Alaska
Fisheries Science
Center

National Marine
Fisheries Service

U.S DEPARTMENT OF COMMERCE

AFSC PROCESSED REPORT 2018-06

Temperature Effects on Larval Walleye
Pollock (*Gadus chalcogrammus*) In the
Gulf of Alaska (1987 - 2010)

November 2018

This document should be cited as follows:

Temperature Effects on Larval Walleye Pollock (*Gadus chalcogrammus*)
In the Gulf of Alaska (1987 - 2010)

A. B. Dougherty, D. T. Jones, K. L. Mier, L. A. Rogers, and T. C. Vance

Resource Assessment and Conservation Engineering Division

Alaska Fisheries Science Center

National Marine Fisheries Service

National Oceanic and Atmospheric Administration

7600 Sand Point Way NE

Seattle, Washington 98115

November 2018

ABSTRACT

Early developmental stages of marine fishes experience high mortality and are particularly sensitive to environmental conditions. Understanding how changes in thermal conditions affect the ecology of early life stages is therefore important for elucidating mechanisms underlying variation in year-class success. In this study, otoliths collected from walleye pollock larvae (*Gadus chalcogrammus*) by NOAA's Alaska Fisheries Science Center from 1987 to 2010 in the western Gulf of Alaska were analyzed for age, growth, and hatch date distributions relative to temperature. These years covered a range of cool to warm years in the Gulf of Alaska. Growth rates of larvae were relatively insensitive to thermal conditions. However, analyses revealed significant shifts in larval length ranges and hatch date distributions relative to temperature. In warm years, larval hatch date distributions spread over a longer time period, whereas in cold years hatching occurred later in a contracted time period. The complex biological and environmental mechanisms favorable for survival of Gulf of Alaska larval pollock are not fully understood; however, a shift towards later hatching due to cold temperatures may affect the match of larval pollock with the production of their preferred prey (copepod nauplii) with consequences for recruitment success.

CONTENTS

INTRODUCTION

Marine fishes are especially sensitive to environmental changes during their early developmental stages. High rates of mortality during the egg and especially the early larval developmental period due to starvation or poor larval condition can be highly detrimental to cohort survival (Bailey et al. 1996). Mortality due to strong wind events during first-feeding is also a source of high mortality for larval fish due to the increased risk of mismatch with prey items (Bailey and Macklin 1994). In years when larval abundance is high, the depletion in available prey items is reduced and may result in poor recruitment (Duffy-Anderson et al. 2002). Changes in environmental conditions associated with the transition from winter to spring in the Gulf of Alaska (GoA) such as nutrient upwelling, phytoplankton blooms, and zooplankton production all must occur prior to the hatching of larval fish. It is critical for larval production to be synchronized with the production of their main food source, copepod nauplii of the genera *Calanus*, *Metridia*, *Pseudocalanus*, and *Oithona* (Napp et al. 1996), at the depth of larval occurrence (approximately 40 m), which also coincides with a defined thermocline and pycnocline (Kendall et al. 1994).

Walleye pollock (*Gadus chalcogrammus*)[1] support a major commercial fishery in the GoA and have been the subject of decades of work to understand the

---

1 Walleye pollock, formerly known as *Theragra chalcogramma*, was reclassified *Gadus chalcogrammus* in 2013 (Page, L. M., H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, N.E. Mandrak, R. L. Mayden, and J. S. Nelson. 2013. Common and scientific names of fishes from the United States, Canada, and Mexico, 7th edition. American Fisheries Society, Special Publication 34, Bethesda, Maryland.).

mechanisms driving variation in early life stage survival and recruitment. Until the completion of juvenile transformation (larval to age-0 life stage), when the fish become capable swimmers and have a higher probability of successfully avoiding predators and locating prey (Brown et al. 2001), larval distribution and food availability are controlled by the Alaska Coastal Current (ACC) which can range in strength from 25 to 100 cm/s (Stabeno et al. 1995). Temperature has been shown to be of considerable importance to the duration of spawning and development rate for walleye pollock eggs. Hinckley (1990) used laboratory and field work to confirm that pollock are batch spawners at depths of 150 to 250 m with females releasing larger eggs first, which produced larger larvae at hatch. Subsequent eggs, released after the first spawn, were smaller resulting in smaller larvae at hatch. Differences in egg size were also found to be correlated with geographic region and temperature in the Hinckley (1990) study. For walleye pollock eggs, the development and hours to 50% hatch under three rearing temperatures (3.8° C, 5.7° C, and 7.7° C) was shown to be inversely related to temperature (Blood et al. 1994). In Porter and Bailey (2007), the authors found that eggs which hatched early within a cohort resulted in larvae that were less responsive to physical stimulus (touched repeatedly with a probe to determine escape response to a predator) in comparison to larvae which hatched later. Larvae which hatched early due to turbulence (hatch at egg stage 15 instead of stage 21, a difference of approximately 154 hours) were observed to be underdeveloped and had low survival (S. Porter, NMFS - AFSC, pers. commun.). Larvae which hatch early have a partial yolk-sac that may be used as a food source while they continue to develop towards first feeding, but the larvae may exhaust their yolk

reserve and starve before they become competent at finding and feeding on copepod nauplii. Underdeveloped larvae would also be less capable of avoiding predators.

In rearing experiments conducted under cold temperatures (2 - 4° C), eggs/larvae developed more slowly, hatched at smaller sizes, but had large yolk-sacs which allowed for continued larval development (Canino 1994). The transition period from yolk-sac to first feeding is temperature-dependent (approximately 5 to 6 days at 6° C, in the laboratory; Theilacker and Shen 1993), and is the time when the larvae are most vulnerable to starvation (Theilacker and Porter 1995). In the field, the transition to first feeding may result in high mortality due to a lack of suitable prey. For instance, in Bailey et al. 1995 the authors compare 2 years (1990 vs. 1991) to demonstrate the effects of the strong wind events on larvae and prey. Strong wind events in the GoA in 1991 resulted in pollock larvae being transported away from concentrations of copepod nauplii resulting in starvation and a high mortality rate. In 1990, when conditions were relatively calm and the larvae and nauplii were concentrated together in an eddy, larval condition, and survival was reported to be higher.

In the GoA, temperatures recorded at the depth of larval occurrence (approximately 40 m) during NOAA-AFSC research surveys in May have fluctuated dramatically. With the growing evidence that changes in thermal conditions are affecting fisheries (Brander 2010), it is important to investigate the potential impact of temperature changes on early life stages of larval walleye pollock. In this study, we examine 24 years of data (1987 to 2010) collected from larval walleye pollock surveys conducted from mid-to late May in

3

the GoA to determine possible effects of in situ temperature changes on hatch date distributions and growth.

METHODS

Larval Pollock Surveys

The Recruitment Processes Program of the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (AFSC) has conducted early and late spring surveys in the GoA since 1984 to assess and understand the mechanisms that support the survival of larval walleye pollock (*Gadus chalcogrammus*). Kendall et al. (1996) summarized the first decade of this work by outlining the oceanographic and biological parameters such as turbulence and eddies, feeding and predation that were studied to understand the observed variations in walleye pollock recruitment.

