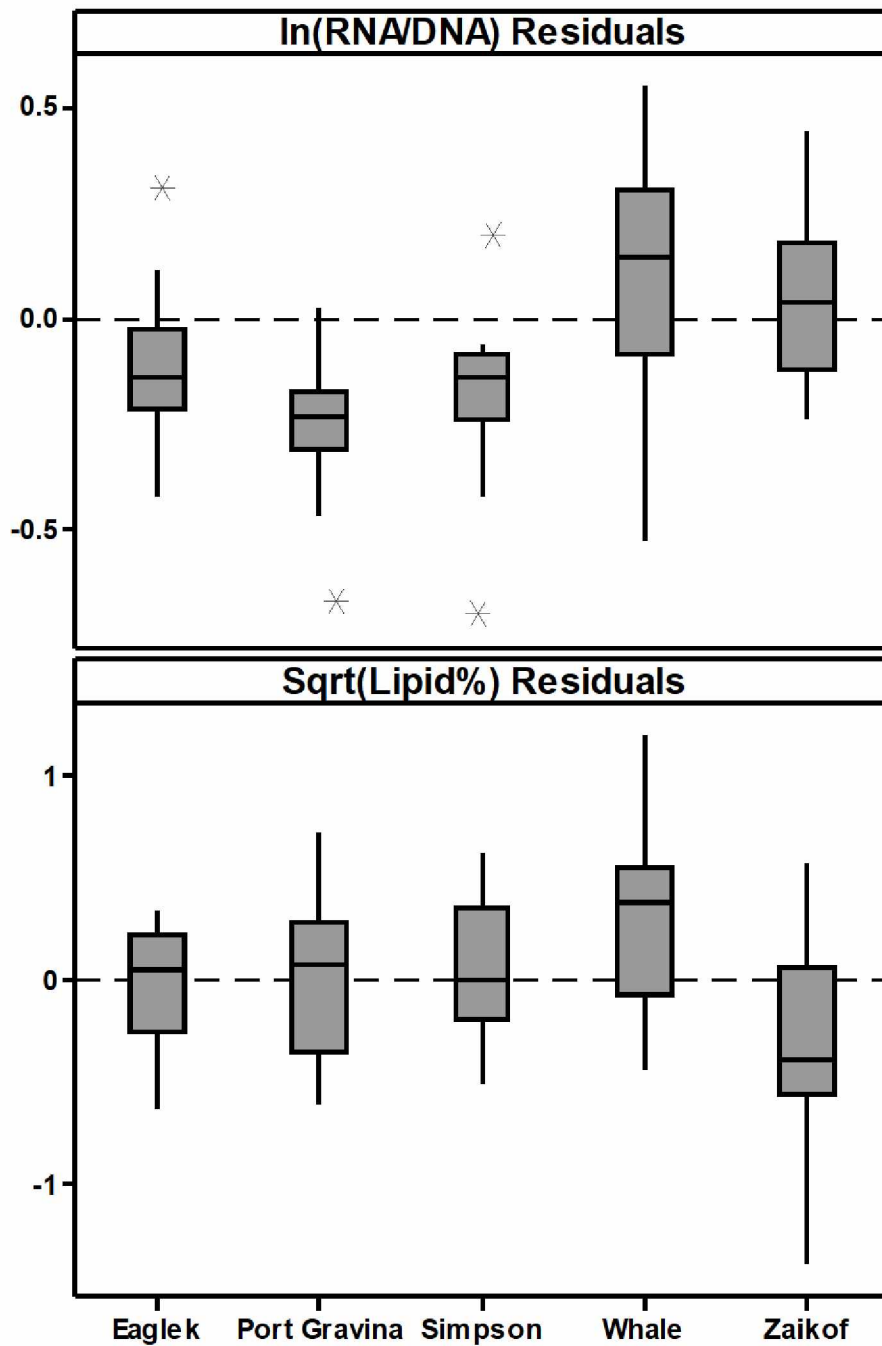


Figure 2.A.7 Residuals from the piecewise regressions of RNA/DNA versus fork length (top panel) and % lipid versus fork length (bottom panel), for large young-of-the-year herring (≥ 76 mm FL) collected from 5 bays in Prince William Sound, AK, in November 2011.

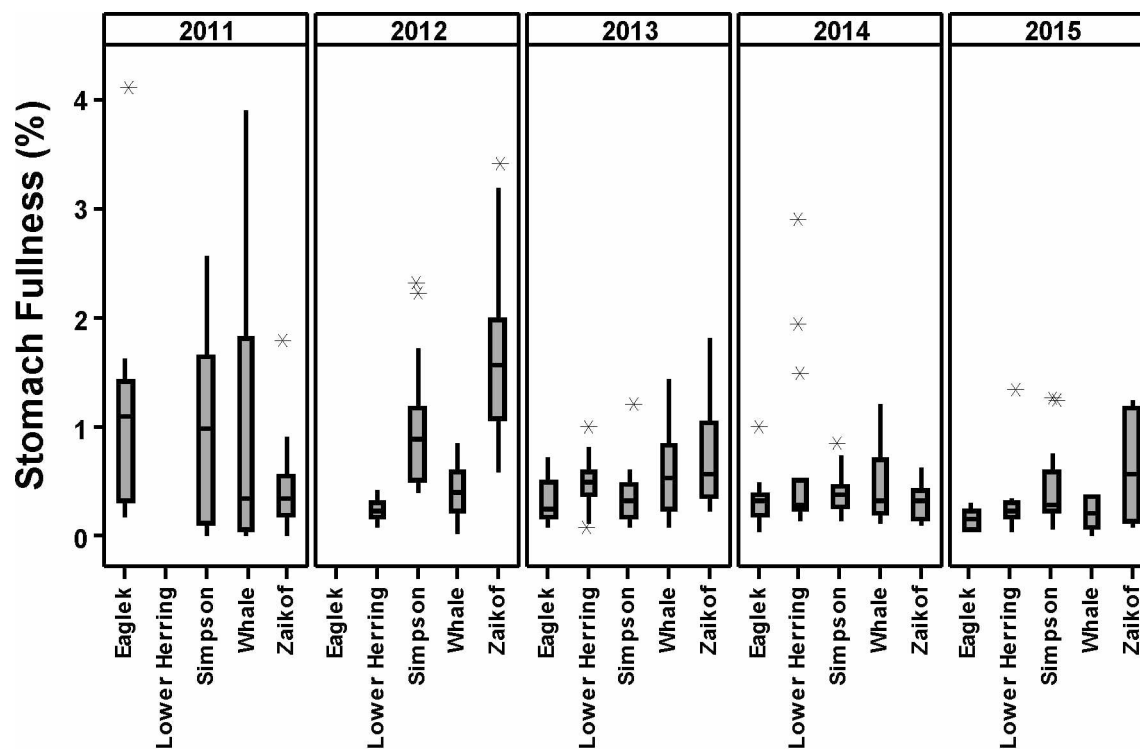


Figure 2.A.8 Stomach content mass as a percentage of body mass for young-of-the-year herring collected from 5 bays in Prince William Sound, AK, in November 2011. One outlier in 2011 is not shown for Whale Bay (6.1%).

Tables

Table 2.1 Tukey pairwise comparisons of residuals from piecewise regression of log-transformed RNA/DNA versus fork length for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015. Differing superscript letters indicate significant differences between years.

Year	N	Mean
2012	80	0.324 ^a
2009	59	0.097 ^b
2010	125	0.038 ^{bc}
2015	77	-0.019 ^{cd}
2013	104	-0.041 ^{cd}
2011	106	-0.046 ^d
2014	99	-0.112 ^d

Table 2.2 As in Table 2.1, for square-root transformed % lipid versus fork length for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

Year	N	Mean
2012	80	0.333 ^a
2014	99	0.084 ^b
2013	103	0.052 ^{bc}
2011	106	-0.023 ^{bcd}
2009	77	-0.119 ^{cde}
2010	95	-0.157 ^{de}
2015	79	-0.277 ^e

Table 2.3 As in Table 2.1, for log-transformed % lipid versus fork length for young-of-the-year herring collected in Prince William Sound, AK, in March 2010–2016.

Year	N	Mean
2013	20	0.795 ^a
2014	78	0.132 ^b
2010	97	-0.022 ^{bc}
2015	64	-0.119 ^c
2011	60	-0.122 ^c
2016	27	-0.175 ^c
2012	38	-0.216 ^c

Table 2.4 Results from rank-based robust regressions of stomach fullness as a function of lipid content for November and March combined (one-slope model) and considered separately (two-slope model), for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015 (n = 710) and March 2010–2016 (n = 444).

One-slope model:	Estimate ± SE	P
Overall intercept	0.622 ± 0.022	<0.001
Overall slope	-0.028 ± 0.004	<0.001
Overall Wald Test: 63.3, $p < 0.001$, $R^2 = 0.053$		
Two-slope model:	Estimate ± SE	P
Mar intercept	0.673 ± 0.034	<0.001
Nov intercept	0.548 ± 0.035	<0.001
Mar slope	-0.034 ± 0.012	0.005
Nov slope	-0.018 ± 0.005	<0.001
Overall Wald Test: 557.9, $p < 0.001$, $R^2 = 0.063$		

Table 2.5 Results from PERMANOVA test of differences in diet composition (proportions by mass) by year, bay, and herring length, for young-of-the-year herring with non-empty stomachs collected in Prince William Sound, AK, in November 2011–2015 (n=284).

	R²	F	p
Year	0.087	7.54	<0.001
Bay	0.070	4.85	<0.001
Length	0.045	15.47	<0.001
Residual	0.792		

Table 2.A.1 Number of young-of-the-year herring samples for biochemical analysis by gear type (CN = cast net | GN = gillnet | MT = midwater trawl) from bays in Prince William Sound, AK, in November 2009–2015 and March 2010–2016. Samples from sites within bays are pooled by bay, and additional bays sampled opportunistically (Port Fidalgo – Mar. 2011, Nov. 2012, Nov. 2013, Mar. 2014; Windy Bay – Mar. 2013) are shown as “other.” (–) No samples analyzed.

	Eaglek Bay			Lower Herring Bay			Simpson Bay			Whale Bay			Zaikof Bay			Port Gravina			Other			PWS Total		
	CN	GN	MT	CN	GN	MT	CN	GN	MT	CN	GN	MT	CN	GN	MT	CN	GN	MT	CN	GN	MT	CN	GN	MT
Nov 2009	–	29	7	–	14	–	–	19	–	–	4	–	–	4	–	–	–	–	–	–	–	70	7	–
Mar 2010	–	36	–	–	30	–	–	–	–	–	10	–	–	22	–	–	–	–	–	–	–	98	–	–
Nov 2010	19	–	–	36	–	–	30	–	–	9	11	–	20	–	–	–	–	–	–	–	114	11	–	–
Mar 2011	20	–	–	10	10	–	20	–	–	–	–	–	–	–	–	–	–	20	–	–	70	10	–	–
Nov 2011	–	20	–	–	–	–	30	10	–	10	16	–	–	20	–	10	10	–	–	–	50	76	–	–
Mar 2012	–	18	–	–	–	–	10	10	–	–	–	–	–	–	–	–	–	–	–	–	10	28	–	–
Nov 2012	–	–	–	20	–	–	20	–	–	–	20	–	20	–	–	20	–	–	20	–	80	40	–	–
Mar 2013	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	20	–	–	40	–	–	–
Nov 2013	–	20	–	20	–	20	–	–	20	5	–	4 ^a	14	–	1	20 ^b	– ^b	–	15	–	59	35	45	–
Mar 2014	–	–	–	–	20	–	–	20	18	–	–	–	20	–	–	17	–	20	–	20	77	18	–	–
Nov 2014	–	10	10	–	20	–	–	10	10	7	7	6	–	–	19	–	17	–	–	–	7	47	45	–
Mar 2015	–	6	–	–	18	–	–	–	–	10	10	–	10	10	–	–	–	–	–	–	20	44	–	–
Nov 2015	–	–	13	–	14	–	–	16	13	–	–	12	–	–	12	–	–	–	–	–	–	30	50	–
Mar 2016	–	–	–	–	–	–	5	14	–	–	–	–	–	9	–	–	–	–	–	–	5	23	–	–
Bay Total	39	139	30	86	126	20	115	99	61	41	78	22	84	85	32	50	27	–	20	75	–	435	629	165

^a Two fish were captured by jig in Whale Bay in November 2013.

^b Mixture of cast net and gillnet gears used for 20 fish in November 2013

Table 2.A.2 Number of young-of-the-year herring samples for biochemical analysis (RNA/DNA, % lipid) from bays in Prince William Sound, AK, in November 2009–2015 and March 2010–2016. Samples from sites within bays are pooled by bay, and additional bays sampled opportunistically (Port Fidalgo – Mar. 2011, Nov. 2012, Nov. 2013, Mar. 2014; Windy Bay – Mar. 2013) are shown as “other.” The number of stomachs analyzed for diets is the same as for RNA/DNA. (–) No samples analyzed.

	Eaglek Bay		Lower Herring Bay		Simpson Bay		Whale Bay		Zaikof Bay		Port Gravina		Other		PWS Total	
	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid	RNA-DNA	Lipid
Nov 2009	19	36	14	14	18	19	4	4	4	4	–	–	–	–	59	77
Mar 2010	19	36	30	30	–	–	10	10	22	21	–	–	–	–	81	97
Nov 2010	19	19	36	20	30	20	20	18	20	18	–	–	–	–	125	95
Mar 2011	20	20	20	20	20	20	–	–	–	–	–	–	20	20	80	80
Nov 2011	20	20	–	–	40	40	26	26	20	20	20	20	–	–	126	126
Mar 2012	18	18	–	–	20	20	–	–	–	–	–	–	–	–	38	38
Nov 2012	–	–	20	20	20	20	20	20	20	20	20	20	20	20	120	120
Mar 2013	–	–	–	–	–	–	–	–	20	20	–	–	20	20	40	40
Nov 2013	20	20	40	39	20	20	9	9	15	15	20	20	15	15	139	138
Mar 2014	–	–	20	20	38	38	–	–	20	20	17	17	20	20	115	115
Nov 2014	20	20	20	20	20	20	20	20	19	19	–	–	–	–	99	99
Mar 2015	6	6	18	18	–	–	20	20	20	20	–	–	–	–	64	64
Nov 2015	12	13	13	13	28	29	12	12	12	12	–	–	–	–	77	79
Mar 2016	–	–	–	–	19	18	–	–	9	9	–	–	–	–	28	27
Bay Total	173	208	231	214	273	264	141	139	201	198	77	77	95	95	1191	1195

Table 2.A.3 Results for alternative model fits to log-transformed RNA/DNA versus length and square-root transformed lipid versus length including number of parameters (df), coefficients of determination (R^2), and differences relative to the lowest Akaike Information Criterion score (ΔAIC). Based on data from young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

Model	df	R^2	$\Delta AICc$
RNA/DNA:			
GAM	4.91	0.343	16.7
Linear	3	0.328	33.2
1-breakpoint piecewise	5	0.345	18.0
2-breakpoint piecewise	7	0.364	0
Quadratic	4	0.332	30.4
Lipid:			
GAM	3.89	0.146	0.8
Linear	3	0.143	3.4
1-breakpoint piecewise*	5	0.152	0
Quadratic	4	0.149	0.8

* No second breakpoint was identified for lipid.

