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Plankton indices explain interannual variability in Prince William Sound herring first year growth

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ABSTRACT

This study examines the relationships between first year growth of juvenile Prince William Sound herring, temperature and their food. We present time series of herring first year growth, determined from scale measurements as a proxy for herring length, water temperature and indices of multiple trophic levels of plankton obtained from Continuous Plankton Recorder (CPR) sampling on the adjacent Gulf of Alaska shelf. We show that there was a significant correlation between herring growth and water temperature, when the three warmest years were excluded (the mean July and August temperatures were greater than 12.5°C in 1989, 2004 and 2005). There were also strong, significant relationships between the abundance of appropriately sized (for first-feeding herring) planktonic prey groups and herring growth. First year herring growth was greater in years with higher abundances of diatoms, microzooplankton and small mesozooplankton but not related to variability in abundance of larger mesozooplankton (such as euphausiids and large copepods). Furthermore, the strong interannual relationship between diatoms and herring growth held true even in the warmest years where the relationship between temperature and growth broke down. We also found seasonal timing and abundance changes in the plankton in warm years that would make the prey more abundant during the summer months immediately after metamorphosis of the herring larvae. We thus conclude that young-of-the-year herring may grow better in warm years because the timing of key prey is a better match for their first feeding.

Key words: Continuous Plankton Recorder, Gulf of Alaska, pacific herring, phytoplankton, Prince William Sound, Zooplankton

INTRODUCTION

Pacific herring (*Clupea pallasii*) has a distribution in the eastern Pacific from the Beaufort Sea to Baja California, Mexico. They are pelagic forage fish that provide an important transfer of energy from phyto- and zooplankton to a suite of larger predators such as other fish, marine mammals, and birds. Herring are also important to humans as a subsistence food and through commercial fisheries. For more than 1500 years herring species from around the world have been captured by subsistence and commercial fisheries for reduction to fish meal, consumption of meat and eggs, and bait for predatory fishes (Hay *et al.*, 2001). Herring are the most abundant forage fish in Prince William Sound (PWS), Alaska (Paine *et al.*, 1996) so are an important component of the marine ecosystem there. Additionally, herring have been commercially harvested in PWS since the early 1900s although there have been gaps in the harvest associated with changes in the markets (Funk and Sandone, 1990). After the *Exxon Valdez* oil spill in 1989 the herring stock in PWS collapsed and by 1994 the commercial fishery was closed. A limited fishery was conducted from 1996 through to 1998 but since 1999 the commercial fishery has remained closed. Many herring stocks have experienced collapses, but unlike other fish species that decline as a result of fishing, herring are more likely to recover after reduced, or zero, levels of harvest (Hutchings, 2000). In spite of fishery closure in PWS, the herring population has not recovered to pre-1993 numbers. While research over the past 16 years has been conducted to help pinpoint the cause(s) of the collapse and the lack of recovery, the conclusions are complex and at times conflicting (Hulson *et al.*, 2008; Thorne and Thomas, 2008; Pearson *et al.*, 2012). One thing that is clear is that there has not been a large

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recruit class since 1988. One hypothesis is that environmental conditions may be limiting growth and hence overwintering survival in the first year of life. A recent effort to image herring scales from PWS collected since the 1970s allows an opportunity to examine the relationship between environmental conditions and growth in the first year of life.

Larval fish growth is expected to be determined by temperature and food, although other environmental properties will almost certainly play a role (e.g., Anderson, 1988; Stokesbury *et al.*, 1999). Temperature will have direct effects on metabolic rates of these ectotherms, so that warmer temperatures will increase growth rates if other factors remain constant and food is plentiful. There is, however, disagreement in the observations of temperature–growth relationships (Haist and Stocker, 1985; Anthony and Fogarty, 1985; Tanasichuk, 1997). Temperature may also have indirect effects on growth by influencing the composition and abundance of planktonic prey available to the young herring. Numerous studies now show that plankton are highly responsive to temperature variability, see for example Mackas *et al.* (2012) and Edwards and Richardson (2004) which review phenological (timing) responses, and Beaugrand *et al.* (2009) which describe extensive biogeographical shifts. Either changing distributions or phenological shifts, or a combination of them, may influence the quantity and composition of the planktonic prey in the water surrounding the young herring.

Variability in near-surface temperatures in the North Pacific has been attributed to several large-scale modes of climate variability, including basin scale connections (Mantua *et al.*, 1997), the El Niño Southern Oscillation (Lluch-Cota *et al.*, 2001) and atmospheric teleconnections (Emery and Hamilton, 1985). In the coastal Gulf of Alaska, an 18.6-year cycle in water temperatures has been observed in several time series and attributed to changes in tidal mixing known as the Lunar Nodal Cycle (Loder and Garrett, 1978; Royer, 1993; McKinnell and Crawford, 2007). The Lunar Nodal Cycle (LNC) arises from variations in the relative tilt of the orbital planes of the earth and moon (Doodson, 1921). Those variations result in changes in the magnitude of tidal mixing, which influences surface temperatures. It has also been suggested that the LNC may influence ecosystem productivity, again through vertical mixing of nutrients (summarized by Royer, 1993; Parker *et al.*, 1995). Distributions of Atlantic herring have been found to vary over an 18.6-year cycle (Maksimov and Smirnov, 1965).

