

AN ABSTRACT OF THE THESIS OF

Erin J. Fedewa for the degree of Master of Science in Fisheries Science presented on May 13, 2015

Title: Pre- and Post-settlement Processes of Northern Rock Sole (*Lepidopsetta polyxystra*) in Relation to Interannual Variability in Temperature and Productivity in the Gulf of Alaska

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Understanding the effects of climate variability on growth dynamics and timing of early life history events in marine fishes can provide insights into survival, recruitment and productivity. Field collections (2005, 2007, 2009-2011) were combined with otolith microstructural analysis to examine interannual variation in larval and juvenile growth rates, size at hatch and metamorphosis, and the timing of metamorphosis of northern rock sole (*Lepidopsetta polyxystra*) collected in two nurseries at Kodiak Island, Alaska, USA. Variation in early life characteristics was quantified and related to phytoplankton production, temperature and juvenile densities in nursery grounds. In addition, monthly sampling of juvenile northern rock sole during the initial post-settlement period (July to August) was used to determine if carry-over effects of size and growth occurred across life history stages. Finally, individual growth trajectories of July and August fish were compared for evidence of selective mortality during the initial post-settlement period. Overall, timing of metamorphosis varied across years and was related to annual and interannual variation in water temperature. Conversely, fish size at metamorphosis was similar across years, suggesting that the competency to metamorphose is related to a minimum size and ontogenetic stage. Post-settlement growth was related to temperatures in coastal nurseries as well as temperatures during the larval period, indicating that thermal conditions experienced by larvae may carry over to influence growth in nurseries. Correlations between pre- and post-settlement traits demonstrate that size and growth advantages could persist across life history stages. Growth selective mortality was

not evident during the initial post-settlement period; however, differences in hatch size and the timing of metamorphosis between July and August fish suggest a selective loss of individuals. The patterns of selection varied among years, indicating that variation in size acquired early in life and temperature influences on the phenology of metamorphosis may determine the direction of selection and directly influence survival of northern rock sole.

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Pre- and Post-settlement Processes of Northern Rock Sole (*Lepidopsetta polyxystra*) in Relation to
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by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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1. GENERAL INTRODUCTION

1.1.1 Growth, development and survival during early life

An important goal of fisheries science is to understand processes that drive recruitment variability. Early life history stages of marine fish are considered “critical” because they encompass periods of disproportionately high and variable rates of mortality and therefore influence survival and recruitment to the adult population (Hjort 1914). Physiological processes such as growth and development are often strong determinants of survival because variation in these traits can limit the duration of critical life stages (Ware 1975, Chambers & Leggett 1987, Houde 2008). Fish size is also a key factor governing survival, mediated through size-dependent susceptibility to starvation and vulnerability to predation (Anderson 1988, Miller et al. 1988). Growth or size advantages acquired during the larval stage may be carried over to juvenile stages and influence performance and survival (O’Connor et al. 2014). For example, these “carry-over effects” between life history stages may lead to selective loss of individuals over time if slower growth rates and/or smaller sizes of larvae are maintained in juvenile stages (Smith & Shima 2011).

Fish ear stones, or “otoliths” are an important tool for describing variation in growth and development during early life history stages. Otoliths serve as a growth record for fish due to the deposition of daily increments that correspond with somatic growth (Pannella 1971). Changes in otolith microstructure also occur during specific developmental events that involve major behavioral and morphological changes such as hatch and metamorphosis. In most cases, otolith size is proportional to fish size so otolith microstructure can be used to estimate both daily growth rates and fish size across life history stages (Campana & Jones 1992). Likewise, because information obtained from otoliths can be resolved at a daily scale and integrated across life history stages, data can be used to examine carry-over effects across early life history stages, selection for growth traits, and environmental effects on growth (Sponaugle 2010).

1.1.2 Environmental influences on marine fish early life history processes in the North Pacific

Variable environmental conditions encountered during early life stages play an important role in recruitment, distribution, growth and phenology of marine fish. Biological responses can often be linked to climatic processes that occur at large spatial and temporal scales. Marine ecosystems of the North Pacific Ocean, for example, have experienced major shifts in ecosystem dynamics that have been attributed to interannual and interdecadal climatic variability (Francis et al. 1998, McGowan et al. 1998). Documented climatic regime shifts can alter the magnitude and direction of biological responses, resulting in persistent changes in ecosystem biomass and community structure and function (Hare & Mantua 2000, deYoung et al. 2008).

Recruitment variability in a number of fish species has been linked to decadal-scale climatic forcing indices in the North Pacific such as the Aleutian Low Pressure System, the Pacific Decadal Oscillation and the El Nino Southern Oscillation (Francis & Hare 1994, Beamish et al. 1995) although the mechanistic linkages between climate forcing and recruitment at such large spatial scales are not well understood. Climate variation can alter oceanographic features and physical mechanisms (e.g. eddies, currents, wind-forcing) that are important for larval transport to suitable nursery grounds in the North Pacific. For example, shifts in wind-driven advection to favorable nurseries coincides with high fisheries recruitment (Wilderbuer 2002) and temperature-driven changes in hydrodynamic features may limit larval delivery to certain nursery grounds as well as modify juvenile nursery habitat use (Cooper et al. 2014).

Temperature is a central aspect of environmental variability, often serving as a direct driver of marine ecosystem productivity and early life history processes. Seasonal and interannual temperature variation is well recognized, although water temperatures in the North Pacific also vary on decadal and interdecadal time scales. These long-term temperature patterns are defined by the persistence of anomalously warm ($\sim 2-3^{\circ}\text{C}$ above the mean) or anomalously cold water temperatures ($\sim 2-3^{\circ}\text{C}$ below the mean) (Janout et al. 2010, Overland et al. 2012). Documented shifts between multi-decadal warm and cold regimes in the Gulf of Alaska have been linked to reorganization in the Northern Pacific marine ecosystem structure

(Anderson & Piatt 1999), marine food web dynamics (Litzow et al. 2006) and fisheries year-class strength (Hollowed et al. 2001). Temperature also directly impacts vital rates such as growth and development (Pepin 1991) and indirectly affects the timing of early life history events such as spawn, hatch and settlement processes in fish species (Genner et al. 2010). Walleye pollock (*Gadus chalcogrammus*) have been the target of many studies on how climate drives distribution and growth dynamics in the North Pacific. Results suggest that temperature is a major driving force in the timing and spatial distribution of spawning, rate of hatch, larval development, larval transport and survival of walleye pollock (Chan et al. 2010, Dougherty et al. 2007, Smart et al. 2012). However, the direct and indirect effects of temperature on early life history characteristics of many other species in the North Pacific have yet to be examined.

Environmental influences on marine fish species are of particular interest in the Gulf of Alaska because the region is extremely productive despite being characterized as a downwelling system. This differs from typical associations between high productivity and persistent upwelling events such as the California Current System. The Gulf of Alaska also experiences strong seasonality in oceanographic conditions in comparison to other regions in the North Pacific, and as a result, phytoplankton communities undergo seasonal changes in growth and abundance (Stabeno et al. 2004). The cessation of winter storms, increasing water temperatures and light, and stratification of the water column in late spring drive an increase in phytoplankton abundance and a subsequent spring phytoplankton bloom in the Gulf of Alaska (Mundy 2005, Waite & Mueter 2013). This “spring bloom” is the source of nutrients for secondary production and characteristics of the bloom are used as a proxy for potential secondary and tertiary production in the Gulf of Alaska.

Changes in phenology, or timing of life cycle events, are often driven by environmental conditions (Edwards & Richardson 2004). Temperature variability can influence the timing of phytoplankton production, possibly leading to a temporal “mismatch” with higher trophic levels. The resulting changes in prey availability can have a significant effect on larval growth, development, survival and recruitment (Brander et al. 2001). Shifts in phenology, therefore, could have implications for the survival of larval and

juvenile fish due to their reliance on matches between early life stages and prey (Cushing 1990).

Temperature-driven spatial mismatches between early life stages and prey have also been suggested as a mechanism for growth and recruitment variability (Siddon et al. 2013). Additionally, environmental conditions can influence the composition, abundance and size distribution of zooplankton, which are also important prey items for larval and juvenile fish (Mackas et al. 2007, Chiba et al. 2015).

1.1.3 Northern rock sole life history and biology

Northern Pacific marine ecosystems are some of the most productive in the world, providing over 40% of commercial fish landings in the United States (NPRB 2005). The Gulf of Alaska supports high abundances of many commercially important fish species. However, large-scale regime shifts and recent warming trends in the Gulf of Alaska have important implications for understanding the role of climate on fisheries in these highly productive waters (Royer & Grosch 2006). Due to the ecological and economic value of flatfishes in the Gulf of Alaska, much effort has focused on understanding recruitment processes of these populations specifically. Early life history dynamics are of specific interest because previous research suggests that flatfish year-class strength is determined in early life stages, primarily during larval and early post-settlement stages (Gibson 1994). Characterized by a complex life cycle, early life stages of flatfish inhabit both pelagic waters and benthic nurseries in the Northern Pacific. This life history exposes individuals to a variety of abiotic (e.g. temperature variability, oceanographic currents) and biotic factors (e.g. prey availability, predation) which likely contribute to observed variability in recruitment strength (Miller et al. 1991, Van der Veer et al. 2000).

Northern rock sole (*Lepidopsetta polyxystra*) is a flatfish species of high commercial value in the Gulf of Alaska and constitutes the second largest flatfish fishery in the United States by catch weight (NPFMC 2010). This abundant flatfish species is distributed from the eastern Bering Sea and the Gulf of Alaska to the west coast of North America south to the Puget Sound (Orr & Matarese 2000). Mature northern rock sole (NRS) spawn demersal eggs from mid-winter to spring in bays and coastal areas (45 m average bottom depth for spawning). In the western Gulf of Alaska, peak spawning time is estimated to occur in

March-April (Stark & Somerton 2002). Pelagic larvae first appear in the plankton in March and are typically found in highest abundances in April, concentrated primarily at depths of 10-40 m until May-June (Lanksbury et al. 2007). After this pelagic larval stage, NRS juveniles metamorphose and settle in shallow, sandy coastal habitats in June and July, transitioning to a primarily benthic lifestyle (Norcross et al. 1995). Peak juvenile densities in nurseries occur at 30 m depth until juveniles move offshore to deeper waters in the fall (Stoner et al. 2007).

Temporal patterns in NRS production are associated with ocean conditions, and previous research has indicated that climate-driven influences on larval advection to favorable nursery grounds can influence survival and recruitment in the Bering Sea (Wilderbuer et al. 2013). Temperature has also been shown to be a strong determinant of NRS year-class strength (Fargo & McKinnell 1989), larval abundance (Doyle et al. 2009) and larval size (Lanksbury et al. 2007). In addition, Hurst et al. (2010) observed that variation in size of age-0 NRS was best explained by temperatures in the earlier larval period, possibly due to temperature-mediated changes in phenology (spawn and hatch time) or larval growth rates. A potential explanation for this observation is the presence of carry-over effects in which the thermal conditions experienced during spawning and larval periods affect development and performance in later life stages. Observed relationships indicate that temperature variation likely plays a critical role in pre-settlement processes of NRS.

Phytoplankton dynamics, such as the magnitude and timing of the spring bloom onset, are also influenced by thermal regimes and can subsequently influence the transfer of energy up marine food webs. Variation in the productivity of fish populations in the North Pacific has been related to the timing of primary production, indicating that climate-mediated changes in phytoplankton phenology could influence early life history processes (Malick et al. 2015). Furthermore, recent findings linked a weak year class of walleye pollock in lower condition to an anomalously cold and low production year in the Eastern Bering Sea (Gann et al. *in press*). These relationships suggest that interannual variation in NRS growth, development and survival may be related to temperatures and primary production as well,

although such environmental influences on NRS early life history characteristics have not been quantified. Recent changes in environmental conditions in the Gulf of Alaska raise concern for how early life stages of NRS will respond to shifts in water temperatures and phytoplankton production and phenology. During the previous decade, the Gulf of Alaska experienced a warming event (2001-2005) followed by a transition year (2006) in which temperatures declined rapidly in early winter months after a warm fall. Below average temperatures continued in 2007 and 2008, marking the lowest water temperatures recorded in the Gulf of Alaska since the early 1970s (Janout et al. 2010). Temperatures directly influence the timing and intensity of the spring bloom as well, making these recent shifts in environmental conditions a probable cause for variation in growth, development and survival of NRS in the Gulf of Alaska.

1.1.4 Hypotheses and objectives

Temperature can have substantial direct and indirect effects on early life history characteristics of marine fish (Blaxter 1991). Therefore, quantifying the effects of temperature as well as determining the relative importance of other environmental factors, such as food availability, on growth and development are necessary steps in understanding and evaluating potential climate-induced shifts in population dynamics and fishery yields. In this study, field collections of NRS juveniles in two nursery sites in the Gulf of Alaska were combined with otolith microstructure analysis to determine the variation in early life history characteristics across years (2005, 2007, 2009-2011) and relate early life history processes to environmental conditions. Chapter 2 describes interannual variation in hatch size, larval growth rates, and the size and timing of metamorphosis of NRS and examines the hypothesis that environmental conditions influence these pre-settlement processes. Chapter 3 focuses on interannual variation in post-settlement processes of NRS in relation to carry-over effects as well as nursery habitat dynamics such as temperature and juvenile NRS densities. Chapter 4 provides an overall synthesis and discusses the relevance of the findings.

Previous research suggests that NRS are a ‘cold-adapted’ species due to their ability to maintain positive growth at lower temperatures (Hurst et al. 2010). However, like most other cold-water species, laboratory-reared NRS larvae hatch smaller and grow and develop relatively faster in warmer temperatures to a point, above which growth declines (Laurel & Blood 2011). Likewise, faster larval growth in elevated temperatures results in a shorter larval stage duration and earlier settlement at larger sizes in laboratory settings (Laurel et al. 2014). The results of these studies suggest that field-collected NRS larvae may also exhibit relatively faster larval growth and development as well as an earlier onset of metamorphosis and settlement at larger sizes in response to warmer thermal regimes in the Gulf of Alaska.

If patterns in growth, size and phenology are not related to temperature variability, food availability could be a more important determinant of variation in early life history characteristics. Growth rates and size should be greatest in years coinciding with oceanic conditions that favor the production of prey resources. Phytoplankton production can be used as a general proxy for secondary production and production of prey for higher trophic levels. If primary production is a reliable indicator of NRS prey, then fish growth and size will be positively related to phytoplankton biomass. Therefore, to quantify the variation in early life history characteristics of NRS larvae and examine the relative importance of temperature and productivity, I completed the following objectives:

- 1) Examine interannual variation in larval growth of NRS;
- 2) Examine interannual variation in the size at hatch, size at metamorphosis and timing of metamorphosis of NRS;
- 3) Determine if size at and timing of metamorphosis of NRS are related to growth during the larval period; and
- 4) Relate variation in growth rates and timing of early life history events to temperature variation and phytoplankton dynamics in the Gulf of Alaska.

Chapter 3 focuses on interannual variation in post-settlement processes of NRS in nursery grounds in the Gulf of Alaska. Interannual variation in larval characteristics described in Chapter 2 was used to determine if larval growth and/or size advantages are carried over to the juvenile stage. Larval characteristics were also integrated with juvenile characteristics to evaluate individual growth trajectories

for evidence of growth and/or size selection that may lead to mortality between July and August post-settlement periods.

Evidence for temperature-dependent growth in NRS larval stages suggests that post-settlement growth of NRS juveniles will also be positively related to temperatures in nursery grounds in the Gulf of Alaska. However, previous research has noted that prey limitation may also be a primary determinant of post-settlement growth variation in NRS (Hurst & Abookire 2006). In addition to temperature, density-dependent processes can affect growth in nursery grounds. For example, slow growth in relation to high densities of juvenile NRS may be due to increased competition for prey resources.

By integrating pre- and post-settlement size and growth traits, I also addressed the hypothesis that carry-over effects contribute to variation in post-settlement growth. If the effects of traits propagate across life history stages in NRS individuals, relatively fast larval growth is expected to result in fast juvenile growth. A larger size at hatch and size at metamorphosis could also affect survival to later stages if, for example, larger size is advantageous for predator evasion or feeding in nursery grounds.

Mortality of flatfish in nursery grounds following metamorphosis is often non-random, favoring larger and faster growing individuals (Witting & Able 1993, Ellis & Gibson 1995). Therefore, juvenile NRS could maintain these traits across life history stages and experience greater survival to late summer during the post-settlement period. Similarly, if variation in growth occurs during the larval stage, there could be continued selection for size or growth traits in the nursery area, giving fast-growing, larger larvae a selective advantage. Chapter 3 evaluated these hypotheses by completing the following objectives:

- 1) Examine spatial and temporal variation in post-settlement growth of NRS in two nursery sites in the Gulf of Alaska;
- 2) Relate post-settlement growth variation to juvenile NRS densities and water temperature in nursery sites;
- 3) Integrate pre- and post-settlement characteristics to determine if relative patterns of covariation in size and growth are maintained across life stages of NRS; and

- 4) Determine the extent to which variation in pre- and post-settlement traits may result in growth and/or size selection and influence survival from July to August during the initial post-settlement period.

1.1.5 Overview of methods

In order to address these research objectives, otoliths of laboratory-reared NRS were used to identify otolith landmarks relating to major developmental stages and verify daily increment formation. To infer NRS growth and fish size at specific life history events, otolith increment widths and otolith size were used as proxies. NRS for the study were collected as post-settled juveniles in two nursery sites near Kodiak Island, AK, so otoliths provided early life history information on juveniles that survived the larval life history stage. This approach, therefore, enabled larval and juvenile growth histories of individuals to be reconstructed and integrated across life stages. Individual growth trajectories were then used to determine variation in growth across pre- and post-settlement life stages and examine evidence for co-variation in growth across life history stages. In addition, growth trajectories of recent settlers captured in July were compared to NRS that were captured in August and thus survived to late-settlement periods. Differences in pre- and post-settlement traits between the two groups served as an indication of selection in the study.

1.1.6 Rationale for study

This study will contribute to a holistic understanding of pre-settlement processes in NRS that could influence post-settlement growth, survival and recruitment. There is a growing need for research that encompasses multiple life stages with the understanding that large-scale processes such as recruitment operate throughout multiple early life stages. To better understand factors that may regulate NRS productivity and to forecast NRS recruitment, it is also necessary to quantify the effects of seasonal and interannual environmental conditions on early life history characteristics of NRS in the Gulf of Alaska.

Likewise, exploring NRS growth and development in relation to environmental variables is an important step towards understanding the potential impacts of large scale climate variability. In order to

predict biological responses to future climate change, an understanding of the effects of temperature on growth dynamics is crucial (Hollowed et al. 2009). Previous research examining thermal effects on laboratory-reared NRS larvae indicated an upper range of temperature tolerance at 12°C, resulting in poor hatch quality and a large decline in larval growth (Laurel & Blood 2011). This suggests that warming conditions due to climate change could be detrimental to the development and survival of NRS. Exploring the effects of climate variability on NRS will also improve our understanding of NRS life stages most vulnerable to climate change.

In a broader context, quantitative baseline information on NRS responses to climate variation can then be used to forecast similar climate-driven responses in other important marine resources in the Gulf of Alaska. Fisheries in the North Pacific, as a whole, are expected to face fluctuations in recruitment success and productivity in response to direct and indirect effects of climate change (Rijnsdorp et al. 2009, Ainsworth et al. 2011). Mechanistic explanations to address the dynamics of fish growth, recruitment and distribution in response to shifting climatic regimes are clearly necessary in order to predict the possible implications of climate change. Variation in climatic conditions also drives interannual variability in plankton phenology, possibly creating more potential for trophic mismatches with larval and juvenile fish and their prey. Specifically, future climate scenarios predict an advancement of spring bloom phenology so it is important to understand how NRS early life stages as well as the Gulf of Alaska ecosystem as a whole will respond to these alterations in marine trophodynamics (Durant et al. 2007).

2. PRE-SETTLEMENT PROCESSES OF NORTHERN ROCK SOLE (*LEPIDOPSETTA POLYXYSTRA*) IN RELATION TO INTERANNUAL VARIABILITY IN TEMPERATURE AND SPRING BLOOM DYNAMICS IN THE GULF OF ALASKA

2.1 INTRODUCTION

High rates of mortality in the egg and larval stages of marine fish indicate that small changes in early life history characteristics have the potential to influence survival to settlement and juvenile residence in nurseries (Bailey & Houde 1989, Van der Veer et al. 2000). For flatfish species, the physiological process of metamorphosis and associated behavior of settlement are critical life history events that link the pelagic larval stage to the benthic juvenile stage. The timing of metamorphosis and settlement as well as fish size at these key transitions reflect variation in growth and development in earlier life stages (Pepin & Myers 1991). Therefore, processes driving metamorphosis and settlement are important for understanding connectivity between life history stages because variation in traits established during the larval period likely propagate through metamorphosis and post-settlement life stages (Chambers et al. 1988).

Studies of metamorphosis in flatfishes indicate that slower growing larvae begin metamorphosis later (Chambers & Leggett 1987). The relatively high level of variability in the timing and age at metamorphosis can be contrasted with less variable size at metamorphosis, which suggests that metamorphosis may be a size-related phenomenon (Geffen et al. 2007). Likewise, the narrow range of observed size at settlement indicates that variation in the timing of settlement in nurseries is primarily regulated by variability in spawn timing (e.g. Lange & Greve 1997) and rates of larval growth and development (e.g. Amara et al. 2000). Variation in these early life history traits is often correlated with environmental variables such as temperature, which affects larval growth and likely also influences the phenology and size at metamorphosis and settlement. However, the extent to which early life history processes vary under different environmental regimes is not well understood.

Environmental conditions encountered during the pelagic larval stage can significantly influence larval survival, delivery to nurseries, and overall population connectivity (Cowen & Sponaugle 2009). Previous research has identified water temperature as a primary environmental determinant in the timing of spawning (e.g. Fincham et al. 2013), size at hatch (Pepin 1991, Benoît & Pepin 1999), larval growth (e.g. Meekan et al. 2003, Sponaugle et al. 2006) and development rate (e.g. Green & Fisher 2004). Shifts in prevailing temperatures during early life stages affect larval growth rates, which determine larval stage duration and the subsequent timing of metamorphosis and settlement (Benoît et al. 2000). For example, northern rock sole (NRS) settlement is both temperature and size dependent in laboratory settings (Laurel et al. 2014). Larvae reared at 10°C were 6.3 times heavier and 1.8 mm longer (SL) at the onset of settlement compared to larvae reared at 2°C. Likewise, settlement occurred ~69 days earlier among fish reared at 10°C than 2°C. Within this temperature range, warmer rearing conditions resulted in faster larval growth, reduced larval stage duration and earlier settlement at relatively larger sizes. Settlement of laboratory-reared NRS is decoupled from metamorphosis because developmental criteria associated with metamorphosis, such as eye migration and pigmentation, can occur both before and after settlement onto tank bottoms. However, results of the study indicate that metamorphosis of NRS in Gulf of Alaska nurseries may be influenced by temperature as well.

Despite links between temperature and the processes of metamorphosis and settlement in laboratory experiments, relatively few field studies have explored the direct and indirect effects of environmental conditions on phenology in flatfish. Doyle et al. (2009) reported a negative correlation between NRS larval abundance and Gulf of Alaska sea surface temperatures during spawning periods in a 21-year ichthyoplankton time series. These temperature-related shifts in larval abundance could be due to phenological shifts in larval production, and specifically, shifts in the time of spawn and hatch in relation to the timing of the annual research survey. Likewise, observed differences in larval size from field collections across years with contrasting thermal regimes suggest that spawning could have occurred later

in response to cooler water temperatures (Lanksbury et al. 2007). Potential temperature-driven shifts in the phenology of metamorphosis and settlement of NRS also have yet to be determined.

In addition to temperature, larval food supply plays an important role in early life history processes because low prey levels limit larval growth and development (Houde 1989). Plankton dynamics determine bottom-up production for higher trophic levels and can thus link environmental conditions and early life history characteristics. Documented interannual changes in phytoplankton blooms in relation to thermal shifts (i.e. warmer waters lead to an earlier spring bloom) could lead to asynchrony with the prey resources necessary for metamorphosis, settlement and juvenile growth (Mackas et al. 1998, Edwards & Richardson 2004). Metamorphosis is an energetically demanding process and it is likely that larval flatfish must meet energy storage requirements prior to initiating metamorphosis (Bogolino et al. 2012, Fraboulet et al. 2010). Winter to early-spring spawning fish such as NRS are more likely to experience prey limitation during the early larval stage than summer-spawned fish because the onset of the spring bloom coincides with later larval stages rather than first-feeding larvae. These potential mismatches with prey may have implications for larval growth as well as energy stores prior to metamorphosis. Alternatively, in warmer waters larval fish may develop faster and would thus be able to take advantage of earlier bloom conditions. It is unknown if bloom-associated production influences larval growth or if the timing of metamorphosis and settlement are linked to the timing of the spring bloom. Clearly there is a need for research examining phytoplankton dynamics in relation to early life history characteristics in flatfish.

Temperatures during NRS spawning and larval periods are thought to affect settlement and post-settlement processes (Hurst et al. 2010) although variation in pre-settlement processes and the relative importance of environmental variables on these early life history characteristics have not been quantified. In an effort to disentangle sources of early life history variation in this study, larval NRS characteristics were compared with temperature and phytoplankton productivity estimates. If temperature is the primary factor regulating larval growth, size and phenology, it is expected that warmer conditions in the Gulf of

Alaska will result in faster growth, larger sizes and earlier phenology due to faster development.