The larval surveys in this study coincide with the late larval developmental period (mid-to late May) from 1987 to 2010 in the GoA, southwest of Shelikof Strait. The study area (referred to as the Main Grid) is illustrated by the box shown in Figure 1. Stations sampled in the Main Grid were 10 nautical miles (nmi) apart (approximately 120 stations total). The number of stations sampled within the box varied depending on survey design and effort. The timing of the surveys was dictated by available ship time. Although the distribution and abundance of larval walleye pollock varied annually, the Main Grid was routinely sampled each year and consistently provided enough larvae for age and growth analyses. A standard double oblique MARMAP 60 cm bongo (see Smith and Richardson, 1977) with 505 μm mesh was the primary gear used for larval sampling during all

4

surveys, except for 1988 and 1989 when a 1-m Tucker trawl was used with 505 µm mesh. A gear comparison study by Shima and Bailey (1994) determined that both gears caught similar numbers and sizes of walleye pollock larvae. Both gear types were fished to a maximum depth of 100 m or 10 m off-bottom with either a mechanical bathythermograph or a Sea-Bird Electronics SBE-19 SeaCat profiler CTD (conductivity-temperature-depth) mounted above the gear frames to obtain temperature data.

Temperature data were grouped into 1-m depth bins using the Sea-Bird Electronics processing program. The temperature at 40 m (average depth of larval pollock occurrence) at each station within the Main Grid in May was tabulated and a mean temperature for each year was calculated. Unfortunately, temperature data were not available for May surveys from 1987 to 1994, and 1996. Out of the 24 years, only 14 years had May temperature data available from the larval surveys. For years with missing data, temperatures were estimated from trawls conducted in March in Shelikof Strait by the Midwater Assessment and Conservation Engineering Program (MACE) Division of AFSC. A linear regression of May temperatures at 40 m versus March temperatures at trawl depth was calculated as

May Temperature = - 0.067 + 1.084 × March Temperature, n = 14, r^2 = 0.75.

Adult Pollock Survey Data

For MACE surveys from 1987 through 1994, temperature profiles were collected using various combinations of CTD or XBT (expendable bathythermograph) deployments at trawl locations. From 1995 through 2000, MBTs (micro-

bathythermographs) were attached to the trawl head rope to obtain in situ temperature data at depth of observed adult pollock. Since 2001, temperature profiles have been obtained using a Sea-Bird Electronics (Bellevue, WA) temperature-depth probe (SBE-39) attached to the trawl headrope. Temperature data for March 1999 were not available.

Larval Growth and Hatch Date Calculations

From the larval sampling gear, two nets were available for sample type selection. Contents from Net 1 were preserved in 10% formalin for quantitative counts and standard length (SL) measurement of up to 50 larval walleye pollock using a dissection microscope (± 0.1 mm) (Matarese et al. 2003). Larval pollock for otolith work were obtained by quickly sorting Net 2 at sea and preserving in 95% ethanol. From each late larval survey, a minimum of 100 larval fish, when available, were randomly selected from the Main Grid Net 2 sample to create an age-length key. The sagitta otoliths were dissected out of larvae using a dissection microscope and mounted to microscope slides using clear nail polish. The daily increments were read at 1,000× magnification using a compound microscope.

Growth equations (Table 1) and hatch date distributions were calculated using a three-stage procedure (as referenced in Bailey et al. 1996). The first part of the procedure adjusted the preserved standard lengths of the aged fish to live lengths, using the shrinkage corrections reported in Theilacker and Porter (1995) to create a live age/length regression for each survey. These data were then used to construct age-length keys to allow assignment of ages to the fish collected from Net 1 (quantitative sample) in the Main Grid. The final part of the procedure calculated adjusted fish ages to the mean

6

survey date, calculated hatch dates (mean survey date – age), and estimated hatch date distributions that represented all fish sampled in the study area for each year weighted by CPUE. An "All Year" average hatch date distribution was calculated by simply averaging the percent frequencies for each hatch date and year across all years.

Linear mixed effects models were used to test for potential effects of thermal conditions on larval size at hatch and growth rate. Data from all aged larvae (n = 3,440) were used in this analysis. Larval length was modeled as a function of age (in days), and compared to models with an effect of temperature on larval size and with an interaction between temperature and age (i.e., an effect of temperature on growth rate). Included is a random intercept and age slope by station within year. The full model considered was

$$Length_{isy} = \beta_0 + b_{0,sy} + \beta_1 Age_{isy} + b_{1,sy} Age_{isy} + \beta_2 Temp_{sy} + \beta_3 Temp_{sy} \times Age_{isy} + \varepsilon_{isy} \qquad \text{Eq. 1}$$

where $Length_{isy}$ is the length of individual i from station s within year y, corrected for ethanol preservation, $Temp_{sy}$ is the temperature at station s within year y, and Age_{isy} is age in days determined from larval otoliths from individual i from station s within year y. The βs are fixed effect coefficients and bs are normally distributed random effects. Temperature from two time periods was considered: actual temperature at station in May, and mean temperature at depth in March. The Temp × Age interaction (slope by temperature) was tested using conditional t-tests comparing models with and without the interaction terms. This was followed by tests of Temp effect (common slope, different intercepts).

Significant year effects were tested with year as a fixed effect using a common slope among years:

$$\text{Eq. 2}$$

Fixed parameters were estimated using restricted maximum likelihood (REML), in the nlme package in R (R Core Team 2016).

Larval Hatch Date Analyses

To investigate differences in hatch date distributions between years, daily hatch dates and their associated abundances were binned into 5-day intervals and plotted as histograms. Abundance per hatch date was extrapolated by multiplying the proportion of fish measured at that hatch date times the total abundance for the survey (catch per unit effort). A two-sample Kolmogorov-Smirnov (KS) test was then conducted (a nonparametric test to determine if two independent populations were drawn from the same distribution (Sokal and Rohlf 1995)). When applied to binned data rather than continuous data, as in this case, the KS test was conservative (Conover 1980). This test was preferred over a Chi-square test as some hatch date distributions had zero or very few observations, and also because the KS test was sensitive to differences in location and scale (i.e., the central tendency as well as the shape of the two distributions).The sample size for the KS tests were based on the number of fish measured. The software used was SYSTAT 13 for Windows (Systat Software, Inc., Chicago, IL). A total of 276

8

KS tests were performed. A Bonferroni correction was made to the significance level, alpha = 0.05/276 = 0.000181, to determine significant differences.