Table 2.A.4 Results for alternative model fits to log-transformed RNA/DNA and lipid versus length, including number of parameters (df), coefficients of determination (R^2), and differences relative to the lowest Akaike Information Criterion score (ΔAIC). Based on data from young-of-the-year herring collected in Prince William Sound, AK, in March 2010–2016.

Model	df	R^2	$\Delta AICc$
RNA/DNA*:			
GAM	3	0.209	0
Linear	3	0.211	0
Quadratic	4	0.212	1.1
Lipid:			
GAM	4.57	0.078	<0.1
Linear	3	0.033	21.1
1-breakpoint piecewise**	5	0.082	1.4
Quadratic	4	0.081	0

* No breakpoints were identified for RNA/DNA.

**No second breakpoint was identified for lipid.

Table 2.A.5 Grouping information from Tukey pairwise comparisons of residuals from piecewise regression of log-transformed RNA/DNA versus fork length for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

Location	N	Mean	Grouping
Zaikof	110	0.119	A
Lower Herring	143	0.108	A
Whale	111	0.061	A
Eaglek	110	-0.021	B
Simpson	176	-0.094	C

Table 2.A.6 Grouping information from Tukey pairwise comparisons of residuals from piecewise regression of square-root transformed % lipid versus fork length for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

Location	N	Mean	Grouping
Whale	109	0.091	A
Lower Herring	126	0.029	A B
Eaglek	128	0.015	A B C
Zaikof	108	-0.095	B C
Simpson	168	-0.118	C

Table 2.A.7 Results from rank-based robust regressions of stomach fullness as a function of length for November and March combined (one-slope model) and considered separately (two-slope model), for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015 (n = 710) and March 2010–2016 (n = 444).

One-slope model:	Estimate ± SE	p
Overall intercept	1.068 ± 0.060	<0.001
Overall slope	-0.007 ± 0.001	<0.001

Overall Wald Test: 99.0, $p < 0.001$, $R^2 = 0.068$

Two-slope model:	Estimate ± SE	p
Mar intercept	1.557 ± 0.124	<0.001
Nov intercept	1.068 ± 0.067	<0.001
Mar slope	-0.011 ± 0.001	0.005
Nov slope	-0.007 ± 0.001	<0.001

Overall Wald Test: 1059.4, $p < 0.001$, $R^2 = 0.134$

Table 2.A.8 Grouping information from Games-Howell pairwise comparisons of log-transformed stomach fullness for young-of-the-year herring collected in Prince William Sound, AK, in November 2009–2015.

Year	N	Mean	95% CI	Grouping
2011	118	−0.357	(−0.619, −0.095)	A
2010	125	−0.513	(−0.619, −0.407)	A
2012	119	−0.565	(−0.718, −0.412)	A B
2013	137	−1.039	(−1.158, −0.919)	C
2014	99	−1.142	(−1.275, −1.008)	C
2009	46	−1.149	(−1.537, −0.761)	B C
2015	79	−1.391	(−1.597, −1.185)	C

Chapter 3. Condition and performance of juvenile Pacific herring with different winter feeding rations³

Abstract

Winter mortality of juvenile fish decreases recruitment and is related directly or indirectly to winter feeding. Distinguishing well-fed from poorly-fed individuals may be useful in assessing mortality risks of fish with different feeding histories. To assess the effects of winter feeding on condition and performance of young-of-the-year Pacific herring (*Clupea pallasii*), captive herring were maintained at one of five feeding rations for 20 weeks under ambient winter conditions and evaluated for changes in size, body composition, and swimming ability. Mortalities due to a combination of restricted rations and disease were highest among fasted herring and among small herring across rations. Lipid and moisture levels were generally inversely related indicators of feeding history, and differed most between full-ration and fasted herring. Fasted herring that were re-fed in spring showed evidence of compensatory growth without apparent cost to swimming ability. Minimal growth and reduced gut mass even among fully-fed herring suggest limits to winter feeding benefits. Metabolic consumption of stored fat rather than foraging may thus be an advantageous strategy regardless of winter food availability.

³ Sewall, F., Norcross, B., Heintz, R. In preparation for journal submission. Condition and performance of juvenile Pacific herring with different winter feeding rations. In preparation for submission to Can J Fish Aquat Sci.

Introduction

For high-latitude juvenile fishes, winter feeding upon scarce prey can be insufficient to meet metabolic demands, resulting in poor condition. Poor condition may increase mortality directly through depletion of stored energy and starvation, and indirectly if swimming performance is impaired (Martinez et al. 2003) and thereby compromises foraging and predator avoidance. Predation and starvation risk in winter may be highest among small fish due to high metabolic rates and susceptibility to predation. Juvenile fish may compensate for winter mass loss by increasing allocation of food energy towards growth and condition with the return of abundant food in spring, but with potential physiological costs and tradeoffs in performance (reviewed in Ali et al. 2003).

Responses to food scarcity can be complex, involving tradeoffs among structural maintenance, growth, energy storage, behavior, and other factors. Modeling these responses is challenging due to incomplete understanding of the processes involved. A variety of indicators have been used to quantify condition, such as length-weight ratios, organ masses, growth rates, and energy content. The sensitivity of these indices to fasting, and thus their usefulness as indicators of mortality risk, varies across life stages and species (Weber et al. 2003).

Pacific herring (*Clupea pallasii*; hereafter herring) is a useful model organism for investigating these issues due to its ecologically important role as a trophic intermediary between zooplankton and higher-level predators such as fishes, seabirds, and marine mammals. Understanding the biology and population dynamics of this key planktivore is vital to understanding the functioning of many northern marine ecosystems. In particular, management of herring stocks would benefit from improved understanding of recruitment variability, much of

which is associated with first winter mortality (Norcross et al. 2001). As a first step, investigating winter mortality processes requires identifying indices that can reliably differentiate feeding and fasting young-of-the-year (YOY) herring.

Discriminating juvenile herring that are healthy from those at high risk of winter mortality is poorly documented. There are limited data regarding juvenile herring energetic response to fasting under controlled conditions (Paul and Paul 1998), and no published work simultaneously considers multiple condition and performance indices. Swimming performance of juvenile herring is scarcely studied, but is known to decline in response to oil exposure (Kennedy and Farrell 2006), but the effects of varied feeding history on swimming ability are unknown.

The goal of this study was to investigate how YOY herring condition, growth, and swimming performance respond to varied winter and spring feeding conditions. Juvenile herring were fed different rations with the expectation that restricted winter rations would be manifested as decreased body mass, gut mass, growth, condition, and swimming performance, plus increased mortality relative to fully fed herring. Spring re-feeding was expected to allow resumption of growth and energy storage, but at some cost to swimming performance. This research strives to provide a framework to assess the likelihood of first winter survival of wild juvenile herring and consequently improve the ability to predict year-class strength.

Materials and methods

Field collection and laboratory conditions

YOY herring were captured on 27 October 2011 by beach seine in Auke Bay, Southeast Alaska, and transported to the NOAA Fisheries Auke Bay Laboratories. Herring were maintained in 189-liter oval fiberglass tanks with sand-filtered seawater flowing through at 5–6 L·min⁻¹ at ambient Auke Bay temperature, which ranged from a daily mean high of 7.7 °C in early November to a low of 3.7 °C in early March (Fig. 1). Herring were exposed to sunlight on a natural photoperiod, which ranged from a minimum of 6.4 hours of daylight in mid-December to 17.3 hours at the study end in mid-May. The timing of the study thus enabled observation of herring under simulated winter and spring conditions. To minimize bias in initial fish size (average length and mass) among treatment tanks, net scoops of 5–6 herring each were distributed into each of six treatment tanks sequentially in repeated rounds until all herring were allocated. Herring densities ranged from 78 to 92 fish per tank initially in November and declined over time due to sampling removals and mortalities.

During a 10-week acclimation period through the first week of January, all herring were fed daily on weekdays in excess of satiation (~15.0 g per tank) with commercially available frozen euphausiid meal (*Euphausia superba*). Ration levels were then manipulated during the study treatment periods that followed, with all herring fed a given ration constituting a treatment group. In the first treatment period, from early January (study week one) through early April (week 14, 93 d), two replicate tanks of herring per treatment were provided one of three winter rations: 1. full ration (fed daily to satiation); 2. reduced ration (fed to satiation twice weekly), and 3. fasted (Table 1). In the second treatment period, from early April through May (week 20, 42

d), in addition to continuing all three groups, the latter two groups were subdivided and half of each distributed to two replicate tanks each (four total) that were re-fed at full ration to create two new spring re-feeding groups: 1. re-fed full ration following reduced ration; and 2. re-fed full ration following fasting. The January to April/May period of food deprivation for fasted herring approximated the conditions potentially experienced by some herring populations in the North Pacific during winter; high proportions of empty stomachs have been observed among juvenile herring in Prince William Sound, Alaska, from autumn (Oct/Nov) through spring (Mar/Apr), a period of 4–6 months (Norcross et al. 2001). The return of food and the increase in temperatures and daylight hours during the April to May re-feeding period likewise reproduced natural conditions during spring.

Sampling

To assess the responses of herring growth and condition to changes in food availability, subsamples of fish were collected on four occasions over the course of the study. To determine the average initial size of captive herring, two weeks into the acclimation period on 10 November (“start acclimation” in results), 40 herring from one tank were captured by random grab sampling using an aquarium fish net, anaesthetized by brief immersion in tricaine methanesulfonate (MS-222) in seawater ($0.3 \text{ g}\cdot\text{L}^{-1}$), measured for fork length and wet body mass, and returned live. Subsamples of 2–4 herring from six replicate tanks were euthanized by prolonged immersion in MS-222 in seawater and frozen for chemical analysis on 6 January (“end acclimation”) after the acclimation period on full ration, followed by subsamples of five herring from two replicate tanks per ration collected on 6 April (“end winter”) after the winter ration period and on 21–22 May 2012 (“end spring”) after the spring re-feeding period (Table 1).

Chemical analyses were conducted on 120 fish in total: 92 euthanized herring from all five ration groups, and 28 natural mortalities from only the full-ration and fasted groups. Natural mortalities were collected opportunistically within 24 hours of death on several dates in April and May; eight mortalities were collected from full-ration tanks, and 18 from fasted tanks. Mortalities from April and May were pooled within each ration group to boost sample sizes for analysis. Four fish (one reduced ration fish collected in April, one fasted fish in May, and two fasted mortalities in April) with data that were incomplete or failed quality control checks were excluded from analysis.

Growth

Growth of herring was inferred from changes in mean length and weight by ration group, and from individual measurements of ribonucleic acid (RNA)/deoxyribonucleic acid (DNA) ratios. The RNA/DNA ratio, which indicates protein synthesis rates over the preceding few days (Buckley 1984; Buckley et al. 1999), was determined using a fluorometric dye-binding assay developed by Caldarone et al. (2001) and modified by Sreenivasan (2011). In brief, 10–15 mg plugs of dorsal white muscle tissue were sonicated in buffered detergent, sequentially treated with fluorescing dye, RNase enzymes, and DNase enzymes, and fluorescence was read by spectrophotometer (Perkin Elmer) at each step. To calibrate fluorescence readings, the fluorescence of known concentrations of RNA and DNA of standard reference materials (calf liver 18s + 28s ribosomal RNA and calf thymus DNA, Sigma) were measured with each batch of 20 samples. Sample RNA/DNA ratios across batches were standardized by multiplying each sample RNA/DNA value by an average reference material DNA to RNA calibration slope ratio of 3.84 divided by the individual batch calibration slope ratio to ensure comparability among

batches and to facilitate comparisons with other studies (Caldarone et al. 2006). Method blanks were run with samples to check for contaminants introduced during processing.

Gut condition

The effects of feeding history on herring gut condition were assessed by monitoring changes in relative gut mass, which is the dry mass of the gastrointestinal (GI) tract as a percentage of body dry mass. Dry masses were preferred to wet masses due to variable moisture loss during handling, and moisture loss from drying excised guts separately from fish bodies had a negligible effect on the total fish wet mass or body composition. GI tracts were excised from esophagus to vent, stomach contents and feces discarded, and gall bladder, liver, and fat deposits returned to the body carcass. GI tracts were dried and weighed to within 0.1 mg, then returned to the body before homogenizing tissues in preparation for whole body composition analysis.

Body condition

To evaluate the effect of feeding history on condition, individual herring were homogenized with mortar and pestle, then chemically analyzed for moisture, lipid, and protein content following procedures described in Vollenweider et al. (2011b). In brief, herring moisture content was determined gravimetrically by heating homogenized wet tissue to 135 °C to evaporate moisture until remaining dry mass stabilized using a Leco Thermogravimetric Analyzer (TGA) 601. Dry and wet homogenate masses were then compared to calculate percent moisture. Percent moisture from homogenates was then multiplied by whole fish wet mass to estimate whole fish dry mass. To determine protein content, dried homogenate was combusted at 850 °C and the released nitrogen measured by thermal conductivity using a Leco TruSpec CHN

instrument following the Dumas method (Sweeney and Rexroad 1987). The measured nitrogen content was multiplied by a factor of 6.25 (Craig et al. 1978) to estimate the dry mass percent protein. Wet mass percent protein for reporting was derived from moisture and dry mass data. To determine wet mass percent lipid, lipid was extracted from 0.1–0.3 g wet homogenate using a modified Folch method (Folch et al. 1957) with a Dionex 200 Accelerated Solvent Extractor (Thermo Scientific), dried, and weighed. Dry mass percent lipid was derived from moisture and wet mass data.

National Institute for Standards and Technology (NIST) reference materials were used for quality control to verify composition analysis. Each batch of 17–20 samples also included in-house reference materials to check accuracy, a sample replicate to check precision, and a method blank to check for contaminants.