Prey availability, and thus the diet of the young herring, will depend not only on the abundance of the prey, but also its escape response and the mouth size of the fish as it grows. Diet analysis of juvenile herring show they consume a variety of zooplankton (Foy and Norcross, 1999). Friedenberg *et al.* (2012) experimentally demonstrated that as well as the traditionally-assumed copepod diet, Pacific herring larvae consumed significant numbers of microplankton in the size range 73 to 200 μm, including protists such as diatoms and athecate dinoflagellates, as well as metazoa such as bivalve larvae and copepod nauplii. While abundant prey density for herring early life stages has long been assumed to be important in good recruitment and strong year classes (Hjort, 1914; Anderson, 1988; Cushing, 1990), prey quality is also believed to be a key factor (Copeman *et al.*, 2002; Malzahn and Boersma, 2009). Paulsen *et al.* (2014), and references therein, describe the importance of Essential Fatty Acids (EFAs) to herring larvae. Larval fish have to obtain necessary quantities of EFAs through diet, specifically from the phytoplankton and herbivorous zooplankton that form the base of their food chain. Different functional groups of phytoplankton produce different EFAs (Dalsgaard *et al.*, 2003), such as docosahexaenoic acid (DHA) which is principally produced by dinoflagellates, and eicosapentaenoic acid (EPA) which is produced by diatoms (although also by dinoflagellates as a precursor to DHA). Interannual variability in forage fish EFA content, specifically the ratio of DHA to EPA, has been shown to be related to oceanographic conditions through changes in the phytoplankton productivity that underpinned the diet (Litz *et al.*, 2010).

This evidence suggests that variability in the phytoplankton and micro- to meso-zooplankton community composition, as well as in its abundance, should influence the growth of first-feeding herring. Time series of plankton data from within PWS itself are currently too short, too sporadic, or too recent to compare with estimates of PWS herring growth. Long-term plankton sampling over the adjacent Gulf of Alaska shelf, however, has occurred since 2000 through the North Pacific Continuous Plankton Recorder (CPR) Survey. CPR sampling is considered to most adequately represent meso- to large-scale patterns in plankton communities by smoothing out the small-scale patchiness that often influences station-based plankton sampling. There are numerous examples in the literature which show that large-scale climate forcing signals are evident in CPR data (e.g., Batten and Mackas, 2009; Beaugrand *et al.*, 2009; Chiba *et al.*, 2015). There is, thus, a rationale for assuming that variability in plankton communities determined by the CPR for the Gulf of Alaska shelf might influence juvenile herring within

PWS as physical forcing within the Sound will also be mediated by the same hydro-meteorological variability. Furthermore, work by Kline (2009, and references therein) using stable isotope ratios in zooplankton concluded that PWS received ocean productivity from the Gulf of Alaska, with mesoscale eddies suggested as one mechanism of exchange.

Here we explore indices from the CPR data and water temperature time series and assess how they explain the interannual patterns in growth of herring scales during the first year of life. The scale growth is expected to be a proxy for the herring length. While early growth is only one factor in the success, or otherwise, of the PWS herring population, we hope that this study can contribute to the understanding of how food and temperature contribute to the population variability.

METHODS

Herring scale measurements

Since the 1970s, scales have been archived from Pacific herring collected from PWS (Fig. 1) by the Alaska Department of Fish and Game for age-sex-length analysis. Each fish was given a unique identification number and scales from 10 fish were mounted on a microscope slide with a second slide used to cover the scales. From this collection, over 8000 scales from 1985–2013 have been imaged on a scanning microfiche. Of those, 5112 scales were found to be usable. Scales were rejected if the age did not agree with that originally assigned or if the image quality was too poor to make the scale measurements. Scale selection was designed to image scales from approximately 30 male and 30 female fish from each of three age classes (4, 5, and 6) for a total of 180 scales from each collection year.

The images were processed to determine annual growth increments. A focus was determined by examining for a point central to the growth ring along the base of the external portion of the scale (Fig. 2). The positions of the annuli along the central axis of the scale were determined and the distance between annuli recorded. First year growth is the distance measured between the focus and the first annuli. All growth increment data were imported into Microsoft Excel and matched with age, sex, and size data. Data were examined for outliers using Microsoft Excel data filtering tools and the SAS software line, scatter, and box plots. Some scales were measured a second time as a quality control measure.

The primary collection period occurs in March or April during the herring spawn. Fish were collected using either a seine or cast net. The brood year of each fish was determined by subtracting the age of the fish from the collection year, thus a 4-year-old fish collected in 1994 had its first year of growth in the summer of 1990. First year growth was determined not to be dependent on sex or age at collection. This allowed pooling of the measurements among sex and age to provide approximately 180 growth increments for all brood years except the two at both ends of the time series.

Scales of age-0 herring were analyzed using the same methods to determine the relationship between scale growth increments and fish length. Fish were captured from 2008 to 2014 in the period of November to March, the fork length measured, and a scale removed for analysis. A subset of all scales were selected based on 5-mm bins to provide approximately 30 fish per bin between 50 and 105 mm according to fork length. The use of the bins was to ensure the subsample included fish across the size range. This range