However, if food availability is the primary determinant of growth, then high phytoplankton biomass should be associated with relatively fast growth and large size of larvae. Alternatively, both temperature and food availability could play a role in larval characteristics and the relative importance of either environmental factor could vary across years. In order to test these hypotheses, the following objectives were completed:

- 1) Examine interannual variation in larval growth of NRS;
- 2) Examine interannual variation in the size at hatch, size at metamorphosis and timing of metamorphosis of NRS;
- 3) Determine if size at and timing of metamorphosis of NRS are related to growth during the larval period; and
- 4) Relate variation in growth rates and timing of early life history events to temperature variation and phytoplankton dynamics in the Gulf of Alaska.

2.2 MATERIALS AND METHODS

2.2.1 Study site

This study was conducted at two sites off the northeast coast of Kodiak Island, Alaska, USA (Fig. 1). Holiday Beach (57° 41.2' N, 152°27.7' W), in Middle Bay, and Pillar Creek Cove (57° 49' N, 152° 25' W), in Monashka Bay, are known nursery grounds for age-0 NRS (Stoner et al. 2007). Both sites are sheltered coves with flat, sandy beaches and benthic structure composed primarily of sandy and muddy substrate. Age-0 NRS are found primarily in water depths of 10-30 m and abundance is negatively correlated with depth, making these shallow, protected nursery grounds around Kodiak Island an ideal study site for NRS field collections.

2.2.2 Northern rock sole field sampling

Age-0 NRS were sampled in July and August from 2004-2013 by the Fisheries Behavioral Ecology Program of the Alaska Fisheries Science Center (AFSC) (Table 1). Field collections were conducted in July and August in order to target post-settlement NRS as previous sampling efforts

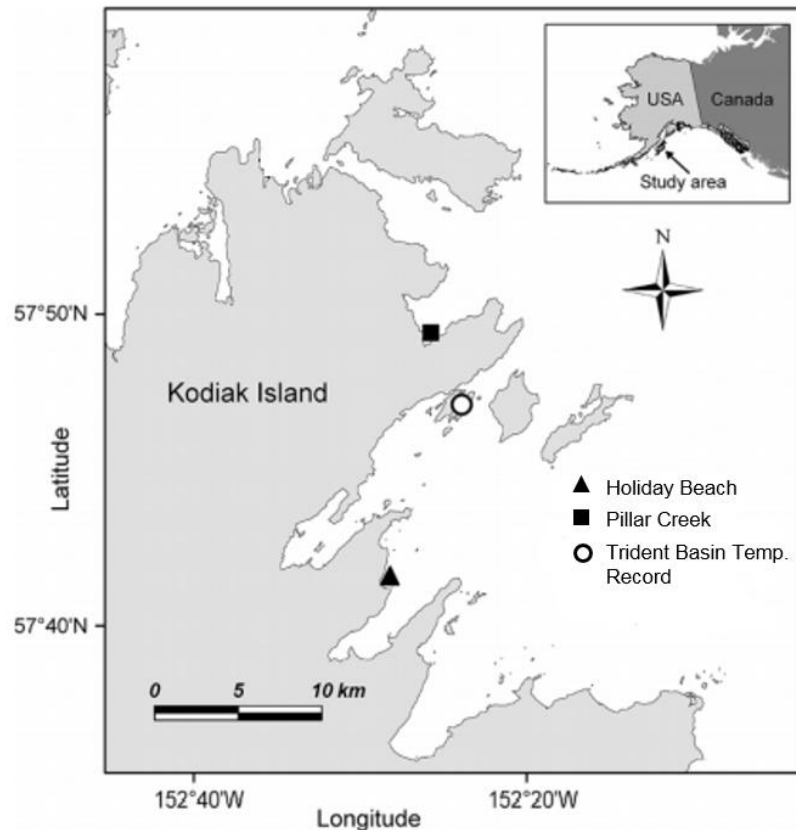


Figure 1. Map of Pillar Creek Cove and Holiday Beach field sampling sites off the northeast coast of Kodiak Island, Alaska, USA.

have indicated that peak settlement likely occurs in May-June (Hurst & Abookire 2006, Laurel et al. 2015). Sampling at nursery sites was conducted with a 2-m beam trawl with a 3-mm mesh codend at fixed transects. Three to five 5-minute trawls were conducted parallel to the shoreline at approximately 10 m depth intervals between 7 and 30 m depth on each sampling day (Hurst et al. 2010). Surface and bottom temperature, salinity and oxygen concentrations were measured upon completion of each tow (YSI model 85). Trawl catches were identified to species, frozen, and shipped to the AFSC laboratory in Newport, OR, U.S.A. Archived NRS collections from field sampling in 2005, 2007, 2009, 2010 and 2011 were selected for otolith extraction and analysis due to adequate sample sizes and suitable otolith condition in these years.

Table 1. Kodiak Island nursery site sampling dates and summary of age-0 northern rock sole (NRS) size at capture. Total length (TL) ranges from field collections were used to distinguish between age-0 and age-1 NRS due to breaks in the size-frequency distribution. NRS used for otolith analyses are a representative subset of the NRS age-0 size distribution.

Year	Site	Sampling Date	TL range (mm) of all NRS collected	TL range (mm) of NRS for otolith analyses
2005	Holiday Beach	July 19-20	21-51	<i>No readable otoliths</i>
		Aug 22	26-76	41-74
	Pillar Creek Cove	July 20	10-50	16-31
		Aug 23	22-61	31-47
2007	Holiday Beach	July 18-19	18-36	25-28
		Aug 23, 25	28-53	27-46
	Pillar Creek Cove	July 20	17-32	21-30
		Aug 24	19-46	21-52
2009	Holiday Beach	July 14	20-41	21-37
		Aug 23	26-59	28-48
	Pillar Creek Cove	July 17, 19	20-41	24-36
		Aug 24-25	20-60	30-50
2010	Holiday Beach	July 14	21-39	24-38
		Aug 23-24	34-59	32-59
	Pillar Creek Cove	July 15	20-38	20-34
		Aug 25-26	20-66	24-66
2011	Holiday Beach	July 16, 20	20-41	31-38
		Aug 26	21-76	32-51
	Pillar Creek Cove	July 15, 17	20-46	29-43
		Aug 23, 29	22-74	34-50

2.2.3 Environmental parameters: temperature variation

For analyses within the larval pelagic period, temperature data were extracted from hydrographic station GAK-1 (<http://www.ims.uaf.edu/gak1/>) from January 1 to May 1. Located near Seward, Alaska at the mouth of Resurrection Bay (~59°51'N, 149°28'W), the GAK-1 time series includes temperature and salinity readings every 15 minutes at standard depths (0, 10, 20, 30, 50, 75, 100, 150, 200, and 250 m). Previous ichthyoplankton surveys conducted in the North Pacific reported highest abundances of NRS larvae at depths of 10-30 m (Lanksbury et al. 2007) so the 20 m depth time series was selected for all further analyses. Yearly temperature records were created by averaging the 15-minute continuous temperature readings to daily, two-week and monthly temporal resolutions across the 5-year dataset.

While the GAK-1 time series data are ~180 miles northeast of Kodiak Island nursery sites, the use of daily temperature data obtained from National Oceanographic and Atmospheric Administration buoy

stations (<http://www.ndbc.noaa.gov/>) in closer proximity to Kodiak Island (Buoy 46080, Portlock Bank: 57.924°N, 149.865°W and Buoy 46078, Albatross Bank: 55.990°N 152.64°W) was not possible due to significant periods of missing data across study years. However GAK-1 daily temperatures were highly correlated with both Portlock Bank ($r > 0.88$, $p < 0.001$) and Albatross Bank ($r > 0.81$, $p < 0.001$) daily temperatures within each year. These relationships indicate that the GAK-1 records reflect general patterns of temporal variation in temperatures and provide a reasonable estimate of thermal conditions experienced during NRS spawning, hatch and larval periods in offshore waters in the Gulf of Alaska. Furthermore, GAK-1 temperature data have previously been used to address similar research objectives in studies examining species distribution, recruitment patterns and biological production in relation to environmental variables in the Northern Gulf of Alaska and specifically the vicinity of Kodiak Island (Royer et al. 2001, Coyle & Pinchuk 2005, Bechtol & Kruse 2011).

For analyses during the metamorphic period (~mid-April to mid-July), temperature data were collected from a continuous temperature record at 10 m depth in Trident Basin on the NE coast of Kodiak Island (Fig. 1). This Trident Basin logging station is in close proximity to Holiday Beach and Pillar Creek Cove sampling sites. Short-term temperature records for Holiday Beach and Pillar Creek indicated that the Trident Basin temperature record was consistently within the range of temperatures measured at the sampling sites (Hurst et al. 2010). Therefore, Trident Basin temperature records were used to describe interannual temperature variation across both sampling sites during NRS metamorphosis and settlement. Daily Trident Basin temperature records across the 5-year dataset were used to determine 15-day and monthly temperature means to characterize interannual temperature variation.

Fifteen-day mean temperature periods of GAK-1 and Trident Bay records were used for all further statistical analyses because the larval stage and metamorphic window in NRS both span several months. Therefore, 15-day time steps are suitable for capturing temperature variability throughout the duration of the two periods. Intra- and interannual autocorrelation was assessed between 15-day temperature means of both GAK-1 and Trident Basin temperature records. Within each year, 15-day mean GAK-1

temperature time series were not significantly autocorrelated and 15-day mean Trident Basin temperatures were positively autocorrelated at a lag of 1. There was no evidence for autocorrelation across years in either temperature record.

2.2.4 Environmental parameters: spring bloom dynamics

To describe interannual variation in timing and magnitude of the spring bloom, satellite-derived chlorophyll-*a* (chl-*a*) concentrations were used as a proxy for phytoplankton biomass and bottom-up production in the Gulf of Alaska. Chl-*a* data were extracted at 9-km spatial resolution from Level-3 MODIS-Aqua 8-day composite time series data for the grid surrounding the Kodiak Island study area (56-60°N, 148-155°W). Data were downloaded from NASA's Giovanni tool (<http://disc.sci.gsfc.nasa.gov/giovanni>, maintained by Goddard Earth Sciences Data and Information Services Center) which subsets MODIS-Aqua data from the Goddard Space Flight Center Ocean Color website (<http://oceancolor.gsfc.nasa.gov>). Eight-day mean chl-*a* concentrations were used for all further statistical analyses because this was the finest temporal resolution of data obtained from MODIS-Aqua time series data.

The onset of the annual spring bloom was defined as the estimated date that chl-*a* concentrations reached 5% above the median chl-*a* concentration of that respective year (Henson 2007, Waite & Mueter 2013). Median chl-*a* concentration was calculated as 50% of the difference between the winter “baseline” and maximum chl-*a* concentrations. Baseline pre-bloom chl-*a* concentrations were determined by averaging chl-*a* concentrations prior to the initial increase of chl-*a* leading into the spring bloom (February 10th-March 29th). The 8-day mean chl-*a* concentration values were assigned to the mid-point of the sampling interval and interpolated to estimate the date of bloom onset (Bloom_{Onset}) each year. The magnitude of the bloom was described by the annual maximum chl-*a* concentration (i.e. largest 8-day mean chl-*a* concentration, referred to as ChlA_{Max}). In addition, the annual spring chl-*a* concentration (ChlA_{Spring}) was determined as the average of March-May chl-*a* concentrations.

2.2.5 Laboratory-reared NRS otolith structure and daily increment validation

Laboratory-reared NRS otoliths were used to verify structural landmarks (e.g. discontinuities or “check marks”) relating to life-history events and then used to identify similar landmarks in field-caught NRS. While otolith growth patterns often coincide with development events, the timing of formation of these otolith landmarks in relation to morphological development differs among flatfish species (Toole et al. 1993, Modin et al. 1996, Neuman et al. 2001). Therefore, laboratory-reared NRS at specific ontogenetic stages were examined.

NRS larvae and juveniles used for validation studies were acquired from laboratory experiments conducted by the Fisheries Behavioral Ecology Program of the AFSC. NRS broodstock was collected from Kodiak, AK and shipped back to Oregon State University’s Hatfield Marine Science Center, Newport, OR. Fertilized eggs were incubated until the onset of hatch (~16-22 days post-incubation). After hatch, yolk-sac larvae were moved to round fiberglass tanks and fed a diet of enriched rotifers for the duration of the larval period. Experiments conducted by AFSC examined growth, condition, development and settlement of NRS reared in various temperature conditions (Laurel et al. 2014, Hurst et al. 2015).

NRS larvae had previously been anesthetized in a solution of tricaine methanesulfonate (MS-222) and preserved in ethanol at different stages of development by staff at the AFSC. Preserved yolk-sac, 2 d, 4 d and 6 d post-hatch larvae were acquired from AFSC collections for verification of a hatch check. Fish standard length (SL) was measured from digital photographs under a stereomicroscope. Sagittal otoliths were removed, placed on a microscope slide in immersion oil and imaged at 1,000x magnification. A check that was ~15-18 μm in diameter was identified in individuals at each age ($n = 20$). Corresponding counts of daily growth increments succeeding the hatch check in 2 d post-hatch, 4 d post-hatch and 6 d post-hatch larvae confirmed that the deposition of this check corresponds with the hatching process in NRS rather than several days post-hatch as documented in other flatfish species (Joh et al. 2005).

To determine if an otolith check corresponds with metamorphosis and/or settlement, preserved fish from experimental collections were selected based on the stage of eye migration. Five to ten individuals from each late larval stage were examined based on Ryland's (1966) morphological classification of larval plaice, starting with initial eye migration and concluding with full pigmentation and complete eye migration. Larvae were individually imaged and sagittal otoliths were extracted. Otoliths were mounted onto glass slides and polished using wet-or-dry paper if necessary (2000 grit) and lapping film (3-30 μm) until increments were visible under a dissection scope. Otoliths were imaged at 200x to 1,000x magnification.

Based on results from image analysis, otoliths from bilaterally symmetric larvae were spherical in shape (Fig. 2a) whereas the initiation of eye migration corresponded with the formation of an accessory growth center along the otolith circumference (Fig. 2b and 2c). Additional accessory growth centers were observed when the migrating eye reached the dorsal edge of the head (Fig. 2d). Completion of eye migration corresponded with full pigmentation, dorsal fin morphology (i.e. the dorsal fin reaches the migrating eye) and deposition of a check around the edge of "petal-like" protrusions formed by accessory growth centers (Fig. 2e and 2f). This "metamorphic check" was observed in all age-0 NRS individuals with completed eye migration (SL range = 10.90 -12.43 mm, mean metamorphic check width = $284.88 \mu\text{m} \pm 24.61 \mu\text{m}$, $n = 10$).

Observed changes in both otolith morphology and shape throughout the larval period are largely attributed to the formation of accessory growth centers (i.e. accessory primordia). The otolith flattens, becoming more asymmetrical and this processes corresponds with a region of indistinguishable daily growth increments, precluding empirical increment counts during metamorphosis. Accessory primordia have been previously noted to correspond with metamorphosis and settlement in other species of flatfish (e.g. Campana 1984, Sogard 1991, Alhossaini et al. 1989) although in NRS, initial formation coincided with the start of eye migration. The formation of a check on the otolith corresponded with completion of eye

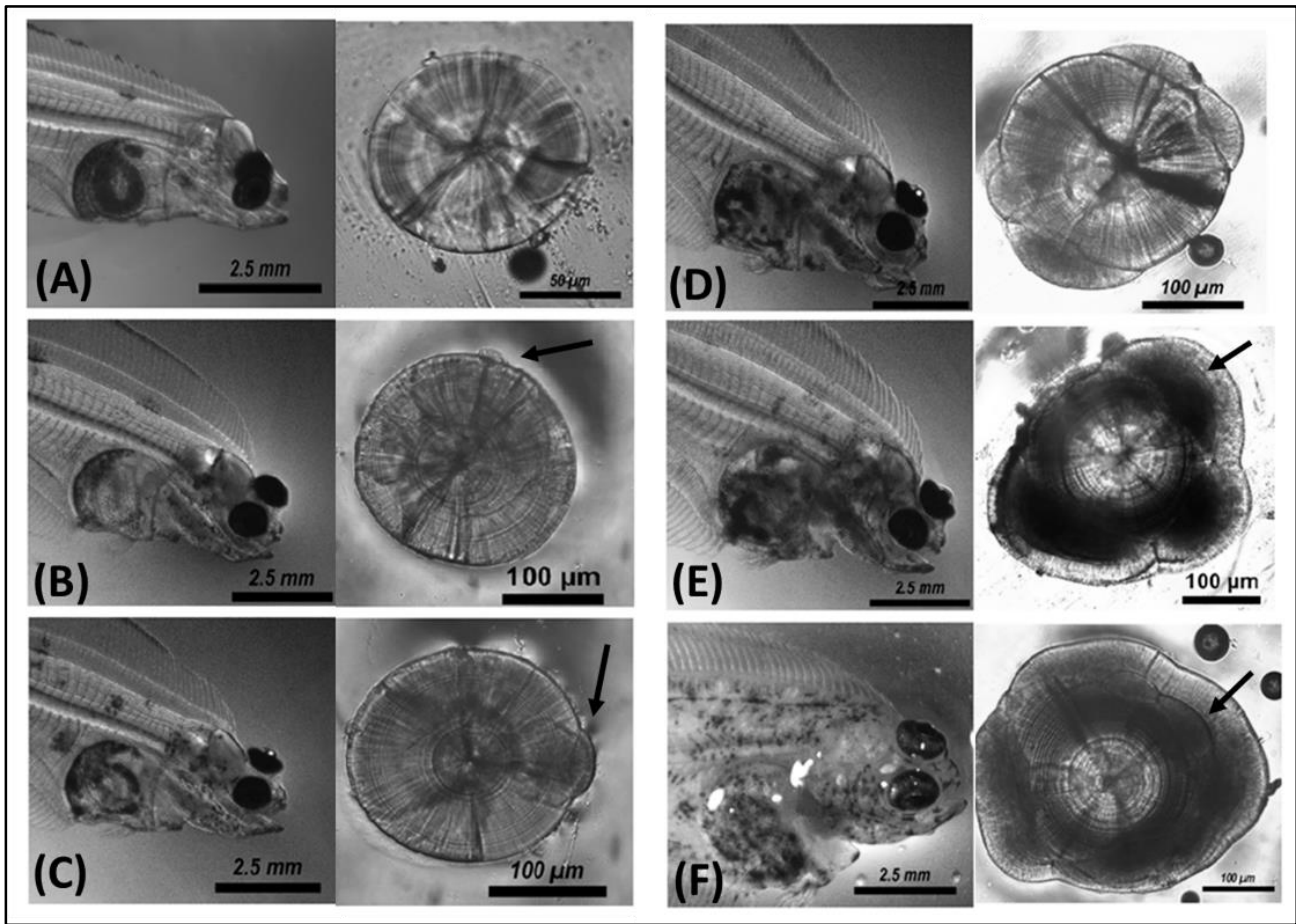


Figure 2. Lab-reared northern rock sole developmental stage and standard length (SL) with corresponding sagittal otolith structure, otolith width (OW) and days-post-hatch (dph): a) Larval stage; bilaterally symmetrical eyes (OW 99.96 μ m, SL 10.40 mm, ~58-63 dph); b) Initial eye migration and formation of accessory primordia (OW 225.54 μ m, SL 12.39 mm, ~85-90 dph); c) Migrating eye at the dorsal edge of head (OW 193.63 μ m, SL 11.49 mm, ~85-90 dph); d) Formation of additional accessory primordia (OW 248.8 μ m, SL 12.40 mm, ~85-90 dph); e) Initial metamorphic check formation (OW 308.39 μ m, SL 12.92 mm, ~85-90 dph); and f) Dorsal fin reaches the migrating eye, enhanced pigmentation and complete formation of metamorphic check (OW 328.85 μ m, metamorphic check width 276.73 μ m, SL 13.98 mm, ~88-93 dph).

migration during metamorphosis. This check was consistently observed in otoliths of field-caught juvenile NRS although at a larger otolith size (mean check width = $328.50 \mu\text{m} \pm 32.28 \mu\text{m}$). Behavioral observations of lab-reared NRS individuals near the completion of eye migration could not verify that the physiological process of metamorphosis coincides temporally with the behavioral process of settlement. Individuals remaining on the bottom of the tank and characterized as “settled” in the laboratory (Laurel et

al. 2014) were often still in the early- to mid-stages of eye migration. This observation suggests that settlement may not be synchronous with completion of eye migration and formation of an otolith check, at least in laboratory culture. Therefore, the observed otolith check was considered a metamorphic check for the remainder of the study.

Laboratory-reared NRS were also used to validate the daily deposition of growth increments. The validation procedure was conducted on age-0 post-settlement NRS and relied on the presence of otolith checks that were formed in response to experimental drops in tank water temperature of $\sim 7^{\circ}\text{C}$. Increment deposition rate was validated by comparing the relationship between increment count and the number of days since the temperature decline. Fish had been euthanized by AFSC staff 5, 10 and 15 d after the temperature change. Sagittal otoliths were acquired from fish that had been euthanized 15 d after the temperature drop and otoliths were extracted, polished and imaged at 400x magnification. Image analysis revealed a clear check near the periphery of the otolith edge. Two independent counts of consecutive daily increments from this check to the otolith edge verified that empirical counts did not statistically differ from the number of days since the temperature drop (mean = 15 ± 1 , t-test, $p > 0.05$, $n = 10$), thereby validating the daily deposition of growth increments.

2.2.6 Preparation and polishing of field-collected juvenile NRS otoliths

Prior to extracting otoliths, field-collected juvenile NRS were thawed and measured (SL, nearest 0.1 mm using a digital caliper). Right and left sagittal otoliths were removed and photographed under a dissecting microscope. Image analysis software (Image-Pro Premier®) was used to measure otolith length (anterior to posterior: longest axis) and otolith width (dorsal to ventral: longest perpendicular axis) from otolith images. Although previous flatfish studies have noted bilateral asymmetry between right and left sagittae (Sogard 1991), no significant differences were found in length or width of right versus left sagittal otoliths across the fish size range examined (13.19-55.76 mm SL) (paired t-test, $p > 0.05$, $n = 52$). Right sagittal otoliths were selected for further otolith analysis and interpretation. A subset of 30-50 otolith samples from each month (July and August) and year (2005, 2007, 2009-2011) at each of the two

nursery sites (Holiday Beach and Pillar Creek Cove) were mounted onto glass slides and polished using wet-or-dry paper (800-2000 grit) and lapping film (3-30 μm) until increments were visible under a dissection scope. Otoliths were then flipped and re-mounted to continue polishing until microstructure was evident and the otolith was transparent. Polished otolith images were acquired with a Leica DC300 camera and Leica DM1000 compound microscope (40-400x magnification).

2.2.7 Microstructural analysis of field-collected juvenile NRS otoliths

Similar to laboratory-reared NRS otoliths, daily increments in field-caught NRS otoliths could not be counted consistently during accessory primordia formation. Therefore, determination of total age was not possible so otolith growth metrics were developed to address the research objectives (Table 2).

Table 2. Northern rock sole otolith size and growth metrics with corresponding methods for microstructural analysis. All measurements were to the nearest 0.01 μm . See Figure 3 for additional information on the otolith landmarks.

Otolith growth metric	Methods
1) Hatch check width (HC_W)	Measure of the diameter of the first opaque check closest to the core of the otolith. Imaged at 1,000x magnification with oil immersion.
2) Early larval growth (EL_IW)	Increment widths of the last 10 daily increments prior to the 45- μm check. Imaged at 400x magnification.
3) Larval growth (L_IW)	Increment widths of the first 10 daily increments after the 45- μm check. Imaged at 400x magnification.
4) Metamorphic check width (MC_W)	Measure of the width (dorsal to ventral otolith axis) of the innermost dark check deposited at the accessory primordial edge, marked by petal-like protrusions in the microstructure.
5) Post-metamorphic growth (PM_IW)	Increment widths of the first 10 daily increments following the metamorphic check. Imaged at 40x and measurements taken from otolith core to edge direction on the ventral axis of otolith.

Daily increment widths were measured to reflect growth rates during specific life history periods whereas the width of both the hatch check (HC_W) and metamorphic check (MC_W) were used as proxies for fish size at these life history events. Ten consecutive otolith increments were measured adjacent to designated otolith landmarks to characterize early larval (EL_IW), larval (L_IW), and post-metamorphic (PM_IW) growth

rates (Fig. 3). The ten consecutive increment widths corresponding with each growth metric were used for longitudinal data analyses. The mean of ten increment width measurements for each growth metric was used in subsequent cross-sectional data analyses. Otolith degradation during storage of field collections prevented the inclusion of additional years and resulted in small sample sizes for 2005 (Table 3).

Table 3. Sample sizes of northern rock sole otoliths with growth metric estimates from microstructural analysis. Sample sizes vary because not all growth metrics were able to be estimated for each individual. ‘*ND*’, or no data, refers to the lack of any readable otoliths during the corresponding period.