Swimming performance

To assess the effect of feeding history on swimming performance, swimming trials were conducted based on modifications to procedures developed by Beamish (1978). Herring randomly selected from each of the three winter ration groups were subjected to critical swimming speed testing in groups of five in a swim chamber during the April sampling event, and from each of the five spring ration groups during the May sampling at the study's end. Critical swimming speed, which is the maximum speed maintained for a defined time interval, is an index of prolonged swim speed that is intermediate between burst and sustained swim speeds and defined as the speed individuals can maintain for 20 s to 200 min before fatiguing (Beamish 1978). Following a swim chamber acclimation period of 5 min with slow water flow ($3 \text{ cm}\cdot\text{s}^{-1}$), swim trials began at a flow speed of $14 \text{ cm}\cdot\text{s}^{-1}$ for 5 min, followed by speed increases of $7 \text{ cm}\cdot\text{s}^{-1}$

every 5 min until herring became fatigued. Time to fatigue was defined as the time when an individual remained against the back of the swim chamber for more than 10 s (Melzner et al. 2009). Individual fish were immediately removed upon fatiguing, euthanized, and frozen for later body composition analysis.

Critical swimming speeds ($\text{cm}\cdot\text{s}^{-1}$) for individual fish were calculated using Brett's (1964) formula:

$$U_{\text{crit}} = u_i + (t_i/t_{ii} * u_{ii})$$

where u_i is the maximum speed ($\text{cm}\cdot\text{s}^{-1}$) maintained for a complete time interval, u_{ii} is the speed increment used ($7 \text{ cm}\cdot\text{s}^{-1}$), t_i is the time (min) fish swam at fatigue speed, and t_{ii} the time interval used (5 min). Speeds in $\text{cm}\cdot\text{s}^{-1}$ were divided by fork length (cm) to express speed in terms of body lengths per second ($\text{BL}\cdot\text{s}^{-1}$).

Mortality

To assess the effects of feeding levels on herring mortality, tanks were checked daily for dead fish, which were removed and their lengths recorded. Due to apparent signs of disease, including bleeding around the head, and the likelihood of high prevalence of naturally-occurring diseases in captive herring, recently dead herring during the acclimation period and at the end of the study were subjected to pathology.

Comparing mortalities among ration groups required several steps. First, daily mortality (M) by tank was calculated as the number of dead fish divided by the number alive the previous day, minus any sample removals. Cumulative percent mortality (A) across a treatment period was then estimated by tank as:

$$A = 1 - e^{(-\bar{M} * t)},$$

where \bar{M} is the average daily mortality over t days in the treatment period. Cumulative percent mortalities were then averaged across replicate tanks to statistically compare ration groups. Illustrating trends in cumulative percent mortalities on a daily basis required a modified approach in which counts of dead fish were first summed across both replicate tanks by ration group on a given day. Deaths were then expressed as a percentage of summed fish alive the previous day, minus any sample removals, and added to the percent mortality from previous days to yield cumulative mortality as of that day.

To evaluate whether mortality was length dependent, median fork lengths were compared between live and dead herring by treatment group in spring. For these comparisons, lengths of sampled herring and all remaining live herring in April within treatment groups were pooled with lengths of herring euthanized for sampling in May. Likewise, lengths of dead herring in April and May were pooled due to low sample numbers.

Statistical analyses

Ration groups were compared over time and among groups for differences in mean fork length, wet mass, percent moisture, dry mass, relative gut mass, RNA/DNA, wet mass percent lipid, wet mass percent protein, and critical swim speed. Changes in mean fork length and wet mass were evaluated from the start to the end of the acclimation period (November-January), during which all herring were fed at full ration. Changes in full-ration, reduced-ration, and fasted groups through April and May were evaluated by comparing them to fish collected at the end of the acclimation period in January, all fed full ration. Ration groups were also compared within April and May. Comparisons in May included dry mass percent lipid and protein to check for agreement with comparisons on a wet basis. Statistical significance ($\alpha = 0.05$) of differences was

determined using ANOVA and post-hoc Tukey pairwise comparisons, unless otherwise specified. Assumptions of equal variances and normal distribution of residuals from ANOVA model fits were checked using Bartlett's test (Bartlett 1937) and Anderson-Darling test (Anderson and Darling 1954), respectively. Groups with unequal variances were compared using Welch's ANOVA (Welch 1951, Day and Quinn 1989) employing weighted least squares and Games-Howell pairwise comparisons (Games and Howell 1976, Day and Quinn 1989). Groups with non-normal data were analyzed using Kruskal-Wallis tests (Kruskal and Wallis 1952) and post-hoc Dunn pairwise comparisons (Dunn 1964). Previous work showed growth and condition indices can vary with herring length (Sewall et al. 2019), so significant relationships between fork length and each body composition index and between fork length and swimming speed were identified using simple linear regressions applied to all samples combined, unless otherwise specified. Regression residuals were then used to compare variables that were length-dependent among groups. This removed effects of the covariate length and facilitated use of non-parametric tests when ANOVA assumptions were violated.

Linear discriminant analysis (LDA; Ripley et al. 2019) was performed to find the morphometric and body composition indices that best classified individual herring membership among all seven groups (five ration groups and two mortality groups) at the study end in May. To make measurement scales comparable for LDA, data for each variable were first standardized by subtracting the mean and dividing by the standard deviation. Model accuracy in classifying samples was estimated as the bootstrapped mean accuracy from randomly resampling the training data (~80 % of data) and test data (~20 % of data) 1000 times.

The statistical significance of differences in mean percent cumulative mortality among ration groups during each treatment period was determined by ANOVA and post-hoc Tukey

pairwise comparisons. To evaluate whether mortality was size dependent, lengths of live and sampled herring versus mortalities by ration during spring were compared using Mann-Whitney rank-based tests due to skew in the length data.

Results

Growth and condition

Full ration

Fully-fed herring showed only modest growth through winter (Fig. 2). Herring mean fork length and wet mass showed statistically significant increases from the start of the acclimation period in November (FL = 69.5 mm, wet mass = 2.44 g; Table 2) through April (FL = 77.4 mm, wet mass = 3.59 g), though size increases were not significant from the end of the acclimation period in January through the end of winter in April, and no increase occurred in spring from April to May. The test for length-dependent effects showed moisture significantly decreased with length for January, April, and May pooled ($R^2 = 14.5\%$, $F = 5.43$, $p = 0.026$); with or without accounting for length as a covariate, moisture did not differ among months. Relative gut mass showed a marginally non-significant decrease from 3.72 % in January to 3.14 % in April, with a slight rebound to 3.19 % in May, despite being fully fed through winter. In agreement with the minimal size increases observed during the study, mean RNA/DNA levels were similarly low in January (5.21) and April (5.66), and did not significantly increase until May (7.10; Table 2). Lipid showed a marginally non-significant increase with length ($R^2 = 10.1\%$, $F = 3.60$, $p = 0.067$), and the nearly 2 % gain in lipid content from January through May was not statistically

significant with or without accounting for length differences. Percent protein was stable through winter and spring (mean range: 14.4–14.6 %).

Reduced ration

Herring on a reduced ration diet from January through May showed no significant differences over time on most measures, with the exception of relative gut mass, which was significantly lower in May than at the end of full-ration acclimation in January (Table 3). Reduced ration herring in May had maintained size relative to the end of full rations in January in terms of mean length (73.1 mm in January and May) and wet mass (2.80 g in January, 2.97 g in May). Moisture showed a marginally non-significant decrease with length ($R^2 = 9.22\%$, $F = 3.15$, $p = 0.086$), but mean moisture did not significantly differ across months (mean range: 75.7–77.4 %) with or without accounting for length. Relative gut mass significantly declined from a median value of 3.57 % in January to 2.67 % by the study end in May. RNA/DNA remained stable across months (mean range: 5.21–5.26 %). Lipid showed a marginally non-significant increase with length ($R^2 = 9.31\%$, $F = 3.18$, $p = 0.084$), but the small differences among months in mean lipid (mean range: 6.49–7.73 %) were not significant regardless of length differences. Percent protein was stable through winter and spring for herring on a reduced ration (mean range: 14.3–14.6 %).

Fasted

Herring that fasted through winter largely maintained body size in length and wet mass, though body composition and gut mass changed. Mean lengths were nearly identical for fish at the end of full-ration acclimation in January (73.1 mm) and those that fasted from then until May

(72.9 mm). Mean wet masses were also similar in January (2.80 g) and April (2.75 g), and showed a non-significant 17 % decrease by May (2.33 g; Table 4). Wet mass loss was mitigated by gains in water mass, shown by significantly higher median moisture levels from January (76.5 %) to May (81.4 %). Mean dry mass declined more rapidly than wet mass, showing a 32 % marginally non-significant decrease from January (0.66 g) to May (0.45 g). Losses in mean wet and dry mass by May could be biologically meaningful although not statistically significant due to low sample sizes of fasted fish in May. Median relative gut mass significantly decreased from January (3.72 %) through May (2.40 %), indicating preferential loss of gut tissue. Mean RNA/DNA generally declined through winter but was highly variable, decreasing from 5.21 in January through 4.35 in April and 4.94 in May, such that month had a significant effect overall but no months differed in pairwise comparisons. The observed decline in dry mass was reflected in significant losses in the two main constituents; lipid declined to 4.25 % of wet mass by May, while protein declined to 12.6 %.

Differences among ration groups

Morphometric and biochemical indices generally differed most between the full-ration and fasted groups over time, with other groups intermediate (Fig. 2). Herring fed at full ration during winter from January through April were larger in mean length (77.4 mm) and wet mass (3.59 g) than reduced ration or fasted herring, though the differences were not significant (Table 5). Differences were still not significant by the study end in May, although full-ration herring again were longest and heaviest and fasted herring were smallest among sampled ration groups (Table 6). In May, surviving full-ration herring were significantly larger than mortalities from the full-ration and fasted groups, the two groups from which mortalities were analyzed. Full-

ration herring exceeded fasted herring in mean or median dry body mass, RNA/DNA, lipid level, and protein, with differences typically increasing from April (Table 5) to May (Table 6). In contrast, moisture content was ~6 % lower in the full-ration group than in the fasted group. Moisture and lipid content showed contrasting relationships to size, as moisture decreased with length for all ration groups pooled in April ($R^2 = 12.2\%$, $F = 3.75$, $p = 0.063$) and May ($R^2 = 9.9\%$, $F = 7.76$, $p = 0.007$), while lipid increased with length in April ($R^2 = 12.6\%$, $F = 3.90$, $p = 0.059$) and May ($R^2 = 19.4\%$, $F = 17.1$, $p < 0.001$). Regardless of length, moisture was strongly inversely-related to lipid content of wet tissue ($R^2 = 84.8\%$, $F = 396.4$, $p < 0.001$) and dry tissue ($R^2 = 73.2\%$, $F = 194.2$, $p < 0.001$) across all herring in May. Lipid levels among full-ration herring were more than twice those of fasted herring and more than three times those of fasted herring mortalities in May (Table 6). Lipids among other groups were largely similar, though full-ration mortalities had more than twice the lipid content of fasted mortalities. Lipid content calculated on a dry mass basis in May increased with length ($R^2 = 21.4\%$, $F = 19.3$, $p < 0.001$) and showed similar contrasts among rations to lipid on a wet mass basis. Mean dry mass lipid significantly differed by ration overall after accounting for length, though the difference between full-ration and fasted herring was marginally non-significant ($p = 0.090$) in pairwise comparisons. Protein as a percentage of wet body mass was less variable than lipid, but showed a significant 2 % difference between full-ration and fasted herring. Protein content on a dry mass basis decreased with length in May ($R^2 = 11.5\%$, $F = 9.19$, $p = 0.003$) and exhibited the reverse pattern among ration groups as protein on a wet mass basis. After accounting for length, mean dry mass protein significantly differed by ration overall, with lower levels among full-ration herring than among fasted herring, though only full-ration mortalities and fasted mortalities significantly differed ($p = 0.044$). Increased percentage of protein and decreased lipid on a dry

mass basis indicate conservation of protein mass relative to lipid mass when body tissues were metabolized by fasted herring.

Moisture and lipid indices were the most useful for distinguishing herring from different ration groups, as indicated by the large moisture and lipid coefficients in LDA functions (Table 7). LDA showed the clearest differences between full-ration and fasted fish, and between mortalities and non-mortalities (Fig. 3). The LDA model classified fish with approximately 54 % accuracy, better than a null model classifying evenly across groups (for seven groups, $100/7 = 14$ %).

Re-feeding

Herring re-fed in spring following a winter period of reduced ration or fasting showed evidence, though not statistically significant, of greater average length, wet mass, relative gut mass, RNA/DNA, lipid, and protein content, and lower moisture in May compared to those not re-fed (Fig. 2, Table 7). Re-fed herring thus showed less separation in the LDA plot from full-ration herring than did herring not re-fed (Fig. 3). Indices for re-fed herring in May were similar to those of reduced ration and fasted herring before they began re-feeding in April. Similar wet mass, lipid, and protein levels from April to May indicate that re-fed herring had stopped metabolizing body tissues, but had not significantly increased energy stores or size. However, RNA/DNA among fasted fish re-fed in spring increased to surpass that of the full-ration group.

Swimming performance

Critical swimming speeds ($\text{BL} \cdot \text{s}^{-1}$) did not significantly differ among rations in April following the winter ration period (ANOVA; $F_{2,27} = 0.14$, $R^2 = 1.03$ %, $p = 0.870$) or in May

following spring re-feeding (ANOVA; $F_{4,43} = 1.11$, $R^2 = 9.43$ %, $p = 0.360$), although the fasted group was slowest (April: $4.49 \text{ BL}\cdot\text{s}^{-1}$; May: $3.88 \text{ BL}\cdot\text{s}^{-1}$), while the re-fed groups in May (reduced re-fed: $4.92 \text{ BL}\cdot\text{s}^{-1}$; fasted re-fed: $4.66 \text{ BL}\cdot\text{s}^{-1}$) exceeded the speed of all other groups (full ration: $4.44 \text{ BL}\cdot\text{s}^{-1}$; reduced ration: $4.48 \text{ BL}\cdot\text{s}^{-1}$; Fig. 4). Critical swimming speed increased linearly with length for herring among all rations pooled in the April swim test ($R^2 = 17.8$ %, $F = 6.06$, $p = 0.020$) and with April and May tests pooled ($R^2 = 5.8$ %, $F = 4.69$, $p = 0.033$), though not in May ($R^2 = 2.29$ %, $F = 1.08$, $p = 0.304$). Regardless, herring did not significantly differ by ration based on residuals from swim-speed length regressions or absolute swimming speed ($\text{cm}\cdot\text{s}^{-1}$).

