

# The potential effects of pre-settlement processes on post-settlement growth and survival of juvenile northern rock sole (*Lepidopsetta polyxystra*) in Gulf of Alaska nursery habitats



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## ABSTRACT

Early life history traits in marine fish such as growth, size, and timing of life history transitions often vary in response to environmental conditions. Identifying the potential effects of trait variation across life history stages is critical to understanding growth, recruitment, and survival. Juvenile northern rock sole (*Lepidopsetta polyxystra*) were collected (2005, 2007, 2009–2011) from two coastal nurseries in the Gulf of Alaska during the early post-settlement period (July–August) to examine variation in early life history traits in relation to water temperature and juvenile densities in nurseries as well as to evaluate the potential for carry-over effects. Size-at-hatch, larval growth, metamorphosis size and timing, and post-metamorphic and recent growth of juveniles were quantified using otolith structural analysis and compared across years and sites. Additionally, traits of fish caught in July and August were compared for evidence of selective mortality. Post-metamorphic and recent growth were related to temperatures in nurseries as well as temperatures during the larval period, indicating a direct influence of concurrent nursery temperatures and a potential indirect effect of thermal conditions experienced by larvae. Correlations between metamorphic traits and fish size at capture demonstrated that interannual variation in size persisted across life history stages regardless of post-settlement growth patterns. No evidence of density-dependent growth or growth-selective mortality were detected during the early post-settlement period; however, differences in hatch size and metamorphosis timing between fish collected in July and August indicate a selective loss of individuals although the pattern varied across years. Overall, variation in size acquired early in life and temperature effects on the phenology of metamorphosis may influence the direction of selection and survival of northern rock sole.

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## 1. Introduction

Marine fish species such as flatfish have a complex life cycle with discrete pelagic larval and benthic juvenile stages. Settlement to the benthos following metamorphosis in flatfish exposes individuals to a novel habitat and a distinct suite of predators. Predation is considered the primary source of mortality in nursery grounds and individuals that grow slowly and settle at small sizes are often the most vulnerable to growth- and size-selective

predation (Ellis and Gibson, 1996; Nash and Geffen, 2000; Joh et al., 2013). These observations indicate that nursery conditions promoting fast growth and large body size are especially important in maximizing survival during post-settlement life stages. Growth in nursery grounds is influenced by density-dependent processes and environmental factors, including temperature and prey availability (Gibson, 1994; Sogard et al., 2001; Ciotti et al., 2013).

Flatfishes are considered particularly vulnerable to density-dependent effects on growth because large concentrations of recently settled juveniles present in nurseries can often result in increased competition (van der Veer, 1986; Bergman et al., 1988). Studies on several flatfish species have observed significant negative effects of high abundance on growth rates and post-settlement

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size (Steele and Edwards, 1970; Modin and Pihl, 1994; Nash et al., 1994). However, in other cases evidence for density-dependent processes in flatfish nurseries is limited, suggesting that environmental factors play a larger role in explaining growth variation. The “maximum growth/optimal food condition” hypothesis predicts that if there is no competition for food then temperature will be the primary driver of growth (Karakiri et al., 1991; van der Veer and Witte, 1993). Although the relative importance of food versus temperature on flatfish growth dynamics remains poorly understood, a large number of studies have documented positive correlations between post-settlement growth and temperature (e.g. Zijlstra et al., 1982; May and Jenkins, 1992; Teal et al., 2008).

Increasing attention has been paid to the relationships and interdependency of early life history stages with the recognition that conditions experienced during the larval stage may have lasting effects on the characteristics of post-settlement juveniles. Life history stages are linked through the processes of “carry-over effects” and selection. For example, environmentally-induced body size variation within and between cohorts tends to persist independent of subsequent growth rate variation (O'Connor et al., 2014). Because predation on juvenile fishes is generally inversely related to size (Ellis and Gibson, 1996; Sogard, 1997), size advantages gained during the larval stage can influence performance and survival in post-settlement periods (Searcy and Sponaugle, 2001; Vigliola and Meekan, 2002; Smith and Shima, 2011). These relationships are complicated by potential changes in magnitude and direction of selective pressures with ontogeny (Gagliano et al., 2007a; Johnson and Hixon, 2010). Correspondingly, while selection operates on phenotypes expressed in the juvenile stage, the covariation in traits across life history stages can effectively act as selection on traits expressed in the larval stage. Ultimately, a better understanding of individual growth histories and patterns of covariation in early life history characteristics is necessary to provide insight into trait-mediated survival of individuals as well as population-level ramifications of selection (McCormick, 1998).

Recent research directed toward understanding the effects of nursery habitat factors and potential carry-over effects on post-settlement growth and survival has focused on reef species (e.g. Shima and Findlay, 2002; McCormick and Hoey, 2004; Smith and Shima, 2011). Early life history processes of many North Pacific species, however, are not well understood despite their economic importance. Northern rock sole (*Lepidopsetta polyxystra*) is a flatfish species of high commercial value in the Gulf of Alaska and Bering Sea. In mid-winter to early spring, adult northern rock sole (NRS) spawn demersal eggs in nearshore bays (Stark and Somerton, 2002). Pelagic larvae metamorphose and settle in shallow nursery grounds in May and June (Norcross et al., 1995; Laurel et al., 2015). While research on the early life history stages of NRS has focused primarily on the post-settlement nursery period (Moles and Norcross, 1998; Hurst and Abookire, 2006; Ryer and Hurst, 2008; Ryer et al., 2012), larval growth exhibits significant interannual variation (Fedewa et al., 2016). Hurst et al. (2010) demonstrated that temperatures in the late-larval period explained >80% of the variation in post-settlement size of NRS and contributed to variation that persisted throughout the first growing season. Furthermore, post-settlement growth was more variable across years than across nursery sites and not related to NRS densities in the nurseries. These observations highlight the need to identify larval traits that may be carried over to post-settlement stages to influence growth and survival.