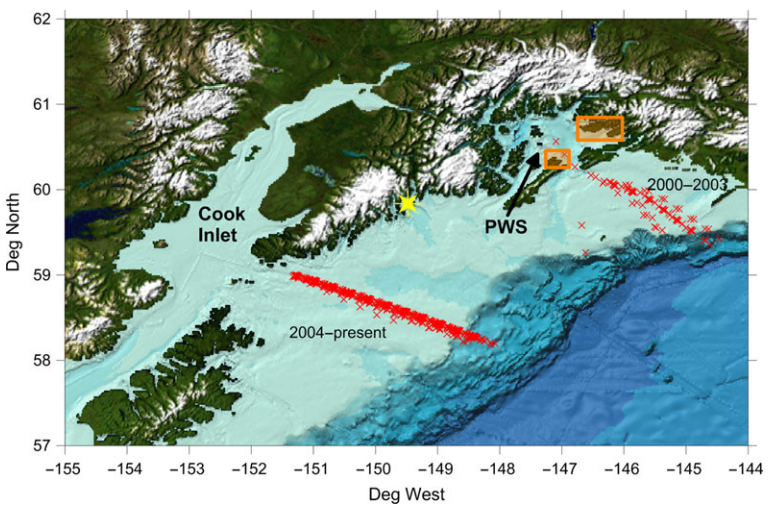
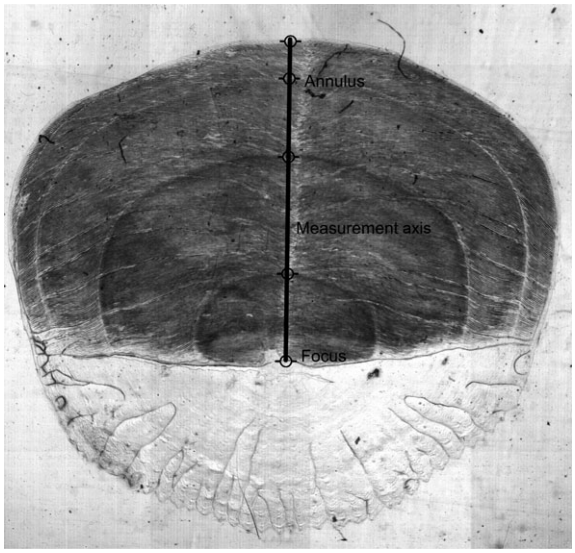


Figure 1. Map showing the sampling locations. Scale measurements were made from adult herring collected in locations marked by orange boxes. Continuous Plankton Recorder (CPR) samples used in this study are shown as red 'x' with the years each transect was sampled indicated. The site of the GAK 1 sampling station is shown as a yellow star.

Figure 2. Example overlay from image analysis software of a herring scale with the focus, measurement axis, and each annulus marked.



was selected by the constraints that few fish were smaller than 50 mm and fish greater than 105 mm could be age-1 fish.

Temperature data

The mean monthly water temperatures were calculated using data from the Cordova tide station, PWS as being most local to the juvenile herring. The temperature is measured approximately 2 m above the sea floor, representing depths of 6–12 m, depending on the tide. All available data each month were collected and visually inspected for outliers (e.g., temperature outside of the range of –1 to 20°C, or > 5°C different from the hour before or after the measurement). Once outliers were removed, the data were averaged to provide a monthly temperature value. It was determined that the strongest correlation was between growth and the average of July and August water temperatures. The mean July–August water temperature was calculated and used in this analysis.

Temperature data were also available from the GAK1 CTD dataset (location shown on Fig. 1), available at http://www.ims.uaf.edu/gak1/, which was judged to be the geographically closest source to the CPR data. Monthly measurements have been made at GAK 1 from 1970 to 2013 from surface to depth. For this study, a mean of the four upper-most water column measurements was calculated (0, 10, 20, and 30 m) from each month to represent sea surface temperature (SST). Where a month was not sampled in a particular year, the long-term mean for that month was used instead to create an unbroken time series.

There was a highly significant positive correlation between the two temperature time series from GAK1 and Cordova ($r^2 = 0.45$, $P < 0.001$) but the tide station data extend further back in time, were closer to where the herring were sampled, and were more continuous than the GAK1 dataset in the early years, therefore most useful for comparison with the herring growth data set.

The PDO is the dominant mode of climate variability at the NE Pacific-basin scale (Mantua *et al.*, 1997) and accounts for much of the interannual variability in the GAK1 dataset. To compare indices of plankton in warm and cold years, particularly changes in phenology, we selected the five warmest and five coldest years in the 14-year plankton time series, using the mean of March to September temperatures (which captures the plankton's productive period and the timing of the CPR sampling season). The warm years were mostly in the earlier part of the time series (warmest to cooler); 2005, 2003, 2006, 2001 and 2000 while the coldest years were mostly later in the time series (coldest to warmer); 2008, 2009, 2012, 2002 and 2007.

Tidal variability

The 18.6-year LNC was approximated by the cosine of the negative of the longitude of the moon's ascending node (N': Doodson, 1921):

$$N' = 100°.8432 + 1934°.1420T - 0°.0021T^2 \quad (1)$$

where T is time, based on a Julian century of 36 525 solar days, with day zero as January 1 1900. Variations in cos(N') correspond to long-term variations in water height observations at tide stations located in Cordova and Seward, Alaska. Geophysical signals like the LNC are often lagged at varying time scales to other variables, such as Pacific Halibut recruitment (Parker *et al.*, 1995) or SST (McKinnell and Crawford, 2007). Thus, the relationship between herring growth increment and the LNC was assessed by calculating the correlation (Pearson's R) between average herring growth increment for each year and cos(N') lagged at 1-year increments. For the purposes of the correlations, cos (N') for each year was calculated for 30th June of each year (i.e., the midpoint day of the year). The significance of each correlation (i.e., that $r \neq 0$) was assessed with the t distribution.

Plankton indices

A summary is given here but for a full description of the CPR instrument and sampling protocols see Batten

et al. (2003) and see Richardson *et al.* (2006) for data analysis methods.