Mortalities

Mortalities in the winter ration and spring re-feeding periods were highest among the fasted herring and lowest among the full-ration herring, with other groups appearing intermediate (Fig. 5), similar to the patterns seen in the morphometric and biochemical indices. Cumulative mortality differences needed to be large to be statistically significant due to comparisons being based on means of only two tanks per group. The differences were not significant during the period from the end of acclimation in January through the end of winter ration treatments in April (ANOVA; $F_{3,2} = 1.14$, $R^2 = 43.3$ %, $p = 0.427$). During the spring re-feeding period (April–May), mortalities significantly differed among groups (ANOVA; $F_{4,5} = 6.58$, $R^2 = 84.0$ %, $p = 0.032$), with the highest mortality (70 %) in the fasted group (Tukey’s post-hoc test; Table 8) and lowest (36 %) in the full-ration group. Resuming feeding at full ration in spring had little effect on mortality of herring previously on restricted winter rations, as cumulative mortalities

among the re-fed groups appeared similar to their fasted and reduced ration cohorts that were not re-fed.

Mortality appeared to be size-dependent, as herring that died were of smaller average size than live or euthanized herring regardless of ration (Fig. 6). Based on spring (April–May) data in which all rations were represented, median fork lengths of herring mortalities (70 mm) were significantly smaller than those of non-mortalities (74 mm) across rations (Table 9). Within rations, median lengths of mortalities were significantly smaller than non-mortalities by 3.5–7 mm in all cases with the exception of reduced ration herring that were re-fed in spring, and mortalities typically included the smallest fish in each group.

Discussion

Winter feeding challenges and benefits

Herring growth was modest over the course of the study, likely due to the relatively cold temperatures and short daylight during the winter months (Stokesbury et al 1999; Foy and Paul 1999), even with abundant food provided. Relatively small decreases in temperature can significantly slow growth, as fully fed captive YOY herring from Puget Sound gained only one-third the mean mass when reared for 10 weeks at 6.5 °C versus 8.5 °C (~1 g versus ~3 g gain; Sreenivasan 2011). In comparison, water temperatures in the present study in southeast Alaska were below 5 °C during winter (January–April), and likely contributed to growth slowing to levels difficult to detect. Growth and metabolism may have also slowed in response to short daylight hours, a winter adaptation seen in other high-latitude visual feeders (Perch *Perca fluviatilis*, Karås 1990). In addition to low temperatures and short daylight, growth is further

constrained for wild herring by winter declines in zooplankton prey availability (McKinstry and Campbell 2018) and herring stomach fullness (Foy and Norcross 1999). However, stomach fullness in late winter is greater among lean herring (Sewall et al. 2019), and high proportions of herring may feed in March before the return of high zooplankton biomass (Foy and Paul 1999). This suggests that winter feeding or fasting do not strictly indicate prey availability, but reflect tradeoffs in costs and benefits to foraging. Winter foraging offers herring limited winter growth potential, as evidenced by minimal size gains despite abundant food in this study. This may explain why an overwintering strategy of metabolically consuming stored fat while maintaining anti-predator schooling behaviors (Sogard and Olla 1997) is preferred to foraging and potentially increasing predation risk, regardless of zooplankton prey availability.

Food quality can affect the growth and condition of herring at early life stages (Foy and Norcross 1999, Malzahn et al. 2007) and should be considered when interpreting responses to feeding, especially under artificial conditions. Growth of some species can be negatively affected by high fluoride levels found in euphausiid exoskeletons (rainbow trout *Oncorhynchus mykiss*, Yoshitomi et al. 2006), though others appear unaffected (Atlantic salmon *Salmo salar*, Julshamn et al. 2004). Food quality was not suspected to constrain growth in this study, as the Antarctic euphausiids provided as food are lipid-rich (Cho et al 1999), and various species of euphausiids are energy-dense prey for PWS herring (Foy and Norcross 1999). Euphausiid diets are commonly used in captive Pacific herring studies (Kocan et al. 1999; Kennedy and Farrell 2008) and promote feeding and growth of other northern marine species (Atlantic salmon, Olsen et al. 2006; juvenile Atlantic cod *Gadus morhua* and Atlantic halibut *Hippoglossus hippoglossus*; Tibbetts et al 2011). However, growth limitation due to an exclusively euphausiid-based diet cannot be ruled out.

Winter zooplankton prey availability may offer limited benefits to herring if assimilation efficiency is reduced by gut atrophy. Relative gut mass apparently declined through winter across all ration groups including fully fed herring. Changes in gut mass in response to seasonally-variable food occur in wild Dolly Varden (*Salvelinus malma*; Armstrong and Bond 2013) to reduce energy spent on gut maintenance. Reductions in gut mass and length also have been observed in response to fasting in laboratory studies in at least eleven fish species (reviewed in Zaldúa and Naya 2014). However, while gut mass losses were greatest among fasted herring in the present study, gut atrophy among fish provided excess food suggests influence by other environmental cues such as limited daylight hours or low temperatures. If gut atrophy commonly occurs in overwintering herring populations, winter feeding benefits could be limited even when conditions support high zooplankton prey abundance.

Resumption of growth in spring with the return of abundant food should be critically important, though low temperatures persisting after winter may constrain its benefits to survival. Herring that resumed feeding in spring after winter fasting showed signs of compensatory growth, increasing their median RNA/DNA levels by 77 % from April to May, moving them up from the lowest RNA/DNA among all rations in April to the highest among rations in May. This renewed growth effort enabled previously fasted herring to maintain sizes only slightly smaller than their continuously fed counterparts through the study's end. Additional time beyond that provided in this study for re-feeding at full ration might have allowed full compensation in size, although growth deficits after fasting for several weeks can be insurmountable even at relatively warm temperatures (e.g., 28 °C for channel catfish *Ictalurus punctatus*; Gaylord and Gatlin 2000). The efficiency of translating RNA into protein-based growth declines with temperature

(Buckley et al. 1999); low temperatures persisting after winter, as observed during April–May (daily mean 5.4 °C), may thus limit compensatory growth in spring.

Compensatory growth effort in spring did not appear to negatively affect swimming performance, as re-fed fasted herring had higher RNA/DNA levels and critical swimming speeds than continuously fully-fed herring. Re-fed fasted herring may have supported high growth without sacrificing physiological capacity for swimming by increasing consumption to levels comparable to or exceeding those of continuously fed cohorts, as reflected by their slightly larger relative gut mass following spring re-feeding. Temporarily increasing consumption is a common response to feeding deficits (Won and Borski 2013), and is how re-fed fasted juvenile walleye pollock (*Gadus chalcogrammus*) are likewise able to achieve compensatory growth without impacting critical swimming speed (Sogard and Olla 2002). Not all species can use this strategy, as re-fed fasted sablefish (*Anoplopoma fimbria*) apparently cannot eat more than continuously fed counterparts and so achieve compensatory growth at the expense of swimming ability (Sogard and Olla 2002). Supporting swimming ability concurrently with growth likely reflects the urgent need of fasted herring to forage efficiently while avoiding size-based predation. In contrast, continuously fed herring had high fat stores and sub-maximal RNA/DNA and swimming speed, suggesting they were not allocating all available energy consumed towards growth. This agrees with previous findings that YOY herring will shift energy allocation away from growth in favor of storing lipids as long as they attain a critical size (Sewall et al. 2019). Spring re-feeding thus appeared to promote swimming ability after winter, and may also allow healthy fish to rapidly resume growth and lipid storage. However, the observed minimal gains in size, lipid levels, and high mortality suggest limited survival benefits to spring re-feeding after winter fasting. These challenges to improving fish size, condition, and survival in spring when

low winter temperatures persist underscore the importance of achieving large size (Beamish and Mahnken 2001) and lipid stores (Paul and Paul 1998) in the critical period before winter.

Lipid and moisture variables clearly made the strongest contributions to the LDA functions distinguishing herring with known winter and spring feeding histories, suggesting they may be the most useful of the variables tested for inferring feeding and condition of wild herring. Given the strong influence of lipid and moisture in the LDA, their utility for distinguishing poorly-fed and well-fed wild herring may be similar to that of the LDA functions, and their biological interpretation is more straightforward. Lipid and moisture were strongly inversely related, as has been reported elsewhere across several species (Anthony et al. 2000, Wuenschel et al. 2019), indicating that either variable alone may be adequate for distinguishing wild fish. If the results had shown instead that several measured variables made similar contributions to the LDA functions, thus making the effect of any specific variable ambiguous, then applying LDA functions derived from lab fish could be especially useful for assessing wild herring with measurements on those variables. Developing LDA functions with non-diseased fed and fasted herring and comparing the results to this study would enable their appropriate application to wild fish of known disease status.

Size-dependent mortality by starvation and disease

Mortalities were unexpectedly high throughout the study, likely due in part to disease. Among full-ration herring for example, with starvation risk minimized, mortalities were anticipated to be under ~5 % in a three-month period (Gregg et al. 2011), but approximately 25 % died during the three-month winter period and more than another ~36 % in the 1.5-month spring period, with higher mortalities at other rations. Herring showed signs of disease including

hemorrhaging around the head throughout the study, and captive juvenile herring can experience increased incidence of naturally-occurring diseases (Hershberger et al. 2006). Tissue and blood samples from freshly dead herring fed full ration near the study start (30 November through 16 December) and pooled across all rations at the study end (30–31 May) were inspected for signs of common herring diseases. Pathology laboratory examination (Ted Meyers, Alaska Department of Fish and Game pathology laboratory, Juneau, AK, USA) detected no ichthyophthiriasis, but found 70 % incidence of viral hemorrhagic septicemia (VHS) and 83 % incidence of viral erythrocytic necrosis (VEN) in dead herring in November–December, and 77 % VEN in May, confirming disease as a likely source of mortality. Disease effects, including mortality and energetic costs, are thus important to consider when applying of these findings to wild juvenile herring populations, and may well have contributed to increased variability that hampered detecting statistically significant treatment effects. Diseases are likely widespread among juveniles (Meyers et al 1994) and may impact recruitment (Marty et al. 2003) though disease effects are not well monitored in field studies.

Disease exposure was not a controlled variable in this study, so it is difficult to attribute deaths to disease versus starvation. It is likely that most of the 25–36 % mortality among full-ration herring in each treatment period was due to disease, but interactive effects of disease and starvation cannot be ruled out for herring on restricted rations. Only a small fraction (~17 %) of dead fish were subjected to pathology due to logistical constraints, and no live fish were sacrificed for testing to avoid compromising other analyses. Additionally, disease prevalence among live fish is not a good predictor of mortalities, because many survive infection (Kocan et al. 2001). Cumulative mortalities among all rations were similar through April, while lipid levels were still relatively high even among fasted fish, suggesting disease and not starvation caused

the deaths of roughly one-third of the herring. An additional doubling of deaths in May among fasted herring was likely due to starvation and disease, based on previous observations of mortalities increasing with starvation duration (Gregg et al. 2011) to similarly high levels among non-diseased fish (~60 % over 18 weeks, Paul and Paul 1998).

Smaller herring appeared to be at higher risk of death regardless of winter feeding history. For herring that died of starvation, this could be due to the combined effects of higher mass-specific metabolic rate (Slotte 1999) and lower lipid stores (Sewall et al. 2019) among smaller herring that caused them to deplete their stored energy more rapidly than larger individuals. However, it is less clear why size-dependent mortality also occurred among fully-fed herring, indicating that smaller herring were also at higher risk than larger herring of dying from disease. Size-dependent disease mortality is poorly documented for herring, but has been observed in juvenile rainbow trout (*Oncorhynchus mykiss*), possibly reflecting developmental differences in immune response (Becker et al. 2005, Overturf et al. 2010). Higher mortality from VHS or VEN among smaller herring could reflect a relationship between body size and viral pathogen dose, though the mechanism is unclear (pers. comm., P. Hershberger, US Geological Survey Marrowstone field station, Nordland, WA, USA). Regardless of the exact mechanism responsible, risk of mortality by starvation, disease, or a combination of the two was greatest for the smallest herring. Across rations, 85 % of herring that died in spring were less than 76 mm long, the length at which YOY herring switch from growth to storing lipid for winter (Sewall et al. 2019). By comparison, only 61 % of survivors and euthanized herring were smaller than 76 mm. Failure to attain that critical size among wild herring likely raises the risk of predation and starvation, and reduces the probability of eating energy-rich euphausiid prey (Sewall et al. 2019). Loss of small herring to predation and starvation are believed to cause the observed increases in

mean size of PWS herring collected before and after winter, when feeding is unlikely to support growth (Foy and Paul 1999, Paul and Paul 1998). In addition to these factors, the present findings suggest smaller herring are also more vulnerable to disease, reinforcing the notion that growing beyond a critical size before winter is essential for reducing herring mortality risk.

Mortality risk can be high due to disease even absent clear signs of poor condition associated with starvation, though disease and poor condition may interact. Cumulative mortalities were similarly high between herring re-fed in spring and those that continued on restricted rations, despite higher lipid levels among re-fed fish as food supplanted lipid stores as an energy source. In addition, lipid levels of fish that died were well above the minimum survival threshold lipid of 1.28 % established in fasting disease-free herring (Sewall et al. 2019), and higher than the mean lipid level of wild herring in PWS in March (2.15 %, Sewall et al. 2019). Based on lipid and protein energetic equivalents (Brett 1995), the energy density of dead herring fasted for 14–20 weeks in this study (3.86 kJ/g wet) was higher than that reported for dead Resurrection Bay herring fasted for 18 weeks (3.2 kJ/g, Paul and Paul 1998) and similar to wild PWS herring winter survivors in March (3.8 kJ/g, Paul and Paul 1998, 3–4 kJ/g Gorman et al. 2018). Taken together, these findings suggest that disease effectively raises the minimum survival threshold level of lipid. That threshold would likely be reached by wild PWS herring more quickly than by fasted herring in this study, given they typically have lower lipid levels near the start of winter fasting (mean November lipid 5.79 %, Sewall et al. 2019).

The condition of fully-fed herring that died was intermediate between fed and fasted survivors, indicating an energetic cost associated with lethal disease, or greater susceptibility among herring in poor condition. Disease energetic cost may be the primary reason fasted herring in this study lost total body energy from January to May at twice the daily rate for

captive herring reported previously (~46 J/d, based on mean lipid and protein losses, versus 23 J/d in Paul and Paul 1998), despite water temperatures 1–2 °C colder. Few studies establish causal relationships between disease lethality and poor fish condition. However, Vollenweider et al. (2011a) demonstrated experimentally that poor juvenile herring condition can be both a consequence of ichthyophoniasis and a contributor to elevated mortality of herring already in poor condition when they acquire the disease, and the same may be true of VHS and VEN. Mortality among herring afflicted by VHS can result from tissue damage to the liver, kidney, and other organs (Kocan et al. 1997), and need not involve depletion of stored energy to lethal levels. While low lipid levels can be useful for identifying fish in poor condition at risk of starvation, assessing disease mortality risk likely requires additional specialized measures such as blood plasma assays that can distinguish herring that have acquired immunity to VHS versus those that are vulnerable (Hart et al. 2017). It is clear that independent indices of starvation and disease mortality risks and their potential interaction are important for modeling and monitoring juvenile herring winter survival.