Consequently, we quantified spatial and temporal variation in post-settlement growth of NRS in relation to water temperature and juvenile NRS densities in two nursery sites in the Gulf of Alaska using otolith structural analysis. Pre- and post-settlement traits of NRS individuals were also examined to determine if relative

patterns of covariation in size and growth were maintained across life stages. In addition, we determined if there was evidence for selection related to timing of metamorphosis, growth or size in the nursery grounds between July and August during the early post-settlement period. Reconstructing and integrating pre- and post-settlement growth histories of “settlers” (July-captured fish) and “survivors” (August-captured fish) enabled the comparison of traits between the two months to determine if pre-settlement growth and size patterns were preserved during juvenile residence in nurseries. We therefore hypothesized that NRS that are larger at hatch, grow faster as larvae, and are larger at metamorphosis will display faster growth and experience greater survival during the early post-settlement period.

## 2. Materials and methods

### 2.1. Fish collection and site characterization

Age-0 NRS were collected off the northeast coast of Kodiak Island, Alaska, USA, at two nurseries: 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 (Fig. 1). Sampling for post-settlement NRS has been conducted annually since 2004 by the Fisheries Behavioral Ecology Program of the Alaska Fisheries Science Center (AFSC) (Hurst and Abookire, 2006; Laurel et al., 2015). Sampling was conducted using a 2-m beam trawl with a 3-mm mesh codend at fixed transects. Three to five 5-min trawls were conducted at approximately 10 m depth intervals between 7 and 30 m depth parallel to the shoreline on each sampling day (Hurst et al., 2010). After each tow, surface and bottom temperature, salinity and oxygen concentrations were measured (YSI model 85). Trawl catches were identified to species, frozen, and shipped to the AFSC laboratory in Newport, OR, USA. Density of age-0 NRS (fish/1000 m<sup>2</sup>) in the nursery areas on each sampling date was calculated from catch rates and GPS-measured trawl lengths (Hurst et al., 2010). Archived

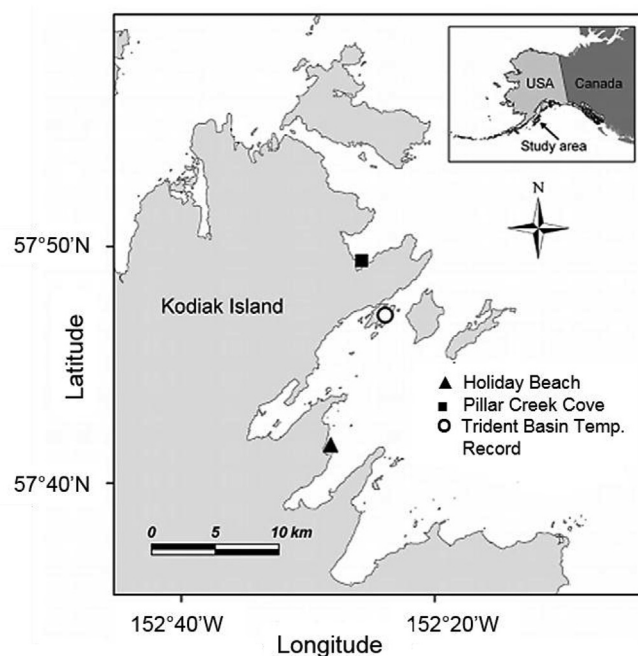


Fig. 1. Map of Pillar Creek Cove and Holiday Beach field sampling sites off the northeast coast of Kodiak Island, Alaska, USA.

NRS samples from field collections in 2005, 2007, 2009, 2010 and 2011 were selected for otolith structural analysis due to adequate sample sizes and suitable otolith condition (Table 1).

Daily, 15-day, and monthly temperature averages corresponding with the late-larval to early post-settlement period (~March–August) were collected from a continuous temperature record at 10 m depth in Trident Basin on the NE coast of Kodiak Island, AK (Fig. 1). This Trident Basin temperature station is close to Holiday Beach and Pillar Creek Cove with daily temperature differences averaging less than 0.5 °C between Trident Basin and the two sampling sites (Hurst et al., 2010). Therefore, Trident Basin temperature records were used as a proxy for regional temperature at both sites during NRS residency in nursery areas. Late-larval and early post-settlement periods span several months so 15-day temperature means were considered a suitable time interval for capturing temperature variability throughout the duration of both periods. Fifteen-day temperature means were used for all further statistical analyses.

## 2.2. Otolith preparation and interpretation

Juvenile NRS were measured using a digital caliper (standard length, SL, and total length, TL, nearest 0.1 mm). Right and left sagittae were removed and photographed using a stereoscope. Image analysis software (Image-Pro Premier®) was used to measure otolith length (anterior to posterior: longest axis) and width (dorsal to ventral: longest perpendicular axis). 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 (13.2–55.8 mm SL) (paired *t*-test,  $p > 0.05$ ,  $n = 52$ ). Right sagittae were selected for further otolith analysis and interpretation. 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. Polished otolith images were

acquired with a Leica DC300 camera and Leica DM1000 compound microscope (40–400× magnification).