Between 2000 and 2003, the CPR was towed behind an oil tanker from ports in California to Valdez, PWS although the CPR was normally brought back on board outside Hinchinbrook entrance. From 2004 until the present, the CPR has been towed by the cargo ship *Horizon Kodiak* on its route from Tacoma to Anchorage (Fig. 1) with recovery of the instrument normally occurring in lower Cook Inlet (but we have excluded Cook Inlet samples from this study). In both cases, the CPR was towed monthly between about April and September (but occasionally in March and October, see Table 1) in the wake of the ship at a depth of about 7 m. Water and associated plankton entered the front of the CPR through a small square aperture (sides of 1.27 cm), and then through silk-filtering mesh (with a mesh size of 270 μm) which retained the plankton and allowed the water to exit at the back of the machine. The movement of the CPR through the water turned an external propeller which, via a drive shaft and gear-box, moved the filtering mesh across the tunnel at a rate of approximately 10 cm per 18.5 km of tow. As the filtering mesh left the tunnel it was covered by a second band of mesh so that the plankton were sandwiched between these two layers. This mesh and plankton sandwich was then wound into a storage chamber containing buffered 40% formaldehyde preservative (which diluted in the seawater to a concentration of about 4%, sufficient to fix and preserve the plankton).

The towed mesh was processed according to standard CPR protocols; first cut into separate samples (each representing 18.5 km of tow and about 3 m^3 of seawater filtered) which were randomly apportioned amongst the analysts for plankton identification and counting. All Alaskan shelf samples were processed. The ship's log was used to determine the mid-point latitude and longitude of each sample (shown in Fig. 1), along with the date and time.

Table 1. Months that were sampled with the Continuous Plankton Recorder (CPR) each year are indicated by an X in the table.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
2000	x	x			x	x		
2001		x	x	x			x	
2002		x			x			x
2003			x			x		
2004	x	x		x	x	x		
2005		x	x		x	x		
2006	x	x			x	x	x	x
2007		x		x		x	x	
2008				x			x	
2009	x	x	x	x		x		
2010			x		x		x	
2011		x	x		x	x	x	
2012		x	x	x	x		x	x
2013		x	x	x	x	x	x	

The formaldehyde preservative used in the CPR does not fix athecate dinoflagellates so it is not possible to quantify their abundance. Hard-shelled phytoplankton were counted under a purpose-built microscope by viewing 20 fields of view (diameter 295 μm) across each sample under high magnification (× 450) and recording the presence of all the taxa in each field (presence in 20 fields is assumed to reflect a more abundant organism than presence in two fields for example). Cell abundances per field (H) were then calculated for each taxon according to Robinson and Hiby (1978):

$$H = -\ln\left(\frac{k}{20}\right) \quad (2)$$

where k is the number of empty microscope fields (out of 20) observed. Multiplication by the proportion of the sample examined gave cell counts per sample.

Small zooplankton were identified and counted from a sub-sample by tracking across the filtering mesh with the microscope objective (a 2-mm-diameter field of view = 2% of the sample width) and counting all zooplankton organisms encountered within the sub-sample.

All zooplankton larger than about 2 mm were removed from the mesh and counted without sub-sampling. Identification in all cases was carried out to the most detailed practicable taxonomic level and was a compromise between speed of analysis and scientific interest. For example, as copepods make up the majority of the zooplankton and remain mostly intact after sampling, most copepods were identified to species level whereas rarer groups, or those more fragile and not preserved well by the sampling mechanism (such as chaetognaths), were identified to a lower level such as phylum.

Calculation of plankton indices

The mean abundance per sampling event (monthly) was calculated for the entire shelf region, excluding Cook Inlet samples, for various taxonomic groupings (e.g., small mesozooplankton, diatom abundance, etc.). The mean seasonal cycles were calculated by averaging the monthly means for each month of the year when sampling occurred. Annual abundance anomalies and phenology were calculated using a

method proposed by Grieve *et al.* (2005) that relies on cumulative integration. In this case, we integrated between day 60 and day 300 each year (assuming 0 abundance on days 60 and 300), and summed daily values to give a cumulative total for the year. Years generally had 4–6 samplings (Table 1), spaced at monthly or greater intervals. An annual abundance anomaly (Log_{10}, based on the geometric mean of all years) was calculated for each year for the cumulative integrated abundance at day 300. The day of the year when 50% of the cumulative abundance occurred was calculated as the mid-season timing. The day of the year when the seasonal midpoint occurred was calculated for each of the five warm and five cold years for groups of plankton.

RESULTS

We use the full time series of first year herring growth (31 years) and plankton (14 years) to explore the relationships between each series and temperature variability but as the scale measurements were made from fish aged 4–6 years old, the growth time series currently extends only to 2009, giving a 10 year overlap with the plankton time series. Note that the CPR data prior to 2004 were collected south of PWS rather than Cook Inlet, where it has been collected since 2004. Data analyses show no discernible differences in plankton community composition from CPR samples between the two regions (unpublished cluster analysis data) so we were comfortable in considering the plankton data as one time series representative of the Alaskan shelf for the purposes of this study.