Herring disease mortality risk may be strongly influenced by winter food scarcity. For YOY herring infected by ichthyophoniasis, cumulative mortality plateaus at 50–70 % after 2–3 months if they are feeding, but continues to increase if they are fasting (Gregg et al. 2011). Herring with VHS and VEN in the present study likewise had lower mortality if continuously fully fed than if fed a reduced ration or fasted in winter and spring. Following the winter period of food scarcity, the return of high food availability in spring did not appear to reduce mortality risk, as cumulative mortalities were similar for herring that resumed feeding in spring and those that continued on restricted rations. Food scarcity and low temperatures can impair immune function, with effects increasing with fasting duration (e.g., in yellow drum *Nibea albiflora*;

Song et al. 2019). Impaired immune response following an extended period of fasting and cold temperatures thus may have contributed to high mortality during and after winter among herring observed in this study. Conditions promoting high zooplankton prey availability may thus need to persist through winter months to benefit survival of diseased herring.

While higher temperatures can hasten starvation mortality among fasting herring by increasing metabolic rates, the effects of temperature on mortality among diseased fish is more complex. Disease mortality can be higher at intermediate (ambient 7.9 °C) temperature than at higher (12.4 °C) or lower (5.6 °C) temperatures among fasting herring infected by ichthyophoniasis (Gregg et al. 2011), and VHS mortality declines with increasing temperature at ~9–15 °C (Hershberger et al. 2013). Ichthyophoniasis mortality may decline at low temperatures due to reduced parasite growth, similar to declines in bacterial parasite growth and mortality of salmon (*Oncorhynchus* spp.) at decreasing temperatures (range: 3.9–20.5 °C; Groberg et al. 1978). In contrast, decreased mortality at high temperatures for diseased herring is likely due to improved herring immune response (Gregg et al. 2011, Hershberger et al. 2013). Increasing temperature may also reduce disease mortality by improving recovery of size and energy stores upon re-feeding after fasting (Vollenweider et al. 2011a). Cold temperatures therefore likely hindered recovery following spring re-feeding among diseased herring in the present study. In wild populations of herring and other species susceptible to VHS along the Pacific coast of North America, the disease appears most commonly in cold northern regions and in winter (Hedrick et al. 2003). Warming ocean conditions thus may reduce disease mortality among YOY herring in northern populations. However, multiple potentially interacting effects of ocean warming on herring and pathogens will likely determine disease outcomes.

Conclusions

In summary, herring growth was minimal during winter months even with abundant food available, supporting the importance of growth before winter to promote survival (Norcross et al. 2001, Sewall et al. 2019). Spring re-feeding following winter food limitation may stop body mass loss and even promote compensatory growth and swimming performance, but may not reduce mortality compounded by disease. Winter feeding benefits to herring growth and condition may be limited not only by cold temperatures but also by gut atrophy, causing lower assimilation efficiency even among fully-fed fish. These constraints suggest why a fat-burning strategy may be favored rather than incurring greater predation risk by foraging during winter, regardless of food availability, and why maximizing fat stores prior to winter is critical. Further, ocean conditions that promote zooplankton prey availability may offer only limited benefits to herring if they are inconsistent or poorly matched to herring needs. If high zooplankton availability occurs too early in the spring, herring may have not yet recovered gut mass lost in winter for efficient assimilation and temperatures may be too low to promote growth. Alternatively, herring may not benefit if spring zooplankton peak too late to counteract effects of limited winter feeding compounded by disease. Reduced disease effects can occur at warmer temperatures, but may be contingent on herring obtaining sufficient energy from food. Timing and magnitude of peak zooplankton prey biomass in spring responds to ocean temperature (Batten et al. 2018), thus recent warming trends in the North Pacific could promote a mismatch between prey availability, herring digestive capacity, and energetic demands that negatively impacts herring survival.

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Figures

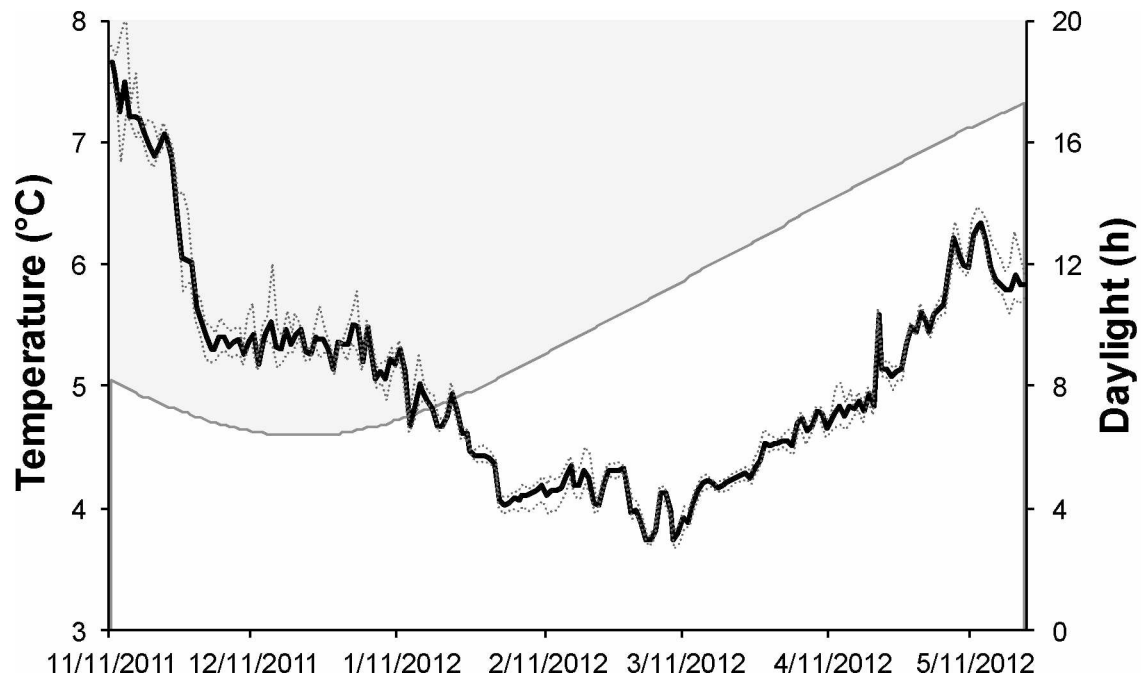


Figure 3.1 Daily mean ambient seawater temperatures (°C) and daylight hours (unshaded) for tanks in the laboratory feeding study of young-of-the-year Pacific herring in Auke Bay, Southeast Alaska throughout the study period, November 2011 to May 2012. Solid black line indicates daily mean temperature averaged across five representative tanks. Dotted gray lines indicate the daily minimum and maximum individual tank means.

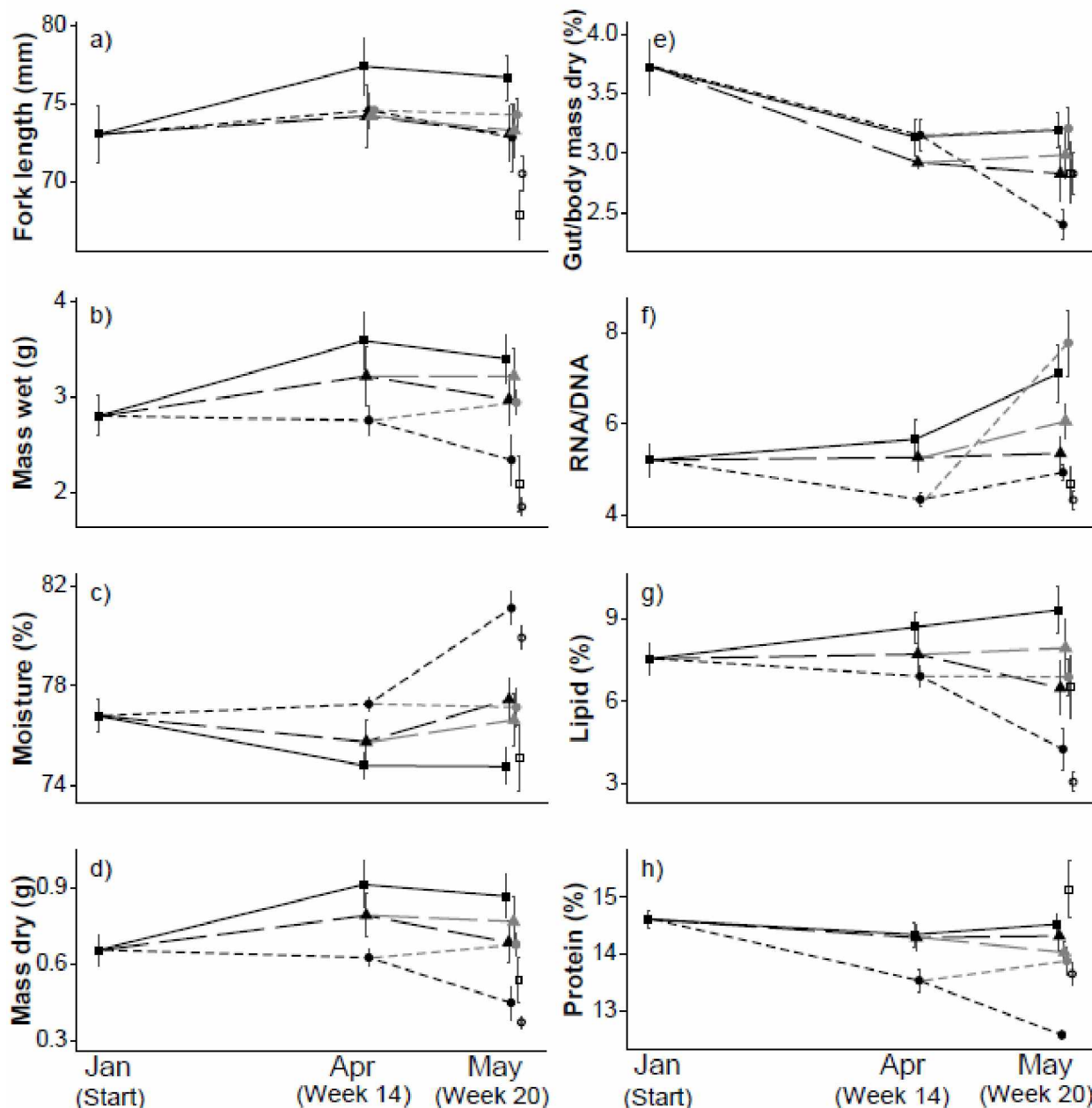


Figure 3.2 Morphometric and biochemical indices (mean \pm 1SE) for young-of-the-year Pacific herring from Auke Bay, Southeast Alaska in the laboratory feeding study, shown at different ration levels: full (■, black line), reduced (▲, black dashes), fasted (●, black dots), reduced then re-fed (▲, gray dashes), fasted then re-fed (●, gray dots), and mortalities from full (□) and fasted (○) groups that occurred on various dates during April and May shown pooled in May for clarity. Panels show *a*) fork length, *b*) body mass on a wet tissue basis, *c*) moisture content as a percentage of body mass, *d*) body mass on a dry tissue mass basis, *e*) dry gut mass as a percentage of dry body mass, *f*) RNA/DNA ratio, *g*) lipid mass as a percentage of wet body mass, and *h*) protein mass as a percentage of wet body mass.

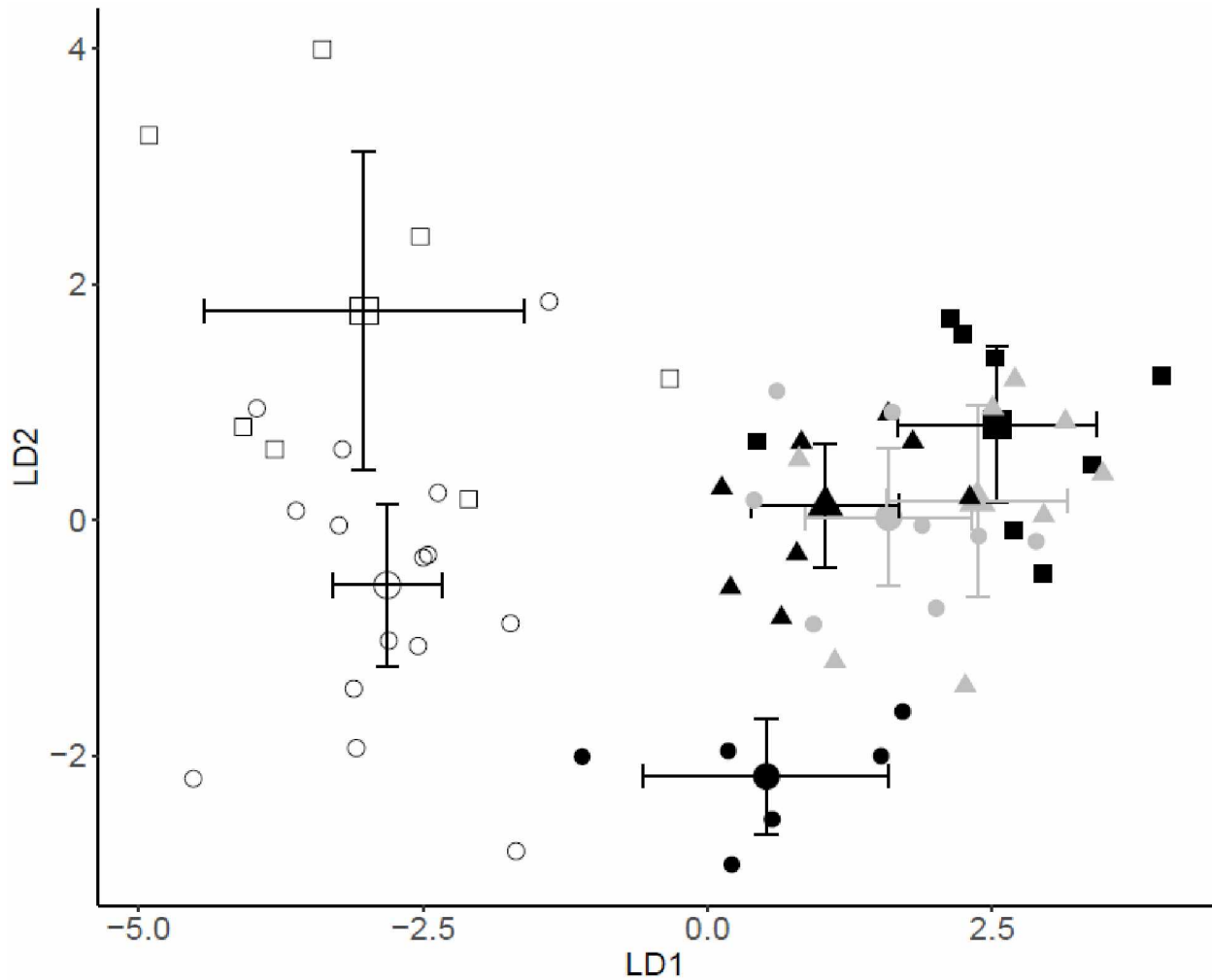


Figure 3.3 Linear discriminant analysis scores with centroids and 95 % CI bars for discriminants LD1 and LD2 derived from all standardized morphometric and biochemical data at the end (May) of the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Points represent individual herring by ration level: full (■), reduced (▲), fasted (●), reduced then re-fed (▲●), fasted then re-fed (●●), and mortalities from full (□) and fasted (○) groups.