Field-caught NRS otoliths displayed otolith morphology similar to laboratory-reared NRS otoliths, which were used to validate otolith landmarks in relation to early life history events (Fedewa et al., 2016). Daily increment widths were measured to reflect growth whereas the widths of the validated hatch check (HC<sub>W</sub>) and metamorphic check (MC<sub>W</sub>) were used as proxies for fish size at these life history events. Body size (SL) and otolith size were positively correlated in recently hatched larvae ( $r = 0.79$ ,  $p < 0.001$ ,  $n = 30$ ) as well as individuals both prior to and during metamorphosis ( $r = 0.87$ ,  $p < 0.001$ ,  $n = 35$ ). Ten consecutive increments were measured at designated otolith landmarks to characterize early larval, larval, post-metamorphic and recent growth for longitudinal data analyses (Fig. 2). The mean of all 10 increment width measurements for each growth metric was used in cross-sectional data analyses.

Early larval growth and larval growth were identified as separate growth metrics due to an increase in otolith increment width corresponding with a ~45-μm diameter check mark. Therefore, the metric of “early larval growth”, EL<sub>IW</sub>, represents ~10–20 d post-hatch, while the “larval growth” metric, L<sub>IW</sub>, represents ~20–30 d post-hatch. Analyses were limited to the first 10 increments in order to standardize measurements across individuals and reduce potential ontogenetic effects; however, there was evidence for strong covariation in growth across the entire larval period of individuals ( $r > 0.48$ ,  $p < 0.05$ ). 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. 2a). The post-metamorphic growth metric (PM<sub>IW</sub>) was measured across a 10-increment range during the first 20–30 days following eye migration whenever possible (73% of the 367 otoliths analyzed, Table 1). “Recent growth” (R<sub>IW</sub>) 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 10–30 day range

**Table 1**  
Sampling dates, size at capture range (TL, in mm), and sample size (TL<sub>n</sub>) of all age-0 northern rock sole (NRS) collected in two Kodiak Island nurseries (Holiday Beach, HB and Pillar Creek Cove, PCC). Individuals included in otolith analyses are a representative subset of the NRS age-0 size distribution, and sample sizes indicate the number of individuals used to estimate hatch check width, (HC<sub>W</sub>); early larval growth, (EL<sub>IW</sub>); larval growth, (L<sub>IW</sub>); metamorphic check width, (MC<sub>W</sub>); post-metamorphic growth, (PM<sub>IW</sub>); date of metamorphosis, (DOM<sup>a</sup>); and recent growth, (R<sub>IW</sub>). Sample sizes vary because not all metrics could be estimated for each individual. ‘ND’, or no data, refers to the lack of any readable otoliths during the corresponding period.

Year	Site	Month	TL	TL <sub>n</sub>	HC <sub>W</sub>	EL <sub>IW</sub>	L <sub>IW</sub>	MC <sub>W</sub>	PM <sub>IW</sub>	DOM <sup>a</sup>	R <sub>IW</sub>
2005	HB	Jul	21–51	71	ND	ND	ND	ND	ND	ND	ND
		Aug	26–76	97	17	16	24	26	21	21 (0)	22
	PCC	Jul	10–50	178	4	4	5	7	ND	ND	4
2007	HB	Jul	18–36	162	4	3	5	8	4	4 (0)	ND
		Aug	28–53	90	17	20	25	25	22	22 (1)	19
	PCC	Jul	17–32	138	6	5	8	9	7	7 (3)	5
2009	HB	Jul	19–46	117	23	22	24	25	23	23 (4)	19
		Aug	20–41	524	20	23	26	26	17	17 (7)	14
	PCC	Jul	26–59	122	9	9	14	18	9	9 (0)	17
2010	HB	Jul	20–41	326	23	24	27	26	22	22 (9)	11
		Aug	20–60	289	14	15	20	21	15	15 (3)	19
	PCC	Jul	21–39	30	18	16	19	22	10	10 (4)	15
2011	HB	Aug	34–59	40	16	15	20	18	19	17 (1)	19
		Jul	20–38	44	15	18	21	20	14	14 (8)	12
	PCC	Aug	20–66	51	22	22	23	26	23	22 (0)	20
2011	HB	Jul	20–41	239	11	12	12	13	11	11 (6)	6
		Aug	21–76	495	11	11	11	13	8	8 (0)	9
	PCC	Jul	20–46	330	9	11	13	13	11	11 (4)	6
		Aug	22–74	276	7	6	9	14	11	11 (0)	10

<sup>a</sup> Sample size represents number of fish for which DOM could be estimated from PM<sub>IW</sub> and ventral otolith growth; the number in parentheses is the number of samples with direct estimates of DOM used in the development of the DOM model.

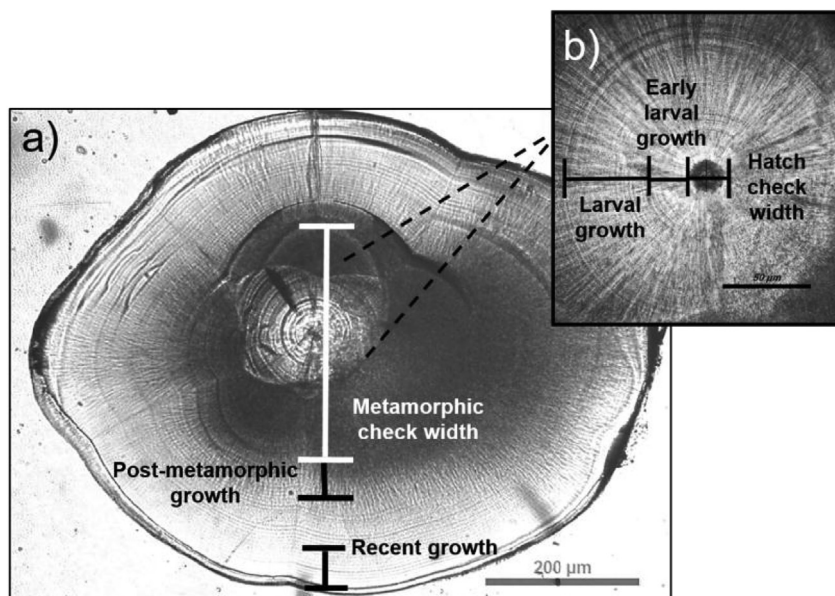


Fig. 2. Northern rock sole sagittal otolith landmarks and a) post-settlement and b) larval growth metrics used in the study.

prior to sampling (66% of the 367 otoliths analyzed).