Year	Site	Month	Hatch check width (HC _w)	Early larval (EL _{IW})	Larval (L _{IW})	Metamorphic check width (MC _w)	Post-metamorphic (PM _{IW})
2005	Holiday Beach	July	<i>ND</i>	<i>ND</i>	<i>ND</i>	<i>ND</i>	<i>ND</i>
		Aug	17	16	24	26	21
	Pillar Creek Cove	July	4	4	5	7	<i>ND</i>
		Aug	20	11	20	27	19
2007	Holiday Beach	July	4	3	5	8	4
		Aug	17	20	25	25	22
	Pillar Creek Cove	July	6	5	8	9	7
		Aug	23	22	24	25	23
2009	Holiday Beach	July	20	23	26	26	17
		Aug	9	9	14	18	9
	Pillar Creek Cove	July	23	24	27	26	22
		Aug	14	15	20	21	15
2010	Holiday Beach	July	18	16	19	22	10
		Aug	16	15	20	18	19
	Pillar Creek Cove	July	15	18	21	20	14
		Aug	22	22	23	26	23
2011	Holiday Beach	July	11	12	12	13	11
		Aug	11	11	11	13	8
	Pillar Creek Cove	July	9	11	13	13	11
		Aug	7	6	9	14	11

Separate growth metrics were identified for early larval growth and larval growth due to the consistent presence of a check ~45 μ m in diameter and change in increment morphology following this check (0.8 μ m increment width average to post-check 1.2 μ m increment width average). Previous research using microstructural analysis with flatfish otoliths noted similar changes in increment morphology during early larval stages, possibly coinciding with notochord flexion (Jenkins 1987, May & Jenkins 1992). Enumeration of increments from hatch check to the 45- μ m check in individual otoliths with clear microstructure ($n = 30$) indicated that this check is formed approximately 20-30 days-post-hatch. However, given that increments near the hatch check were often indistinct, the last ten increments

prior to the 45- μm check (i.e. ~10-20 days-post-hatch) were measured for all otoliths and used as a metric of early larval growth (Fig. 3b). Larval growth was characterized by the first ten increments following the 45- μm check (i.e. ~30-40 days-post-hatch).

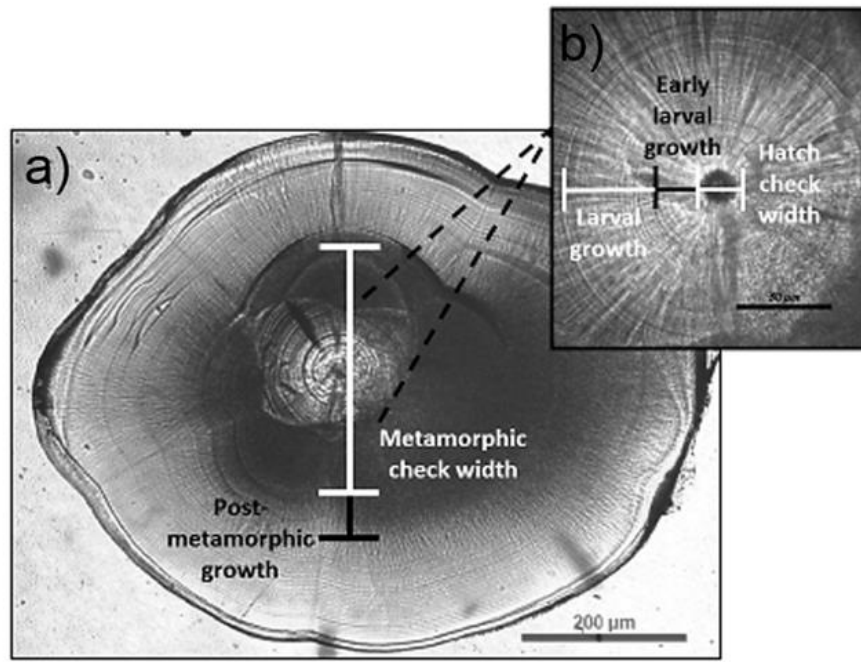


Figure 3. Northern rock sole sagittal otolith landmarks and a) post-metamorphic and b) early larval and larval growth metrics used in the study

Otolith data were organized into longitudinal and cross-sectional data structures for each individual fish. Longitudinal early larval and larval growth estimates consisted of ten consecutive increment widths for each otolith metric. Cross-sectional early larval and larval and growth estimates were the average increment width of all 10 daily increments measured at each respective otolith metric.

2.2.8 Size and date of metamorphosis

Daily increments were counted from the ventral edge of the metamorphic check towards the otolith edge, representing post-metamorphic growth immediately following eye migration (Fig. 3a). The post-metamorphic growth metric (PM_{IW}) was measured across a 10-increment range during the first twenty to thirty days following eye migration whenever possible (73% of the 367 otoliths analyzed).

Continuous daily increment counts from the ventral edge of the metamorphic check to the ventral otolith edge provided an estimate of days from metamorphosis to capture (referred to as days post-metamorphosis). Consecutive increments were counted on the ventral axis of otoliths because daily increments were consistently clearer than all other axes. Two independent counts of days post-metamorphosis increments (average percent error 1.99%) were averaged for further analyses. However, due to difficulties in resolving daily increments continuously from the ventral edge of the metamorphic check to the ventral edge of the otolith, empirical estimates for days post-metamorphosis could be directly determined for only ~15% of analyzed otoliths ($n = 49$). Otoliths with empirical increment counts were primarily fish collected in July because the additional post-settlement growth observed in August fish complicated interpretation of daily increments to the otolith edge (Table 4). In addition, small sample sizes in 2005 and 2011 due to otolith degradation prevented direct counts of days post-metamorphosis for 2005 and August 2011.

Table 4. Summary of otoliths used to empirically estimate the number of days post-metamorphosis. 'ND' refers to the lack of any otoliths with direct counts during the corresponding period.

Year	Month	# of otoliths with direct counts of days post-metamorphosis
2005	July	ND
	August	ND
2007	July	3
	August	3
2009	July	17
	August	3
2010	July	12
	August	1
2011	July	10
	August	ND

A simple model was developed to estimate days post-metamorphosis for all otoliths. Post-metamorphic age determination can be completed by numerically integrating the average width of daily increments across a specified otolith distance (Ralston & Williams 1989). In this study, post-metamorphic ventral otolith growth was highly correlated with days-post-metamorphosis ($r > 0.90$, $p < 0.001$, $n = 49$).

This relationship supports the assumption that post-metamorphic ventral otolith growth is a result of variation in growth and/or time since metamorphosis.

To estimate days post-metamorphosis (D_{PM}), the subset of otoliths with direct counts of days post-metamorphosis were used to develop a relationship between 1) mean post-metamorphic increment width (PM_{IW}) and 2) post-metamorphic ventral otolith growth (V_{OG}) (Equation 1).

$$D_{PM} = \alpha + \beta_1(PM_{IW}) + \beta_2(V_{OG}) \quad (\text{Eq. 1})$$

To assess performance of the multiple linear regression models, individual coefficient of variation (CV) was calculated between direct counts of days post-metamorphosis versus model results of days post-metamorphosis for the 49 individuals with empirical estimates of days since metamorphosis. Calculations indicated an overall CV less than 7% between days post-metamorphosis estimates. Furthermore, normality of residuals was evaluated to ensure that estimates were not systematically over- or under-estimated and model fit was assessed ($r^2 > 0.89$, $p < 0.001$). Date of metamorphosis was then determined for each fish by subtracting days post-metamorphosis model estimates from the known date of capture (73% of the 367 otoliths).

2.2.9 Data Analyses

Statistical analyses of growth variation were completed on otolith measurements (EL_{IW} and L_{IW}) rather than back-calculations of somatic growth. Similarly, measurements of HC_W and MC_W were used to reflect variation in fish “size at hatch” and “size at metamorphosis”, respectively. Data were first tested for normality and homogeneity of variance, and log-transformed when necessary. All statistical analyses were conducted in R, version 3.1.2 (R Development Core Team 2012). Due to missing data in some sites and months, intra-annual nursery site (i.e. Pillar Creek and Holiday Beach) and sampling month (i.e. July or August) effects on larval characteristics were evaluated with Student’s t-tests. Bonferroni corrections were used to account for multiple comparisons and possible Type 1 error associated with such repeated tests. Within-year mean size at hatch, mean early larval growth, mean larval growth and mean size at

metamorphosis of NRS did not vary significantly between nursery sites or sampling month (Student's t-test, $p > 0.05$). Therefore, samples were pooled for each of the growth or size metrics and tested for interannual differences with a one-way Analysis of Variance (ANOVA) and Tukey-Kramer *post-hoc* analyses. Within-year date of metamorphosis comparisons did vary significantly between nursery sites and sampling month (Student's t-test, $p < 0.05$) so a three-way ANOVA with year, month and site main effects was used.

Early larval and larval growth trajectories (i.e. sequential ten-increment width measurements) were compared across years with repeated-measures ANOVA tests. Consecutive ten-increment measures for larval growth metrics are not independent. Therefore, a repeated measures ANOVA was used to examine within-subject (growth between day 1 to day 10) as well as between-population (interannual variation in growth across 10 days) effects.

Relationships between mean size or growth metrics and environmental parameters across years were examined with correlation analyses (Pearson's correlation coefficient). Eight-day mean chl-*a* concentrations and 15-day mean GAK-1 temperatures (herby referred to as larval temperatures) across the time period corresponding with the pelagic larval stage (January 1st to mid-March) were compared with size at hatch, early larval growth and larval growth. Likewise, 15-day mean Trident Bay temperatures (herby referred to as metamorphosis temperatures) across the range of metamorphic dates (Mid-March to mid-July) were compared to mean size at metamorphosis and mean date of metamorphosis. To refine comparisons between size at and date of metamorphosis in relation to temperatures just prior to metamorphosis, pre-metamorphosis temperature (Pre_{Met}) was determined as the mean temperature across the 14-day period prior to the first date of metamorphosis estimate for each year. As NRS metamorphosis may coincide temporally with the spring bloom in the Gulf of Alaska, spring bloom dynamics ($Bloom_{Onset}$, $ChlA_{Max}$ and $ChlA_{Spring}$) were also examined in relation to mean size at and date of metamorphosis. There is the potential for post-settlement selection, which could influence characteristics of fish collected in August compared with those collected in July. Therefore, additional correlation

analyses were performed with growth and size metrics of only July individuals to determine if patterns were similar to analyses using all individuals. Similar patterns would indicate that relationships between growth metrics and environmental parameters were not substantially altered by including August fish.

Correlation analysis was also used to determine if metamorphic metrics were related to prior growth during the larval period. Mean size at metamorphosis and date of metamorphosis were compared with mean early larval and mean larval growth metrics. All α values for correlations were Bonferroni corrected to account for multiple comparisons.

Based on the results of correlation analyses, the greatest variation was observed in the timing of metamorphosis. Therefore, to further explore variation in the timing of metamorphosis that may be introduced from annual and individual-based variability in thermal and productivity conditions experienced by NRS, additional environmental variables were determined for analyses. To describe annual variability in temperatures during metamorphosis, mean temperature across the range of estimated metamorphosis dates for each year was calculated (T_{MetRange}). To characterize individual-based temperature patterns, the mean temperature across the 14-day period prior to each individual fish's date of metamorphosis estimate was determined (T_{Indv}). In addition, to describe annual variability in productivity regimes, mean chl-*a* concentration was calculated across the 14-day period prior to the mean estimated date of metamorphosis for each year ($\text{ChlA}_{\text{PreMet}}$). To characterize individual-based chl-*a* conditions, the mean chl-*a* concentration across the 14-day period prior to individual date of metamorphosis estimates was determined ($\text{ChlA}_{\text{Indv}}$). The annual date of the spring bloom onset ($\text{Bloom}_{\text{Onset}}$) was also included in analyses.

To quantify the relative influence of environmental variables on the timing of metamorphosis, multivariate linear regression models were fit and evaluated with Akaike information criteria adjusted for small sample size (AIC_c) (Burnham & Anderson 2004). Due to inherent collinearity between temperatures and chl-*a* concentrations, variable selection for model inclusion was contingent on variance inflation factor (VIF) values for each predictor to estimate how much the variance of the coefficient was

“inflated” due to linear dependence with other predictors. Variables with the highest VIF were sequentially dropped from models until all VIFs were smaller than the selected threshold ($VIF < 2$) (Zuur et al. 2009). Model fitting consisted of comparing a series of candidate models across values for 1) the difference between the AICc of the best fitting model and that of model i , (Δ_i); 2) Akaike weight, (w_i); and 3) coefficient of determination, (R^2) (R package ‘AICcmodavg’). The relative importance of each model was also assessed to quantify each individual parameter’s contribution to the regression model (R package ‘relaimpo’).

2.3 RESULTS

2.3.1 Environmental parameters: temperature variation

Annual minimum larval temperatures (3.1-4.6°C) were consistently observed in February and March with temperatures increasing in mid-April to May. Average temperatures in 2005 and 2010 were at least 1°C warmer than average temperatures in 2007 and 2009 (Fig. 4a, one-way ANOVA, $p < 0.001$), with 2007 being one of the coldest winters in the central Gulf of Alaska in the past 40 years (Fig. A1). Notably, 2010 was the warmest year during the larval period (average 4.8°C). Nursery ground temperatures steadily increased from April to July and temperatures were consistently the warmest in 2005, averaging at least 1°C warmer than those in any other year and at least 1.5°C warmer than 2007 and 2009 temperatures (Fig. 4b, one-way ANOVA, $p < 0.001$). May to September nursery temperatures in 2005 were anomalously warm in relation to the 17-year Trident Basin temperature record as well (Fig. A2).

2.3.2 Environmental parameters: spring bloom dynamics

The spring bloom in the proximity of Kodiak Island was evident in satellite-derived chl- a data. In early April, chl- a concentrations increased from winter baseline pre-bloom conditions and by late-April to early-May, chl- a concentrations had exceeded the annual median concentration, signifying the onset of the spring bloom (range 1.47-2.97 mg m⁻³) (Fig. 4c). Annual maximum chl- a concentrations were reached by mid-May (max range 2.50-7.07 mg m⁻³). Following the peak of the spring bloom, chl- a concentrations

decreased until June when moderate blooms occurred (max range 2.18-5.59 mg m⁻³). Chl-*a* concentrations in July declined, though levels still remained fairly high for the duration of the summer period. Chl-*a* concentrations and date of the bloom onset also differed among years. The largest spring bloom occurred in 2009 (max concentration 7.07 mg m⁻³) and the smallest occurred in 2007 (2.50 mg m⁻³). The earliest date of bloom onset occurred in 2011 (3 April) while the latest date of onset occurred in 2009 (7 May).

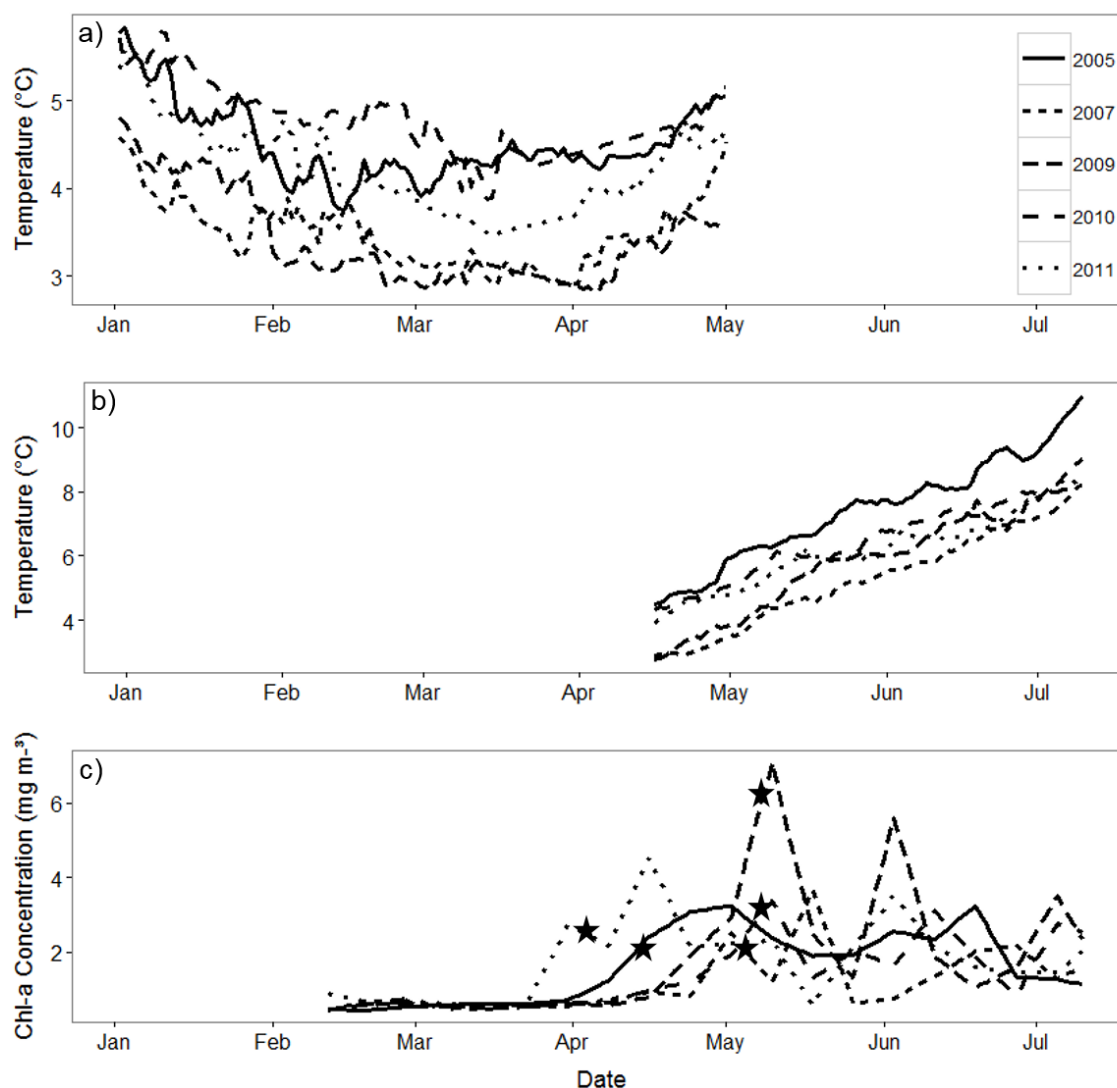


Figure 4. Interannual variability in a) mean GAK-1 temperature records corresponding with northern rock sole larval stages; b) mean Trident Basin temperature records corresponding with northern rock sole metamorphosis; c) mean chl-*a* concentrations and the annual date of spring bloom onset in waters surrounding Kodiak Island, Alaska. Annual bloom onset dates are indicated by black stars.

Interpolated chl-*a* concentrations from mid-February to June were positively correlated with daily temperatures during the larval period in 2005, 2007, 2009 and 2010 ($r > 0.30$, $p < 0.001$). Chl-*a* concentrations in 2011, however, were not correlated with temperatures, likely due to the previously noted early spring bloom date and simultaneous increase in chl-*a* concentrations despite fairly low temperatures. Daily chl-*a* concentrations from mid-February to late-August were correlated with metamorphosis and post-settlement temperatures in 2007, 2009, 2010 and 2011 ($r > 0.30$, $p < 0.001$). Very high metamorphosis temperatures but moderate chl-*a* concentrations in 2005 likely resulted in decoupling of the two environmental parameters.

2.3.3 *Size at hatch, early larval and larval growth patterns*

Size at hatch differed significantly across years with a larger mean size at hatch in 2010 compared to 2011 (Fig. 5a, Kruskal-Wallis ANOVA, $p < 0.001$). Log-transformed mean early larval growth also differed significantly across years, with larvae exhibiting faster growth in 2005 than all other years (Fig. 5b, ANOVA, $p < 0.001$). Likewise, interannual comparisons of mean larval growth indicated that growth was faster in 2005, 2009 and 2010 than in 2007 and 2011 (Fig. 5c, Kruskal-Wallis ANOVA, $p < 0.001$).

Repeated-measures analysis of early larval growth trajectories revealed a significant interaction between increment widths and year, indicating that early larval growth varied interannually over the 10-day growth period (Fig. 6a, $p < 0.001$). Increment width increased from day 1 to day 10, which resulted in significant within-subject growth differences ($p < 0.001$). Likewise, the between-subject year effect was significant, with larvae growing faster across 10 days in 2005 than any other year ($p < 0.01$). Results were similar for longitudinal data analysis of larval growth. There was a significant interaction between day 1 to day 10 increment widths and year (Fig. 6b, $p < 0.05$) as well as significant differences between within-subject growth across 10 days. Between-subject growth differences across years indicated that larval growth across 10 days was faster in 2005 compared to 2007 ($p < 0.01$).

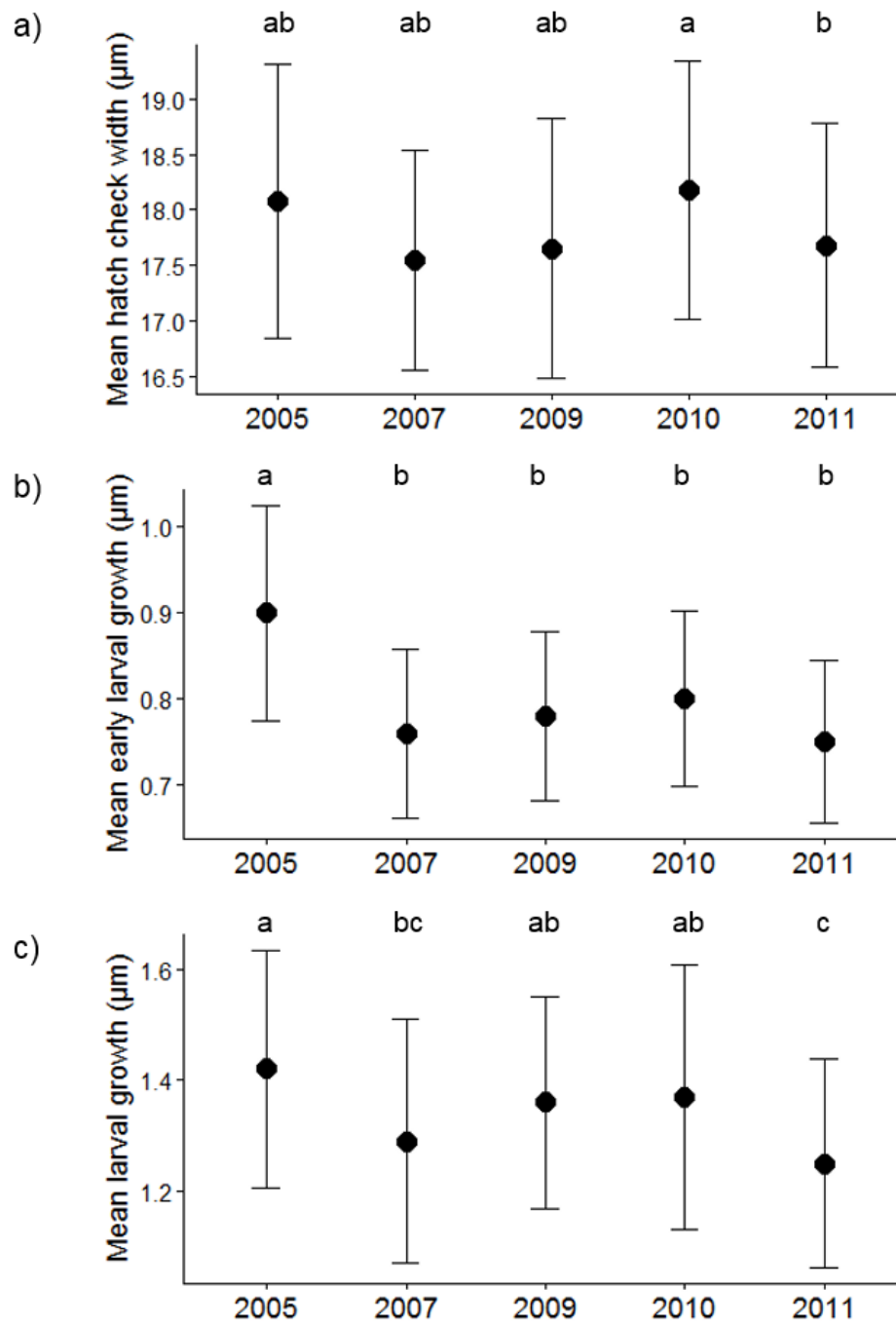


Figure 5. Annual mean (\pm SD) of a) hatch check width, b) mean early larval growth and c) mean larval growth of northern rock sole. Letters indicate significant differences from Tukey-Kramer post-hoc analyses (ANOVA, $p < 0.05$).