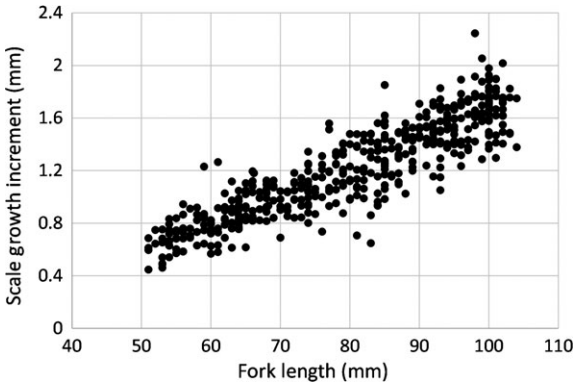
Scale increment and herring length

The first-year scale growth increment is strongly positively correlated with the length of age-0 herring in the size range of 50–105 mm ($r^2 = 0.79$, $P < 0.0001$, Fig. 3). There is a slight increase in the residuals with increasing fork length.

Herring growth and temperature

Tide gauge data were used to calculate an annual mean temperature for the months July and August, to best reflect water conditions when much of the first year of growth occurred. It is during these months that the fish metamorphose from larvae and begin their scale growth. Figure 4a shows the time series of scale-growth measurements and annual water temperature. As expected, there is a significant, positive relationship between temperature and growth ($n = 31$, $r^2 = 0.25$, $P < 0.01$). The three warmest years (1989, 2004, and 2005) do not follow the growth versus temperature relationships. These 3 years do not provide enough information to determine if there is a non-linear temperature-growth relationship. Removal of those 3 years strengthens the relationship between temperature and growth ($n = 28$, $r^2 = 0.63$, $P < 0.0001$, Fig. 4b). Herring growth and N' (variations in water height observations from the LNC) were almost perfectly out of phase (Fig. 4a), with the best correlations between growth and N' at lags of 9–10 years (Fig. 4c).

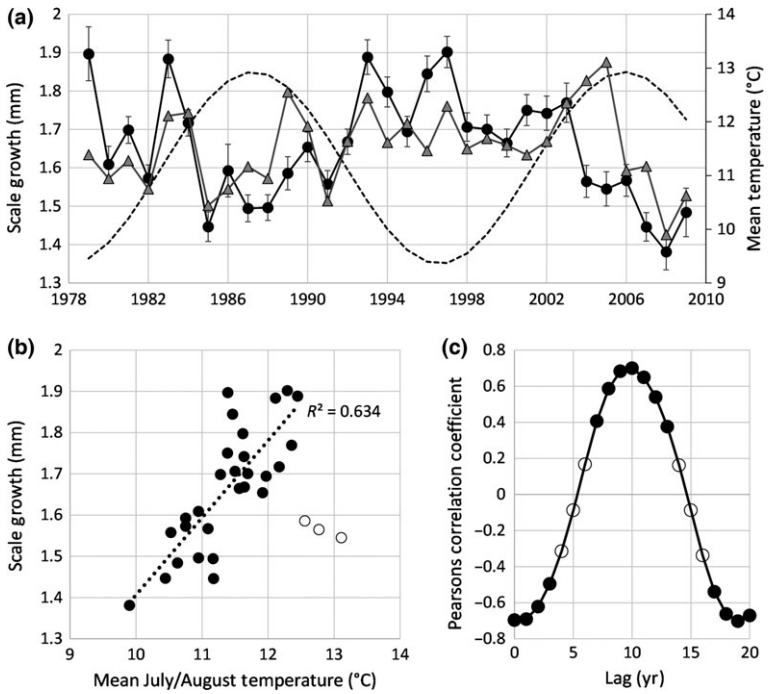
Figure 3. Scale growth increment as a function of fork length of age-0 herring.



Herring growth and plankton indices

The several hundred plankton taxa that occurred in the CPR dataset were reduced to five groupings that reflected the size and trophic level of the organisms identified. Annual anomaly time series of large zooplankton (copepods > 2 mm, euphausiids, pteropods etc.), small zooplankton (copepods < 2 mm, copepod nauplii, larvaceans, cirripede nauplii etc.), microzooplankton (hard-shelled single-celled ciliates such as tintinnids, foraminifera and radiolaria), diatoms and dinoflagellates (only thecate cells) were calculated. These time series are shown in Fig. 5, with the herring first-year scale growth data overlaid and the relationship between the two time series indicated by the r^2 value on each graph. Large zooplankton were not correlated with the herring growth but the smaller, lower trophic level groups did have positive relationships, particularly the diatoms where the r^2 of 0.76 ($n = 10$) had a significance value of $P = 0.0005$ indicating highly correlated data. Dinoflagellates were weakly correlated ($r^2 = 0.17$, $P = 0.12$) and the microzooplankton were also significantly correlated ($r^2 = 0.45$, $P = 0.02$). We had expected that the small zooplankton would also show a positive relationship but this was not apparent when all 10 years were compared ($r^2 = 0$). However, the number of small zooplankton

Figure 4. Herring growth and temperature. (a) Upper panel. The mean first year herring scale growth (circles), with error bars indicating 95% confidence intervals, the mean annual July/August temperature from the tide gauge at Cordova (triangles) and the Lunar Nodal Cycle [cos(N'), dashed line]. An arbitrary offset and multiplier (1.6 and 0.25 respectively) have been applied to the N' curve to line it up with the other data. See main text for discussion on the strength of the relationship between these time series. (b) Lower left panel. The mean first year herring scale growth and the mean annual July–August temperature from the Cordova tide station. Unfilled points indicate the three warm years of 1989, 2004 and 2005 which are excluded from the correlation shown by the dashed line. See text for more details. (c) Lower right panel. Lagged correlations between cos(N') and mean first year herring scale growth. Solid points indicate where $P < 0.05$.



in 2003 was unusually low and in fact the summer months of June and July were not sampled in this year (Table 1), a time when small copepods especially would be quite abundant. We removed this year and the correlation between small zooplankton and herring growth became significant ($n = 9$, $r^2 = 0.34$, $P = 0.05$).