RESULTS

Mean larval length, age, hatch date distributions, and temperature varied between years (Tables 1, 2). For example, in 1990 the mean SL was 10.6 mm, but in 2007-2009 the mean SLs were considerably smaller (5.8, 6.7, 6.6 mm, respectively), coinciding with cold temperatures. Mean temperature versus year for March at trawl depth and May at 40 m are shown in Figure 2 (estimated values represented by black and white dots, respectively). The overall mean temperature at trawl depth in March was 4.75°C (SD ± 0.47) and the mean depth for all trawls/years was 215 m, approximately 50 m off bottom. In May the mean temperature at 40 m was 5.09° C (SD ± 0.57). A warm or cold year was defined to be one standard deviation above or below the mean temperature in March (± 0.47º C) and in May (± 0.57º C). Cold years in March were 1989, 1991, 1999, and 2007 and warm years were 1998, 2001, 2003, and 2005. In May, cold years were 1989, 1991, 2007, 2008, and 2009. Warm years in May were 1998, 2001, 2003, and 2005. See Appendix for examples of cold and warm years at adult and larval sampling depths in March and May. In general, temperature patterns at 40 m in May reflected temperature patterns at depth in March (i.e., if it was cold (or warm) in March at depth, then the temperature at 40 m in May was also cold (or warm) relative to the calculated mean May temperature). However, a few years provided interesting changes in the mean temperature pattern. For instance, in 1995 there was little increase in temperature

9

between the adult (March) and larval (May) sampling periods. In 2006 and 2008, recorded temperatures at 40 m in May were colder than in March at depth. Starting in 1998 and ending in 2005, the temperatures in March and May fluctuated considerably relative to their respective means in comparison to earlier years. In 1998, 2001, and 2003 - 2005, the temperatures in March and May were above their respective means for this time period. Although 2007 was a cold year in March, it did warm up in May at 40 m, but it was still below the calculated mean temperature for May.

Growth Model

We did not find evidence for an effect of temperature on growth rates of larval pollock. In a linear mixed effects model with an interaction between temperature and age, the interaction coefficient (β_3) was not significantly different from zero (conditional t-test on β_3). This was the result for a model with average yearly temperatures during the spawning period (P > 0.5) and a model with May temperatures at time of capture (P > 0.4). There was a tendency for larvae to be smaller for a given age (i.e., have smaller sizes at hatch) during warm years, particularly for 1998 and 2005. This was statistically supported as an overall trend for May temperature at capture (conditional t-test on β_2, Eq. 1, P = 0.02), but not for average yearly March temperatures. When a common slope among years was fit to the data (no interaction between year and age, Eq. 2), some years showed a significantly different length at hatch (illustrated by inequalities in Table 2).

10

Hatch Date Distributions

The calculated hatch date distribution for all years (see Fig. 3b, d, f, black line) were skewed towards later hatching (maximum hatch dates represented at 13-18 May, Julian dates 133-138). Relative to this "All Years" distribution, the comparison of hatch date distributions revealed a shift to the right (later hatching) for years with cold egg/larval developmental periods, while in warm years the hatch date distributions were spread out over a longer time period. Growth equations for 2003 (warm year) and 2007 (cold year) are similar, but the hatch date distributions are significantly different (Fig. 3a, b and Table 1). In 2007, the larvae hatched early to mid-May whereas the 2003 hatch occurred mid-April to late May. The larval size range in 2007 (5-9 mm) was within the size range reported for 2003 (6-14 mm), with a mean larval size of 5.8 mm in 2007 and 9.3 mm in 2003. This suggests that the mean size of larvae in 2007 is weighted towards smaller larvae due to either mortality during the egg stage, only eggs spawned later were viable, mortality of earlier hatched larvae, or spawning occurred later in the cold year. This is also seen in other cold years such as 2008 (6.7 mm) and 2009 (6.6 mm). The hatch date distribution for 2007 suggests that the larvae hatched significantly later over a much shorter time period. In fact, the hatch date distribution for 2007 was significantly different from all other years except 2008, which was the second coldest year observed (Tables 1 and 2).

Further evidence of a temperature effect on the larval stage of pollock can be seen in Figures 3c and d. In this example, the warm year 2005 and the cold year 2008 are compared. The growth rates are similar but the hatch date distributions are significantly different with the size range of larvae sampled in 2005 being much broader at 5 -17 mm

(mean 8.9 mm) than in 2008 (5 -10 mm, mean 6.7 mm). The linear growth regressions

also suggest that the 2005 larvae hatched at a smaller size (2.9 mm) than the 2008 larvae

(4.6 mm) and considerably earlier. The 2008 sampled larvae, although later to hatch,

were larger at hatch, which was shown to be significant from the pairwise tests of the

year effect in the model. The year 2008 is also unique in that the mean temperature did

not increase by time of sampling in May relative to March (see Fig. 2). The hatch date

distribution for 2008, as in the cold year 2007, is shifted towards later hatch dates relative

to the hatch date distribution for all years.

In a final example, we compare 1989 and 1998 (Fig. 3e, f). The comparison of these

two years was chosen to illustrate that even though a larger number of samples were

available and aged in 1989 (n = 220) and in 1998 (n = 131), relative to more recent years,

the trends discussed in the previous examples are viable even though fewer otolith

samples were aged. Temperature at depth in 1989 was estimated as cold (4.11° C) and

1998 was observed as a warm year (6.11º C). In Table 1, we see from the growth

equations that the estimated size at hatch was 5.1 mm in 1989 (a cold year) and 3.3 mm

in 1998 (a warm year) but with very similar growth rates (0.20 and 0.21 mm/day). In

1989, the surviving larvae sampled were larger at hatch compared to those in 1998 but

the pairwise tests from the model did not show this to be significant. However, the hatch

date distributions were significantly different. In 1989, the range of the hatch dates is

considerably wider compared to the previous examples given, with more of the early

hatch dates represented (mid-April) which may be a result of multiple strong year classes

returning to spawn in conjunction with good larval survivorship. Also to be considered

when trying to analyze the 1989 data is that the processing and reading techniques for

pollock that are beginning juvenile transformation (10-12 mm) as defined in Brown et al. (1992) had not yet been established when the 1989 otoliths were originally analyzed. Even though the haul dates for these two surveys do not overlap (see Table 1), the hatch date distributions are still reasonable compared to the "All Years" distribution (black line in Fig. 3f).

DISCUSSION

In this study, we analyzed almost three decades of larval walleye pollock data from mid-to late May from the western GoA to study the potential effect of temperature on larval growth and hatch date distributions. Our data suggest that in cold years, egg development was slower which resulted in larvae hatching later over a shorter time span with fewer large larvae represented in our samples compared to warm years. In our study, most of the surveys had occurred during or after the highest period of mortality, the first feeding stage, and hence a reduction in the representation of the smaller larvae would be expected. But, in the coldest of years examined (1989, 2007, and 2008), the youngest larvae were still present in the larval population. For a given age, larvae tended to be larger in cold years relative to warm years. The strategy of slower development and later hatching in cold years may be a survival advantage for pollock (resulting larvae hatch with larger yolk sacs as a food reserve allowing growth/development to continue until prey is available and the larvae are more capable of feeding). The results from laboratory experiments reported in Canino (1994) confirm this strategy. The rearing of pollock eggs at 3° C produced larger larvae with large yolk reserve whereas at 6° C and 12° C the resulting larvae hatched smaller with significantly reduced yolk reserve and increased mortality. In warm years in the GoA, the eggs developed more quickly but produced

13

larvae that may have been prone to a high rate of mortality due to a lack of energy reserve (yolk sac). The size range and hatch date range of the larvae in warm years was protracted, but this scenario may have made the larvae subject to higher mortality due to starvation since they were competing for food with not only earlier hatched pollock larvae but other larval fish species. On the other hand, by spreading out hatch dates over a number of weeks in warm years, the likelihood of some larvae encountering conditions conducive to survival may be increased (Mertz and Myers 1994).