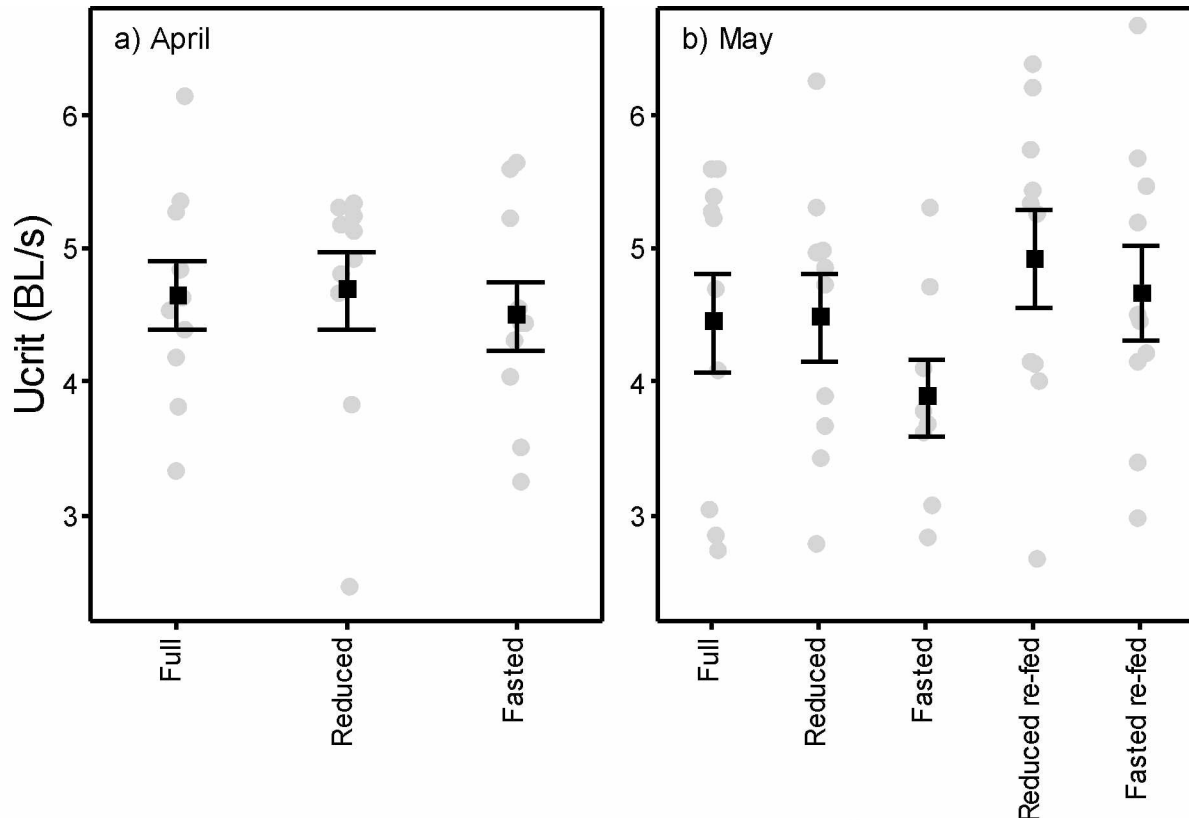


Figure 3.4 Critical swimming speeds (body lengths per second) of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska in the laboratory feeding study, shown by ration level after a) the end of winter ration treatments in April and b) the end of spring re-feeding treatments in May. Individual speeds (\bullet), means (\blacksquare) and SE bars shown. Sample sizes: $n = 8$ for fasted group in May; $n = 10$ for all other groups.

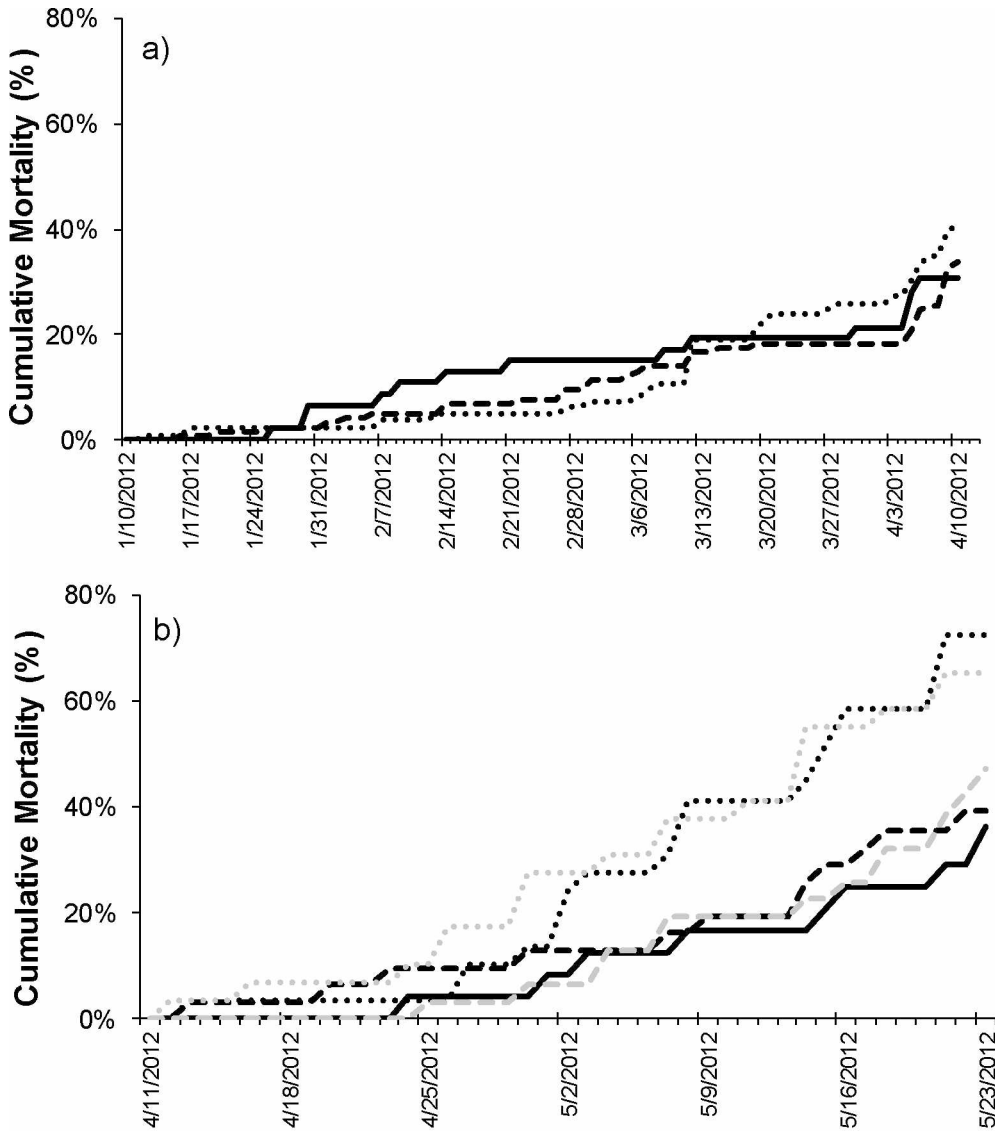


Figure 3.5 Cumulative daily mortality (% initial n) in the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska by ration level, for *a*) winter ration period (January–April; 3 ration levels), and *b*) spring re-feeding period (April–May; 5 ration levels). Lines indicate sums across replicate tanks by ration level: full (black line), reduced (black dashes), fasted (black dots), reduced then re-fed (gray dashes), and fasted then re-fed (gray dots).

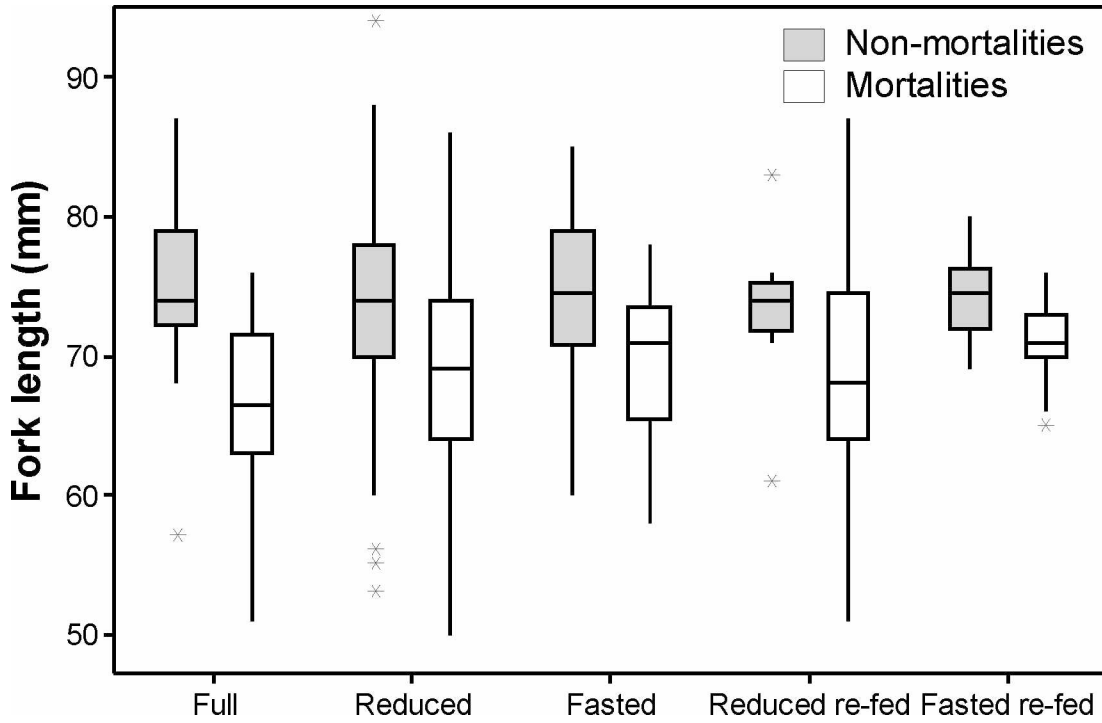


Fig. 3.6 Fork length (mm) of live and sampled fish (non-mortalities) and fish that died (mortalities) by ration level during spring (April–May) in the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Medians, interquartile ranges (IQR), whiskers (≤ 1.5 IQR) and outliers (*, > 1.5 IQR) are shown.

Tables

Table 3.1 Study design for laboratory feeding experiment with number of individuals analyzed (*n*) by ration level at the end of each treatment period, for young-of-the-year Pacific herring from Auke Bay, Southeast Alaska.

Tank	Acclimation (Nov–Jan)		Winter (Jan–Apr)		Spring (Apr–May)	
	Ration	<i>n</i>	Ration	<i>n</i>	Ration	<i>n</i>
1			Full*	5	Full	5
2			Full*	5	Full	5
3	Full	2	Reduced	5	Reduced	5
4			→		Reduced re-fed**	5
5	Full	2	Reduced	5	Reduced	5
6			→		Reduced re-fed**	5
7	Full	2	†		†	
8	Full	2	†		†	
9	Full	2	Fasted	5	Fasted	5
10			→		Fasted re-fed**	5
11	Full	4	Fasted	5	Fasted	3
12			→		Fasted re-fed**	5
Total:		14		30		48

*Separate full-ration tanks established in winter after January acclimation period sampling.

**Re-fed tanks established in spring after April winter sampling using transplants from tank 3 to 4, 5 to 6, 9 to 10, 11 to 12.

†Two full-ration tanks discontinued after January acclimation period sampling.

Table 3.2 Full-ration herring morphometric and biochemical indices (mean \pm 1SD or median [95 % CI in brackets] for non-normal data) by sampling event (month) during the laboratory feeding study (November–May) of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values with shared superscript letters did not differ in Tukey’s pairwise comparisons (or Dunn’s for non-normal data) among sampling events, with each index tested separately. Letters are shown only when some values differed. R^2 = coefficient of determination for ANOVA, F = ANOVA test statistic, H = Kruskal-Wallis test statistic, p = significance value.

	Sampling event (month)				ANOVA / Kruskal-Wallis		
	Start acclimation (*Nov)	End acclimation (Jan)	End winter (Apr)	End spring (May)	R^2	F/H	p
<i>n</i>	40	14	10	10			
Fork length mm	69.5 \pm 9.0 ^b	73.1 \pm 6.8 ^{ab}	77.4 \pm 5.8 ^a	76.7 \pm 4.5 ^{ab}	15.4	4.26	0.008
Mass wet g	2.44 \pm 0.92 ^b	2.80 \pm 0.79 ^{ab}	3.59 \pm 0.95 ^a	3.40 \pm 0.81 ^a	21.7	6.45	0.001
[†] Moisture %	--	76.8 \pm 2.5	74.8 \pm 1.6	74.8 \pm 2.3	10.6	1.83	0.177
**Mass dry g	--	0.63[0.48, 0.81]	0.85[0.65, 1.14]	0.74[0.68, 1.06]	--	5.61	0.061
Gut/body mass dry %	--	3.72 \pm 0.88	3.14 \pm 0.48	3.19 \pm 0.47	15.6	2.87	0.072
RNA/DNA	--	5.21 \pm 1.33 ^b	5.66 \pm 1.43 ^{ab}	7.10 \pm 2.01 ^a	21.9	4.35	0.022
[†] Lipid %	--	7.56 \pm 2.20	8.72 \pm 1.80	9.34 \pm 2.74	6.53	1.08	0.351
Protein %	--	14.6 \pm 0.6	14.4 \pm 0.7	14.5 \pm 0.6	3.45	0.55	0.580

* No chemical analyses conducted on fish collected in November.

** Medians, Kruskal-Wallis test, and Dunn pairwise comparisons of ranked data using Bonferroni-adjusted significance values.