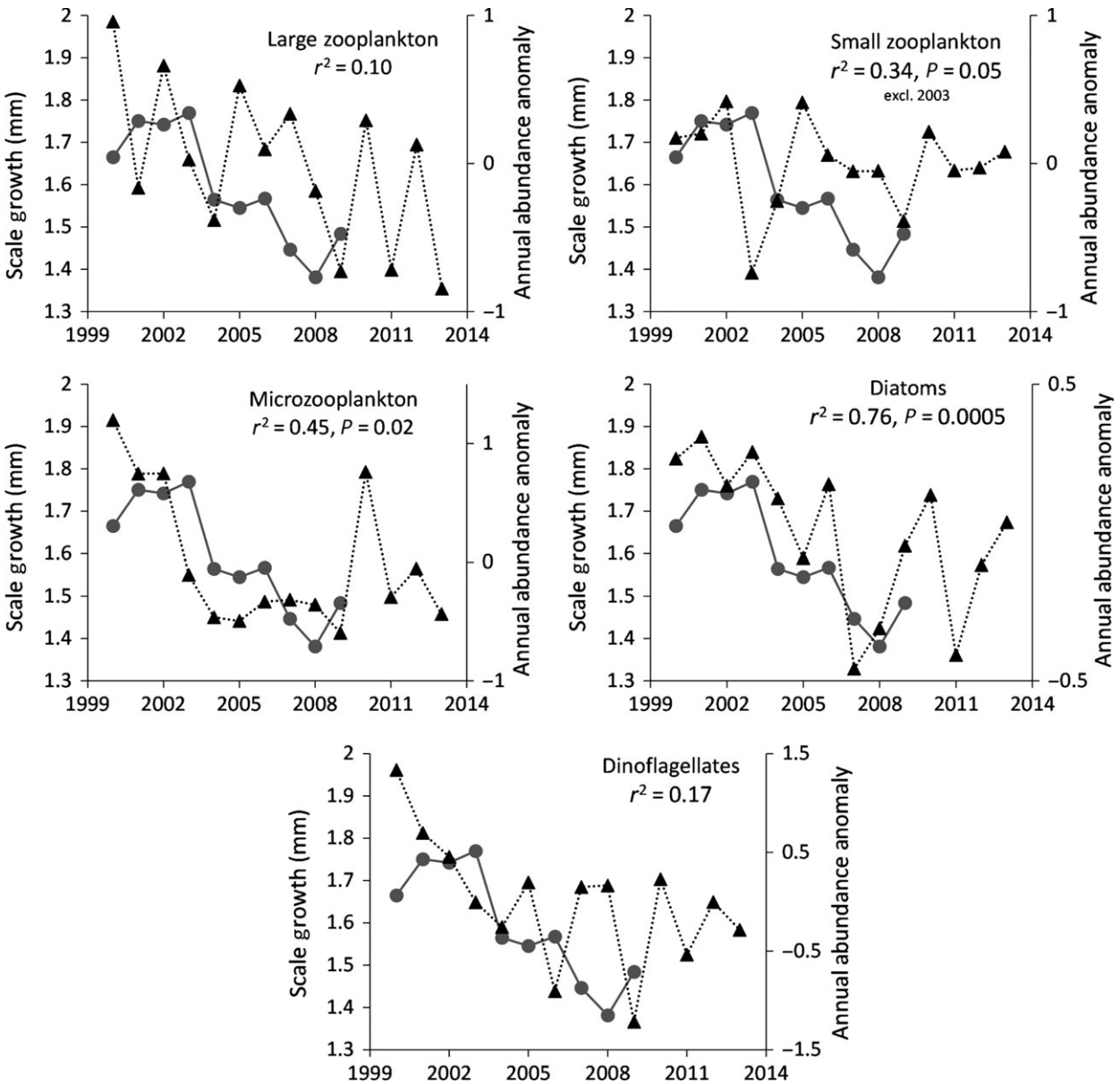
Plankton and temperature

The plankton abundance anomaly time series for the five trophic/size-based groups, when compared with the annual time series of surface temperature (as an annual mean), were all positively correlated with temperature (i.e., generally more abundant in warm years) but the only significant relationship was with the diatoms (data not shown but $n = 14$, $r^2 = 0.34$ $P = 0.01$). This comparison and the results described in the previous section relate to annual anomalies only and thus ignore any changes in seasonal timing between years that may not actually result in a change in overall abundance within a year. Given that changes in phenology as a response to temperature variability are commonly recorded in the plankton (e.g., Mackas *et al.*, 2012), and that timing of prey abundance may be as important to the herring as prey density, we compared the data from the five warmest and five coldest years to determine whether such timing differences were evident. Where possible we used more highly resolved taxonomic data to account for the quite different taxon-specific life history strategies that exist.