An estimated date of metamorphosis was also determined for NRS individuals. Due to accessory primordia formation corresponding with metamorphosis, consecutive daily increments from the metamorphic check to the otolith edge could not be counted for all fish. These ageing difficulties were attributed to the obscure otolith region accompanying accessory primordia formation; therefore, we have no reason to believe that our results are biased towards the potential exclusion of individuals based on otolith microstructure.

Date of metamorphosis estimates were based on a model developed from a subset of otoliths with direct counts ( $n = 49$ ) of days post-metamorphosis ( $D_{PM}$ ). The model related post-metamorphic increment widths ( $PM_{IW}$ ) to cumulative post-metamorphic ventral otolith growth ( $V_{OG}$ ;  $R^2 = 0.90$ ; Fedewa et al., 2016, Eq. (1)).

$$D_{PM} = 34.986 - 10.942 \cdot PM_{IW} + 0.333 \cdot V_{OG} \quad (1)$$

Date of metamorphosis ( $DOM$ ) was then determined by subtracting estimated days post-metamorphosis from the known date of capture.

### 2.3. Data analyses

All data were tested for normality and homogeneity of variance assumptions for parametric tests. If assumptions could not be met after transformation, non-parametric tests were used. All statistical analyses were conducted in R, version 3.1.2 (R Development Core Team, 2012). The combination of small sample sizes and poor otolith quality due to degradation during storage precluded some data from statistical analyses, including: 1) post-metamorphic growth estimates for all July fish in 2005; 2) recent growth estimates for July fish in Pillar Creek in 2005; and 3) recent growth estimates for July fish in Holiday Beach in 2007. Therefore, 2005 was eliminated from July post-metamorphic analyses and 2005 and 2007 were eliminated from July recent analyses.

#### 2.3.1. Spatial and interannual patterns in growth and size metrics

To quantify spatial and temporal variation in growth and size, two-way Analysis of Variance (ANOVA) with site and year as factors and Tukey-Kramer post-hoc analysis were used to examine post-metamorphic growth, recent growth, and size at capture. July and August collections were examined separately. Statistical analyses examining July and August size at capture (TL, in mm) included all age-0 NRS collected whereas analyses examining growth metrics were limited to a representative subset of NRS used for otolith analyses.

#### 2.3.2. Environmental and growth carry-over effects

To evaluate the relationship between temperature and growth, correlation analyses (Pearson's correlation coefficient) were used to quantify interannual relationships between mean post-metamorphic growth metrics and 15-day mean Trident Bay temperatures corresponding with the post-settlement juvenile period prior to capture (June 2 - August 31). To determine if post-metamorphic and recent growth were related to temperatures experienced during earlier life stages, post-metamorphic, July recent, and August recent growth were compared to 15-day mean water temperatures during the late-larval to peak metamorphosis period (March 19 - June 1). Peak metamorphosis period (May 4 - June 1) was defined as the range of annual mean date of metamorphosis estimates. We adjusted the significance level of all correlation analyses to account for multiple comparisons and also adjusted degrees of freedom to account for temporal autocorrelation in temperature stanzas (Pyper and Peterman, 1998).

In addition, we compared average NRS densities between July and August using a paired  $t$ -test, which included 10 comparisons for each site by year combination. Correlation analyses were used to examine relationships between mean recent growth metrics and densities in July and August.

To further evaluate potential carry-over effects, we determined if growth and size metrics covaried across life history stages by comparing individual pre- and post-settlement growth and size metrics across all 5 years with partial correlation analysis. To account for annual differences among traits, we determined the



residuals from regression analyses of each metric by year and then performed correlation analysis on the resulting residuals. While we do not consider fish collected in the same year independent samples, correlation analyses do not assume data are independent (Fisher, 1915). In addition, all  $\alpha$  values in analyses were Bonferroni corrected to account for multiple comparisons and possible Type 1 error associated with multiple tests.

### 2.3.3. Selective mortality during the early post-settlement period

To determine if there was evidence for selection based on timing of metamorphosis, growth, or size during the July to August early post-settlement period, comparisons were made between July fish (referred to as July “settlers”) and August fish (referred to as August “survivors”). To evaluate phenological changes in the sample population of juvenile NRS, the date of metamorphosis between July settlers and August survivors was examined with a two-way ANOVA with month and year as main effects. One year (2005) was eliminated from the analysis due to missing data.

Additionally, a Gaussian linear model with a linear covariance structure (Clifford and McCullagh, 2006) was used to assess evidence for growth selection by examining growth histories of July settlers and August survivors after integrating all pre- and post-settlement growth metrics. The incorporation of a 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 response variable of the model was the growth curve of individual fish as given by a vector of the growth metrics across life stages (hereafter referred to as “individual growth histories”). In the full model, the linear mean structure of a growth metric was:

$$\text{Metric} \sim \text{stage} + \text{year} + \text{collection month} + \text{all two} \\ \text{— way interactions} \quad (2)$$

where the explanatory variables in the model included: 1) stage, a categorical variable whose levels are early larval growth ( $EL_{IW}$ ), larval growth ( $L_{IW}$ ), post-metamorphic growth ( $PM_{IW}$ ), and recent growth, which was represented by either July ( $JulyR_{IW}$ ) or August ( $AugR_{IW}$ ) growth depending on when juveniles were collected; 2) year, a categorical variable with 5 levels; and 3) month of collection (July and August). The two-way interactions between factors allowed stage-specific growth histories to have different “shapes” across years. A covariance structure was specified to allow for heterogeneous variability of the growth metrics across stages as well as a correlation between any two life stages within a fish. Restricted maximum likelihood (REML) was used to estimate mean and covariance parameters (R package Gaussian ‘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 using linear models with 1) year and 2) month as categorical factors. 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 factor in the size at metamorphosis model.