Ship scheduling and weather shifted the timing of several surveys so that the mean and range of sampling dates were not consistent each year. It is difficult to determine how these shifts in survey dates affected our data since the mean larval size, age, abundance, and distribution of the larvae in the Main Grid area varied from year to year even when surveys were conducted within the same time frame (i.e., 2001 and 2002). The size and age of spawning adult pollock (older/bigger females produce more large eggs) as well as the viability and mortality of developing eggs and survivorship of early stage larvae are all determining factors in the larvae that would be present during the larval surveys. The early larval stage (mid-April to early May) of walleye pollock has the highest rate of mortality which means by mid-to-late May we are sampling the larval lengths and hatch dates of the larvae which have survived the transition to first feeding. Comparing the growth equations from late larval surveys addresses the growth of the larval fish which have survived mortality "hurdles" such as successful avoidance of predators during the egg and yolk-sac stages and the transition to feeding on live prey (yolk reserve to copepodites). The mean size-at-age and size range of the larvae at the time of sampling does not provide definitive results as to how temperature affected earlier larval

development. With the addition of the hatch date analyses, we have established a much clearer picture about the life history of the larvae which have survived the earlier life stages.

Temperature and food production during the egg and early larval stages of walleye pollock may be the most important of environmental factors affecting larval fish survival. The abundance of the primary food source of larval pollock, copepod nauplii, varies geographically, seasonally, and interannually (Incze and Ainaire 1994, Napp et al. 1996). The spatial and temporal overlap of larvae with their food source will determine survivorship, baring predation from other organisms. The position of larvae relative to a sustainable food supply will be highly influenced by oceanographic conditions such as strength and direction of currents in their early life stages since they are not capable swimmers until the age-0 life stage (Brown et al. 2001). In years when there were frequent strong wind events observed in the GoA, larvae were transported away from suitable feeding areas resulting in a decreased food supply. This was discussed in Bailey et al. (1995) suggesting poor condition of larval pollock during the spring of 1991, which resulted in a weak year class. Results from starvation experiments found pollock larvae to be the most vulnerable to starvation 2 weeks after first-feeding (Theilacker and Porter 1995). In 1991, there was a high occurrence of starving pollock larvae sampled in the survey preceding the survey used in this study suggesting a mismatch with prey (Theilacker et al. 1996). Density-dependent starvation has also been observed in large aggregations of larvae in 1981 resulting in over-grazing of available prey which led to starvation, poor condition, and increased mortality (Duffy-Anderson et al. 2002).

Although a warmer environment would seem to be more beneficial in that the larvae would grow faster and transition into the age-0 life stage sooner, this could only occur successfully if food was available in quantities necessary to support increasing metabolism and body size. In the GoA during cold years, when the larvae are slower to develop and hatch, a reduced metabolism would allow the larvae more time to synchronize with their food source and decrease the potential for depletion of food resources. As water temperature gradually increases throughout spring and summer, body size and weight increase and produce age-0 pollock that are capable of increasing their energy reserves (lipid content of liver) for the approaching winter, as long as a thermal tolerance is not exceeded. From the research reported by Houde (1989) involving the comparison of growth, mortality, and energetics of larvae in regards to temperature, it was found that starvation of first feeding larvae was more likely to occur in warmer water due to high feeding requirements paired with low assimilation efficiency. In Mueter et al. (2011), the authors model the effect of increased sea surface temperature in the Bering Sea in relation to over-wintering success of walleye pollock. The authors suggest that even though larval pollock grew and survived well when ice retreated earlier due to warmer temperatures, it was the continued warming before the onset of winter that caused poor over-wintering success. Litvak and Leggett (1992) suggested from the results of laboratory experiments that bigger is not always better in regards to larval fish survival especially when a predator has a choice of different larval sizes. In this case, the larger larvae become more noticeable to predators and hence may increase the number of fast-growing larvae removed from the cohort due to predation. Pörtner and Peck (2010) reviewed research that had been conducted to understand the effect of climate change on

numerous fisheries. It was concluded that not all life stages of fishes will be affected the same by warming temperatures.

In our study, the hatch date distributions for larval walleye pollock have been useful in demonstrating the effects of temperature. The hatch date distributions for warm years were more spread out in time resulting in a broader size range of larvae competing for prey items. Larger pollock larvae present during warm years would be capable of consuming a broader size range of prey, including the smaller copepods that the younger larvae depend upon at first feeding. Also to be considered is that pollock larvae were not the only larval fish species in the study area during the May surveys. When temperature increased, other species of larval fish may have experienced favorable growth and survivorship conditions and forced pollock towards starvation. Laurel et al. (2011) investigated the match-mismatch hypothesis for Pacific cod larvae in regards to temperature in their laboratory experiments and determined that warm rearing temperatures increased the potential for the mismatch of larvae and prey. Mazur et al. (2007) used bioenergetics modeling and determined that the spatial variability of age-0 walleye pollock growth and condition in the GoA was explained by temperature and prey quality.

There are many dynamic interactions affecting larval fish survival that are linked to changing environmental parameters that we may not be able to monitor consistently or well enough (changes in larval and age-0 condition, competition with other species, balance of predator and prey, etc.) to define only one or two model parameters that would accurately predict survivorship. For walleye pollock, we have been able to monitor the fluctuations in hatch date distributions, growth, and in situ temperature during spawning

17

(March) and the late larval period (May) to demonstrate the results of the changes that pollock eggs and larvae experience in warm and cold conditions. The possibility of being able to predict species sensitivity and potential responses to changing climate (e.g., Hare et al. 2016) will improve by gaining a mechanistic understanding of the effects of temperature on different life stages, including the critical larval stage.

ACKNOWLEDGMENTS

CITATIONS

Bailey, K. M., M. F. Canino, J. M. Napp, S. M. Spring, and A. L. Brown.

    1995. Contrasting years of prey levels, feeding conditions and mortality of larval

    walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. Mar. Ecol.

    Progr. Ser. 119:11-23.

Bailey, K. M., S. J. Picquelle, and S. M. Spring.

    1996. Mortality of larval walleye pollock *Theragra chalcogramma* in the western

    Gulf of Alaska, 1988-91. Fish. Oceanogr. 5 (Suppl. 1): 124-136.

Blood, D. M., A. C. Matarese, and M. M. Yoklavich.

    1994. Embryonic development of walleye pollock, *Theragra chalcogramma*, from

    Shelikof Strait, Gulf of Alaska. Fish. Bull., U. S. 92:207-222.

Brander, K.

    2010. Impacts of climate change on fisheries. J. Mar. Systems 79(3):389-402.

Brown, A. L., and K. M. Bailey.

    1992. Otolith analysis of juvenile walleye pollock (*Theragra chalcogramma*) from

    the western Gulf of Alaska. Mar. Biol. 112:23-30.

Brown, A. L., M. S. Busby, and K. L. Mier.

 2001. Walleye pollock *Theragra chalcogramma* during transformation from the

 larval to juvenile stage: Otolith and osteological development. Mar. Biol. 139:845-

 851.

Canino, M. F.