Note that one each of the warm years (2003) and of the cold years (2008) had reduced sampling frequency so that mid-season timing may be less well resolved in these years. With, at most, five values for each group of years the ability to detect a significant difference in mean abundance or timing is quite limited, however, three patterns emerged in the groups that were examined. Figure 6 shows an example of each. Pattern i; For some taxa there was a significant change in seasonal timing but no change in abundance between warm and cold. This was the case for both small and large copepods ($P < 0.05$, *t*-test comparing mid-season

timing). Pattern ii; Some taxa showed no change in timing but there was a change in abundance, such as the microzooplankton (*t*-test comparing abundance, $P = 0.1$). Euphausiids also had higher abundances in warm years ($P = 0.07$) with no significant change in seasonal timing. Pattern iii; Diatoms showed a significant change in abundance (greater in warm years, $P < 0.05$, *t*-test comparing abundances) as well as a change in timing. There are two peaks in diatoms in most years, representing spring and autumn blooms, and this method was not sensitive to such a bi-modal pattern. We also know from just considering the spring diatom data that warm springs have a significantly earlier increase in abundance (unpubl. data). Other groups that were examined; pteropods, copepod nauplii, dinoflagellates and larvaceans showed no significant difference in timing or abundance, although the group of warm years had higher mean abundances and earlier seasonal timing than the group of cold years throughout.

Figure 5. The annual mean abundance anomalies of plankton groups (triangles with dashed lines) and the latest 10 years of herring growth measurements (circles). The strength of correlation between the two time series is also shown, and the *P*-value if less than or equal to 0.05.



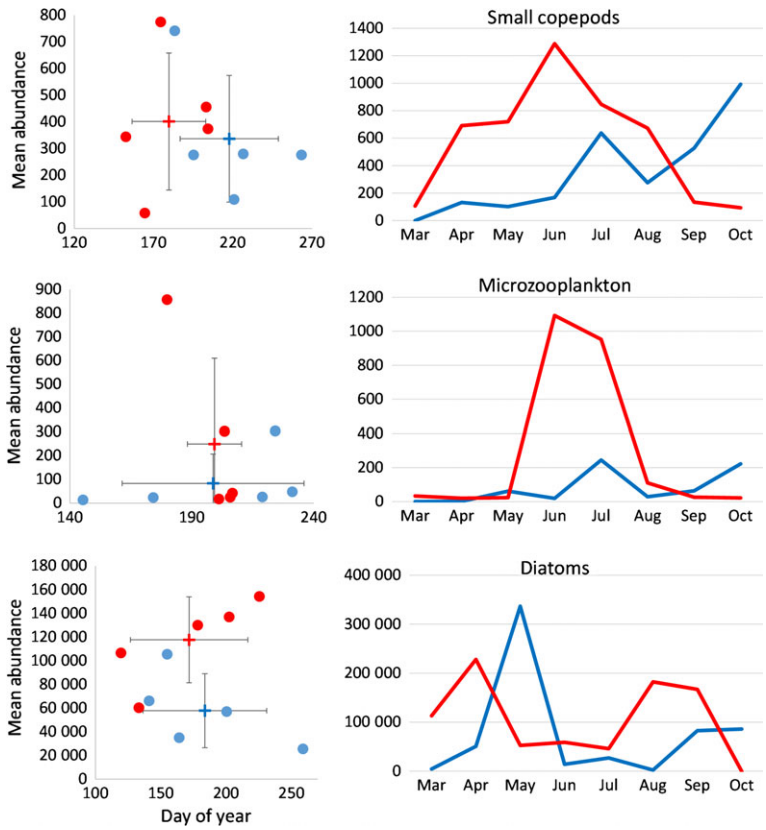


Figure 6. Data for three representative plankton groups showing the relationship between seasonal timing and abundance in warm and cold years. Left-hand panels show the mid-season timing plotted against the mean daily abundance for each of the five warm (red dots) and cold (blue dots) years. The crosses indicate the mean value for each group of years, together with standard deviations shown by the error bars. The right-hand panels show the monthly mean abundance data for each group of 5 years (red line = warm years, blue line = cold years). Abundances are expressed as the number of organisms (zooplankton) or cells (diatoms) per Continuous Plankton Recorder (CPR) sample.

Figure 6 shows the data for the warm and cold years for three groups of plankton that represent the noted patterns; (i) a change in seasonal cycle but no change in abundance, shown by small copepods, (ii) A change in abundance but no change in seasonal cycle shown by microzooplankton, and (iii) a change in both abundance and seasonal cycle shown by diatoms (where earlier peaks in both spring and autumn in warm years are evident). Graphs to the right show the monthly mean data for the two groups of years to better represent the seasonal cycles, whereas variability within the data is indicated in the left hand plots of mid-season timing and average abundance.

DISCUSSION

Experimental results have shown relationships between growth of juvenile fish and food (Werner and Blaxter, 1980; Folkvord *et al.*, 2000) and temperature (Houde, 1989; Pepin, 1991). While we, therefore, assume that these factors are also important in the wild, demonstrating such relationships in the natural environment is more complex because of the difficulties in adequately sampling the larval and juvenile herring, their environment and their prey base simultaneously and with sufficient resolution. A modelling study using coupled nutrient–phytoplankton–zooplankton and bioenergetics models concluded that at least some of the aspects of the population dynamics of herring in British Columba were due to climate 'regime' effects and not to fishing (Rose *et al.*, 2008). This analysis suggests that combined food and environmental factors are important to capture.

We found a strong relationship between summer (July and August) water temperatures and herring growth. Part of the temperature variability is driven by local weather patterns, but variations in water temperatures are also probably tied to the 18.6-year LNC. Increased growth with increased water temperature may stem from increased metabolism leading to faster growth, but it is also possible that a change in the food availability is also important. Warmer temperatures may also increase the larval development rate allowing metamorphosis to occur earlier. The earlier metamorphosis provides a greater time for growth during the first summer. The relationship between temperature and growth appears to break down once summer water temperatures exceed 12.5°C. This only occurred in 3 years (1989, 2004 and 2005) so there are limited data available. However, 12.5°C exceeds by some

margin the 0–10°C range of temperature that Alderdice and Hourston (1985) suggest as the range normally encountered by Pacific herring. They report that a combination of high temperatures with other stressors such as high salinity adversely affects herring larvae.