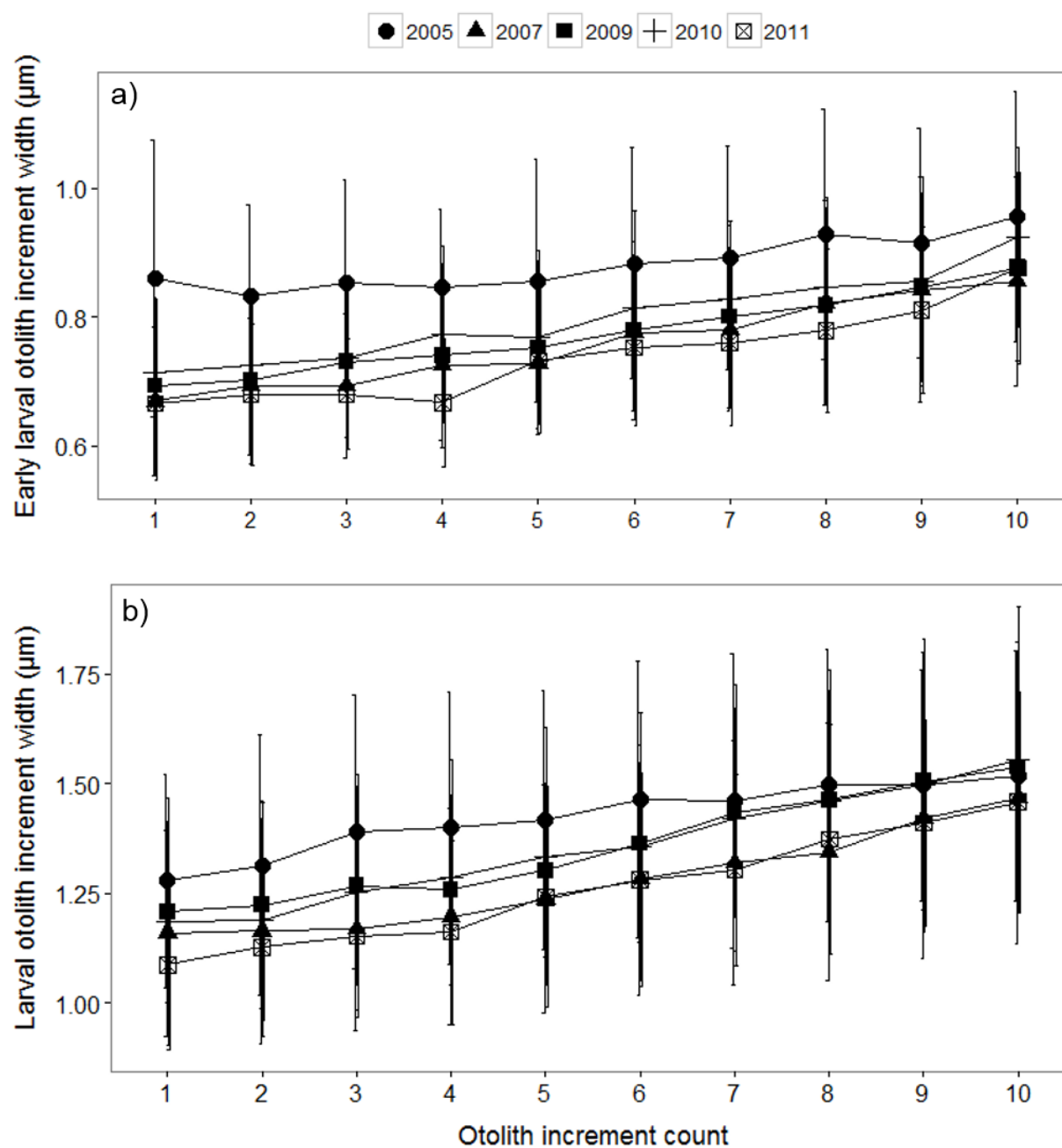


Figure 6. Annual mean (\pm SD) of a) early larval and b) larval daily growth trajectories (otolith increment widths) across consecutively measured increments 1 through 10, beginning at specified otolith microstructural landmarks.

2.3.4 Size at and date of metamorphosis

Overall mean metamorphic check width was $328.50 \pm 32.28 \mu\text{m}$ ($n = 357$) and there was no significant year effect on size at metamorphosis (ANOVA, $p > 0.05$). Date of metamorphosis estimates for all NRS individuals spanned nearly 4 months from late March to mid-July (Fig. 7). Distributions were fairly protracted with a continuous distribution of dates within each year. Interannual variation in date of metamorphosis was characterized by a significantly earlier mean date of metamorphosis in 2005 (4 May) compared to all other years. Conversely, later mean dates of metamorphosis in 2009 (28 May) and 2007 (5 June) differed significantly from each other as well as the other three years (3-way ANOVA, $p < 0.01$). In addition, there were significant interactions between month and year as well as month and site on individual date of metamorphosis estimates. Site differences were driven by earlier dates of

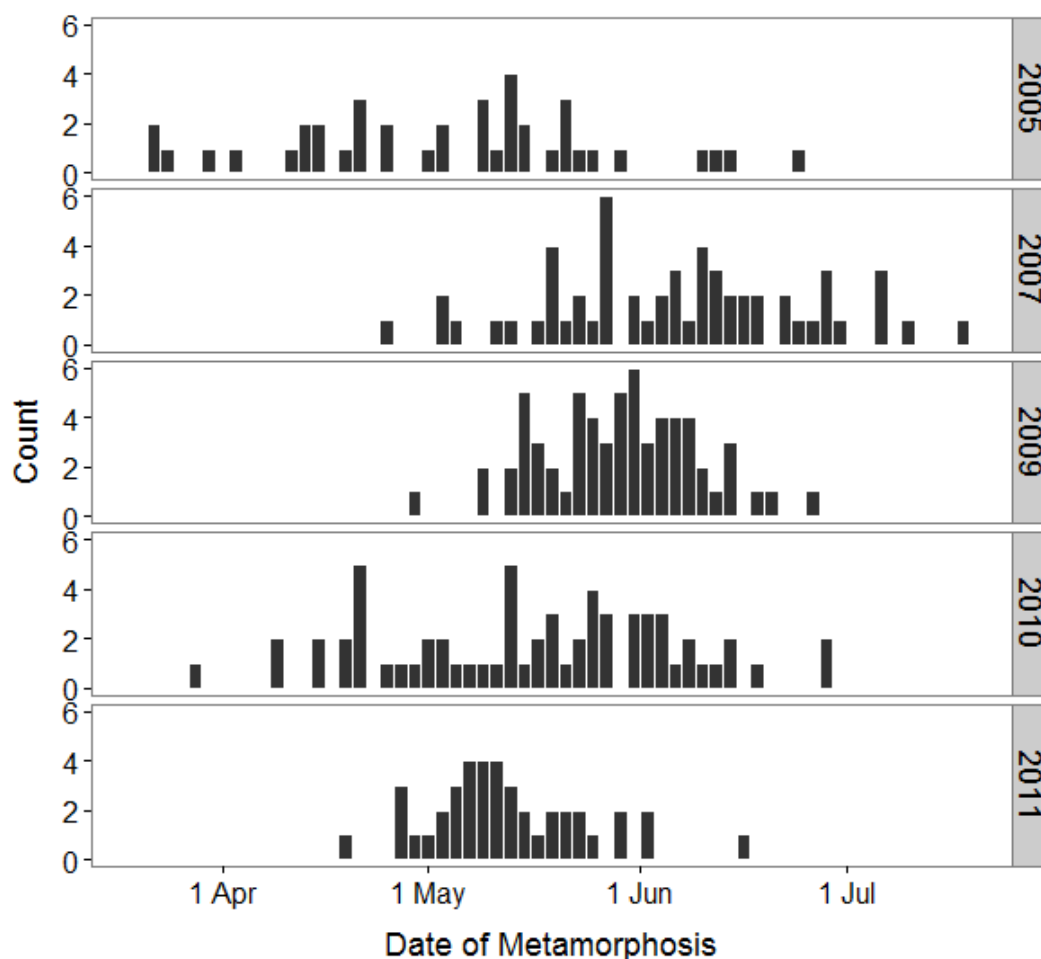


Figure 7. Interannual variation in estimated date of metamorphosis of northern rock sole individuals.

metamorphosis in Holiday Beach in 2005 and 2007 (site x year interaction, $p < 0.01$). July fish in 2010 had later dates of metamorphosis than August fish, driving the significant month x year interaction ($p < 0.01$).

2.3.5 Environmental parameters in relation to larval and metamorphic characteristics

Size at hatch, early larval growth, larval growth and size at metamorphosis of July individuals were not significantly correlated with temperatures or spring bloom dynamics (r -values < 0.48). For July fish dates of metamorphosis, there was a non-significant negative trend with temperatures from late March to early May (r -values = -0.53 to -0.70). When all fish were included in the analyses, mean size at hatch was positively correlated with several of the 15-day mean temperature periods (r -values = 0.69 - 0.93, Table 5), but none of these were significant after Bonferroni correction for multiple tests. Contrary to the hypotheses, early larval growth and larval growth were not related to 15-day mean temperatures or 8-day mean chl-*a* concentrations (Tables 5 and 6). Similarly, size at and date of metamorphosis were not correlated with spring bloom dynamics (Table 7). While size at metamorphosis was not correlated with temperatures, mean date of metamorphosis was negatively correlated with temperatures two weeks prior to the annual onset of metamorphosis ($r = -0.99$) as well as mean temperatures in late April and early May (Table 8, $r > -0.97$, $p < 0.01$). This relationship suggests that cooler years resulted in a shift to later dates whereas in warmer years, metamorphosis occurred earlier.

Table 5. Pearson product-moment correlation coefficients (r) for comparisons between annual means of northern rock sole larval growth metrics and 15-day mean larval temperatures from the GAK1 buoy (20 m depth).

Larval growth metric	15-day mean temperatures				
	Jan 1-14	Jan 15-29	Jan 30-Feb 13	Feb 14-28	Mar 1-15
Mean size at hatch	0.88*	0.89*	0.69	0.86	0.93*
Mean early larval growth	0.50	0.49	0.15	0.33	0.60
Mean larval growth	0.39	0.46	0.00	0.25	0.46

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** ($p < 0.01$). $n = 5$ for all comparisons.

Table 6. Pearson product-moment correlation coefficients (r) for comparisons between annual means of northern rock sole larval growth metrics and 8-day mean chlorophyll- a concentrations (MODIS-Aqua, 9 km).

Larval growth metric	8-day mean chlorophyll- a concentration				
	Feb 10-17	Feb 18-25	Feb 26-Mar 5	Mar 6-13	Mar 14-21
Mean size at hatch	-0.23	-0.67	0.00	-0.43	0.75
Mean early larval growth	-0.38	-0.96*	-0.71	0.02	0.46
Mean larval growth	-0.66	-0.93*	-0.52	-0.35	0.26

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** ($p < 0.01$). $n = 5$ for all comparisons.

Table 7. Pearson product-moment correlation coefficients (r) for comparisons between annual means of northern rock sole metamorphosis growth metrics and timing of the spring bloom (Bloom_{Onset}), magnitude of the bloom (ChlA_{Max}) and March-May average chl- a concentration (ChlA_{Spring}) using 8-day mean chlorophyll- a concentration data (MODIS-Aqua, 9 km).

Metamorphosis growth metric	Spring bloom dynamics		
	Bloom _{Onset}	ChlA _{Max}	ChlA _{Spring}
Mean size at metamorphosis	-0.03	0.33	0.47
Mean date of metamorphosis	0.65	0.38	-0.51

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** ($p < 0.017$). $n = 5$ for all comparisons.

Table 8. Pearson product-moment correlation coefficients (r) for comparisons between annual means of northern rock sole metamorphosis growth metrics and 15-day mean metamorphosis temperatures from Trident Bay, AK (10 m depth). Pre-metamorphosis temperature (Pre_{Met}) was determined as the mean temperature across the 14-day period prior to the onset of metamorphosis each year.

Growth metric	15-day mean temperatures								
	Pre _{Met}	Mar 19-Apr 2	Apr 3-17	Apr 18-May 2	May 3-17	May 18-Jun 1	Jun 2-16	Jun 17-Jul 1	Jul 2-16
Mean size at metamorphosis	0.44	0.22	0.13	0.27	0.40	0.74	0.66	0.74	0.86
Mean date of metamorphosis	-0.99**	-0.95	-0.96	-0.98**	-0.97**	-0.87	-0.87	-0.79	-0.64

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** ($p < 0.006$). $n = 5$ for all comparisons.

2.3.6 Size at and timing of metamorphosis in relation to early larval and larval growth

Mean size at metamorphosis and date of metamorphosis were not significantly correlated with mean larval growth metrics. However, the trends for all comparisons were in the expected direction (i.e. faster larval growth associated with larger size at metamorphosis and earlier dates of metamorphosis). Visual examination of mean early larval and larval growth comparisons with mean date of metamorphosis indicated that 2011 appeared to be an outlier, likely resulting in non-significant overall patterns.

Table 9. Pearson product-moment correlation coefficients (r) for comparisons between annual means of northern rock sole larval growth metrics and metamorphosis growth metrics.

	Larval growth metric	
	Mean early larval growth	Mean larval growth
Mean size at metamorphosis	0.73	0.74
Mean date of metamorphosis	-0.66	-0.35

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** ($p < 0.025$). $n = 5$ for all comparisons.

2.3.7 Variation in timing of metamorphosis in relation to environmental conditions:

All five environmental variables were included in candidate models to estimate time of metamorphosis, although multicollinearity ($VIF > 2$) resulted in exclusion of the majority of interaction terms in models. Fifteen models were evaluated and results were only included for those models with Akaike weight (w_i) > 0 . Based on results of performance criteria, models containing both temperature parameters T_{Indv} and $T_{MetRange}$ received considerably more support ($\Delta_i < 2$, M1-M4, Table 10) than models including spring bloom dynamics (M3-M5). Model M5, which included neither of the temperature parameters, performed poorly ($w_i < 0.001$). The model selected by performance criteria (M1, $w_i = 0.4223$) indicates that temperature conditions experienced by individuals two weeks prior to metamorphosis (T_{Indv}) as well as temperatures during the overall temporal window of metamorphosis across years ($T_{MetRange}$) reflect the variation in timing of metamorphosis (Fig. 8). Calculations of the relative importance of variables in each model indicated that T_{Indv} accounted for $>60\%$ of the variation in timing of metamorphosis in M2-M4 and $>70\%$ of the variation in M1.

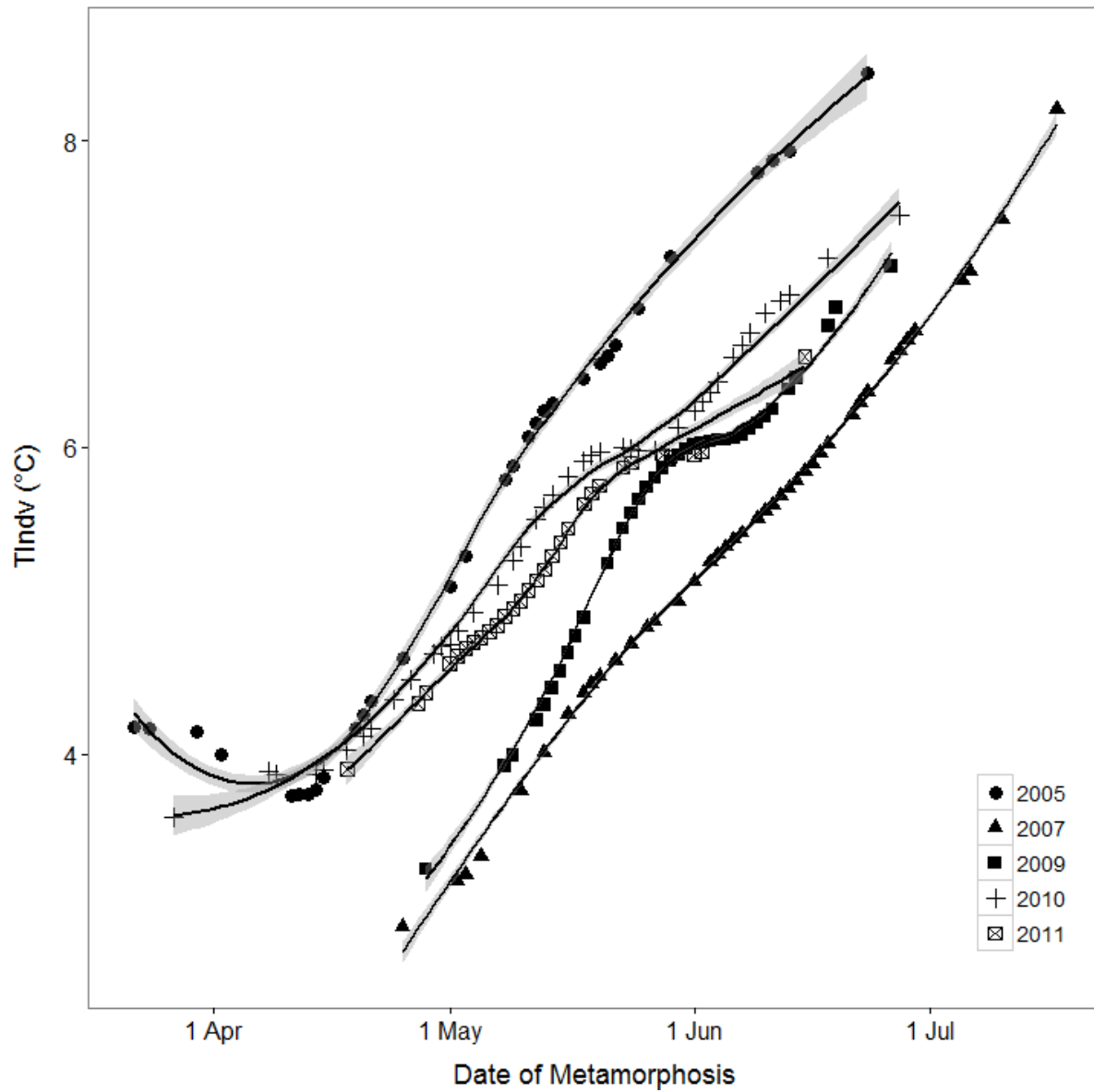


Figure 8. Estimated date of metamorphosis of northern rock sole individuals in relation to temperatures experienced during the two weeks prior to metamorphosis (T_{Indv}). Fitted lines (\pm SE) represent the temperature range experienced by individuals across each year during metamorphosis.

Table 10. Top five model results to evaluate spring bloom dynamics and temperate effects on individual date of metamorphosis in northern rock sole.

Model	Environmental variables	AIC _c	Δ_i	w_i
M1	T _{Indv} , T _{MetRange}	1543.98	0.00	0.42
M2	T _{Indv} , T _{MetRange} , T _{Indv} X T _{MetRange}	1545.34	1.37	0.21
M3	T _{Indv} , T _{MetRange} , ChlA _{Indv} , Bloom _{Onset}	1545.41	1.43	0.21
M4	T _{Indv} , T _{MetRange} , Bloom _{Onset}	1545.94	1.96	0.16
M5	ChlA _{Indv} , ChlA _{PreMet} , Bloom _{Onset}	2256.34	712.36	<0.01

Note: T_{Indv}, mean temperature across 14 day period prior to individual date of metamorphosis estimates; T_{MetRange}, annual mean temperature across range of all estimated metamorphic dates; ChlA_{Indv}, mean chl-*a* concentration across 14-day period prior to individual date of metamorphosis estimates; ChlA_{PreMet}, annual mean chl-*a* concentration across 14-day period prior to the mean estimated date of metamorphosis for each year; Bloom_{Onset}, Julian date of spring bloom onset. Akaike information criteria adjusted for small sample sizes (AIC_c), difference between AIC_c of the best model (Δ_i) and Akaike weight (w_i) are given for each model.

2.4 DISCUSSION

This study combined multiple years of field collections with otolith structural analysis to document interannual variation in early life history characteristics of NRS and present the first estimates of size at and timing of metamorphosis of field-caught NRS. Evaluating the relative influence of environmental conditions in the Gulf of Alaska on early life history characteristics revealed that temperature conditions experienced prior to and during metamorphosis were the primary driver of the timing of metamorphosis. Conversely, size at metamorphosis displayed little variability and appears to be driven by ontogeny rather than environmental conditions or earlier larval growth. These results suggest that temperature variability in the Gulf of Alaska may exert a stronger influence on the phenology of critical life history events compared to other early life history characteristics such as size and growth.

Temperature is assumed to be one of the primary influences on fish growth and previous research indicates that warmer temperatures lead to faster growth in larval flatfish (Benoit & Pepin 1999, Bidwell & Howell 2001, Hutchinson & Hawkins 2004, Laurel & Blood 2011). In this study, the patterns of variation in NRS larval growth metrics were generally consistent with these thermal effects, despite the lack of significant correlations with temperature. However, several factors reduced the power of these analyses. Because the formation of accessory primordia in the otolith at the time of metamorphosis

obscured daily increment formation, larval growth increments could not be assigned to specific dates. Therefore, analyses were based on temperatures in fixed temporal windows across years. Additionally, the lack of a significant correlation with temperature across years appeared to be due to the occurrence of anomalously slow growth in 2011 despite moderate temperatures. The fastest larval growth occurred in 2005, the warmest year in the study period, while in the cold year, 2007, growth was relatively slow. The years 2009, 2010 and 2011 are fairly “intermediate” in regard to temperature across the 40-year GAK-1 temperature record, particularly when compared to more anomalous conditions in 2005 and 2007. Similarly, larval growth in 2009 and 2010 was intermediate although the apparent anomalously slow growth in 2011 suggests that warm temperatures may be necessary, but not sufficient to promote rapid growth of larval NRS.

Although not significant after Bonferroni correction, mean size at hatch was positively correlated with temperatures during the winter-spring spawning period. Interestingly, this pattern differs from results in Laurel and Blood (2011). Laboratory incubation in colder temperatures resulted in larger, rather than smaller, sizes at hatch and larvae were able to more efficiently utilize endogenous resources for growth after hatch. The difference between these two observations could suggest that size at hatch is influenced by selective mortality in the field that is not observed in the laboratory. In addition, maternal effects could play a larger role than rearing and spawning temperatures on size at hatch in field-collected NRS in the Gulf of Alaska. For example, female condition prior to spawning as well as conditions during spawning and egg stages may result in interannual variability in size at hatch and larval growth. Variation in size at hatch has been linked to variability in egg size, which is often a consequence of maternal effects and rearing temperatures (as well as their synergistic interactions) (Howell 1980, Chambers & Leggett 1996, Benoit & Pepin 1999). In a recent study, size at hatch of larval NRS differed among four different females (Hurst et al. 2015). Results suggest that feeding conditions and water temperatures prior to spawning could influence a female’s condition, which may then lead to influences on egg size and size at hatch. Studies also demonstrate that variation in larval growth, pelagic larval duration and survival to settlement

can be influenced by maternal effects in addition to the environmental conditions larvae experience (McCormick 1999, Kerrigan 1997). Maternal effects on size at hatch and early larval growth could then influence growth and size in later stages (i.e. larger size at hatch correlated with fast larval growth).

There was little interannual variation in size at metamorphosis, suggesting that metamorphosis in NRS is a strongly size-dependent process. This “competent” size for metamorphosis as well as a constraint in variation in size at metamorphosis has been noted in other flatfish species (Chambers & Leggett 1987, Keefe & Able 1993, Amara et al. 2000). Results indicate that metamorphosis is a time of convergence in the life history of NRS despite interannual variation in hatch size and larval growth rates. Metamorphosis may act as a compensatory processes in response to larval growth or size depression, dampening variability in traits induced from hatch to late larval stages as sizes converge at the onset of metamorphosis. However, as growth during the larval period was not associated with size at metamorphosis in NRS, ontogeny is likely more dependent on size and instead, can be uncoupled from growth (Fuiman 1997).

If larval growth metrics vary interannually but size at metamorphosis does not, the most parsimonious explanation for the ability of NRS to reach the competent size range for metamorphosis is that the timing of metamorphosis, instead, must vary. For instance, fast larval growth means that larvae must reach the optimal size for metamorphosis earlier. Despite fairly protracted metamorphosis dates within each year as well as differences in the scale of variation among years, there were interannual differences in the timing of metamorphosis. Negative correlations between the timing of metamorphosis and water temperatures were evident from mid-March to mid-July, suggesting that temperature has a cumulative effect on the entire range of metamorphic dates observed within years. Analyses limited to July fish indicated that correlations between mean date of metamorphosis and temperature were also negative, although insignificant. The difference between the July data set versus the overall data set could be due to lack of data on the date of metamorphosis for July fish in 2005 and, hence, a smaller sample

size. While overall patterns between both data sets were similar, the potential for month effects on the timing of metamorphosis as well as additional analyses examining selection are addressed in Chapter 3.

Results also indicated that temperature is the primary driver of the date of metamorphosis of NRS individuals as well as the annual mean date of metamorphosis. Thermal conditions experienced by individuals ~2 weeks prior to metamorphosis explained more than 70% of the variation in timing of metamorphosis. While variation in individual temperature conditions (T_{Indv}) explained the majority of metamorphosis phenology, annual temperature means (T_{MetRange}) across the date range of metamorphosis also influenced the timing of metamorphosis. The overall thermal regime represents the effect of interannual variation in temperature experienced by the entire cohort, driving earlier dates of metamorphosis in warmer years and later dates in colder years. The individual temperature metric provides a seasonal signal where individuals experiencing warmer temperatures two weeks prior to metamorphosis are those metamorphosing later in that year while individuals experiencing colder temperatures metamorphosed earlier in the season. The effects of this seasonal increase in temperatures in combination with an observed delay in metamorphosis in colder years would be expected to reduce the variation in metamorphosis timing compared to that which may be generated by variation in hatch time within a year. Early-spawned individuals would experience colder temperatures and exhibit relatively slow larval growth such that phenology is delayed until later in the season when water temperatures are warmer. On the contrary, late-spawned individuals develop faster due to warmer temperatures so metamorphosis occurs before temperatures reach their maximum for the season.

Another possible contributing factor for correlations between the timing of metamorphosis and pre-metamorphosis temperatures is that temperatures may influence the phenology of earlier life history events such as spawning and hatching. In the absence of strong compensatory mechanisms, a temperature-dependent shift in the time of spawn would result in associated shifts in the timing of hatch and metamorphosis. Rather it is more likely that if low temperatures delay spawning activity, the temporal autocorrelation of conditions would mean that lower temperatures during the egg and larval

stages would further delay hatch and metamorphosis. The effects of thermal history may be carried across life history stages, contributing to variation in phenology across years with varying thermal regimes (Dougherty et al. 2007). The timing of metamorphosis and settlement have been associated with temporal variation in spawning in other flatfish studies (Beggs & Nash 2007, Genner et al. 2010) and a strong relationship between late-larval temperatures and the timing of metamorphosis in NRS suggests that cohorts may display temperature-driven phenological shifts in earlier life stages as well.