[†]ANOVA and Tukey post-hoc tests based on residuals from regressions versus length. Means (\pm 1SD) not adjusted for length are shown.

Table 3.3 Reduced ration herring morphometric and biochemical indices (mean \pm 1SD or median [95 % CI in brackets] for non-normal data) by sampling event (month) from January through May during the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values with shared superscript letters did not differ in Tukey's pairwise comparisons (or Dunn's for non-normal data) among sampling events, with each index tested separately. Letters are shown only when some values differed. R^2 = coefficient of determination for ANOVA, F = ANOVA test statistic, H = Kruskal-Wallis test statistic, p = significance value.

	Sampling event (month)			ANOVA / Kruskal-Wallis		
	End acclimation (Jan)	End winter (Apr)	End spring (May)	R^2	F/H	p
<i>n</i>	14	9	10			
Fork length mm	73.1 \pm 6.8	74.2 \pm 5.9	73.1 \pm 5.7	0.72	0.11	0.897
Mass wet g	2.80 \pm 0.79	3.22 \pm 0.94	2.97 \pm 0.82	4.43	0.70	0.507
[†] Moisture %	76.8 \pm 2.5	75.7 \pm 2.7	77.4 \pm 2.8	5.71	0.91	0.414
Mass dry g	0.66 \pm 0.23	0.79 \pm 0.26	0.69 \pm 0.26	5.45	0.86	0.432
**Gut/body mass dry %	3.57[3.10, 4.09] ^a	2.92[2.81, 3.03] ^{ab}	2.67[2.34, 3.33] ^b	--	9.83	0.007
RNA/DNA	5.21 \pm 1.33	5.27 \pm 0.95	5.36 \pm 1.08	0.30	0.05	0.956
[†] Lipid %	7.56 \pm 2.20	7.73 \pm 2.49	6.49 \pm 3.12	4.33	0.68	0.515
Protein %	14.6 \pm 0.6	14.3 \pm 0.7	14.3 \pm 0.8	5.19	0.82	0.449

** Medians, Kruskal-Wallis test, and Dunn pairwise comparisons of ranked data using Bonferroni-adjusted significance values.

[†]ANOVA and Tukey post-hoc tests based on residuals from regressions versus length. Means (\pm 1SD) not adjusted for length are shown.

Table 3.4 Fasted herring morphometric and biochemical indices (mean \pm 1SD or median [95 % CI in brackets] for non-normal data) by sampling event (month) from January through May during the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values with shared superscript letters did not differ in Tukey's pairwise comparisons (or Dunn's for non-normal data, Games-Howell comparisons for unequal variances) among sampling events, with each index tested separately. Letters are shown only when some values differed. R^2 = coefficient of determination for ANOVA, F = ANOVA test statistic, H = Kruskal-Wallis test statistic, p = significance value.

	Sampling event (month)			ANOVA / Kruskal-Wallis		
	End acclimation (Jan)	End winter (Apr)	End spring (May)	R^2	F/H	p
<i>n</i>	14	10	7			
Fork length mm	73.1 \pm 6.8	74.6 \pm 3.5	72.9 \pm 5.6	1.91	0.27	0.763
Mass wet g	2.80 \pm 0.79	2.75 \pm 0.48	2.33 \pm 0.70	7.60	1.15	0.331
**Moisture %	76.5[75.9, 78.2] ^b	77.0[76.6, 77.9] ^b	81.4[80.6, 82.2] ^a	--	13.4	0.001
Mass dry g	0.66 \pm 0.23	0.63 \pm 0.15	0.45 \pm 0.17	17.8	3.04	0.064
*Gut/body mass dry %	3.72 \pm 0.88 ^a	3.15 \pm 0.42 ^a	2.40 \pm 0.33 ^b	40.6	15.71	<0.001
*RNA/DNA	5.21 \pm 1.33	4.35 \pm 0.52	4.94 \pm 0.44	14.2	4.25	0.031
Lipid %	7.56 \pm 2.20 ^a	6.92 \pm 1.21 ^a	4.25 \pm 2.03 ^b	34.4	7.33	0.003
*Protein %	14.6 \pm 0.6 ^a	13.5 \pm 0.6 ^b	12.6 \pm 0.2 ^c	71.8	72.10	<0.001

* Welch's ANOVA and Games-Howell pairwise comparisons.

** Medians, Kruskal-Wallis test, and Dunn pairwise comparisons of ranked data using Bonferroni-adjusted significance values.

Table 3.5 April herring morphometric and biochemical indices (mean \pm 1SD or median [95 % CI in brackets] for non-normal data) and pairwise comparisons by ration level following the winter ration period during the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values with shared superscript letters did not differ in Tukey's pairwise comparisons (or Dunn's for non-normal data, Games-Howell comparisons for unequal variances) among sampling events, with each index tested separately. Letters are shown only when some values differed. R^2 = coefficient of determination for ANOVA, F = ANOVA test statistic, H = Kruskal-Wallis test statistic, p = significance value.

	Ration level			ANOVA / Kruskal-Wallis		
		Full	Reduced	Fasted	R^2	F/H p
	n	10	9	10		
Fork length mm		77.4 \pm 5.8	74.2 \pm 5.9	74.6 \pm 3.5	7.9	1.12 0.341
Mass wet g		3.59 \pm 0.95	3.22 \pm 0.94	2.75 \pm 0.48	17.0	2.66 0.089
* \dagger Moisture %		74.8 \pm 1.6 ^b	75.7 \pm 2.7 ^{ab}	77.3 \pm 0.9 ^a	22.1	8.04 0.004
*Mass dry g		0.91 \pm 0.29 ^a	0.79 \pm 0.26 ^{ab}	0.63 \pm 0.11 ^b	22.7	4.95 0.023
*Gut/body mass dry %		3.14 \pm 0.48	2.92 \pm 0.12	3.15 \pm 0.42	7.60	2.09 0.161
**RNA/DNA		5.61[4.75, 6.08] ^a	5.05[4.59, 6.33] ^{ab}	4.40[4.03, 4.70] ^b	--	9.37 0.009
\dagger Lipid %		8.72 \pm 1.80	7.73 \pm 2.49	6.92 \pm 1.21	10.8	1.57 0.228
**Protein %		14.6[13.9, 14.8]	14.6[13.3, 14.8]	13.4[13.1, 14.0]	--	6.86 0.032

* Welch's ANOVA and Games-Howell pairwise comparisons.

** Medians, Kruskal-Wallis test, and Dunn pairwise comparisons of ranked data using Bonferroni-adjusted significance values.

\dagger ANOVA and Tukey post-hoc tests based on residuals from regressions versus length. Means (\pm 1SD) not adjusted for length are shown.

Table 3.6 May herring morphometric and biochemical indices (mean \pm 1SD or median [95 % CI in brackets] for non-normal data) and pairwise comparisons by ration level following the spring re-feeding period during the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values for mortalities represent full-ration ("Full mort") and fasted ("Fasted mort") herring that died during spring (April–May). Values with shared superscript letters did not differ in Tukey's pairwise comparisons (or Dunn's for non-normal data, Games-Howell comparisons for unequal variances) among sampling events, with each index tested separately. Letters are shown only when some values differed. R^2 = coefficient of determination for ANOVA, F = ANOVA test statistic, H = Kruskal-Wallis test statistic, p = significance value.

	Ration level						
	Full	Reduced	Fasted	Reduced re-fed	Fasted re-fed	Full mort	Fasted mort
<i>n</i>	10	10	7	10	10	8	18
Fork length mm	76.7 \pm 4.5 ^a	73.1 \pm 5.7 ^{ab}	72.9 \pm 5.6 ^{ab}	73.3 \pm 5.5 ^{ab}	74.3 \pm 3.2 ^{ab}	67.9 \pm 4.4 ^b	70.6 \pm 4.6 ^b
**Mass wet g	3.09[2.80, 4.04] ^a	2.89[2.60, 3.44] ^{ab}	2.11[1.84, 3.14] ^{abc}	2.97[2.69, 3.43] ^{ab}	3.05[2.51, 3.27] ^{ab}	1.97[1.30, 3.00] ^{bc}	1.90[1.52, 2.09] ^c
†Moisture %	74.8 \pm 2.3 ^c	77.4 \pm 2.8 ^{abc}	81.1 \pm 1.7 ^a	76.6 \pm 3.2 ^{bc}	77.1 \pm 2.4 ^{bc}	75.1 \pm 3.8 ^c	79.9 \pm 1.9 ^{ab}
**Mass dry g	0.74[0.68, 1.06] ^a	0.63[0.51, 0.90] ^{ab}	0.38[0.32, 0.59] ^{bc}	0.64[0.55, 0.89] ^{ab}	0.71[0.54, 0.82] ^{ab}	0.51[0.26, 0.83] ^{abc}	0.36[0.31, 0.42] ^c
Gut/body mass dry %	3.19 \pm 0.47	2.83 \pm 0.76	2.40 \pm 0.33	2.99 \pm 0.62	3.21 \pm 0.57	2.84 \pm 0.71	2.83 \pm 0.74
**RNA/DNA	6.86[5.40, 9.26] ^{ab}	5.23[4.61, 5.82] ^{abc}	4.99[4.48, 5.35] ^{abc}	5.99[4.96, 6.94] ^{ab}	7.78[5.80, 8.38] ^a	4.71[3.62, 5.17] ^{bc}	4.49[3.77, 4.89] ^c
†Lipid wet %	9.34 \pm 2.74 ^a	6.49 \pm 3.12 ^{abc}	4.25 \pm 2.03 ^{bc}	7.95 \pm 3.29 ^{ab}	6.89 \pm 2.04 ^{abc}	6.50 \pm 3.24 ^{ab}	3.05 \pm 1.50 ^c
†Lipid dry %	36.5 \pm 7.5 ^a	27.6 \pm 10.3 ^a	21.9 \pm 8.4 ^{ab}	32.9 \pm 9.6 ^a	29.6 \pm 6.4 ^a	24.9 \pm 10.5 ^a	14.7 \pm 5.7 ^b
*Protein wet %	14.5 \pm 0.6 ^a	14.3 \pm 0.8 ^{ab}	12.6 \pm 0.2 ^c	14.0 \pm 0.6 ^{ab}	13.9 \pm 0.8 ^{ab}	15.1 \pm 1.4 ^{ab}	13.7 \pm 0.8 ^b
*Protein dry %	58.1 \pm 6.1 ^{ab}	64.4 \pm 8.5 ^{ab}	67.1 \pm 5.4 ^{ab}	61.0 \pm 8.2 ^{ab}	61.3 \pm 6.9 ^{ab}	61.4 \pm 6.4 ^a	68.3 \pm 3.9 ^b

	ANOVA / Kruskal-Wallis		
	R^2	F / H	P
Fork length mm	23.2	3.33	0.006
**Mass wet g	--	36.3	<0.001
†Moisture %	43.2	8.37	<0.001
**Mass dry g	--	36.2	<0.001
Gut/body mass dry %	12.3	1.55	0.177
**RNA/DNA	--	34.7	<0.001
†Lipid wet %	38.0	6.73	<0.001
†Lipid dry %	39.4	7.15	<0.001
*Protein wet %	41.5	29.8	<0.001
Protein dry %	22.1	3.11	0.010

* Welch's ANOVA and Games-Howell pairwise comparisons.
 ** Medians, Kruskal-Wallis test, and Dunn pairwise comparisons of ranked data using Bonferroni-adjusted significance values.
 † ANOVA and Tukey post-hoc tests based on residuals from regressions versus length. Means (\pm 1SD) not adjusted for length are shown.

Table 3.7 Coefficients of linear discriminants (LDs) from analysis of standardized data for all morphometric and biochemical indices at the end (May) of the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Top three discriminants explaining ~93 % of between-group variability (“Separation achieved %”) are shown.

	Linear discriminants		
	LD1	LD2	LD3
Fork length mm	-0.439	-0.496	0.686
Mass wet g	0.405	0.947	1.981
Moisture %	7.529	-2.589	-4.096
Mass dry g	0.384	-0.639	-3.510
Gut/body mass dry %	0.159	0.493	0.185
RNA/DNA	0.601	-0.023	1.058
Lipid %	7.054	-1.594	-2.526
Protein %	1.670	0.090	-1.359
Separation achieved %	73.4	14.4	5.5

Table 3.8 Cumulative percent mortality (mean \pm 1SD) across replicate tanks (n), adjusted for sampling and other removals, during the winter ration period (Jan–Apr; 93 d) and spring re-feeding period (Apr–May; 42 d) in the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values with shared superscript letters did not differ in Tukey’s pairwise comparisons among ration levels within a period, with winter and spring periods tested separately. Letters are shown only when some values differed.

Winter (Jan–Apr)						Spring (Apr–May)				
Ration Level	n	# fish start	# fish removed	# fish died	Mortality (%)	n	# fish start	# fish removed	# fish died	Mortality (%)
Full	2	46	10	12	24.6 \pm 13.3	2	24	10	8	35.5 \pm 1.1 ^b
Reduced	2	123	26	35	33.4 \pm 5.2	2	31	10	12	37.5 \pm 1.7 ^{ab}
Fasted	2	133	29	43	36.6 \pm 0.8	2	29	8	21	69.6 \pm 2.6 ^a
Reduced re-fed*						2	31	10	14	44.4 \pm 16.8 ^{ab}
Fasted re-fed*						2	29	10	19	62.0 \pm 7.5 ^{ab}

*Re-fed groups established after spring (April) sampling.

Table 3.9. Median length and range (mm) of live and sampled fish (“non-mortalities”) versus fish that died (“mortalities”) by ration level during April and May in the laboratory feeding study of young-of-the-year Pacific herring from Auke Bay, Southeast Alaska. Values include the end of “winter” and all of “spring” treatment periods. W = Mann-Whitney test statistic, p = significance value adjusted for ties.

Ration Level	Non-mortalities		Mortalities		Mann-Whitney	
	n	Length (range)	n	Length (range)	W	P
Full	44	74 (57–87)	10	66.5 (51–76)	116	<0.001
Reduced	94	74 (53–94)	26	69 (50–86)	1024.5	<0.001
Fasted	90	74.5 (60–85)	33	71 (58–78)	1327.5	<0.001
Reduced re-fed*	10	74 (61–83)	13	68 (51–87)	133.5	0.171
Fasted re-fed*	10	74.5 (69–80)	19	71 (65–76)	236.5	0.027
All pooled	248	74 (53–94)	101	70 (50–87)	11706.5	<0.001

*Re-fed groups established after April sampling.