### 2.3.4. Interannual variability in pre- and post-settlement traits

To compare interannual variability across early life stages during the study period, we determined annual anomalies for each growth and size metric. Anomalies were calculated by subtracting the 5-year mean from annual means for each trait and then dividing by the 5-year mean. Anomalies were presented as percentages of the

5-year mean.

## 3. Results

### 3.1. Environmental variation in nursery sites

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. Inter-annual 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. 3, one-way ANOVA,  $F_{4,360} = 4.28$ ,  $p < 0.01$ ) as well as all 17 years in the Trident Bay temperature record. 2007 was the coldest year during the early post-metamorphic period with lower than average temperatures observed from mid-April to mid-July.

### 3.2. Spatial and interannual patterns in growth and size metrics

Mean post-metamorphic growth of July fish varied interannually (Fig. 4a, two-way ANOVA,  $F_{3,88} = 6.53$ ,  $p < 0.001$ ) but not between nursery sites ( $p > 0.05$ ). July post-metamorphic growth was significantly higher in 2010 and 2011 than in 2007 (Tukey HSD,  $p < 0.01$ ). There was no significant effect of site or interaction with year on mean recent growth of July fish (two-way ANOVA,  $p > 0.05$ ; analysis of 2009–2011 due to missing data in 2005 and 2007). A one-way ANOVA of data pooled across sites revealed a significant effect of year on July recent growth (Fig. 4a,  $F_{4,68} = 3.90$ ,  $p < 0.01$ ) with significantly faster growth in 2010 than in 2005 (Tukey HSD,  $p < 0.01$ ). There were no significant differences in mean post-metamorphic growth of August fish across years or between sites (Fig. 4b, two-way ANOVA,  $p > 0.05$ ). August recent growth varied

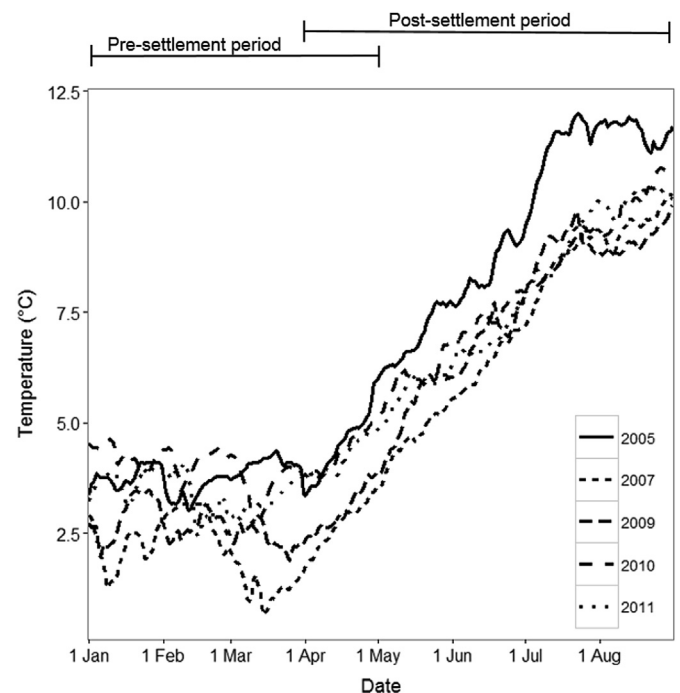
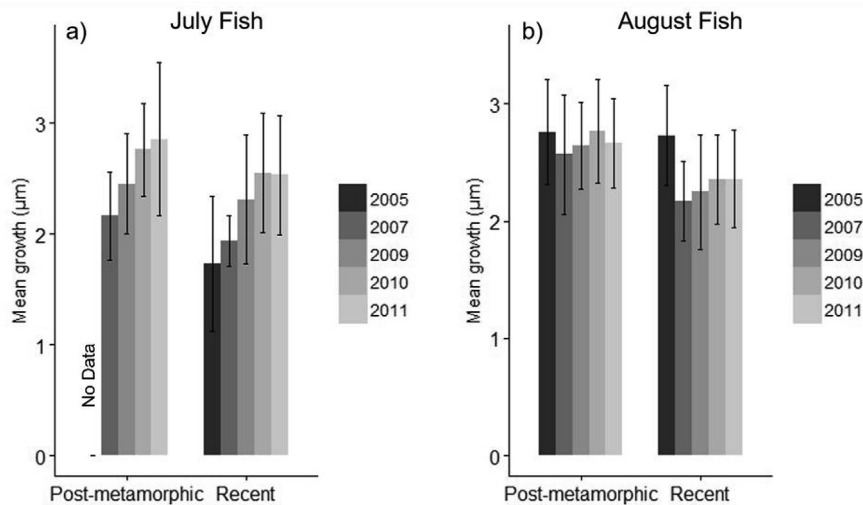


Fig. 3. Temporal trends in Trident Basin daily temperatures off the northeast coast of Kodiak Island, Alaska corresponding with the pre-settlement period (~January–May) and post-settlement period (~May–August). Overlap in the pre-settlement and post-settlement periods represent individual as well as interannual variation in northern rock sole date of metamorphosis.



**Fig. 4.** Northern rock sole annual mean post-metamorphic and recent growth ( $\pm$ SD) of a) July fish and b) August fish. July post-metamorphic growth estimates in 2005 were excluded from statistical analyses.