In addition to environmental conditions, many other studies have attributed shifts in the size at and timing of metamorphosis and settlement to larval growth characteristics (Burke et al. 1999, Fernández-Díaz et al. 2001, Laurel et al. 2014). Laurel et al. (2014) concluded that NRS were more likely to settle earlier in warmer rearing conditions due to faster larval growth. The lack of a strong relationship between temperature and growth during the larval stage suggests that growth may be uncoupled from the timing of key early life history events. An explanation for this is through the potential for NRS individuals to grow moderately faster in cold temperatures than would be predicted due to less thermal sensitivity in growth rates (Hurst et al. 2010, Ryer et al. 2012, Matta et al. 2010). This suggests that as a “cold-adapted” species, NRS larvae may be less subject to temperature-mediated influences on growth and not as responsive to cooler thermal regimes as hypothesized (Laurel & Blood 2011).

Little evidence for temperature effects on larval growth metrics suggests that food availability could have a larger influence on larval growth and size, although this hypothesis was not supported with correlation analyses. The highly variable and frequently negative correlations between spring bloom dynamics and larval growth metrics suggest that limited availability to food or starvation may not be the primary factors driving larval growth dynamics, or that primary production is not a reliable indicator of NRS prey. Given the cooler winter to early-spring water temperatures that NRS larvae experience in the Gulf of Alaska, larvae may be able to tolerate low-food conditions due to lower metabolic rates. The NRS life history strategy is an intermediate to “early production” (i.e. winter spawners) and “late production” phenologies (i.e. summer spawners). Therefore, early larval stages coincide with low- production, pre-

bloom conditions well before the onset of the spring bloom and peak of chl-*a* concentrations (Doyle & Mier 2012). It is hypothesized that mid-winter to spring spawning species such as NRS could use protracted spawning as a mechanism to compensate for this potential mismatch with food resources (Mertz & Myers 1994). Interannual variation in phytoplankton production, for example, could be mediated by the protracted spawning window of NRS (~January to April), resulting in a subset of larvae that may be less sensitive to trends in phytoplankton dynamics.

Insignificant correlations between spring bloom dynamics and NRS growth metrics could also suggest that chl-*a* concentrations are not a suitable proxy for the NRS larval feeding environment. While little research has been done on NRS larval feeding ecology, walleye pollock, another mid-winter spawner, primarily consume copepod eggs, nauplii and copepodites as larvae (Hillgruber et al. 1995). Pollock recruitment in the Bering Sea has been linked to secondary production, with zooplankton production being more closely tied to water temperatures than spring bloom dynamics (Hunt et al. 2011, Hunt et al. 2002). Furthermore, secondary production can be out of sync with primary production as overwintering zooplankton and nauplii provide important food resources to larval fish prior to the onset of the spring bloom in the Gulf of Alaska (Napp et al. 1996). These observations suggest that secondary production is a more direct proxy of larval food availability for NRS and therefore could be more closely linked to NRS growth dynamics rather than primary production and chl-*a* concentrations.

In conclusion, this study provides valuable insight on temperature-driven shifts in the timing of metamorphosis in NRS. Temperatures in the Gulf of Alaska were the best predictor of variation in the date of metamorphosis and NRS display phenological plasticity in relation to both annual thermal regimes and individual temperature conditions experienced. Results indicated that temperature may be related to growth during the larval stage as well. The size at which NRS metamorphosed, however, was fairly constrained and appeared to be driven by ontogeny. This study provides further evidence that metamorphosis is a size-dependent process and acts as a point of convergence, reducing variability induced during larval stages. However, links between phenology and temperature require further research

to understand how temperatures influence the timing of earlier life history events such as spawn and hatch. Determining temporal influences on phenology across several life history stages could help clarify if, and how, phenologies are coupled across a variety of environmental conditions. Similarly, research exploring shifts in the timing of early life history events could have implication for understanding long-term shifts in phenology in response to climate change that may affect survival and recruitment of NRS.

3. POST-SETTLEMENT GROWTH AND SELECTIVE MORTALITY OF JUVENILE NORTHERN ROCK SOLE (*LEPIDOPSETTA POLYXYSTRA*) IN GULF OF ALASKA NURSERY HABITATS IN RELATION TO EARLY LIFE HISTORY CHARACTERISTICS AND ENVIRONMENTAL VARIABILITY

3.1 INTRODUCTION

Marine fish species such as flatfish are characterized by a complex life cycle with discrete pelagic larval and benthic juvenile stages. The stages are inherently connected across the life history of individuals and the effects of conditions in one stage may “carry-over” to the subsequent stage and influence performance (Harrison et al. 2011). Relatively fast larval growth, for example, may lead to fast juvenile growth (Chambers et al. 1988) and enhanced survival in post-settlement stages (Shima & Findlay 2002, McCormick & Hoey 2004). Understanding an individual’s history can also provide insight into future life history processes such as recruitment and population dynamics (Shima & Swearer 2009). The strength and direction of carry-over effects may vary across spatial and temporal scales as well as across environmental conditions (Smith & Shima 2011, Gagliano et al. 2007a). Ultimately, identifying the potential effects of variation in traits that are carried over across life history stages is crucial because this variability enables selective processes to act on both individuals and populations (McCormick 1998).

As early life history stages are subject to high mortality rates, many studies have focused on identifying which members of a cohort survive non-random mortality events. Often, the likelihood of survival is directly linked to individual growth and size through selective mortality (Sogard 1997). The growth-mortality hypothesis predicts that faster-growing and larger individuals have a higher probability of survival (Anderson 1988). Three mechanisms have specifically been proposed to explain the hypothesis: 1) the “bigger-is-better” mechanism in which faster growing larvae will be bigger, thus enabling more effective predator evasion and prey capture (Miller et al. 1988, Fuiman 1994, Leggett & Deblois 1994); 2) the “stage-duration” mechanism which predicts that faster growing larvae will spend less time in the vulnerable larval stage and therefore reduce mortality risk (Houde 1987); and more recently 3) the “growth selective predation” hypothesis in which slower growing individuals are more

prone to predation independent of size or stage duration (Takasuka et al. 2003, 2004). These hypotheses have been an important focus of research on the early life history of marine fishes and are the basis of a large number of studies (e.g. Meekan & Fortier 1996, Hare & Cowen 1997, Searcy & Sponaugle 2001, Vigliola & Meekan 2002). The likelihood of predation events may be influenced by prior growth, making the growth-mortality hypothesis a means to examine carry-over effects in relation to post-settlement survival. The magnitude and direction of selective pressures can change with ontogeny, demonstrating the importance of integrating analyses across life history stages to understand underlying processes driving trait-mediated survival.

Settlement to the benthos following metamorphosis in flatfish exposes individuals to a novel habitat with a distinct suite of predators which may increase the vulnerability of recently settled individuals to mortality. Predation is considered the primary source of mortality in nursery grounds and individuals that settle small are the most vulnerable to size selective predation (Ellis & Gibson 1995, Nash & Geffen 2000). These observations indicate that growth and size characteristics are especially important in nurseries and small changes in nursery conditions could therefore influence growth and subsequent survival. The quality of a nursery is defined by its capacity to optimize growth and survival. Growth in these often highly concentrated nursery grounds is influenced by factors such as density-dependent processes, the quantity and quality of prey, and environmental factors such as temperature (Gibson 1994). Nursery habitat characteristics can vary spatially and temporally and these differences may lead to distinct selective environments that drive variation in size and growth traits as well as the intensity of subsequent selection (Smith & Shima 2011).

Density dependence is a fundamental concept in flatfish growth dynamics. Nurseries are the initial sites for settlement in flatfish and contain a high density of juveniles, often resulting in increased competition and possible density dependent effects on growth. Studies on several flatfish species have observed a significant negative effect of abundance on growth rates and post-settlement size (Steele & Edwards 1970, Modin & Pihl 1994, Nash et al. 1994, Peterman & Bradford 2011). Northern rock sole

(NRS) specifically exhibit negative density-dependent habitat selection in laboratory experiments, leading to use of habitats that are less favorable (Laurel et al. 2007, Camp et al. 2011). This finding suggests that processes such as growth may be sensitive to increased conspecific densities and competition in Gulf of Alaska nurseries. Decreasing length-at-age of NRS populations has also been documented in years with high recruitment (Walters & Wilderbuer 2000), suggesting that density dependent processes may be exerting an effect on growth, especially in nursery grounds with high NRS abundance and limited space. However, previous research examining growth variability of NRS in Kodiak Island nurseries reported that juvenile growth rates were not correlated with fish density (Hurst et al. 2010). Despite observed relationships, the carrying capacity and range of densities a nursery can support is still not well understood though these nursery site characteristics could affect post-settlement survival and recruitment to the adult population (Rijnsdorp et al. 1995).

For juvenile flatfish, food quality and quantity have been shown to influence growth and survival within nursery habitats as well (van der Veer & Witte 1993, Gibson 1994). Food availability in nurseries can be driven by top-down (i.e. density-dependent competition) or bottom-up (i.e. production rates) processes. Flatfish growth rates are sensitive to changes in the feeding rate (Malloy et al. 1996) and growth variation is often attributed to prey availability (Berghahn et al. 1995, Hurst & Abookire 2006). However, evidence for food limitation in nurseries is often limited, suggesting that environmental factors play a larger role in explaining growth variation. The “maximum growth/optimal food condition” hypothesis predicts that if there are no density-dependent effects on growth (i.e. no competition for food), then temperature should be the primary driver of growth (Karakiri et al. 1991). This hypothesis has been supported in a large number of studies exploring variation in post-settlement growth and results indicate positive correlations between temperature and growth (e.g. Zijlstra et al. 1982, May & Jenkins 1992, Teal et al. 2008).

In addition to nursery habitat factors driving variation in post-settlement growth dynamics of flatfish, conditions experienced during earlier life history stages prior to settlement may modify juvenile

characteristics of individuals. Predation on juvenile flatfish has been shown to occur primarily in the period immediately following settlement into nurseries and is generally inversely related to fish size (Witting & Able 1993). Therefore, larval size or growth advantages that persist into the juvenile stage may result in a higher probability of survival to later post-settlement periods. Research on the early life history stages of NRS in particular has focused primarily on the post-settlement period in nurseries (Moles & Norcross 1998, Hurst & Abookire 2006, Ryer & Hurst 2008, Ryer et al. 2012). However, Hurst et al. (2010) demonstrated that temperatures in the late-larval period explained cumulative first year growth of NRS cohorts, indicating that pre-settlement characteristics and thermal conditions experienced during larval periods may play an important role in driving post-settlement size variation. Larval growth of NRS varies interannually (see Chp. 2), suggesting that prior growth patterns and larval history may contribute to interannual variation in post-settlement growth and size. Furthermore, the abundances of NRS juveniles in nurseries often decline between July and August (Hurst et al. 2010), indicating significant mortality in this post-settlement period but it is not yet known if mortality is non-random. Furthermore, despite potential evidence for carry-over effects in NRS, little is known about the degree of selective mortality on juveniles in relation to particular traits (i.e. development rates, growth rates and size) acquired during larval stages and metamorphosis.

Otolith microstructural analysis is a useful technique for examining carry-over effects because larval and juvenile growth and size metrics of individual fish can be compared across life history stages to determine if size or growth advantages persist. Likewise, integration of larval and juvenile traits provides individual growth trajectories which can be compared across individuals to identify traits that may only be present in survivors. This approach was used in the following study to draw inferences of the extent and direction of selective mortality in the post-settlement juvenile stage based on comparisons between recently settled NRS individuals captured in July to surviving individuals captured in August. Reconstructing and integrating detailed pre- and post-settlement growth histories of “settlers” (July-captured fish) and “survivors” (August-captured fish) enabled the comparison of traits between the two

periods to determine if pre-settlement growth and size patterns were preserved during juvenile residence in nurseries. Ultimately, understanding these patterns of co-variation in early life history characteristics provides insight into processes that may influence mortality in nurseries as well recruitment regulation in NRS.

This study examined variation in NRS growth and survival during the post-settlement juvenile period in relation to environmental conditions, fish density and carry-over effects from the larval period. It is hypothesized that variation in post-settlement growth of NRS is positively related to water temperatures. If temperature is the primary determinant of growth in nurseries, there should be little evidence for density-dependent growth effects, suggesting that intraspecific competition for resources does not have a major influence on post-settlement processes. By integrating pre-and post-settlement growth metrics, variation in post-settlement growth can also be related to larval growth and size. If carry-over effects exist, larval size and growth metrics should be positively correlated with post-settlement growth and size metrics. High post-settlement mortality of NRS between July and August suggests that mortality may be non-random and mediated by carry-over effects of prior traits and thermal conditions experienced by larvae. NRS that display faster larval growth, larger sizes at hatch and metamorphosis, and faster post-metamorphic growth are expected to experience greater survival from July to August during the initial post-settlement period. Therefore, I evaluated these hypotheses by completing the following objectives:

- 1) Examine spatial and temporal variation in post-settlement growth of NRS in two nursery sites in the Gulf of Alaska;
- 2) Relate post-settlement growth variation to water temperature and juvenile NRS densities in nursery sites;
- 3) Integrate pre- and post-settlement characteristics to determine if relative patterns of covariation in size and growth are maintained across life stages of NRS (i.e. carry-over effects); and
- 4) Determine the extent to which variation in pre- and post-settlement traits may result in growth and/or size selection and influence survival from July to August during the initial post-settlement period.

3.2 MATERIALS AND METHODS

3.2.1 Study site

This study was conducted at two sites off the northeast coast of Kodiak Island, Alaska, USA (Fig. 9). Holiday Beach ($57^{\circ} 41.2' \text{ N}$, $152^{\circ} 27.7' \text{ W}$), in Middle Bay, and Pillar Creek Cove ($57^{\circ} 49' \text{ N}$, $152^{\circ} 25' \text{ W}$), in Monashka Bay, are known nursery grounds for age-0 NRS (Stoner et al. 2007). Both sites are sheltered coves with flat, sandy beaches and benthic structure composed primarily of sandy and muddy substrate. Age-0 NRS are found primarily in water depths of 10-30 m and abundance is negatively correlated with depth, making these shallow, protected nursery grounds around Kodiak Island an ideal study site for NRS field collections.

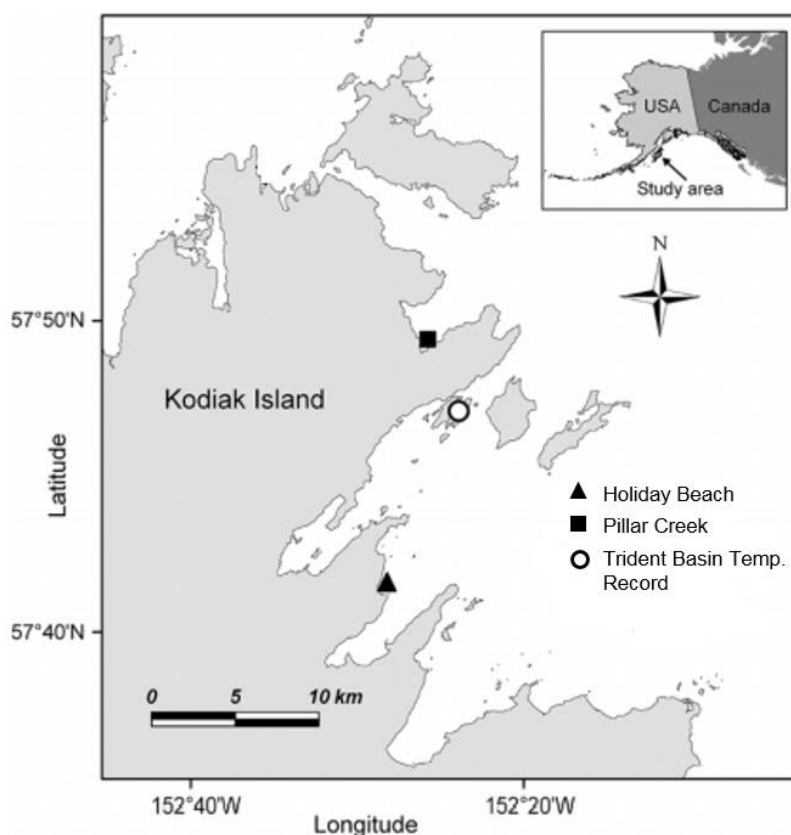


Figure 9. Map of Pillar Creek Cove and Holiday Beach field sampling sites off the northeast coast of Kodiak Island, Alaska, USA.

3.2.2 Northern rock sole field sampling

Age-0 NRS were sampled in July and August from 2004-2013 by the Fisheries Behavioral Ecology Program of the Alaska Fisheries Science Center (AFSC) (Table 11). Field collections were

conducted in July and August in order to target post-settlement NRS as previous sampling efforts have indicated that peak settlement likely occurs in May-June (Hurst & Abookire 2006, Laurel et al. 2015). Sampling at nursery sites was conducted with a 2-m beam trawl with a 3-mm mesh codend at fixed transects. Three to five 5-minute trawls were conducted parallel to the shoreline at approximately 10 m depth intervals between 7 and 30 m depth on each sampling day (Hurst et al. 2010). Surface and bottom temperature, salinity and oxygen concentrations were measured upon completion of each tow (YSI model 85). Trawl catches were identified to species, frozen, and shipped to the AFSC laboratory in Newport, OR, U.S.A. Archived NRS collections from field sampling in 2005, 2007, 2009, 2010 and 2011 were selected for otolith extraction and analysis due to adequate sample sizes and suitable otolith condition in these years.

Table 11. Kodiak Island nursery site sampling dates and summary of age-0 northern rock sole (NRS) size at capture. Total length (TL) ranges from field collections were used to distinguish between age-0 and age-1 NRS due to breaks in the size-frequency distribution. NRS used for otolith analyses are a representative subset of the NRS age-0 size distribution.

Year	Site	Sampling Date	TL range (mm) of all NRS collected	TL range (mm) of NRS for otolith analyses
2005	Holiday Beach	July 19-20	21-51	<i>No readable otoliths</i>
		Aug 22	26-76	41-74
	Pillar Creek Cove	July 20	10-50	16-31
		Aug 23	22-61	31-47
2007	Holiday Beach	July 18-19	18-36	25-28
		Aug 23, 25	28-53	27-46
	Pillar Creek Cove	July 20	17-32	21-30
		Aug 24	19-46	21-52
2009	Holiday Beach	July 14	20-41	21-37
		Aug 23	26-59	28-48
	Pillar Creek Cove	July 17, 19	20-41	24-36
		Aug 24-25	20-60	30-50
2010	Holiday Beach	July 14	21-39	24-38
		Aug 23-24	34-59	32-59
	Pillar Creek Cove	July 15	20-38	20-34
		Aug 25-26	20-66	24-66
2011	Holiday Beach	July 16, 20	20-41	31-38
		Aug 26	21-76	32-51
	Pillar Creek Cove	July 15, 17	20-46	29-43
		Aug 23, 29	22-74	34-50

3.2.3 Temperature variation

Daily, 15-day and monthly temperature averages corresponding with the early post-settlement period (~April-August) were collected from a continuous temperature record at 10 m depth in Trident Basin on the NE coast of Kodiak Island, AK (Fig. 9). This Trident Basin logging station is in close proximity to Holiday Beach and Pillar Creek Cove sampling sites. Short-term temperature records for Holiday Beach and Pillar Creek indicated that the Trident Basin temperature record was consistently within the range of temperatures measured at the sampling sites (Hurst et al. 2010). Therefore, Trident Basin temperature records were used as a proxy to describe regional temperature variation across both sampling sites during NRS post-settlement residency in nursery areas.

Fifteen-day mean temperature periods of Trident Basin records were used for all further statistical analyses because the post-settlement period spans several months. Therefore, 15-day time steps effectively capture temperature variability during nursery residence in order to determine if temperatures during specific temporal windows are related to post-settlement processes. In addition, intra- and interannual autocorrelation was assessed between 15-day temperature means of Trident Basin temperature data. Within each year, 15-day temperature time series were positively autocorrelated at a lag of 1. There was no evidence for autocorrelation across years.

3.2.4 Preparation and polishing of field-collected juvenile NRS otoliths

Prior to extracting otoliths, field-collected juvenile NRS were thawed and measured (SL, nearest 0.1 mm using a digital caliper). Right and left sagittal otoliths were removed and photographed under a dissecting microscope. Image analysis software (Image-Pro Premier®) was used to measure otolith length (anterior to posterior: longest axis) and otolith width (dorsal to ventral: longest perpendicular axis) from otolith images. Although previous flatfish studies have noted bilateral asymmetry between right and left sagittae (Sogard 1991), no significant differences were found in length or width of right versus left sagittal otoliths across the fish size range examined (13.19-55.76 mm SL) (paired t-test, $p > 0.05$, $n = 52$). Right sagittal otoliths were selected for further otolith analysis and interpretation. A subset of 30-50

otolith samples from each month (July and August) and year (2005, 2007, 2009-2011) at each of the two nursery sites (Holiday Beach and Pillar Creek Cove) were mounted onto glass slides and polished using wet-or-dry paper (800-2000 grit) and lapping film (3-30 μm) until increments were visible under a dissection scope. Otoliths were then flipped and re-mounted to continue polishing until microstructure was evident and the otolith was transparent. Polished otolith images were acquired with a Leica DC300 camera and Leica DM1000 compound microscope (40-400x magnification).

3.2.5 Microstructural analysis of field-collected juvenile NRS otoliths

Field-caught NRS otoliths displayed similar otolith morphology as laboratory-reared NRS otoliths that were used to validate otolith landmarks in relation to early life history events in previous experiments (see Chp. 2). Determination of total age from microstructural analysis was not possible so otolith growth metrics were developed to address the research objectives (Table 12). Daily increment widths were measured to reflect growth whereas the width of both the validated hatch check (HC_w) and metamorphic check (MC_w) were used as proxies for fish size at these life history events. Ten increments were measured at designated otolith landmarks to characterize early larval (EL_{IW}), larval (L_{IW}), post-metamorphic (PM_{IW}) and recent (R_{IW}) growth (Fig. 10). The mean of all ten-increment width measurements for each growth metric was used in cross-sectional data analyses. Otolith degradation during storage of field collections resulted in small sample sizes for 2005 and 2007, which prevented many cross-sectional estimates for growth metrics (Table 13).

Early larval growth and larval growth were identified as separate growth metrics due to the consistent presence of a check $\sim 45\ \mu\text{m}$ in diameter and change in increment morphology following this check (0.8 μm increment width average to post-check 1.2 μm increment width average). Previous research using microstructural analysis with flatfish otoliths noted similar changes in increment morphology during early larval stages, possibly coinciding with notochord flexion (Jenkins 1987, May & Jenkins 1992). Enumeration of increments from hatch check to the 45- μm check in individual otoliths with clear microstructure indicated that this check is formed approximately 20-30 days-post-hatch ($n = 30$).

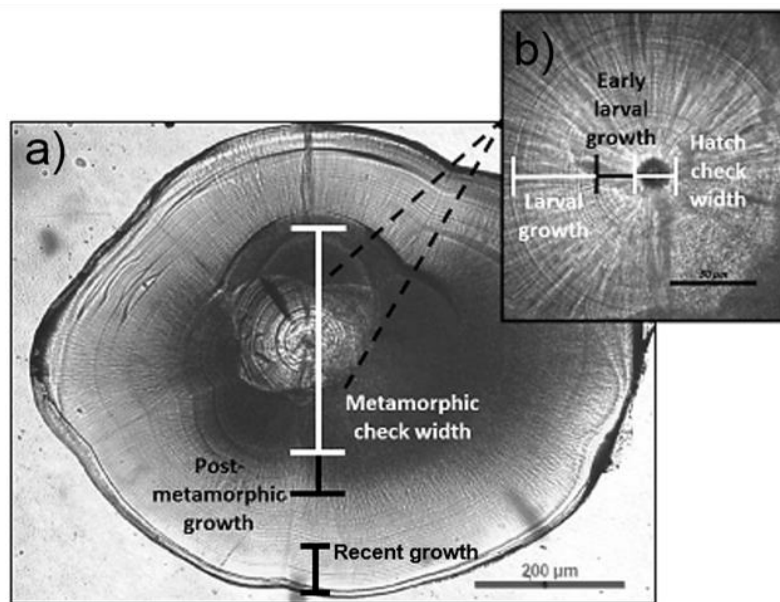


Figure 10. Northern rock sole sagittal otolith landmarks and a) post-settlement and b) larval growth metrics used in the study.

Table 12. Northern rock sole otolith growth metrics and corresponding early life history characteristics. All measurements were to the nearest 0.01 μm . See Figure 10 for additional information on otolith landmarks.

Larval and post-settlement growth metrics	Methods
1) Hatch check width (HC_w)	Measure of the diameter of the first opaque check closest to the core of the otolith. Imaged at 1,000x magnification with oil immersion.
2) Early larval growth (EL_{IW})	Increment widths of the last 10 daily increments prior to the 45 μm check. Imaged at 400x magnification.
3) Larval growth (L_{IW})	Increment widths of the first 10 daily increments after the 45- μm check. Imaged at 400x magnification.
4) Metamorphic check width (MC_w)	Measure of the width (dorsal to ventral otolith axis) of the innermost dark check deposited at the accessory primordial edge, marked by petal-like protrusions in the microstructure.
5) Post-metamorphic growth (PM_{IW})	Increment widths of the first 10 daily increments following the metamorphic check. Imaged at 40x and measurements taken from otolith core to edge direction on the ventral axis of otolith.
6) Recent growth (R_{IW})	Increment widths of the last 10 daily increments preceding the ventral otolith edge. Imaged at 40x and measurements taken from otolith core to edge direction on the ventral axis of otolith.