General Conclusions

This dissertation used a combination of quantitative modeling, field observations, and a laboratory experiment to describe how oceanographic and biological factors may affect recruitment of PWS herring by influencing survival through their first winter. The work included three prominent aspects: a demonstration of the improvement in herring recruitment forecasting gained by incorporating ecosystem components that operate during their first year, observations of a size-based shift from autumn growth to lipid storage that reflect first winter mortality risks, and evidence for first winter constraints on growth and disease recovery that can persist through spring. Taken together, this work described the importance of size- and energy-dependent mortality processes related to variable environmental conditions such as temperature, food availability, and predation that drive the need for YOY herring to attain critical size and energy levels to survive their first winter.

Survival of juvenile PWS herring to recruitment at age three was associated with the abundance of age-one GOA pollock from the same brood year, which improved predictions of herring recruitment when incorporated in a stock-recruitment model. The association with juvenile pollock, which share similar nearshore areas and diets with juvenile herring (Sturdevant et al. 2001), suggests herring recruitment is likely driven by gulf-wide ecosystem processes influencing the abundance or quality of zooplankton prey or predation pressure common to both species. Gulf-wide processes may strongly influence feeding conditions for herring in PWS (Kline 1999, Gorman et al. 2018) and both the GOA and PWS zooplankton communities may show broadly similar responses to warming conditions (Batten et al. 2018, McKinstry and Campbell 2018). When oceanographic conditions support large numbers of juvenile pollock and

herring, their high abundance may promote higher survival by overwhelming predators such as Pacific cod (*Gadus macrocephalus*) and adult pollock (Bishop and Powers 2013).

Predation risk appears closely linked to YOY herring size and condition. YOY herring that grew beyond ~ 76 mm fork length shifted from growth to lipid storage. Herring that failed to store sufficient lipid to support metabolism through winter were compelled to forage during winter to avoid starvation. Foraging and hunger can compromise anti-predator schooling behavior (Sogard and Olla 1997). Predation risk appears highest for small herring that are known to make up a large part of PWS predatory groundfish diets (Bishop and Powers 2013). Predation pressure on small herring is thus likely a key reason why YOY herring store lipid only after growing to a critical size.

Critical size and subsequent lipid storage must be achieved in the critical period before winter. Winter growth was minimal for YOY herring reared under ambient winter conditions of cold water temperatures and short daylight hours, even with abundant food provided. Food assimilation efficiency was likely reduced due to gut atrophy (Lee and Houston 1994), which was most severe among fasted herring but also occurred among fully-fed herring. Food availability for PWS herring declines during winter (Foy and Norcross 1999), which should reduce gut mass (Zaldúa and Naya 2014) and limit growth (Beauchamp et al. 2007). Low winter growth potential due to cold temperatures, alone or in combination with limited food, may explain why winter foraging is avoided in favor of metabolizing stored lipid. Re-feeding during spring, when temperatures rose only modestly from winter lows, offered limited benefits to recovery of size, lipid levels, or reducing size-dependent mortality following winter fasting, reinforcing the importance of attaining large size and energy stores in autumn.

Autumn condition of YOY PWS herring during the seven years examined was best for the 2012 brood year, prompting expectation of strong recruitment at age three in 2015. Herring survival appeared high through the winter of 2012–13, as indicated by schools of age-one herring an order of magnitude more abundant during June 2013 than during other recent years observed by aerial surveys (Pegau 2014). This observation appeared to support the hypothesis that good autumn condition promotes first winter survival. After surviving the first winter, relatively lower mortality at ages two and three were expected to enable a strong recruiting class in 2015. However, the PWS herring population abundance during 2015 remained near historically low levels (Vega et al. 2019) and evidence for strong recruitment was equivocal. Low abundance resulted in limited sampling to determine population age structure. Spring spawning herring catches used by managers to determine PWS herring stock age composition were limited to two samples from different locations collected two weeks apart during April 2015. The 2012 cohort accounted for only 3 % of spawners in the first sample, but 60 % in the second (S Moffitt, Alaska Department of Fish and Game, pers. comm.). Such large variance allows only tentative inferences regarding recruitment strength, but subsequent spawning herring surveys showed only a moderately strong 2012 cohort (Vega et al. 2019). The herring spawning population likely would have been substantially smaller if not for the good condition and high first winter survival of the 2012 brood year.

Similar to the high survival shown by the 2012 brood year herring, the 2012 brood year of GOA pollock during 2013 yielded one of the highest age-one pollock abundance estimates in the 1970–2017 pollock stock assessment time series (Dorn et al. 2017), indicating high survival through their first winter of 2012–13. Unlike herring however, that brood year of GOA pollock persisted into subsequent years at historically high abundances; during 2015 for example, the

2012 brood year at age three accounted for over 80 % of the abundance of all GOA pollock (ages 1–10; based on data in Dorn et al. 2019, Table 1.20). High survival of the 2012 brood year of GOA pollock and PWS herring at least through summer 2013, followed by poor herring recruitment in 2015, suggests high mortality of herring ages 1–3 due to unusual conditions at some time during late 2013–2015.

Ocean conditions were anomalously warm during 2014–16, which could have indirectly contributed to high herring mortality through changes to zooplankton prey or predators. This period was marked by a persistent marine heat wave in the North Pacific (Di Lorenzo and Mantua 2016) associated with numerous changes in primary productivity, zooplankton, and fish stocks (Batten et al. 2018, Zador and Yasumiishi 2017). Biological responses to heat wave conditions may not have followed relationships present before the heat wave. For example, GOA diatom abundance and zooplankton biomass were both positively correlated with temperature in 2000–2013, but not during the subsequent heat wave (Batten et al. 2018). The heat wave was associated with positive anomalies in GOA zooplankton abundance during 2014–2015 (Batten et al. 2018, Batten 2019), with relatively low but increasing zooplankton abundance in PWS (McKinstry and Campbell 2018, Campbell and McKinstry 2019). In both the GOA and PWS, the heat wave was associated with changes in zooplankton community composition, including increased proportions of small copepod species, which could reduce diet quality for herring. Meanwhile, higher temperatures likely raised metabolic rates of predatory fish such as adult pollock (Smith et al. 1988) and their consumption of forage fish (Imsland et al. 2005, Petersen and Kitchell 2001). Predation on herring may have been unusually high during that extended period of high temperatures, when nutritionally-stressed herring were more susceptible to predation (Sogard and Olla 1997), resulting in relatively fewer herring surviving to spawn during

the spring of 2015. In contrast, the 2012 cohort of pollock may have survived in greater numbers than herring during 2014–15 if the differing size or depth distributions seen for YOY herring and pollock (Stokesbury et al. 2000) diverge further with age (Sigler and Csepp 2007), contributing to different predation mortality.

Mortality during the heat wave may also have been unusually high for juvenile herring within PWS if poor condition and high predation were compounded by disease, though direct supporting evidence is lacking for disease effects during that period. While increasing water temperature can improve herring immune response, it is unclear whether the response breaks down at some upper temperature limit, similar to the observed switch at 12 – 12.5 °C from positive to negative effects on growth (Haist and Stocker 1985, Batten et al. 2016). Regardless of temperature, disease response can incur an energetic cost to herring (Vollenweider et al. 2011). If herring energy stores were low during the marine heat wave (e.g., for YOY herring in 2015, Sewall et al. 2019) due in part to low quality zooplankton prey (Batten 2019; Campbell and McKintstry 2019), then disease would likely have further increased predation mortality due to negative impacts of poor condition on anti-predator schooling behavior. Additionally, diseases such as ichthyophoniasis that affect heart function can impair swimming ability, with effects increasing with temperature (Kocan et al. 2006, 2009), further limiting the ability of herring to avoid predators. Though unrelated to warming, a combination of poor condition and disease are among leading candidates for the debated causes of the herring population collapse during the 1990s (Pearson et al. 2012), in which mortality ultimately may have been caused by selective predation on weakened herring (Kramer-Schadt et al. 2010). As an example, combinations of disease, poor condition, and predation may contribute to declines in some Pacific salmon populations in association with climate warming (Miller et al. 2014). Evidence for negative

impacts of climate warming on herring recruitment are suggested in the negative relationship between PWS herring recruitment and increased freshwater discharge into the GOA, an indication of high snow and ice melt and changes in precipitation, though the specific mortality mechanisms involved are unresolved (Ward et al. 2017).

This study provided evidence for mechanisms of PWS herring first winter mortality that likely play a large role in determining recruitment strength. I show that the critical size and critical period concepts that have been applied to first winter survival of juvenile salmon are also useful in understanding juvenile herring. In addition, the reported historical association between juvenile pollock and juvenile herring survival offers useful clues regarding the gulf-wide mechanisms determining both, as does their more recent divergence during the marine heat wave.

While my dissertation work focused on survival of herring through their first winter, processes operating at various early life stages may impact herring recruitment (Stokesbury et al. 1998, Norcross et al. 2001). For example, the effect of ocean temperatures on the timing match/mismatch of larval fish hatching, feeding, and the spring plankton bloom (Cushing 1990) is a key determinant of recruitment for herring in the Strait of Georgia (Schweigert et al. 2013), and has been invoked in past observations of low PWS herring recruitment following cold temperatures prior to spawning (Zebdi and Collie, 1995; Williams and Quinn, 2000). While the present recruitment modeling study found no such relationship, temperature-driven seasonal timing mismatches between food availability and critical feeding periods are predicted to reduce recruitment of many temperate species under continued ocean warming (Asch et al. 2019).

In addition to the potential effects of variability in the seasonal timing of food, quality and quantity of food likely also influence recruitment. In the present modeling study, recruitment

appeared unrelated to the first-order primary productivity index (chlorophyll-*a*), and high quality and quantity diets did not ensure good YOY condition across seven years of field study. However, recruitment among some Atlantic herring (*C. harengus*) stocks in the Baltic Sea can be influenced by zooplankton biomass (Cardinale et al. 2009). Furthermore, changes in food quality resulting from climate-driven alterations in plankton community composition reduce larval survival and ultimately recruitment of Atlantic herring in the North Sea (Payne et al. 2009). In PWS, insufficient zooplankton production leading to poor fish condition decreased juvenile survival, thereby contributing to the herring stock crash of the 1990s and their subsequent failure to recover (Pearson et al. 2012). Poor juvenile survival related to food limitation may be compounded by competition with juvenile pink salmon (*Oncorhynchus gorbuscha*) released from hatcheries in PWS (Deriso 2008, Pearson et al. 2012).

The present study found that the abundances of selected predators did not appear to affect herring recruitment, and quantitative demonstrations of predation effects in herring recruitment models are scarce. However, patterns in YOY herring feeding, growth, energy storage and energy use suggested the importance of predation, and predation impacts on pre-recruit herring survival are widely reported. For example, herring eggs in PWS experience heavy predation by seabirds, with gulls eating up to 26 % of total spawn (Bishop and Green, 2001). Jellyfish predation on larval herring, though poorly documented in PWS, can reduce recruitment of Atlantic herring in the North Sea (Lynam et al. 2005) and causes an inverse relationship between the abundances of jellyfish and larval herring in the Baltic Sea (Möller 1984). At the juvenile stage, predation by Pacific cod has controlled recruitment of Pacific herring in Hecate Strait, British Columbia (Walters et al., 1986), though that relationship may have recently broken down (Ahrens et al., 2012). The correlation between the biomass of Pacific hake (*Merluccius*

productus) and recruitment of herring in the West Coast Vancouver Island stock is also likely driven by predation on YOY herring (Tanasichuk, 2017). There are few estimates of juvenile herring removal by predation in PWS, though the biomass of juveniles eaten by murre (*Uria* spp.) and other seabirds is equivalent to more than 10 % of stock biomass (Bishop et al., 2015).

Viewed in context with previous research, the findings of this work suggest several avenues for future research and management applications. Although the most recently available management report states that no stock modeling was done (Vega et al. 2019), an age-0 GOA pollock index could be incorporated in future PWS herring stock assessment models to improve recruitment forecasts. As described in the modeling study (Chapter 1), a pollock index would be useful if assessments adopt a proposed Bayesian framework (Muradian, 2017), which uses a similar rolling average recruitment in forecasting. Recruitment forecasting may further benefit by adding annual indices of autumn YOY herring size and condition estimated from samples representative of the PWS stock. Size and condition reflect environmental conditions and mortality risks as they enter their first winter, and have shown promise as recruitment indices for walleye pollock in the Bering Sea (Heintz et al. 2013). In addition to the management application, the GOA pollock–PWS herring association suggests that research into either stock may help understand the dynamics of both, as well as the broader functioning of the GOA ecosystem.

The effects of first winter survival on PWS herring recruitment were important under past conditions (Norcross et al. 2001) and will likely remain so into the future, though anomalously warm conditions in the North Pacific and associated GOA ecosystem changes during recent years (Zador et al. 2019, Piatt et al. 2020) may pose new challenges for pre-recruit survival. High mortalities among older juvenile herring during the marine heat wave indicate that understanding

and forecasting recruitment will require research and monitoring targeting herring ages 0–3 as well as environmental drivers. Monitoring and modeling several GOA ecosystem components will likely be required:

- water temperatures, which drive numerous other effects (Zador et al. 2019);
- abundance and quality of zooplankton prey, because species composition may change with warming (McKinstry and Campbell 2018, Batten et al. 2018);
- herring diets, because herring selectively feed on available prey (Purcell and Sturdevant 2001);
- predator biomass and diets, to estimate removals of juvenile herring and other forage fishes, especially given the likelihood of increased consumption by predatory fish at warmer temperatures (Piatt et al. 2020);
- and disease, which may have contributed to the herring stock collapse and subsequent low recruitment (Marty et al. 2003), can kill high proportions of juveniles (Kocan et al 1997), and may be especially important if it is compounded by poor juvenile condition in warmer water.

The statistical significance of many of these factors in recruitment models may be difficult to demonstrate due to high variability, non-linearity, and complex interactions. These may inform management through tiered qualitative recruitment influences (positive, neutral, negative), such as described for the use of autumn abundance of YOY herring as a predictor of relative recruitment strength in the Strait of Georgia (Schweigert et al. 2009), and ecosystem status reports in Alaskan fisheries (Zador et al. 2019). Recruitment modeling efforts informed by annual monitoring data specific to herring as well as broader ecosystem components will be

needed to understand how current unprecedented and persistent warm conditions affect herring and their role in the GOA ecosystem.

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Appendix



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April 18, 2012

To: Brenda Norcross
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [322986-2] Pacific herring YOY overwinter survival and recruitment forecasting in Prince William Sound

The IACUC reviewed and approved the Revision referenced above by Designated Member Review.

Received: April 3, 2012
Approval Date: April 18, 2012
Initial Approval Date: April 18, 2012
Expiration Date: April 18, 2013

This action is included on the April 24, 2012 IACUC Agenda.

The PI is responsible for acquiring and maintaining all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol, and could result in revocation of IACUC approval.

The PI is responsible for ensuring animal research personnel are aware of the reporting procedures on the following page.