 1994. Effects of temperature and food availability on growth and RNA/DNA ratios of

 walleye pollock *Theragra chalcogramma* (Pallas) eggs and larvae. J. Exp. Mar. Biol.

 Ecol. 175:1-16.

Conover, W. J.

 1980. Practical Nonparametric Statistics, 2nd ed. John Wiley & Sons: New York.

 493 p.

Duffy-Anderson, J. T., K. M. Bailey, and L. Ciannelli.

 2002. Consequences of a superabundance of larval walleye pollock *Theragra*

 chalcogramma in the Gulf of Alaska in 1981. Mar. Ecol. Progr. Ser. 243:179-202.

Hare J. A., W. E. Morrison, M. W. Nelson, M. W. Stachura, E. J. Teeters, and R.B.

    Griffis, M. A. Alexander, J. D. Scott, L. Alade, R. J. Bell, A. S. Chute, K. L. Curti, T.

    H. Curtis, D. Kicheis, J. F. Kocik, S. M. Lucey, C. T. McCandless, L. M. Mike, D.E.

    Richardson, E. Robillard, H. J. Walsh, M. C. McManus, K. E. Marancik, C. A.

    Griswold.

    2016. A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the

    Northeast U.S. Continental Shelf. PLoS One

    11(2):e0146756.doi.10.1371/journal.pone.0146756.

Hinckley, S.

    1990. Variation of egg size of walleye pollock *Theragra chalcogramma* with a

    preliminary examination of the effect of egg size on larval size. Fish. Bull., U. S.

    88:471-483.

Houde, E. D.

    1989. Comparative growth, mortality, and energetics of marine fish larvae:

    Temperature and implied latitudinal effects. Fish. Bull., U. S. 87:471-495.

Incze L. S., and T. Ainaire.

    1994. Distribution and abundance of copepod nauplii and other small (40-300 μm)

    zooplankton during spring in Shelikof Strait, Alaska. Fish. Bull., U. S. 92:67-78.

Kendall A. W., Jr, L. S. Incze, P. B. Ortner, S. Cummings, and P. K. Brown.

    1994. Vertical distribution of eggs and larvae of walleye pollock, *Theragra*

    chalcogramma, in Shelikof Strait, Gulf of Alaska. Fish. Bull., U. S. 92:540-554.

Kendall, A. W., Jr., J. D. Schumacher, and S. Kim.

    1996. Walleye pollock recruitment in Shelikof Strait: Applied fisheries

    oceanography. Fish. Oceanogr. 5 (Suppl. 1):4-18.

Laurel, B. J., T. P. Hurst, and L. Ciannelli.

    2011. An experimental examination of temperature interactions in the match-

    mismatch hypothesis for Pacific cod larvae. Can. J. Fish. Aquat. Sci. 68:51-61. DOI:

    0.1139/F10-130.

Litvak, M. K., and M. C. Leggett.

    1992. Age and size-selective predation on larval fishes: the bigger-is-better

    hypothesis revisited. Mar. Ecol. Progr. Ser. 81:13-24.

Matarese, A. C., D. M. Blood, S. J. Picquelle, and J. L. Benson.

    2003. Atlas of abundance and distribution patterns of ichthyoplankton from the

    northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by

    the Alaska Fisheries Science Center (1972-1996). U. S. Dep. Commer., NOAA Prof.

    Paper NMFS 1, 281 p.

Mazur, M. M., M. T. Wilson, A. B. Dougherty, A. Buchheister, and D. A. Beauchamps.

    2007. Temperature and prey quality effects on growth of juvenile walleye pollock

    Theragra chalcogramma (Pallas): A spatial explicit bioenergetics approach. J. Fish.

    Biol. 70:816-836. DOI:10.1111/j.1095-8649.2007.01344.x.

Mertz, G., and R. A. Myers.

    1994. Match/mismatch predictions of spawning duration versus recruitment

    variability. Fish. Oceanogr. 3(4):236-245.

Mueter, F. J., N. A. Bond, J. N. Ianelli, and A. B. Hollowed.

    2011. Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*)

    in the eastern Bering Sea under future climate change. ICES J. Mar. Sci. 68(6):1284-

    1296. DOI:10.1093/icesjms/fsr022.

Napp, J. M, L. S. Incze, P. B. Ortner, D. L. W. Siefert, and L. Britt.

    1996. The plankton of Shelikof Strait, Alaska: Standing stock, production, mesoscale

    variability and their relevance to larval fish survival. Fish. Oceanogr. 5 (Suppl. 1):19-

    38.

Pörtner, H. O., and M. A. Peck.

    2010. Climate change effects on fishes and fisheries: Towards a cause-and-effect

    understanding. J. Fish Biol. 77: 1745-1779.

Porter, S.M., and K.M. Bailey.

2007. The effect of early and late hatching on the escape response of walleye pollock (*Theragra chalcogramma*) larvae. J. Plankton Res. 29(3): 291-300.

R Core Team.

2016. R: A language and environment for statistical computing. R-Foundation for Statistical Computing, Vienna, Austria. URL://www.R-project.org/.

Shima, M., and K. Bailey.

1994. Comparative analysis of ichthyoplankton sampling gear for early life stages of walleye pollock (*Theragra chalcogramma*). Fish. Oceanogr. 3(1):50-59.

Smith, P. E., and S. R. Richardson.

1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Rep. 175, 100 p.

Sokal, R. R., and F. J. Rohlf.

1995. Biometry, 3rd ed. WH Freeman and Co., New York. 887 p.

Stabeno, P. J., R. K. Reed, and J. D. Shumacher.

1995. The Alaska Coastal Current: Continuity of transport and forcing. J. Geophys. Res. 100:2477-2485.

Theilacker, G. H., K. M. Bailey, M. F. Canino, and S. M. Porter.

    1996. Variation in larval walleye pollock feeding and condition: a Synthesis. Fish
Oceanogr (Suppl. 1):112-123.

Theilacker, G. H., and S. M. Porter.

    1995. Condition of larval walleye pollock, *Theragra chalcogramma*, in the western
Gulf of Alaska assessed with histological and shrinkage indices. Fish. Bull., U. S.
93:333-344.

Theilacker, G. H., and W. Shen.

    1993. Fish larval condition analyzed using flow cytometry, p. 346-355. *In* B. T.
Walther and H. J. Fyhn (eds.), Physiological and Biochemical Aspects of Fish
Development. Univ. Bergen, Norway. ISBN 82-992402-0-4.

Table 1. -- Survey data and analyses results for Gulf of Alaska larval walleye pollock, 1987 - 2010.
(E) denotes temperature estimated from linear regression. Years highlighted in gray compared in Fig. 3.