**Table 2**

Pearson product-moment correlation coefficients ( $r$ ) for relationships between annual means of northern rock sole post-metamorphic growth metrics versus 15-day mean water temperatures in Trident Bay, AK. 'NA' indicates correlations that were not applicable.

15-day temp	Growth metric		
	Post-metamorphic growth	July recent growth	August recent growth
<b>Late-larval to peak metamorphosis period</b>			
Mar 19–Apr 2	0.98	0.26	0.76
Apr 3–17	<b>0.99</b>	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
<b>Post-settlement juvenile period</b>			
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	NA	NA	0.95
Aug 1–15	NA	NA	0.97
Aug 16–31	NA	NA	0.93

Note: Critical values were adjusted to account for multiple comparisons and autocorrelation. Significant values after correction are indicated in **bold** ( $r = 0.99$ ).  $n = 5$  for all comparisons.

across years and between sites (two-way ANOVA,  $p < 0.05$ ) with significantly faster growth in 2005 and in Pillar Creek (Tukey HSD,  $p < 0.05$ ).

July size at capture analysis revealed a significant interaction between site and year (two-way ANOVA,  $F_{4,2032} = 3.19$ ,  $p < 0.05$ ) that was driven by larger fish in Holiday Beach every year, although the magnitude of variation in fish size between sites differed from 0.05 mm in 2011 to 2 mm in 2010. Across years, NRS were largest in 2011 and smallest in 2007. August size at capture analyses indicated that the interaction between site and year was significant (two-way ANOVA,  $F_{4,1760} = 82.28$ ,  $p < 0.001$ ), primarily driven by relatively large fish size in 2005 at Holiday Beach compared to Pillar Creek. Across years, August fish were significantly larger in 2010, whereas the smallest mean size at capture was observed in 2007. As observed in July, Holiday Beach fish were larger than Pillar Creek fish in August collections.

### 3.3. Environmental and growth carry-over effects

Correlation analyses 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 2,  $r > 0.97$ ). Mean July recent growth was not correlated with water temperatures during the late-larval or post-metamorphic periods. However, mean August recent growth was positively correlated with water temperatures from the peak of metamorphosis to sampling in August.

There were significant differences in NRS densities between months (paired  $t$ -test,  $p < 0.05$ ). Maximum densities were generally observed in July, likely corresponding with the completion of metamorphosis and settlement. We did not see evidence of density-dependent growth rates among NRS in the nursery area. Across years, July and August recent growth metrics were not correlated with NRS densities at the time of capture when examined independently for each site or when pooled across sites (Fig. 5, all correlations  $p > 0.05$ ).

Partial correlation analyses to evaluate the potential for carry-over effects related to individual growth and size metrics indicated that recent growth of July fish was positively correlated with post-metamorphic growth (Table 3). Additionally, July size at capture was positively correlated with size at metamorphosis and negatively correlated with date of metamorphosis (i.e. small size

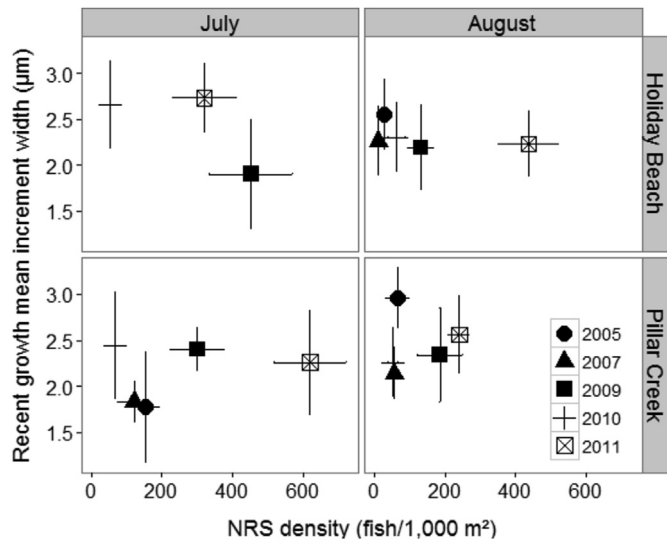


Fig. 5. Mean ( $\pm$ SD) recent growth of northern rock sole in July and August in two Kodiak Island nursery sites, Holiday Beach and Pillar Creek, in relation to northern rock sole densities in nurseries ( $\pm$ SE).

was associated with later metamorphosis). Recent growth of July fish was positively correlated with size at hatch, and post-metamorphic growth was negatively correlated with larval growth, although these relationships were not statistically significant after Bonferroni adjustments. Among August fish, recent growth was positively correlated with early larval growth and post-metamorphic growth, although the relationship between August recent and post-metamorphic growth was not significant after Bonferroni adjustments. Similar to July, size at capture in August was positively correlated with size at metamorphosis and post-metamorphic growth, and negatively correlated with date of metamorphosis.

#### 3.4. Selective mortality during the early post-settlement period

Analyses to examine evidence for selection on the timing of metamorphosis between July and August revealed a statistically significant interaction between year and month (Fig. 6, two-way ANOVA,  $F_{3,215} = 6.31$ ,  $p < 0.05$ ). In both 2009 and 2010, the mean metamorphosis date observed among August survivors was

significantly earlier than that observed among July settlers. However, in 2007, August survivors had later dates of metamorphosis than July settlers.

An integrated linear model of individual growth histories was used to assess evidence for growth selection between July and August. A stepwise selection of main effects and interactions resulted in the inclusion of an interaction between year and stage as well as significant year and stage main effects (Fig. 7a,  $p < 0.001$ ). However, month of collection was not significant ( $p = 0.090$ ). Therefore, pre- and post-metamorphic growth histories did not differ significantly between July settlers and August survivors, indicating that there was no evidence for strong selection related to growth rates of earlier ontogenetic stages.