However, given that increments near the hatch check were often indistinct, the last ten increments prior to the 45- μm check (i.e. ~10-20 days-post-hatch) were measured for all otoliths and used as a metric of early larval growth (Fig. 10b). Larval growth was characterized by the first ten increments following the 45- μm check (i.e. ~30-40 days-post-hatch).

Daily increment widths were also measured from the ventral edge of the metamorphic check towards the otolith edge, representing post-metamorphic growth immediately following eye migration (Fig. 10a). The post-metamorphic growth metric was measured across a 10-increment range during the first twenty to thirty days following eye migration whenever possible (73% of the 367 otoliths analyzed, Table 13). Recent growth prior to July and August sampling dates was determined by measuring 10 increments as close to the ventral otolith edge as possible, representing growth during the twenty-thirty day range prior to sampling (66% of the 367 otoliths analyzed).

Table 13. Sample sizes of northern rock sole otoliths with growth metric estimates from microstructural analysis. Sample sizes vary because not all growth metrics were able to be estimated for each individual. ‘*ND*’ refers to the lack of any readable otoliths during the corresponding period.

Year	Site	Month	Hatch check width (HC _w)	Early larval (EL _{lw})	Larval (L _{lw})	Metamorphic check width (MC _w)	Post-metamorphic (PM _{lw})	Recent (R _{lw})
2005	Holiday Beach	July	<i>ND</i>	<i>ND</i>	<i>ND</i>	<i>ND</i>	<i>ND</i>	<i>ND</i>
		Aug	17	16	24	26	21	22
	Pillar Creek Cove	July	4	4	5	7	<i>ND</i>	4
		Aug	20	11	20	27	19	14
2007	Holiday Beach	July	4	3	5	8	4	<i>ND</i>
		Aug	17	20	25	25	22	19
	Pillar Creek Cove	July	6	5	8	9	7	5
		Aug	23	22	24	25	23	19
2009	Holiday Beach	July	20	23	26	26	17	14
		Aug	9	9	14	18	9	17
	Pillar Creek Cove	July	23	24	27	26	22	11
		Aug	14	15	20	21	15	19
2010	Holiday Beach	July	18	16	19	22	10	15
		Aug	16	15	20	18	19	19
	Pillar Creek Cove	July	15	18	21	20	14	12
		Aug	22	22	23	26	23	20
2011	Holiday Beach	July	11	12	12	13	11	6
		Aug	11	11	11	13	8	9
	Pillar Creek Cove	July	9	11	13	13	11	6
		Aug	7	6	9	14	11	10

An estimated date of metamorphosis was also determined for NRS individuals. Estimates were based on a model relating post-metamorphic growth to cumulative otolith growth along the ventral otolith edge from metamorphosis to capture. The model was parameterized using a subset of fish that could be reliably aged from metamorphosis to capture (see Chp. 2 for details).

Otolith data were organized into cross-sectional and longitudinal data structures for each individual fish. Longitudinal early larval, larval, post-metamorphic and recent growth estimates consisted of ten consecutive increment widths for each otolith metric. Cross-sectional early larval, larval, post-metamorphic and recent growth estimates were the average increment width of all 10 daily increments measured at each respective otolith metric.

3.2.6 Statistical Analyses

To examine spatial and temporal patterns in growth and size of NRS juveniles, post-settlement growth metrics (i.e. post-metamorphic, July recent and August recent growth) from cross-sectional otolith measurements and size at capture data were used. All data were tested for normality and homogeneity of variance assumptions for parametric tests. If assumptions were still violated after log-transformation, non-parametric tests were used. All statistical analyses were conducted in R, version 3.1.2 (R Development Core Team 2012).

Due to fairly small sample sizes and issues with otolith preparation and interpretation, no post-metamorphic growth estimates could be obtained for July fish in 2005. In addition, estimates for mean post-metamorphic and recent growth could not be obtained for July fish in Pillar Creek in 2005. Small sample sizes in July 2007 also resulted in no July recent growth estimates for fish collected from Holiday Beach. Therefore, spatial and interannual patterns in post-metamorphic growth were examined by pooling July and August fish. To examine spatial patterns in July recent growth, a one-way Analysis of Variance (ANOVA) was used to test for growth differences between nursery sites in 2009, 2010 and 2011. When sample sizes permitted, spatial and interannual variation in post-settlement growth and size metrics across

years were examined with a two-way ANOVA with site and year as main effects. Interannual as well as spatial variation in average NRS densities during July and August sampling periods were also examined with a three-way ANOVA, using site, month and year as main effects.

Correlation analyses (Pearson's correlation coefficient) were used to examine interannual relationships between the three mean post-settlement growth metrics and 15-day mean Trident Bay temperatures. To examine if temperatures during earlier pre-settlement periods were related to post-settlement growth, 15-day mean water temperatures coinciding with the late-larval to peak metamorphosis period (March 19-June 1) were compared to post-metamorphic, July recent and August recent growth. Peak metamorphosis period (May 4-June 1) was determined as the range of annual mean date of metamorphosis estimates. Likewise, growth metrics were compared with water temperatures coinciding with the culmination of metamorphosis to the August sampling period (June 2-August 31). Correlation analyses were also used to examine carry-over effects of growth and size metrics across life history stages. Correlations compared all larval and post-settlement growth and size metrics for NRS individuals across all five years. To control for potential confounding effects of annual differences among traits, the year trend was removed by fitting and analyzing the residual data. All α values in analyses were Bonferroni corrected to account for multiple comparisons and possible Type 1 error associated with such repeated tests.

To examine evidence for growth and size selection during the July to August initial post-settlement period, comparisons were made between July fish (referred to as July "settlers") and August fish (referred to as August "survivors"). Variation in date of metamorphosis and post-metamorphic growth between July settlers and August survivors were each examined with a two-way ANOVA with month and year as main effects. 2005 was eliminated from both statistical analyses due to missing July date of metamorphosis and post-metamorphic growth data.

A multivariate statistical approach was used to assess evidence for growth selection between July and August while incorporating potential carry-over effects from larval growth metrics. Specifically,

analyses were used to determine whether growth histories of August survivors differed from July settlers by integrating all pre- and post-settlement growth metrics. A linear model with a linear covariance structure was used to compare individual growth trajectories of July settlers and August survivors. The incorporation of a specified linear covariance structure makes the model an ideal approach for analyses of longitudinal data, owing to the model's ability to account for correlations and unequal variances across multiple growth metric measurements within an individual.

The explanatory variables in the linear model included 1) pre-and post-settlement growth metrics with levels: early larval growth, (EL_{IW}); larval growth, (L_{IW}); post-metamorphic growth, (PM_{IW}); July recent growth, ($JulyR_{IW}$); and August recent growth, ($AugR_{IW}$), 2) Year and 3) Month (July and August). A covariance structure was specified to allow for non-homogeneous variances of growth metrics and correlation between any two pairs of growth metrics. However, correlations between July recent growth and August recent growth were not included, as the two metrics correspond to July settlers and August survivors, rather than consecutively measured growth metrics. Restricted maximum likelihood (REML) was used to estimate model parameters (R package 'regress') and stepwise selection with likelihood ratio tests was used to select the final model.

To examine evidence of size selection between July settlers and August survivors, size at hatch and size at metamorphosis metrics were evaluated in separate linear models with 1) Year and 2) Month as covariates. To determine if hatch size and metamorphic size co-vary to explain differences across years and months, the size at hatch metric was included as an additional covariate in the size at metamorphosis model.

3.3 RESULTS

3.3.1 Temperature variation

Seasonal patterns in Trident Basin nursery temperatures were characterized by minimum temperatures in February and March with an increase in mid-April and a maximum in late-July. Interannual variation in post-settlement temperatures was characterized by higher temperatures in 2005 which were at least 1.5°C warmer than average temperatures in all other study years (Fig. 11, one-way ANOVA, $p < 0.01$) as well as all 17 years in the Trident Bay temperature record (Fig. A2). 2007 was the coldest year during the early post-settlement period with lower than average temperatures observed from mid-April to mid-July.

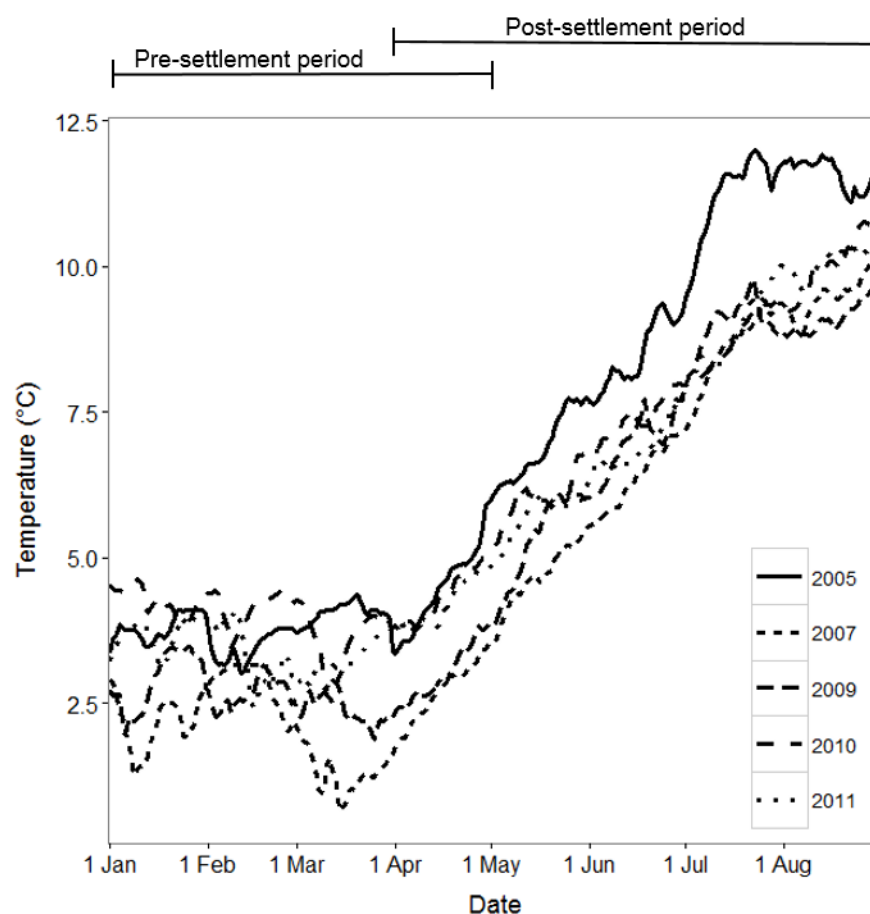


Figure 11. Temporal trends in Trident Basin daily temperatures (10 m) off the northeast coast of Kodiak Island, Alaska. Temperatures ranging from ~April-August are associated with the post-settlement period in Kodiak Island nurseries. Overlap in the pre-settlement and post-settlement periods represent individual as well as interannual variation in northern rock sole date of metamorphosis.

3.3.2 Spatial and temporal patterns in post-metamorphic growth

Post-metamorphic growth did not differ between Holiday Beach and Pillar Creek nursery sites after pooling July and August fish. However, post-metamorphic growth did vary interannually (Fig. 12, two-way ANOVA, $p < 0.001$) with significantly higher mean growth in 2010 than in 2007 and 2009.

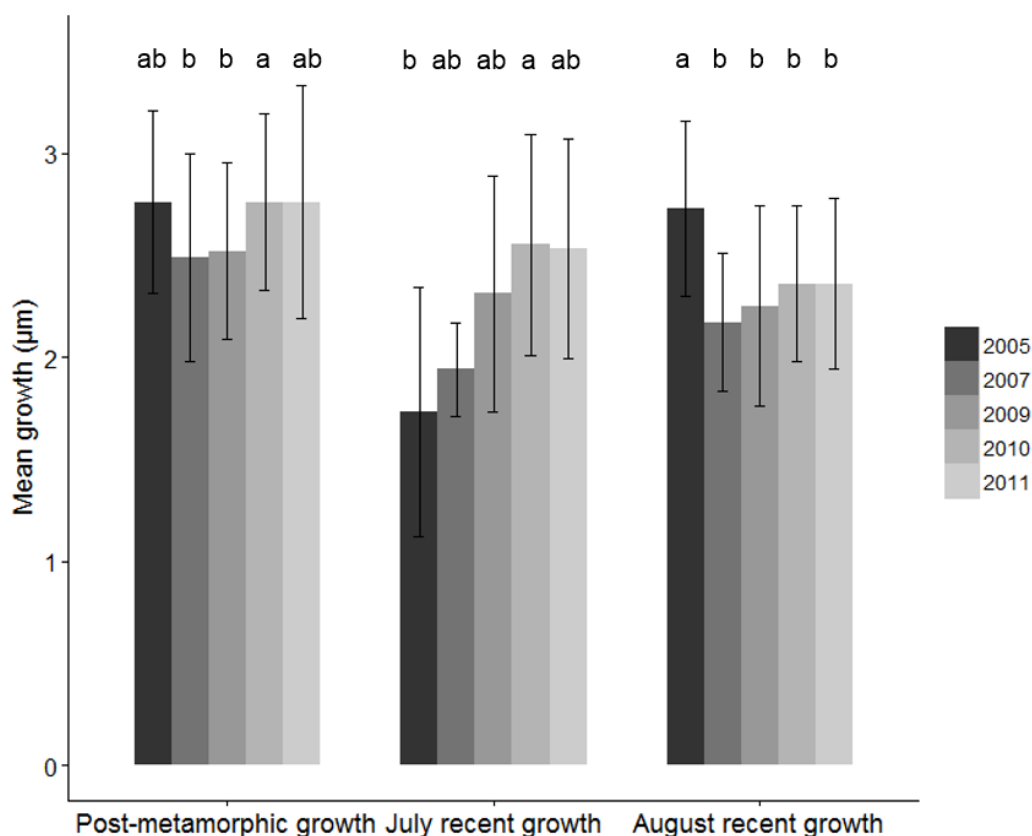


Figure 12. Interannual variation in northern rock sole (NRS) post-settlement growth metrics in Pillar Creek and Holiday Beach, Kodiak, Alaska (\pm SD). Growth metrics include post-metamorphic, July recent and August recent growth. Error bars represent the standard deviation of all individual NRS measures for each growth metric and letters indicate significant differences across years from Tukey-Kramer post-hoc analyses.

3.3.3 Spatial and temporal patterns in July recent growth

No significant differences in July recent growth were found between nursery sites in 2009, 2010 and 2011 (one-way ANOVA, $p > 0.05$). To test for differences in recent growth across all years, sites were pooled to allow for the inclusion of 2005 and 2007 in the analysis. Results indicated that recent

growth of July fish differed significantly across years (Fig. 12, two-way ANOVA, $p < 0.001$). Mean July recent growth rate in 2010 was significantly higher than mean growth rate in 2005.

3.3.4 Spatial and temporal patterns in August recent growth

A significant interaction between year and site on August recent growth was driven by relatively fast growth in 2005 at Pillar Creek (two-way ANOVA, $p < 0.05$). Across years, August recent growth in 2005 was significantly higher than all other years (Fig. 12) and growth was significantly higher in Pillar Creek than Holiday Beach, primarily driven by growth in 2005 at Pillar Creek (Fig. 13).

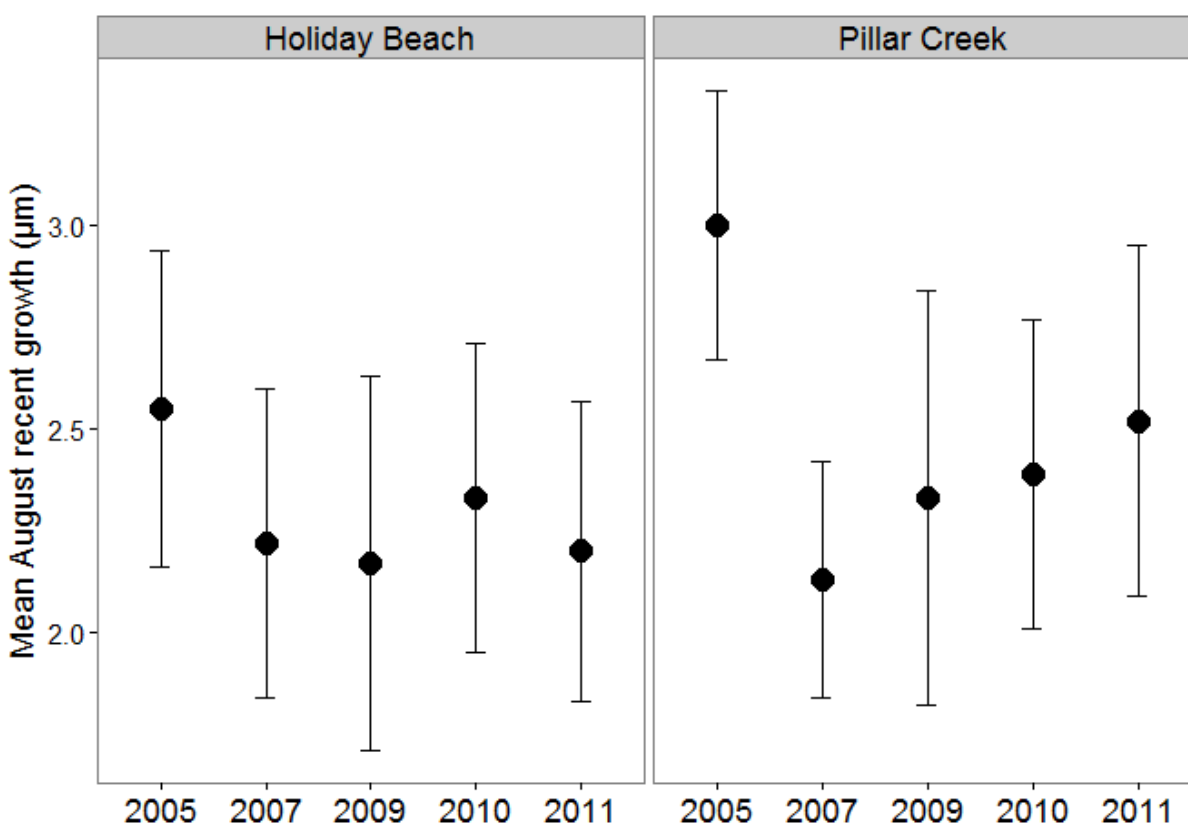


Figure 13. Spatial patterns in northern rock sole mean August recent growth (\pm SD) in two Kodiak Island nursery sites, Holiday Beach and Pillar Creek.

3.3.5 Spatial and temporal patterns in NRS juvenile size at capture

Due to missing data in 2005, a one-way Kruskal-Wallis test was used to examine spatial patterns in NRS size at capture in July across the four remaining years. There was no significant variation in size between nursery sites (Fig. 14a and 14b). Therefore, sites were pooled and 2005 data were included in tests for interannual variation in July size at capture. Across years, fish size differed significantly (one-way Kruskal Wallis test, $p < 0.001$). July fish were largest in 2011 and smallest in 2005 and 2007.

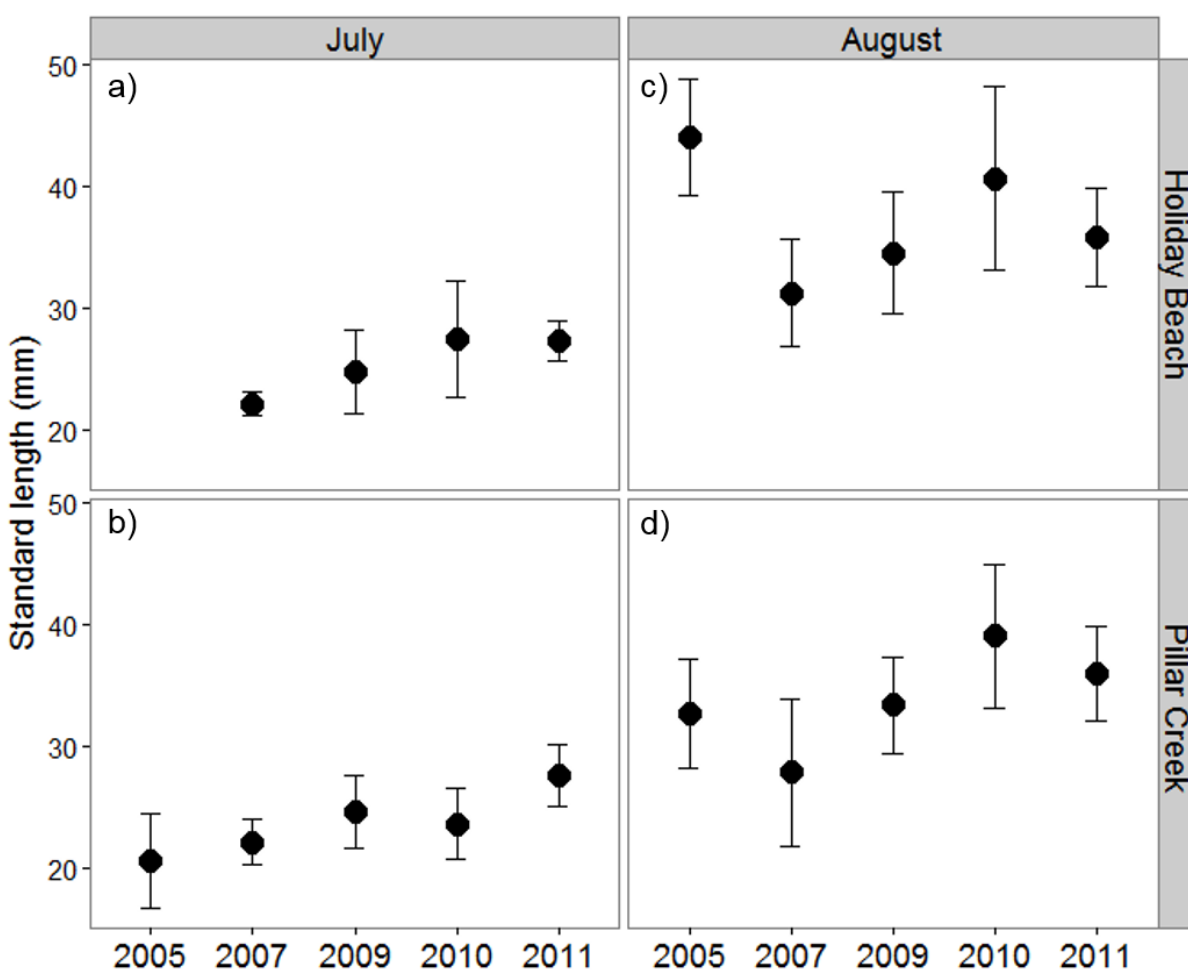


Figure 14. Interannual patterns in mean standard length (SL) of July- and August-captured northern rock sole (\pm SD) in two Kodiak Island nursery sites, Holiday Beach and Pillar Creek.

August size at capture analyses indicated that the interaction between site and year was significant (Fig. 14c and 14d, two-way ANOVA, $p < 0.001$), primarily driven by relatively large fish size in 2005 at

Holiday Beach. Across years, August fish were significantly larger in 2005 and 2010 whereas the smallest mean size at capture was observed in 2007 at both sites. Holiday Beach fish tended to be larger than Pillar Creek fish in August collections.

3.3.6 Temperature variation in relation to post-settlement growth metrics

Correlation analyses examining the hypothesis that the effects of temperature variation in pre-settlement stages may carry-over to influence post-settlement growth indicated that mean post-metamorphic growth was positively correlated with temperatures during the late-larval to peak-metamorphosis periods (mid-March to early-May; Table 14, $r > 0.97$). Mean July recent growth was not correlated with water temperatures during the late-larval or post-settlement periods. However, mean August recent growth was positively correlated with water temperatures from the peak of metamorphosis to sampling in August.

Table 14. Pearson product-moment correlation coefficients (r) for correlations between annual means of northern rock sole post-settlement growth metrics versus 15-day mean water temperatures from the late-larval to the post-settlement August sampling period in Trident Bay, AK.

15-day mean temperatures	Post-settlement growth metric		
	Mean post-metamorphic growth	Mean July recent growth	Mean August recent growth
Late- larval to peak metamorphosis period			
Mar 19-Apr 2	0.98**	0.26	0.76
Apr 3-17	0.99***	0.22	0.76
Apr 18-May 2	0.97**	0.08	0.85
May 3-17	0.92*	-0.01	0.90*
May 18-Jun 1	0.67	-0.32	0.96**
Post settlement juvenile period			
Jun 2-16	0.71	-0.25	0.94*
Jun 17-Jul 1	0.58	-0.49	0.97**
Jul 2-Jul 16	0.33	-0.69	0.90*
Jul 17-31	0.47	-0.67	0.95*
Aug 1-15	0.65	-0.54	0.97**
Aug 16-31	0.78	-0.36	0.93*

Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold** for late-larval to peak metamorphosis period ($p < 0.01$) and the post-settlement period ($p < 0.008$). $n = 5$ for all comparisons.

3.3.7 NRS juvenile density patterns

NRS densities differed significantly across years during July and August sampling periods (three-way ANOVA, $p < 0.001$). Densities between July and August did not differ significantly, however maximum densities within each year were generally observed in July, likely corresponding with the completion of metamorphosis and settlement. Interannual variation was characterized by significantly higher densities in 2011 in both the Holiday Beach and Pillar Creek sites, with the lowest densities occurring in 2007 and 2010. July and August recent growth metrics were not correlated with July and August densities across or within years (Fig. 15).