Year	# of hauls	Haul Dates (mean) in Julian Days	SL Range (Mean SL, mm)	Age Range (Mean Age)	Growth Equation	n	r²	Hatch Range in Julian Days (Mean Hatch)	Temperature at 40m in May (Mean ± SE, ºC)
1987	42	140-145 (141)	4 - 11 (7.6)	4 - 34 (17)	5.12 + 0.18(age)	176	0.58	107 - 137 (124)	5.62 (E)
1988	59	142 - 146 (144)	4 - 13 (7.6)	5 - 54 (30)	4.35 + 0.20(age)	279	0.83	90 - 139 (115)	5.32 (E)
1989	95	149 - 156 (153)	5 - 21 (9.4)	7 - 54 (31)	5.07+0.20(age)	220	0.77	99 - 146 (123)	4.11 (E)
1990	104	150 - 156 (153)	5 - 13 (10.6)	7 - 46 (27)	4.98+0.20(age)	145	0.85	107 - 146 (127)	4.82 (E)
1991	75	139 - 144 (142)	4 - 10 (7.7)	6 - 32 (19)	4.12 + 0.22(age)	113	0.79	110 - 136 (123)	4.37 (E)
1992	114	138 - 146 (144)	5 - 13 (8.9)	9 - 52 (30)	5.52 + 0.15(age)	219	0.85	92 - 135 (115)	5.16 (E)
1993	70	147 - 152 (149)	4 - 18 (8.9)	5 - 75 (26)	4.70 + 0.19(age)	140	0.86	74, 94 - 144 (123)	5.24 (E)
1994	102	145 - 151 (148)	5 - 17 (9.7)	9 - 68 (39)	4.83 + 0.18(age)	210	0.84	80 - 139 (109)	4.95 (E)
1995	66	143 - 148 (146)	5 - 17 (9.5)	7 - 64 (34)	4.66 + 0.17(age)	309	0.89	82 - 139 (112)	4.78 ± 0.07
1996	103	146 - 152 (149)	6 - 18 (11.1)	14 - 64 (37)	4.30 + 0.20(age)	200	0.84	85 - 135 (112)	4.79 (E)
1997	98	144 - 150 (147)	5 - 14 (10.4)	6 - 51 (29)	4.07 + 0.19(age)	125	0.91	96 - 141 (119)	5.15 ± 0.08
1998	72	143 - 148 (146)	5 - 14 (8.9)	12 - 56 (34)	3.34 + 0.21(age)	131	0.86	90 - 134 (112)	6.11 ± 0.04
1999	50	146 - 152 (148)	4 - 13 (7.3)	5 - 47 (26)	4.22 + 0.18(age)	79	0.89	101 - 143 (122)	4.53 ± 0.08
2000	92	149 - 155 (152)	5 - 20 (9.5)	6 - 83 (45)	4.50 + 0.18(age)	109	0.94	69, 87 - 146 (108)	5.61 ± 0.06
2001	77	147 - 151 (149)	5 - 14 (8.6)	6 - 70 (38)	4.78 + 0.16(age)	77	0.92	79, 91 - 143 (111)	5.85 ± 0.05
2002	48	147 - 150 (149)	5 - 12 (7.6)	5 - 41 (23)	4.60 + 0.22(age)	107	0.87	108 - 144 (126)	4.94 ± 0.11
2003	67	148 - 152 (150)	6 - 14 (9.3)	8 - 43 (26)	4.90 + 0.21(age)	99	0.87	107 - 142 (125)	6.16 ± 0.06
2004	75	145 - 151 (150)	6 - 11 (7.9)	8 - 36 (22)	4.38 + 0.19(age)	78	0.83	114 - 142 (128)	5.20 ± 0.06
2005	78	146 - 150 (148)	5 - 17 (8.9)	11 - 67 (39)	2.89 + 0.23(age)	94	0.89	81, 95 - 137 (109)	5.92 ± 0.09
2006	71	146 - 149 (148)	5 - 14 (9.8)	11 - 49 (30)	4.32 + 0.18(age)	93	0.83	99 - 137 (118)	4.96 ± 0.06
2007	75	143 - 147 (145)	5 - 9 (5.8)	5 - 24 (15)	4.59 + 0.21(age)	97	0.81	121- 140 (131)	4.44 ± 0.06
2008	75	144 - 148 (148)	5 - 10 (6.7)	6 - 33 (20)	4.64 + 0.21(age)	103	0.86	115,126 - 142 (129)	4.34 ± 0.06
2009	76	150 - 153 (152)	5 - 10 (6.6)	6 - 36 (21)	5.00 + 0.17 (age)	109	0.86	116, 122 - 146 (131)	4.49 ± 0.10
2010	76	144 - 148 (145)	5 - 11 (7.2)	4 - 36 (20)	5.04 + 0.18(age)	109	0.91	109 - 141 (125)	5.17 ± 0.06

Table 2. -- KS test results for hatch date distributions. Gray box indicates significant difference at 5%. Inequality symbol indicates length at hatch for year on left is significantly greater or less than year on right at 5% (with Bonferroni correction).

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
1987	1987																							
1988		1988																						
1989			1989																					
1990				1990																				
1991					1991																			
1992						1992																		
1993							1993																	
1994								1994																
1995	<								1995															
1996										1996														
1997	<										1997													
1998	<					<						1998												
1999	<												1999											
2000														2000										
2001															2001									
2002									<		>	>	>		<	2002								
2003				>			>	>	>	>	>	>	>	>	>		2003							
2004																<		2004						
2005	<					<	<									<			2005					
2006	<														<	<				2006				
2007												>								>	2007			
2008								<												>		2008		
2009																				>			2009	
2010									>			>	>		>		>	>		>	>			2010

Figure 1.-- Study area in the Gulf of Alaska. The rectangle represents the area
          referred to as the Main Grid where larval walleye pollock (Gadus
          chalcogrammus) were collected for age and growth analyses.
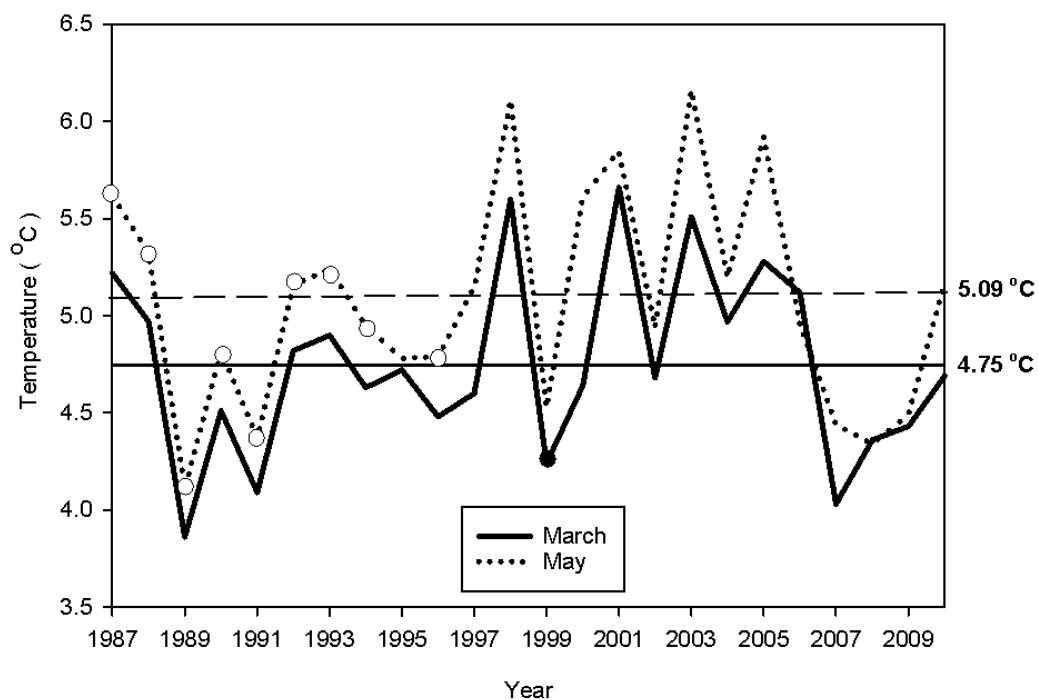   Arrows depict mean current pattern during spring.