The study we describe here has made the assumption that our plankton data collected outside the Sound also reflect changes in PWS plankton, where herring are expected to spend their first year. We found a particularly strong relationship between the abundance anomalies of diatoms, as indexed by the CPR, and first-year herring growth, as indexed by scale measurements. This relationship held even in 2004 and 2005 when the relationship between growth and water temperature broke down. There were also significant, positive relationships between the abundance anomalies of microzooplankton and small mesozooplankton from the CPR and herring growth. Years when larger zooplankton were more abundant show no such relationship with better herring growth. The preservative used in the CPR storage tank does not fix naked flagellates, and naked ciliates are too fragile to survive the sampling process intact. Furthermore, although the mesh is only 40% porous, the mesh size of 270 μm will allow many of the small, non-chain forming phytoplankton cells and microzooplankton through, thus they will be significantly under-sampled. Only an undefined proportion of the phytoplankton and microzooplankton community, therefore, is enumerated by CPR sample analysis. The data shown here then do not necessarily indicate whether more or less chlorophyll or ciliates were available, but as the CPR is an internally-consistent sampler, they do indicate when relatively more, or less, of the large diatoms and hard-shelled microzooplankton were present and available as a food source. The abundance of small plankton groups that significantly correlated with herring growth fit within the likely prey size range of first-feeding herring; diatoms, microzooplankton, copepods (calanoid and harpacticoid) <2 mm, copepod nauplii, barnacle nauplii and larvaceans. Undoubtedly dinoflagellates were important too, but we could only enumerate those with hard shells. Small zooplankton groups have all been found in the stomachs of first-year PWS herring (Foy and Norcross, 1999) and whether or not diatoms and dinoflagellates were consumed directly by the herring as suggested by experimental work (Friedenberg *et al.*, 2012), or first by the herbivorous zooplankton, it is reasonable that higher numbers would be beneficial to the young herring.

The EFAs that herring must derive from their diet differ between the phytoplankton groups. Diatoms have more EPA and less DHA, while dinoflagellates are the converse with high amounts of DHA and less EPA (Dalsgaard *et al.*, 2003). The relative amount of EFA is also higher in the exponential growth phase of the phytoplankton (e.g., during a spring bloom) when cell division occurs frequently (Kattner *et al.*, 1983; Falk-Petersen *et al.*, 1998). It has also been noted that timing and composition of seasonal phytoplankton blooms was critical to the fatty acid accumulation of some zooplankton groups (Richoux *et al.*, 2005). Paulsen *et al.* (2014) showed that high food quality was sometimes able to compensate for low prey abundance and vice versa for larval fish in the Western Baltic Sea, so that when a constant rate of EFAs are consumed the growth rate of the fish is maintained. While we have no direct measurements of the nutritional content of the phytoplankton contributing to the PWS herring during their first months of feeding, it is reasonable to assume from these studies that variability in the density and timing of preferred prey will determine its nutritive value. Schweigert *et al.* (2013) found that the greatest abundances of young of the year herring in September, in the Strait of Georgia, occurred in years when spawning spanned a period 2 weeks before and after the beginning of the spring phytoplankton bloom, suggesting that timing was important there.

Variability in seasonal timing of plankton taxa can be quite large (Mackas *et al.*, 2012), and likely more variable than the timing of herring spawning and, thus, the appearance of the larvae. This presents the opportunity for a mis-match between the young fish and most beneficial prey. PWS herring larvae usually metamorphose and begin scale growth in July. We have shown that in warm years large diatoms are significantly more abundant and the timing of both spring and autumn peaks is earlier (Fig. 6). An earlier increase for the autumn peak (in August in warm years rather than September) may make these especially nutritious cells (they have relatively more EFAs when rapidly dividing) more available to the juvenile herring or their prey. Ciliates, and other small zooplankton are also generally more abundant in the summers particularly of warm years than they are in cold year summers. In other words, young-of-the-year herring may grow better in warm years because the timing of key prey is a better match for their first feeding.

Overall then, we provide evidence that the scale-growth increment is a good indicator of herring length and that first year herring growth is better in years with positive anomalies of suitable-sized prey such as large diatoms, microzooplankton and small mesozooplankton (Fig. 5). Herring growth is also better in warm years that do not exceed the threshold of 12.5°C

(Fig. 4) and in addition to direct effects of temperature on metabolic rates it is also apparent that the seasonal timing of key plankton prey is likely more beneficial (Fig. 6); after all, good growth in warm years would only be possible if food were sufficiently plentiful and nutritious. The strong relationship between diatom abundance held even in the 2 years (2004 and 2005) that the growth-temperature relationship failed, suggesting that food quantity and/or quality are the strongest drivers of growth.

Water temperatures are likely to increase in the future (Collins *et al.*, 2013) and as well as a direct effect on the marine biota will likely alter the timing and/or magnitude of fresh-water run-off in the Alaska shelf region with consequent impacts on local currents and water column properties such as water column stability and nutrient supply (Royer, 1979; Stabeno *et al.*, 2004; Weingartner *et al.*, 2005). We can thus expect changes in the planktonic prey-base of the herring in response to these environmental changes. Early growth is also only one factor in the success of a herring year class. It is, therefore, necessary that time series such as those described here continue to be maintained.

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