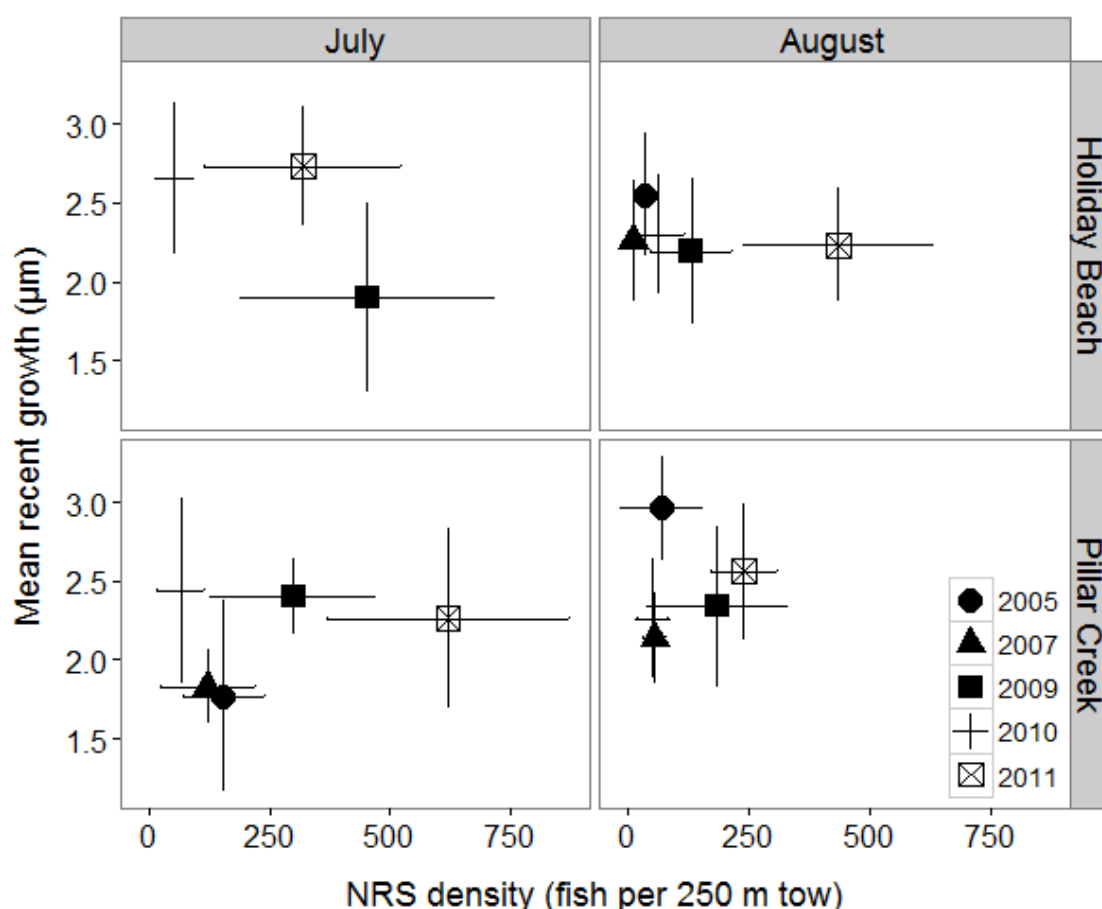


Figure 15. Mean recent growth of northern rock sole in July and August in two Kodiak Island nursery sites, Holiday Beach and Pillar Creek, in relation to northern rock sole densities in nurseries (\pm SE).

3.3.8 NRS growth and size carry-over effects

Correlation analyses examining carry-over effects of individual growth and size metrics across pre- and post-settlement stages of July-caught fish indicated that recent growth was positively correlated with size at hatch and that post-metamorphic growth was negatively correlated with larval growth, although neither pattern was statistically significant after Bonferroni adjustments (Table 15). However, recent growth was positively correlated with post-metamorphic growth and size at capture in July was correlated with size at metamorphosis and date of metamorphosis. Comparisons between growth metrics

Table 15. Correlations of pre- and post-settlement growth and size metrics of northern rock sole (NRS) individuals across all five years. Metrics include size at hatch, (HC_W); early larval growth, (EL_{IW}); larval growth, (L_{IW}); size at metamorphosis, (MC_W); July post-metamorphic growth (JulyPM_{IW}); August post-metamorphic growth (AugPM_{IW}); July recent growth, (JulyR_{IW}); August recent growth, (AugR_{IW}), July size at capture, (July_{SL}) and August size at capture (Aug_{SL}). ‘NA’ indicates correlations that were not possible between July and August fish.

	JulyPM _{IW}	AugPM _{IW}	JulyR _{IW}	AugR _{IW}	July _{SL}	Aug _{SL}
HC _W	0.09 (n = 79)	0.04 (n = 124)	0.28* (n = 55)	0.11 (n = 122)	0.07 (n = 110)	0.12 (n = 156)
EL _{IW}	0.03 (n = 77)	0.06 (n = 120)	0.11 (n = 59)	0.24** (n = 118)	-0.10 (n = 116)	0.09 (n = 145)
L _{IW}	-0.26** (n = 92)	-0.10 (n = 152)	-0.04 (n = 67)	0.06 (n = 150)	-0.12 (n = 136)	-0.12 (n = 190)
MC _W	-0.04 (n = 94)	-0.10 (n = 167)	0.10 (n = 70)	-0.12 (n = 166)	0.34*** (n = 144)	0.19** (n = 213)
Date _{Met}	0.25* (n = 96)	-0.04 (n = 167)	0.24 (n = 46)	-0.07 (n = 137)	-0.37*** (n = 96)	-0.83*** (n = 167)
PM _{IW}			0.65*** (n = 46)	0.22* (n = 140)	0.16 (n = 96)	0.21** (n = 170)
JulyR _{IW}				NA	0.14 (n = 73)	NA
AugR _{IW}					NA	0.07 (n = 168)

Note: *p < 0.05, **p < 0.01, ***p < 0.001. Critical values were adjusted to account for multiple comparisons (Bonferroni adjustment) and significant values after correction are indicated in **bold**.

of August individuals revealed that recent growth was positively correlated with early larval growth and post-metamorphic growth. Size at capture in August was correlated with size at metamorphosis, date of metamorphosis and post-metamorphic growth.

3.3.9 Selective mortality during the initial post-settlement period

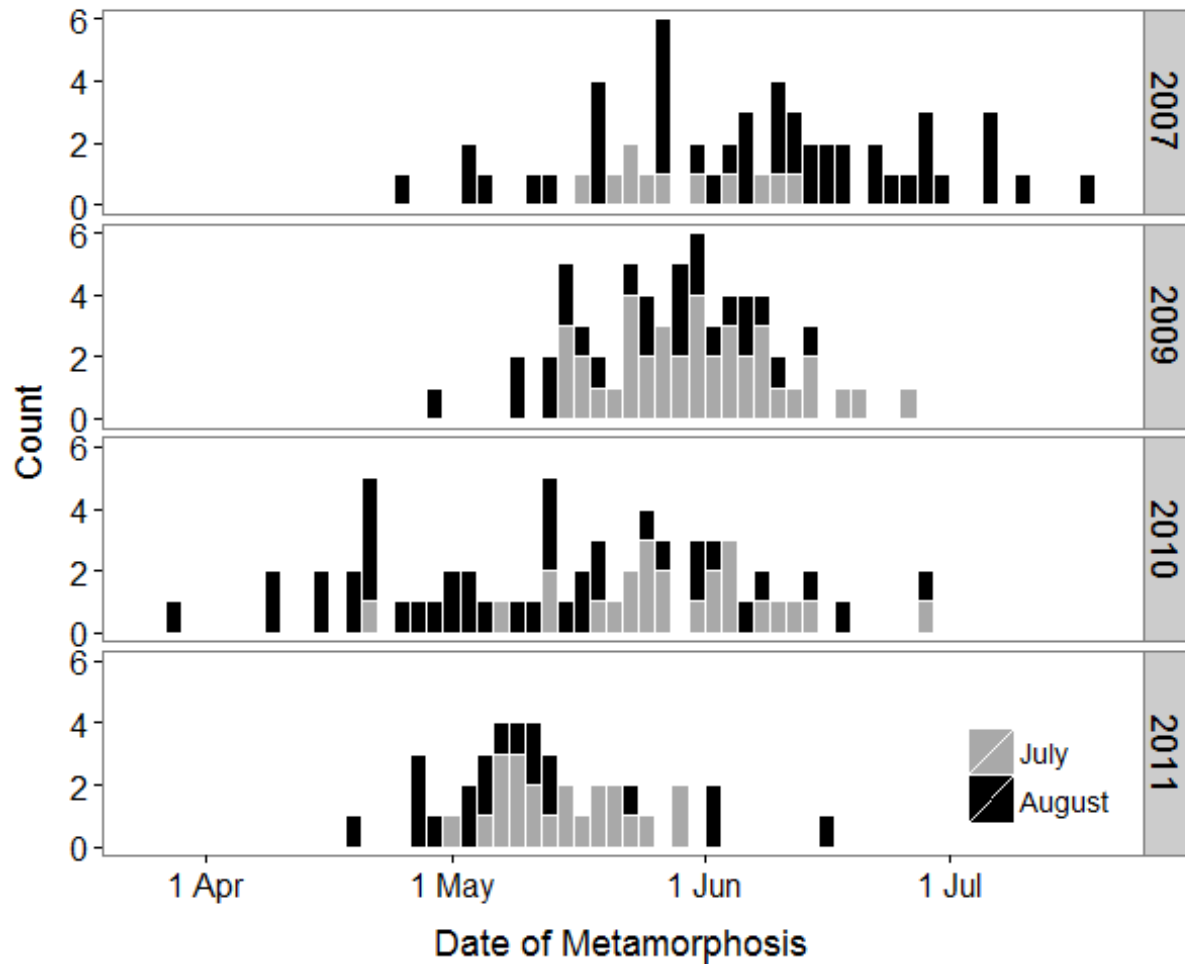


Figure 16. Distributions of estimated date of metamorphosis for July settlers and August survivors.

Analyses to examine evidence for selection on the timing of metamorphosis comparing July settlers to August survivors revealed a statistically significant interaction between year and month (Fig. 16, two-way ANOVA, $p < 0.05$). In both 2009 and 2010, the mean metamorphosis date observed among August survivors was significantly earlier than that observed among July settlers whereas in 2007, August survivors had later dates of metamorphosis than July settlers.

Post-metamorphic growth of July settlers and August survivors indicated that a significant interaction between year and month was driven primarily by slow growth of July fish in 2007 (Fig. 17, two-way ANOVA, $p < 0.05$). There was no significant main effect of capture month on post-metamorphic growth, but growth did differ across years with the highest mean growth rate occurring in 2010 and the lowest mean growth rate in 2007 (as described above).

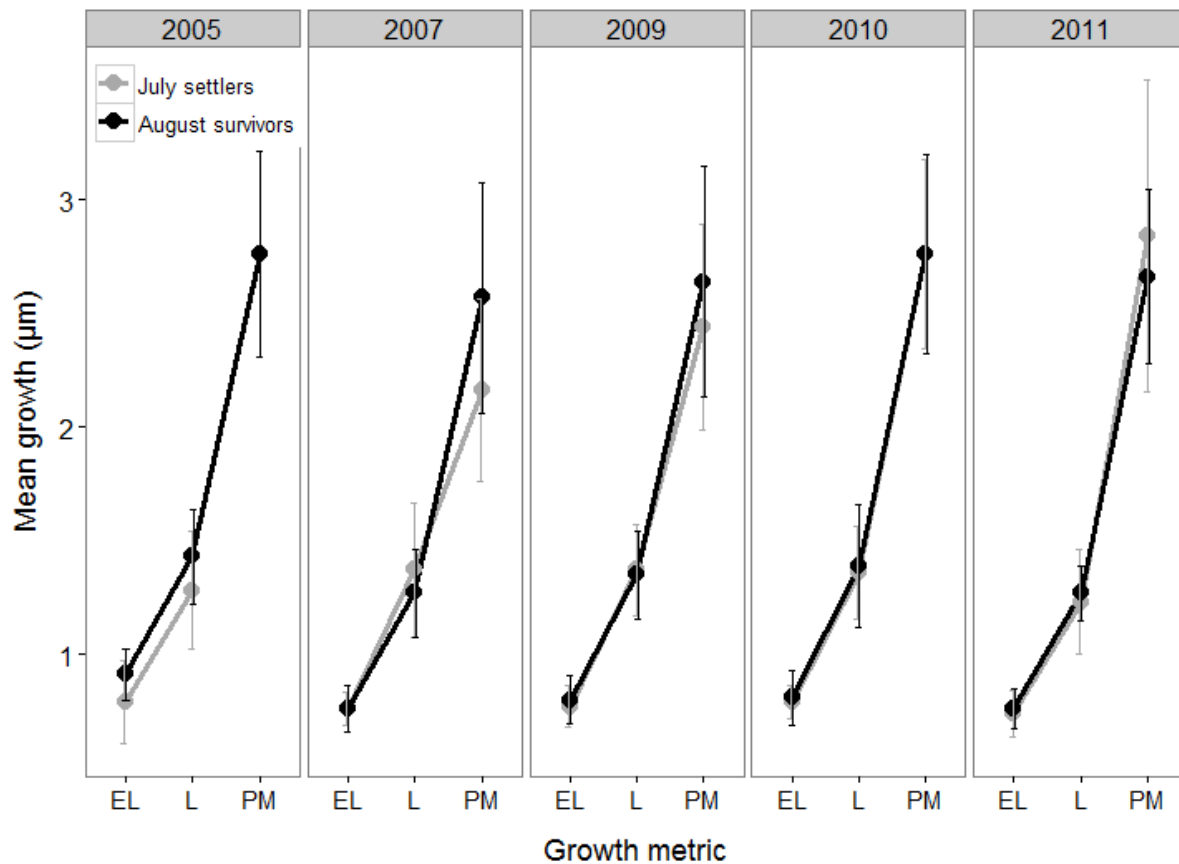


Figure 17. Mean growth trajectory of July settlers and August survivors (\pm SD). Otolith growth metrics include early larval growth (EL), larval growth (L) and post-metamorphic growth (PM). Small sample sizes prevented post-metamorphic growth estimates for July settlers in 2005.

A linear model approach to assess evidence for growth selection between individual growth trajectories of July settlers and August survivors revealed that neither pre- nor post-settlement growth rates differed significantly between July-caught settlers and August-caught survivors. Based on the stepwise selection approach, the best fit model included an interaction between year and growth metric as well as year and growth metric main effects (Table 16 and Fig. 18, $p < 0.001$). In the covariance structure, correlation between non-neighboring growth metrics (e.g. early larval growth and post-metamorphic growth) was not strong enough to be included in the model (Table 17). However, a significant positive correlation was found between early larval and larval growth of all fish and a significant negative correlation was found between larval and post-metamorphic growth. In addition, significant positive correlations were found between post-metamorphic and recent growth of July settlers as well as post-metamorphic and recent growth of August survivors.

Table 16. Final model parameter p -values after stepwise selection of a linear model to examine growth trajectories of northern rock sole across pre- and post-settlement growth metrics among years.

Parameter	p -value
Year	$p < 0.001$
Growth Metric	$p < 0.001$
Year x Growth Metric	$p < 0.001$

Table 17. REML variance, covariance and correlation estimates for the covariance structure of growth metrics in the final model. Growth metrics include: early larval growth, (EL_{IW}); larval growth, (L_{IW}); post-metamorphic growth, (PM_{IW}); July recent growth, ($JulyR_{IW}$); and August recent growth, ($AugR_{IW}$).

	EL_{IW}	L_{IW}	PM_{IW}	$JulyR_{IW}$	$AugR_{IW}$
EL_{IW}	0.011 (0.0009)	0.30***			
L_{IW}	0.007 (0.001)	0.044 (0.0035)	-0.19**		
PM_{IW}		-0.018 (0.006)	0.223 (0.0196)	0.60***	0.17*
$JulyR_{IW}$			0.153 (0.017)	0.292 (0.048)	
$AugR_{IW}$			0.032 (0.016)		0.170 (0.0188)

Note: Variance estimates and standard errors (in parentheses) of each growth metric are listed on the diagonal, in bold. Correlation coefficients between neighboring growth metrics are above the diagonal and significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Covariance estimates and standard errors (in parentheses) between neighboring metrics are below the diagonal. Non-neighboring correlations as well as a correlation between July recent growth and August recent growth are not listed because they were excluded from the final model.

A linear model to examine selection in hatch size of July settlers and August survivors indicated a significant interaction between month and year as well as significant main effects for month and year (Fig. 19). August survivors were significantly larger at hatch than July settlers in 2005, 2009 and 2011. However, in 2010 size at hatch was larger in July settlers. Analysis of size at metamorphosis revealed insignificant month and year effects. Likewise, no association was found between hatch size and metamorphosis size when size at metamorphosis was fitted against size at hatch.

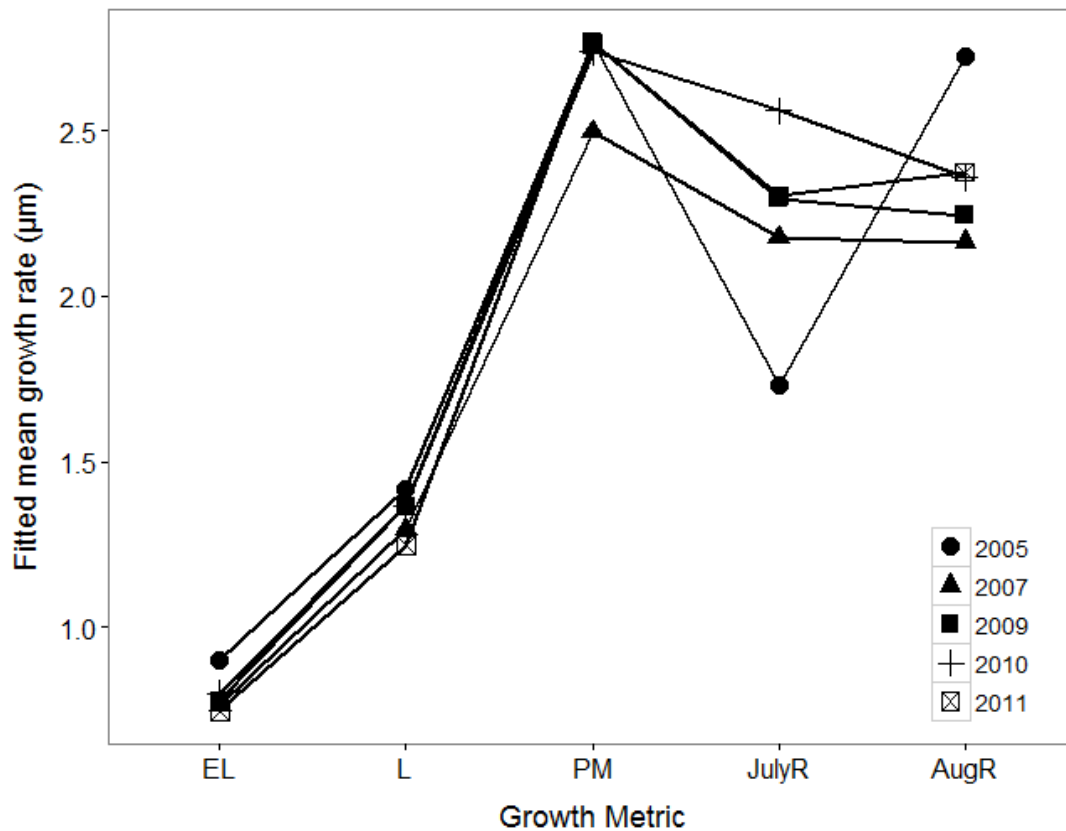


Figure 18. Fitted values for annual mean growth rates across pre- and post-settlement growth metrics. Growth metrics include: early larval growth, (EL); larval growth, (L); post-metamorphic growth, (PM); July recent growth, (JulyR); and August recent growth, (AugR).

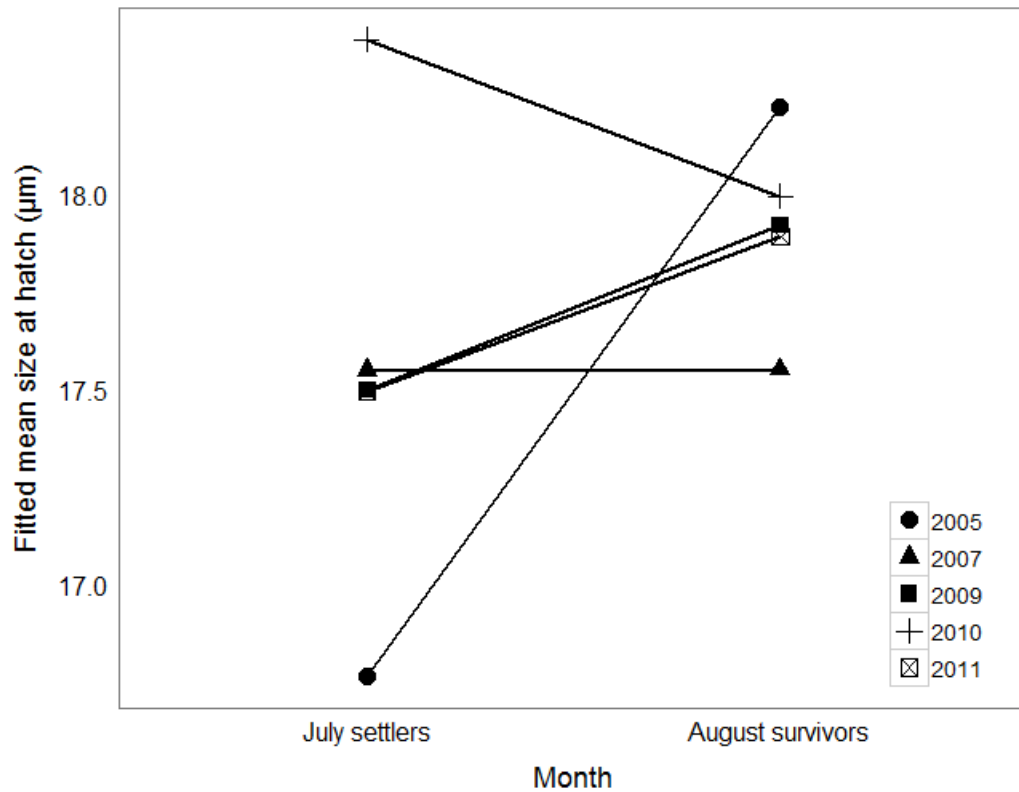


Figure 19. Fitted values for July settlers and August survivors mean size at hatch across years.

3.4 DISCUSSION

Variation in temperatures, food availability and fish densities in nursery grounds can have a significant influence on growth rates of juvenile fish, which may subsequently influence survival and recruitment to the adult population (Houde 1987, Gibson 1994). Larval growth history can also carry over to post-settlement stages, leading to variation in juvenile growth and the potential for growth or size selective mortality (Searcy & Sponaugle 2001, Shima & Findlay 2002). This study was the first to integrate analyses of NRS pre- and post-settlement processes in relation to growth and survival during the initial post-settlement period. Results indicated that early post-settlement growth was associated with concurrent nursery temperatures as well as temperatures during the larval period, suggesting a potential carry-over effect of thermal conditions experienced as larvae. Likewise, carry-over effects on individual-based growth and size metrics were evident with the coupling of traits across the larval-juvenile stage

transition. These observed patterns of co-variation in growth did not result in differences between growth trajectories of July settlers and August survivors. However, differences in size at hatch and timing of metamorphosis between settlers and survivors indicate that hatch size and phenology drive selective mortality during the initial post-settlement period and may have consequences for survival to the adult population.

3.4.1 Influences on temporal and spatial patterns of post-settlement growth

Post-settlement growth varied interannually although little variation was observed across months and nursery sites. Significant positive correlations between temperatures and post-settlement growth metrics suggest that temperature has a larger influence on growth variation than spatial differences in nursery habitat characteristics. A significant association between mid-March to mid-May temperatures and post-metamorphic growth specifically suggests that the effects of temperatures experienced during the larval period carry over to explain growth variation following metamorphosis. This finding is in agreement with Hurst et al. (2010) who concluded that larval temperatures explained more variation in NRS post-settlement size than concurrent nursery site temperatures. August recent growth was also positively correlated with both late larval and post-settlement temperatures, indicating a direct influence of concurrent nursery temperatures on growth as well as an indirect carry-over effect from thermal conditions experienced by larvae. Observed temporal autocorrelation between March-May larval temperatures and nursery temperatures could be a mechanism linking larval temperatures with post-settlement growth metrics. Warm temperatures and temperature-dependent growth during the larval period may result in relatively fast post-settlement growth as temperatures continue to get warmer throughout the post-settlement period in nursery grounds.

Although July recent growth was not significantly correlated with any temperature periods, the lack of a significant correlation appeared to be driven by anomalously slow growth in July 2005 despite very warm temperatures. Nursery temperatures in July 2005 were well above July temperatures in the entire 17-year Trident Basin temperature record. This observation suggests that the temperature anomaly

could be responsible for indirect effects on recent growth such as temperature-mediated shifts in prey quantity and quality in relation to increased metabolic requirements of NRS juveniles in warmer conditions.

While temperatures were associated with variation in post-metamorphic and August recent growth in NRS, juvenile nursery densities were not related to recent growth in July and August. Years with high densities across July and August often coincided with relatively fast recent growth rates. Lack of evidence for density dependent growth suggests that post-settlement growth rates were not likely influenced by food limitation via intraspecific competition. This is consistent with previous studies on juvenile NRS that reported no evidence for density dependent effects on growth (Hurst et al. 2010). Similarly, previous flatfish research suggests that densities during settlement on nursery grounds are not high enough to invoke competition for food and prey availability is likely not a limiting factor in early post-settlement growth (Van der Veer et al. 1990, Sogard 2001, Nash et al 2007). Although prey availability could be more variable later in the post-settlement growing season, the carrying capacity of nurseries in the Gulf of Alaska may not be a limiting factor on post-settlement processes.