30

Figure 2.-- Mean temperature at trawl depth in March (black line) and at 40 m in May
(dotted line) from 1987 to 2010. March temperature means were calculated
from all trawl stations (1999 estimated, black dot), whereas May temperature
means were calculated from stations in the Main Grid study area only (1987-
1994, and 1996 estimated, white dots). Black and dotted lines represent mean
temperature for March and May, respectively.

31
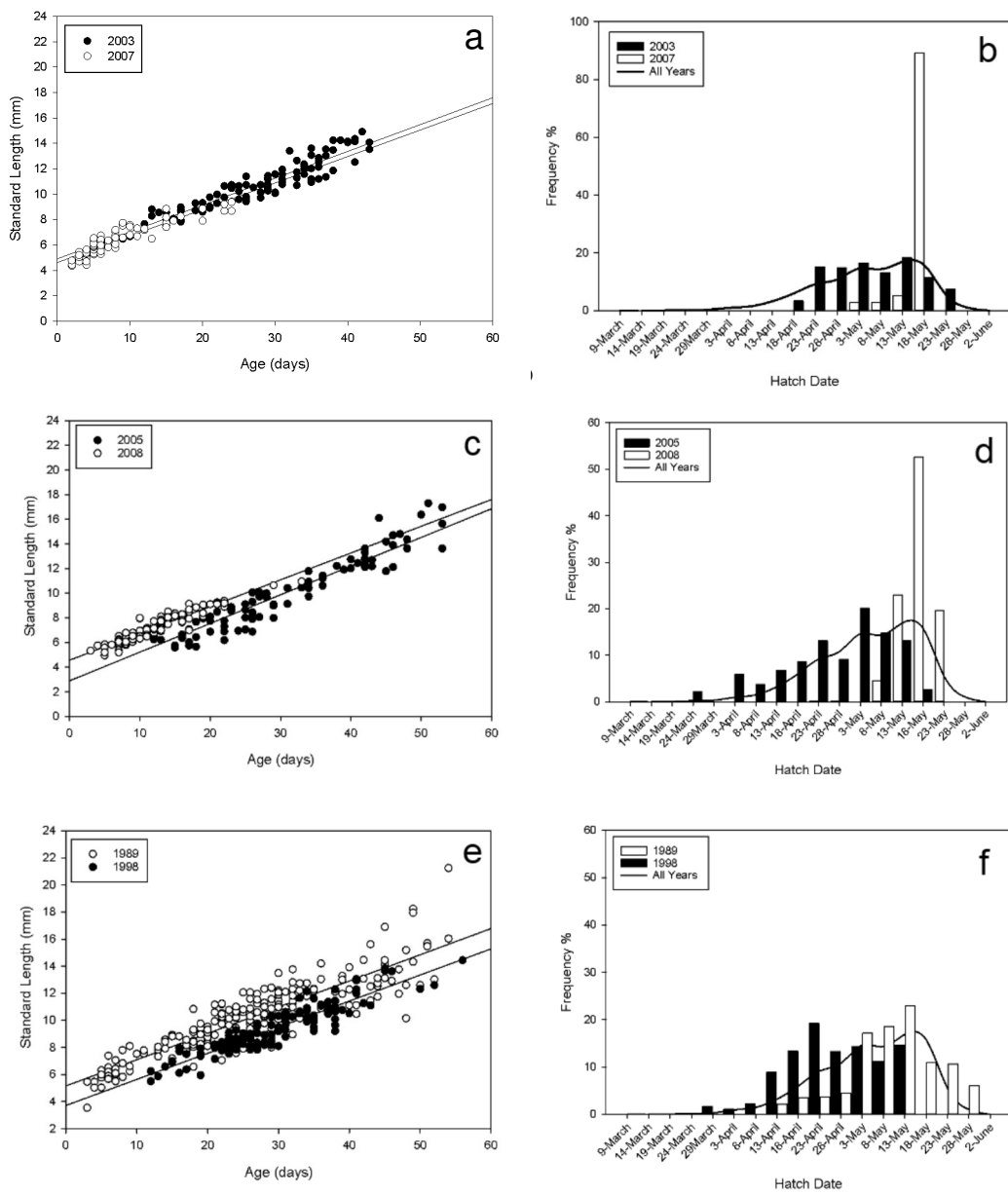
Figure 3.-- Examples of length-at-age and hatch date distributions for warm and cold years. Warm years in black, cold years in white. Black line in Figures b, d, f represent average distribution for all years.
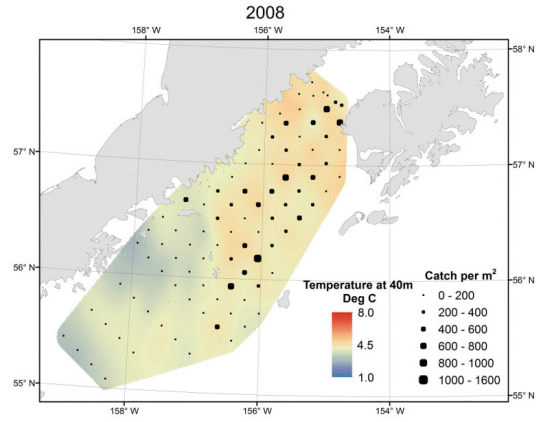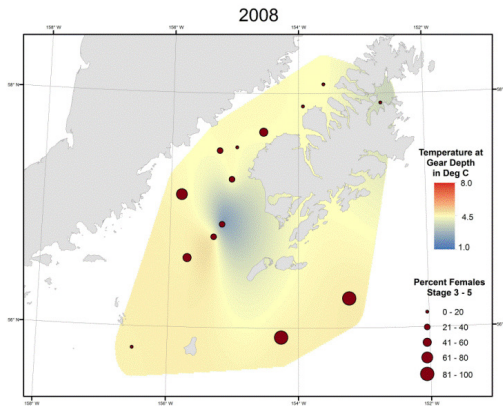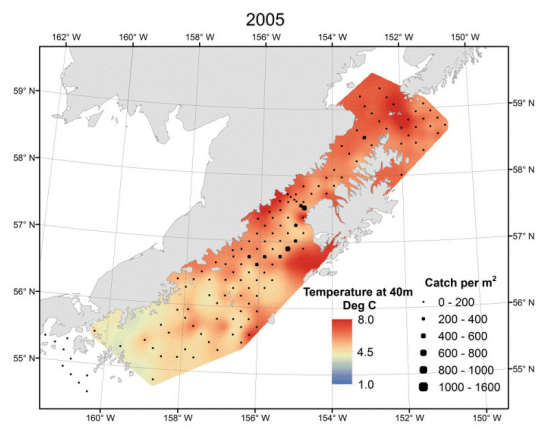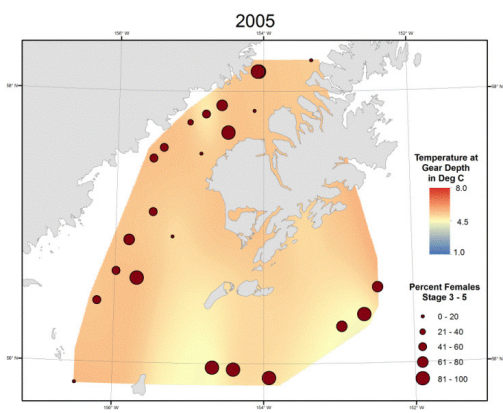
32