A linear model to assess evidence for size selection indicated a significant interaction between month of capture and year on hatch size (Fig. 7b). In 2005, 2009 and 2011, the size at hatch of August survivors was significantly greater than those of July settlers. Conversely, the 2010 size at hatch of August survivors was smaller than among July settlers. There were no significant effects of capture month, year, or their interaction on size at metamorphosis.

#### 3.5. Interannual variability in pre- and post-settlement traits

The relative magnitude of variation across early life stages varied both across years and between traits (Fig. 8). The least variation was observed for metamorphic check width, and there was the greatest variability in recent growth and size-at-capture. 2005 growth metric anomalies were all positive with the exception of July recent growth and July size-at-capture. Conversely all metrics in 2007 displayed negative anomalies.

## 4. Discussion

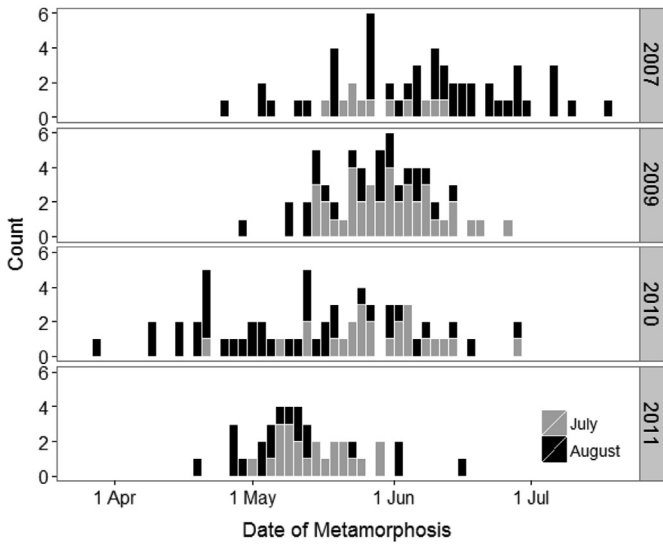
Variation in growth and development during the larval stage can carry over to subsequent post-settlement stages, potentially influencing future growth and survival (Shima and Findlay, 2002; McCormick and Hoey, 2004). To the best of our knowledge, this study is the first to integrate pre- and post-settlement processes of a North Pacific flatfish in relation to growth and survival during the early post-settlement period. Overall, post-metamorphic and August recent growth of NRS were positively associated with temperatures in the nursery habitat as well as temperatures experienced during the larval period. Size at capture metrics were correlated with metamorphosis size and timing, which indicates a coupling of traits across major life history transitions. These results suggest that both carry-over effects of temperature conditions

Table 3

Partial correlations of pre- and post-metamorphic 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, ( $MC_W$ ); date of metamorphosis, ( $DOM$ ); 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, ( $JulyS_C$ ) and August size at capture ( $AugS_C$ ). 'NA' indicates correlations that were not applicable.

	JulyPM <sub>IW</sub>	AugPM <sub>IW</sub>	JulyR <sub>IW</sub>	AugR <sub>IW</sub>	JulyS <sub>C</sub>	AugS <sub>C</sub>
HC <sub>W</sub>	0.07 (n = 79)	0.04 (n = 124)	0.28 (n = 55)	0.11 (n = 122)	0.07 (n = 110)	0.12 (n = 156)
EL <sub>IW</sub>	0.03 (n = 77)	0.06 (n = 120)	0.11 (n = 59)	<b>0.24</b> (n = 118)	-0.10 (n = 116)	0.09 (n = 145)
L <sub>IW</sub>	-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 <sub>W</sub>	-0.04 (n = 94)	-0.10 (n = 167)	0.10 (n = 70)	-0.12 (n = 166)	<b>0.34</b> (n = 144)	<b>0.19</b> (n = 213)
DOM	0.25 (n = 96)	-0.04 (n = 167)	0.24 (n = 46)	-0.07 (n = 137)	<b>-0.37</b> (n = 96)	<b>-0.83</b> (n = 167)
JulyPM <sub>IW</sub>			<b>0.65</b> (n = 46)	NA	0.16 (n = 96)	NA
AugPM <sub>IW</sub>				0.22 (n = 140)	NA	<b>0.21</b> (n = 170)
JulyR <sub>IW</sub>				NA	0.14 (n = 73)	NA
AugR <sub>IW</sub>					NA	0.07 (n = 168)

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



**Fig. 6.** Frequency distributions of estimated date of metamorphosis for northern rock sole collected in July and August in two Kodiak Island nursery sites. July collections are considered “settlers” and August collections are considered “survivors”.