Interestingly, spatial patterns in post-settlement growth were not consistently observed among growth metrics and were most apparent in August fish. This may be due to the fact that July sampling occurs fairly early in the post-settlement period and conditions between the nursery sites could diverge during the growing season. In previous studies exploring spatial variation in NRS juvenile growth, Holiday Beach supported the fastest growth rates and largest age-0 fish (Hurst & Abookire 2006, Hurst et al. 2010). In this study, site effects on July recent growth were primarily driven by relatively fast growth in 2011 at Holiday Beach whereas site effects on August recent growth were due to fast growth in 2005 at Pillar Creek. Variation in spatial patterns across years and months suggests that nursery habitat conditions may be fairly dynamic although it appears that interannual variation in post-settlement growth may be more important than spatial variation.

3.4.2 *Carry-over effects of size and growth traits across pre- and post-settlement stages*

Other potential mechanisms proposed to explain post-settlement growth variation are carry-over effects in which earlier growth or size traits influence post-settlement stages. In this study, carry-over effects of size and growth as well as the timing of metamorphosis were evident, suggesting that interconnections between life history stages play an important role in post-settlement processes of NRS. Negative correlations between larval and post-metamorphic growth indicate that growth advantages during the larval period can be lost in the juvenile period. Studies on laboratory-reared flatfish have noted a similar inverse relationship between larval and juvenile growth, resulting in compensation in size-at-age during the juvenile stage (Bertram et al. 1993). Given that NRS larvae metamorphose at a fairly consistent size range (see Chp. 2), size and growth advantages acquired in larval stages may be dampened by the convergence of size at metamorphosis. However, negative correlations could also suggest that larvae and juveniles respond differently to factors that regulate growth. NRS juveniles are risk-adverse, displaying conservative foraging behavior in nursery grounds (Hurst et al. 2007). Previous research suggests that faster growing NRS larvae are in better condition (Laurel et al. 2014), therefore fast growing larvae with increased energy stores may have the ability to reduce risk-prone foraging behaviors as juveniles, slowing growth rates in this stage. Conversely, slow-growing larvae may display more risk-prone foraging behavior in nurseries to increase food consumption, likely resulting in faster post-metamorphic growth rates and the negative correlation between growth metrics.

While covariance in growth and size metrics can vary across ontogenetic stages, carry-over effects are often non-linear and may not be revealed until later life history stages (Gagliano et al. 2007b). In this study, carry-over effects were apparent on July and August size at capture. Size at capture of July individuals was positively correlated with size at metamorphosis and date of metamorphosis while size at capture of August individuals was similarly related to size at metamorphosis, date of metamorphosis and post-metamorphic growth. Variation in post-settlement size integrates the previous growth history with these results demonstrating that size at capture was influenced by processes associated primarily with

metamorphosis and growth rates shortly thereafter. The direction of correlations between growth metrics of July and August fish suggests that individuals that metamorphose earlier and at larger sizes display relatively faster post-metamorphic growth rates and larger sizes at capture. Furthermore, these patterns of co-variation may be mediated by thermal effects. While size-at and timing of metamorphosis as well as post-metamorphic growth are correlated with July and August size, similar patterns were not evident with July and August recent growth just prior to capture. This suggests that differences in relative size persist despite a period of uncorrelated growth. Furthermore, although metamorphosis is a size-dependent process, evidence of carry-over effects suggest that even small advantages in size at metamorphosis can be maintained and appear to influence size at capture later in the growing season. Overall, size and growth patterns can be carried over across larval and juvenile life history stages and larval history and processes linked to metamorphosis in NRS are important determinants of post-settlement growth and size.

3.4.3 Growth and size selective mortality during the initial post-settlement period

Although several growth and size traits were maintained across life history stages, there were no significant differences in growth trajectories between July settlers and August survivors. This suggests that during the initial post-settlement period from July to August there was no direct selection on growth rates of earlier life history stages or that such growth selection was not strong enough to detect here. However, there was a significant difference in size at hatch between July settlers and August survivors, suggesting a size advantage that persists to the post-settlement period to influence survival. Previous research that observed links between size at hatch and survival of several marine fish species indicates that advantageous traits may be present from hatch (Meekan & Fortier 1996, Meekan et al. 2006, D'Alessandro et al. 2013). Survival advantages associated with hatch size could point towards maternal effects, i.e., maternal condition prior to spawning influences offspring survival and fitness (McCormick 2006). It is also interesting to note that while differences in hatch size between settlers and survivors were largely driven by a larger size at hatch of survivors in 2005, overall patterns in hatch size of settlers and survivors varied across years. August survivors in 2010 were smaller at hatch than settlers, suggesting

that “bigger is better” may not always be the mechanism driving selection and instead, the direction of selection may be influenced by other factors such as ontogeny or environmental conditions. Furthermore, in some cases, individuals that maintain smaller sizes possess a survival advantage and are less vulnerable to predation (Litvak & Leggett 1992).

The timing of metamorphosis also differed between July settlers and August survivors, suggesting that variability in phenology could play an important role in selective mortality processes. While most studies have explored selection in terms of size and growth traits, this study indicated that the timing of metamorphosis could influence post-settlement survival. Similar selective processes have been noted in plaice, indicating that the timing of metamorphosis may be a contributing mechanism for overall nursery dynamics and survival (Geffen et al. 2011). In this study, August survivors metamorphosed significantly earlier than July settlers in two of the study years, 2009 and 2010. In contrast, in 2007, August survivors had a later mean date of metamorphosis than July settlers. A switch in the direction of selection coinciding with the coldest year in the study suggests that the pattern of selection varies among years and thermal regimes. Several studies have demonstrated that the selective loss of individuals was linked to environmental variables such as temperature and variable environmental conditions often drive the intensity and direction of trait-mediated survival (Rankin & Sponaugle 2011, Grorud-Colvert & Sponaugle 2011, Woodson et al. 2013). Similarly, this may suggest that a cold year, such as 2007, in the Gulf of Alaska could result in survival advantages that favor later dates of metamorphosis, as individuals that metamorphosis early may experience unfavorable temperature conditions. Conversely, selection towards earlier dates of metamorphosis in warmer years suggests an advantage to a shorter pelagic larval duration and more time spent in the nursery grounds. Nursery grounds presumably maximize growth potential for juvenile fish (Gibson 1994) so individuals that metamorphose and settle earlier may be able to take advantage of a longer growing season and have more time to obtain larger sizes to avoid size-selective predation.

An important caveat to this study is that the lack of significant differences between growth metrics of settlers and survivors does not imply that growth selection does not occur in earlier life stages. The approach of inferring pre-settlement traits from otoliths of post-settlement juveniles in this study means that selection occurring in early life history stages would not be detected because only fish surviving to mid-July were sampled. A more comprehensive approach would, for example, entail repeated sampling of the cohort during both pre- and post-settlement life history stages to identify selection in both stages.

Overall, interannual variation in post-settlement growth of NRS juveniles was best explained by the cumulative effect of temperatures from the late-larval to juvenile nursery period. The relative magnitude of interannual variation in post-settlement growth compared to spatial variation suggests that nursery site variation may be less important in post-settlement growth processes. Likewise, there was no evidence for density dependent regulation of growth among nursery sites. The role of larval temperatures on post-metamorphic growth suggests that thermal conditions experienced as larvae can have effects that influence post-settlement growth processes. Evidence for post-settlement selection was detected for hatch size and the timing of metamorphosis, although the patterns of selection varied across years. This observation suggests that interannual variation in thermal regimes plays a significant role in determining patterns of survival during the post-settlement period in addition to the direct temperature-dependent effects on post-settlement growth. Additional research to determine the direction and strength of selective mortality across variable environmental conditions is needed. Furthermore, examining selective processes that operate prior to the post-settlement period may provide context for carry-over effects of prior growth or thermal conditions experienced as larvae. Ultimately, a better understanding of the nature of selection will provide further insight into survival and recruitment of NRS in the Gulf of Alaska.

4. GENERAL DISCUSSION AND CONCLUSIONS

Using otolith microstructural analysis, this study applied the unique longitudinal nature of otolith data to examine variation in northern rock sole (NRS) larval and juvenile characteristics, interconnections between traits across life history stages, and pre- and post-settlement growth trajectories of post-settled juveniles. This approach was used to quantify environmental factors in relation to early life history characteristics as well as integrate pre- and post-settlement growth dynamics to examine carry-over effects and selective mortality during the post-settlement period. Ultimately, identifying mechanisms that drive variation in early life history characteristics will result in a better understanding of processes that influence growth and survival of NRS.

This study identified patterns of interannual variation in both pre-settlement and post-settlement characteristics, indicating that temperature is a major determinant of the phenology of metamorphosis as well as post-settlement growth rates. Temperatures during the larval period also appear to indirectly influence post-metamorphic growth, possibly suggesting that larvae carry “thermal histories” across life stages. Furthermore, results demonstrated that density-independent regulation of growth persists into post-settlement stages. Unfortunately, the inability to age NRS individuals from hatch to capture limited the ability to directly test temperature effects on traits such as the timing of hatch and limited the ability to link larval growth rates to temporally-specific environmental conditions. However, results of cohort-based analyses indicated that positive trends between larval growth and temperature were apparent, but not all growth rates across life history stages in NRS were directly driven by temperature. Warm temperatures appear necessary, but not sufficient to promote rapid growth of individuals and temperature appeared to have the largest effect on date of metamorphosis and post-settlement growth rates in NRS. These observations have important implications for understanding which life history stages in NRS may be most vulnerable to climate variability.

While the phenology of metamorphosis in NRS is temperature-dependent, timing is influenced by both individual temperature conditions prior to the date of metamorphosis and annual thermal regimes. The overall thermal regime during the metamorphic period appears to drive earlier dates of metamorphosis in warmer years and later dates in colder years, which is related to variation in larval growth rates to attain a competent size for metamorphosis. Growth variation immediately prior to settlement may be related to both temperature and the timing of metamorphosis and this hypothesis is an important direction for future research. Conversely, the physiological process of metamorphosis is size-dependent and appears to be primarily influenced by ontogenetic effects rather than environmental conditions. NRS individuals undergo metamorphosis within a narrow size range and the observation that larval and post-metamorphic growth are negatively correlated suggests that metamorphosis is a criticality in the life history of NRS, reducing variation in larval growth rates and decoupling growth or size advantages across the larval to juvenile transition.

Integration of pre- and post-settlement growth and size metrics illustrated that the advantages acquired from traits coinciding with metamorphosis, (specifically size, timing and growth immediately following metamorphosis) are carried over to size at capture. These interconnections across larval and juvenile stages reveal that pre-settlement processes play an important role in post-settlement size and growth variation. By comparing trajectories of July settlers and August survivors, covariance in growth across stages did not provide support for growth selection between the two cohorts, suggesting that faster growth may not be a mechanism that increases the likelihood of survival in NRS during post-settlement nursery residence from July to August. However, there was evidence of selection on hatch size and the phenology of metamorphosis. The timing of metamorphosis is temperature-dependent, suggesting that interannual variation in thermal regimes could result in subsequent shifts in the direction and intensity of selection from July to August as exemplified in variation in the patterns of selection of date of metamorphosis across years.

To describe the relative magnitude of variation in pre- and post-settlement processes, Figure 20 presents the annual patterns of larval and juvenile traits, represented as residuals from the 5-year mean. Very small residuals for size at hatch and size at metamorphosis indicate that these events are critical life history transitions for reducing variability induced in earlier stages. Ultimately, identifying interconnections in traits across life history stages allows for a better understanding of post-settlement growth dynamics and survival that may be mediated by carry-over effects. Furthermore, determining the relative importance of environmental conditions on these life history traits is an important step towards

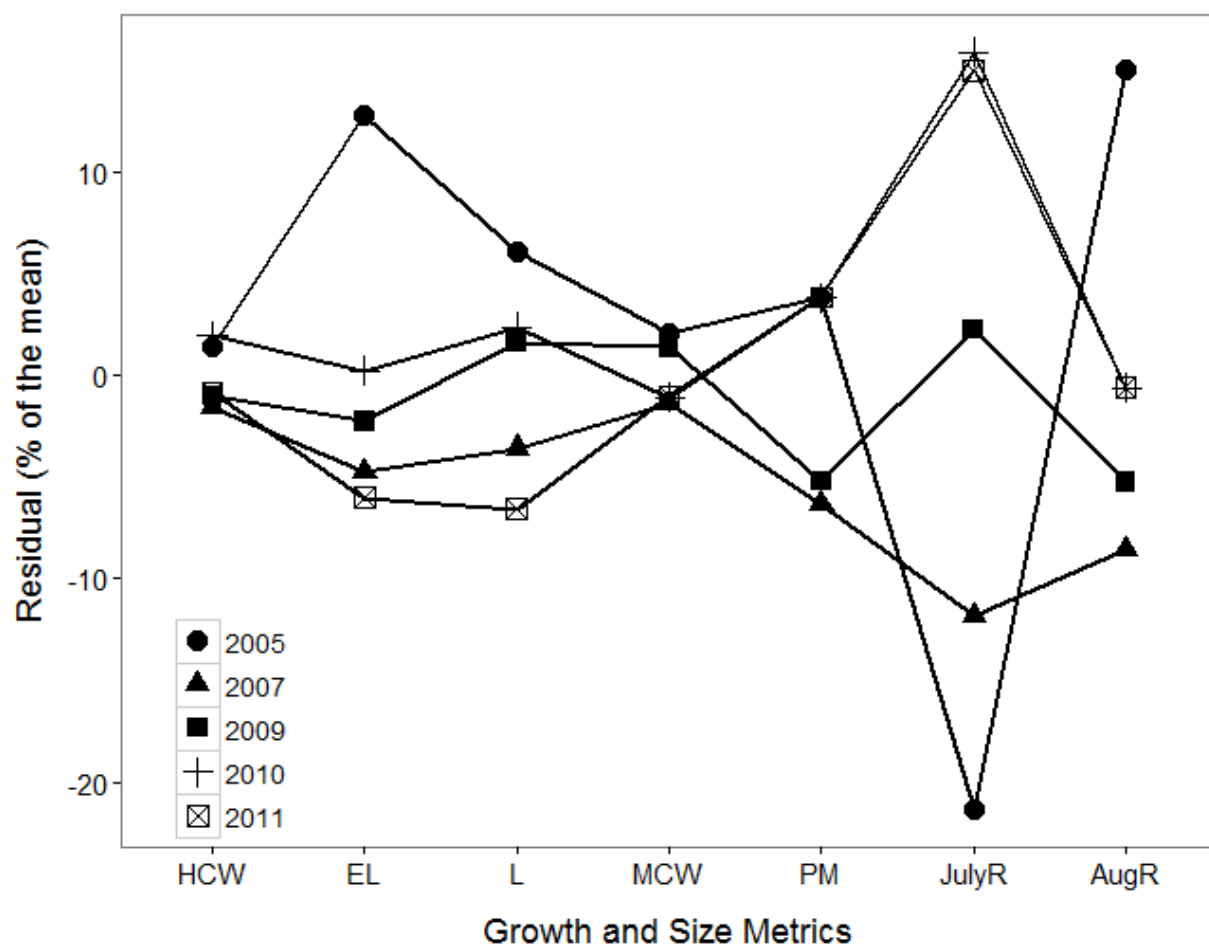


Figure 20. Residual plot from the five-year average of growth and size metrics across northern rock sole pre- and post-settlement stages. Metrics include size at hatch (HCW), early larval growth (EL), larval growth (L), size at metamorphosis (MCW), post-metamorphic growth (PM), July recent growth (JulyR) and August recent growth (AugR).

predicting the implications for future climate variability on NRS growth and survival. 2005, the warmest year in the study, revealed positive residuals across six of the seven traits, suggesting potentially strong and persistent temperature effects on growth and development across life history stages. However, contrary to hypotheses, results did not demonstrate direct temperature effects on growth during the larval period and recent growth in July. Instead, the most prevalent temperature effects on early life history characteristics corresponded with the period during metamorphosis. The finding that phenology is driven by temperature suggests that the timing of key life history events in NRS may shift in response to climate variability, but that stabilizing selection may limit the degree of variation associated with short-term climate variation in the Gulf of Alaska.

Overall, temperature conditions in the Gulf of Alaska explained both physiological effects on growth rates and phenological shifts in metamorphosis of NRS, emphasizing the importance for understanding these thermal drivers in order to evaluate the potential for climatic control on fisheries production. Correlations between water temperatures, growth and phenology of NRS suggest that earlier processes such as spawn and hatch may also be temperature dependent and that thermal effects could be carried throughout the life history of individuals. However, further work is needed to understand how temperatures may influence these earlier life history events. This study reported variation in growth, size and phenology of NRS, warranting research on the links between variation in early life history characteristics, climate variation and recruitment patterns in NRS. Recruitment estimates of age-0 NRS in the Gulf of Alaska predict that 2005 was one of the strongest year-classes in the 40-year time series (A'mar & Pálsson 2014). 2005 was one the warmest years in the past few decades in the Gulf of Alaska and the coinciding high recruitment of NRS could suggest that strong year classes are associated with warm regimes. This hypothesis differs from recruitment patterns of gadids in the North Pacific in which fast larval and juvenile growth in warmer conditions have been linked to weak year classes (Duffy-Anderson et al. *in press*). The difference between these two observations indicates the necessity to

identify mechanisms that drive early life history variation and year class strength in NRS in order to predict future recruitment success or failure.

Continued research on NRS early life history processes is also central to understanding the magnitude, extent and direction of selection which directly influences survival of NRS to the adult population. In a broader context, NRS responses to temperature variation observed in this study may be used to forecast similar climate-driven responses in other important marine resources in the Gulf of Alaska. For example, fisheries in the North Pacific, as a whole, may display phenological plasticity in response to temperatures, which could be important to population productivity and overall ecosystem structure. Mechanistic explanations to address the dynamics of fish growth, development and survival are clearly necessary in order to understand recruitment regulation and predict the possible implications of climate change on economically and ecologically important marine species.

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APPENDIX

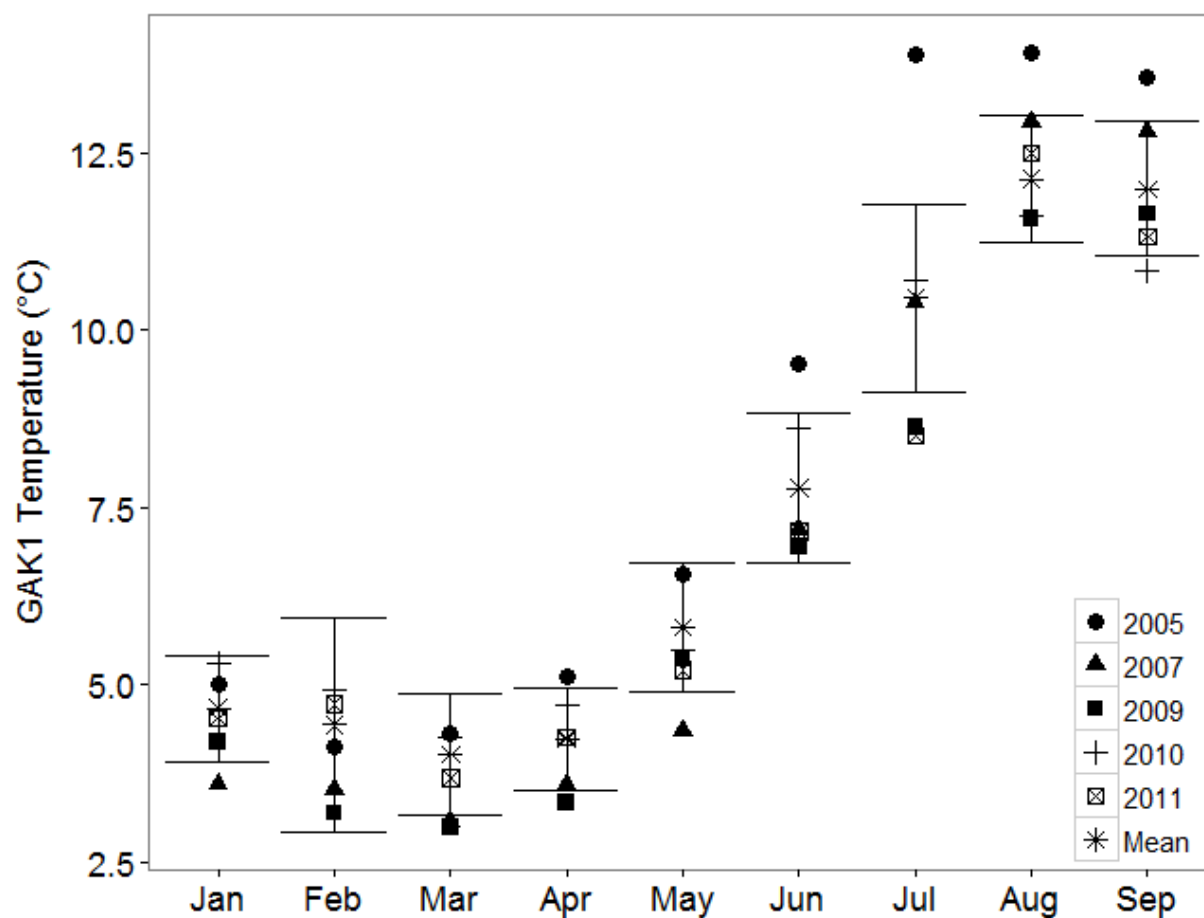


Figure A1. Monthly temperature averages of study years (2005, 2007, 2009-2011) and the 43-year time series (1971-2014) from GAK-1 temperature records at 20 m depth (\pm SD of the time-series mean).

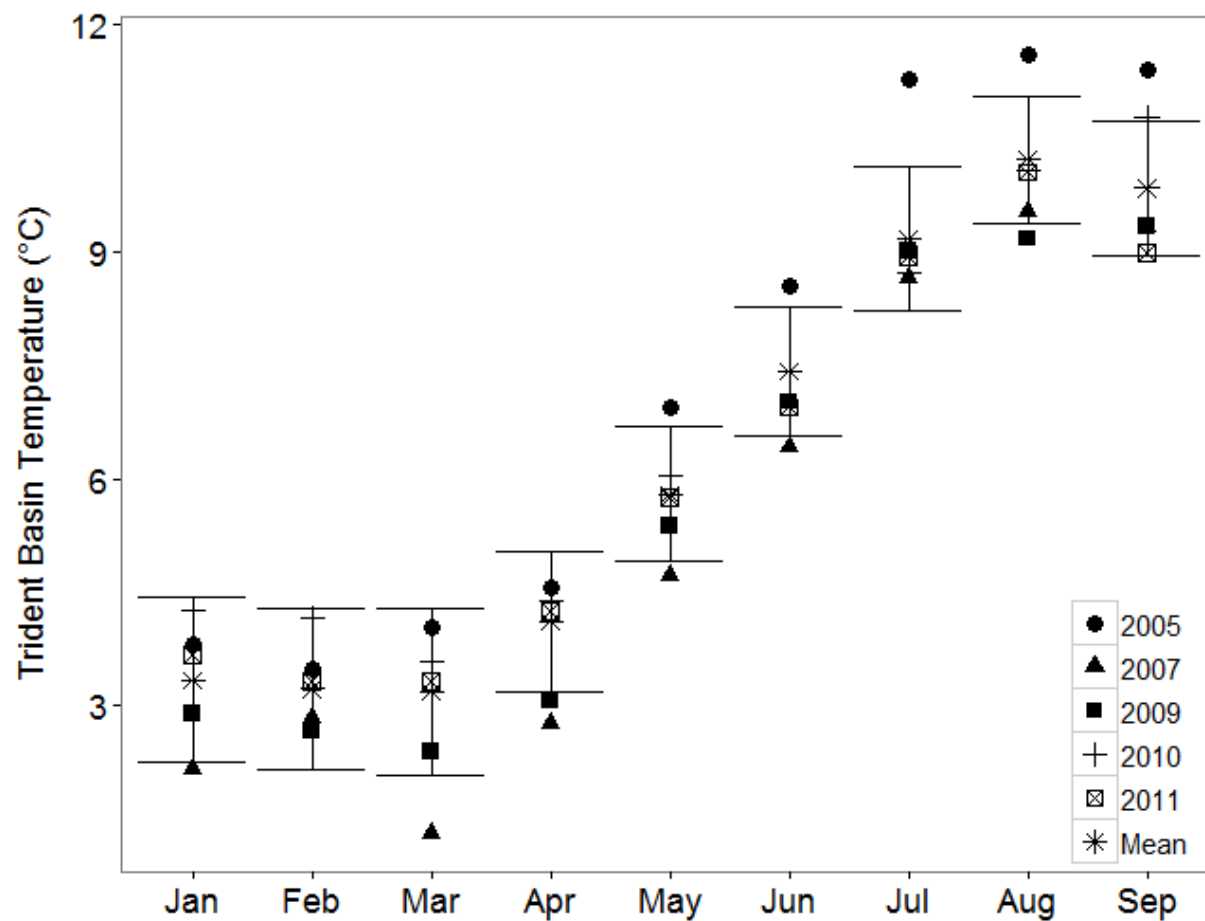


Figure A2. Monthly temperature averages of study years (2005, 2007, 2009-2011) and the 17-year time series (1997-2014) from Trident Basin temperature records (\pm SD of the time-series mean).