APPENDIX

Temperature maps at trawl depth in March and at 40 m in May discussed in Results.
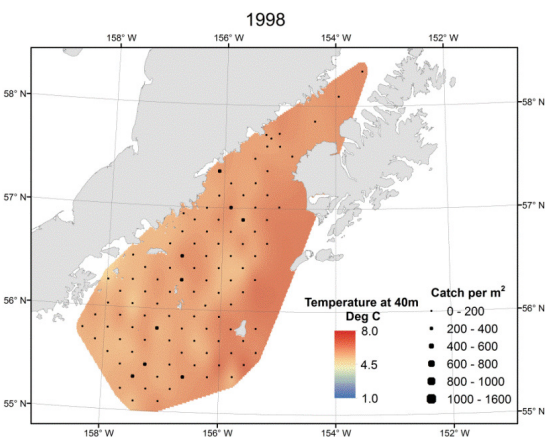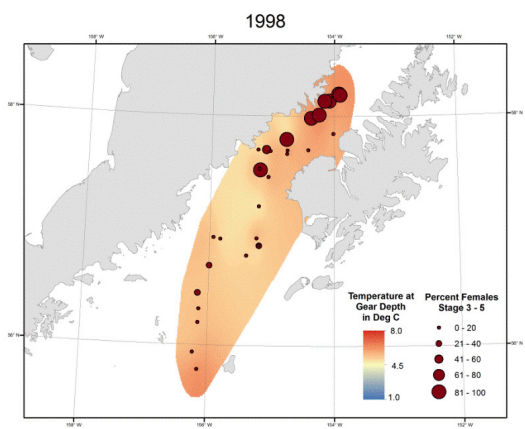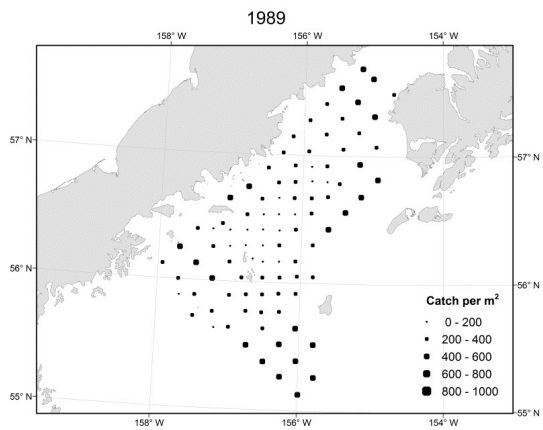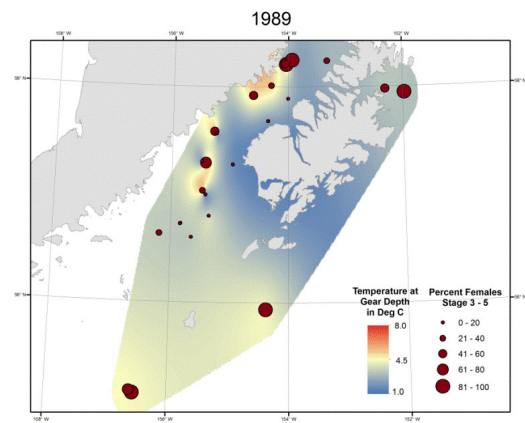
Temperature maps at trawl depth in March (left column) and at 40 meters in May (right column) for 1989 and 1998. No temperature data was available for May 1989.
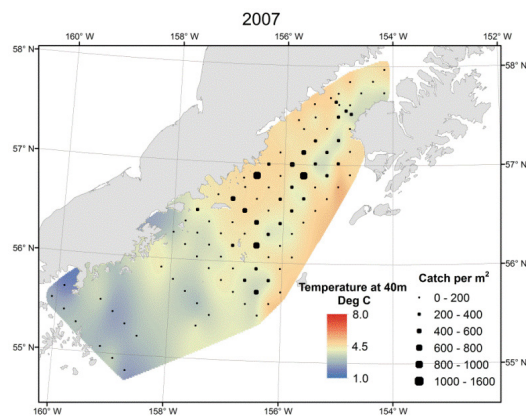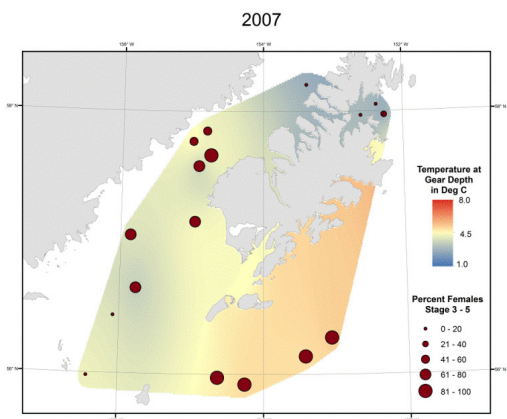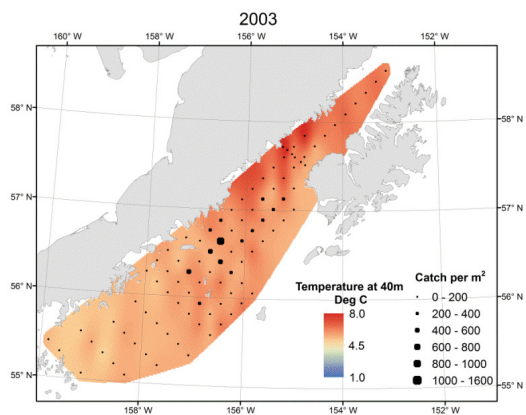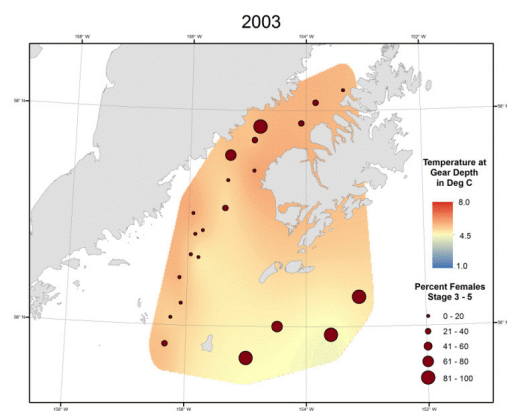
35

Temperature maps at trawl depth in March (left column) and at 40 meters in May (right column) for 2003 and 2007.

36

Temperature maps at trawl depth in March (left column) and at 40 meters in May (right column) for 2005 and 2008.