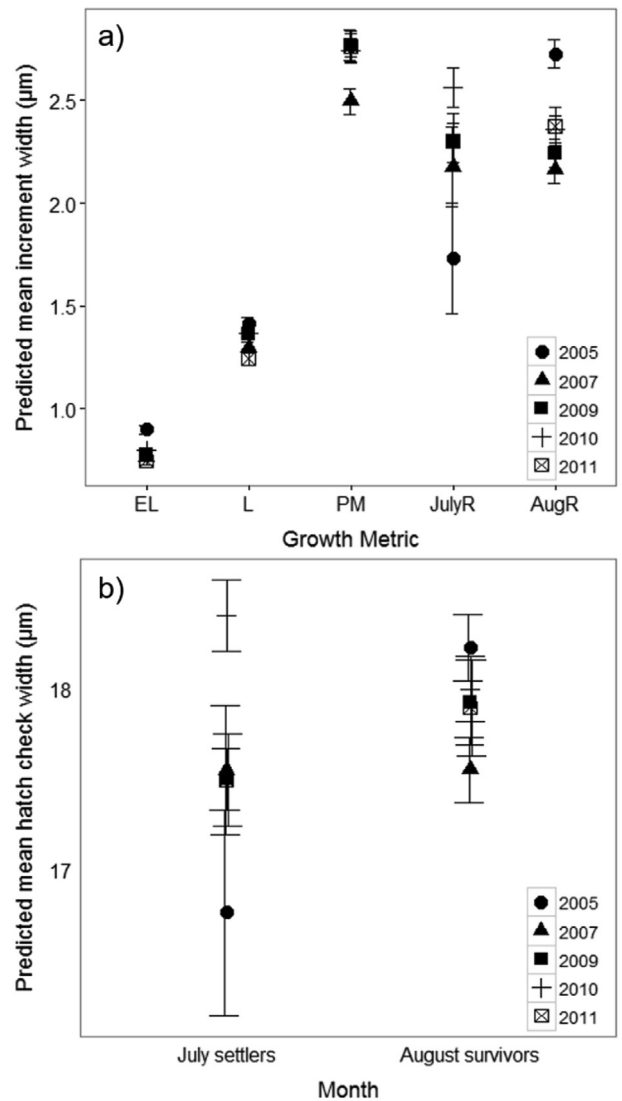
experienced as larvae as well as growth and size carry-over effects across life history stages may play an important role in post-settlement processes of NRS. We detected no evidence for density-dependent growth or selective mortality related to growth metrics during the post-settlement period from July and August. However, some post-settlement growth selection may have occurred prior to our May sampling. On the other hand, differences in size at hatch and timing of metamorphosis between July settlers and August survivors indicate that hatch size and phenology are related to factors influencing survival during the early post-settlement period and may have consequences for recruitment to the adult population.

**4.1. Influences on spatial and interannual patterns in growth and size metrics**

Growth during the post-settlement period was more variable among years than between nursery sites. Significant positive correlations between temperatures and annual post-metamorphic and recent growth means suggest that temperatures in the nursery grounds have a significant influence on growth variation during the post-settlement period. This is in partial contrast to Hurst et al. (2010) who found (based on cohort tracking) that mean summer temperatures were not strongly correlated with overall growth rates in nurseries. However, by measuring individual fish growth rates from otoliths and relating these to temperatures in specific time periods, we were able to provide a clearer understanding of these patterns. In this study, July recent growth was not correlated with temperature stanzas during the pre- and post-settlement periods, indicating that temperature may not have contributed to the observed interannual variation in growth. Conversely, measures of post-metamorphic and August recent growth were positively correlated with temperatures during and preceding the growth window, indicating a direct influence of concurrent nursery temperatures on growth as well as an indirect effect from thermal conditions experienced by larvae.

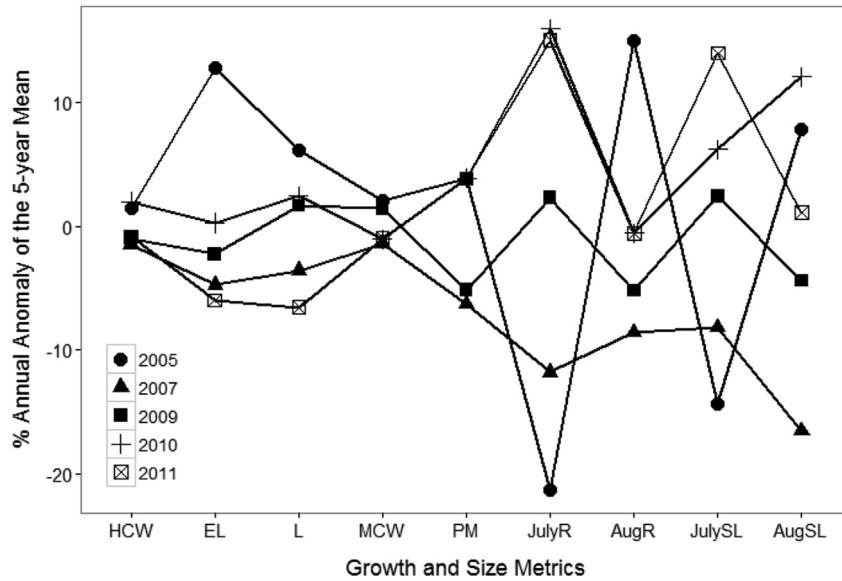
These results support the suggestion of Hurst et al. (2010) that patterns of body size variation through the first growing season are significantly affected by the effects of temperature during the larval

and metamorphosis periods. The observed positive association between mid-March to mid-May temperatures and post-metamorphic growth specifically suggests that the effects of temperatures experienced during the larval period may carry over to influence growth following metamorphosis. This finding that temperatures during earlier life history stages are more highly correlated with post-metamorphic growth than temperatures during the juvenile nursery period is also 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. Another likely mechanism linking larval temperatures with post-settlement growth metrics is the observed temporal correlation between March–May larval temperatures and nursery temperatures. As temperatures continue to get warmer throughout the pre- and post-settlement periods, individuals could exhibit a consistent temperature sensitive growth response across life history stages. However, a decline in July recent growth during



**Fig. 7.** a) Predicted values for annual mean growth rates across pre- and post-metamorphic growth metrics and b) predicted values for mean size at hatch for July settlers and August survivors across years ( $\pm$ SE for the fitted values). Growth metrics include: early larval growth (EL); larval growth (L); post-metamorphic growth (PM); July recent growth (JulyR); and August recent growth (AugR).





**Fig. 8.** Percent anomaly of the 5-year mean for growth and size metrics of 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), August recent growth (AugR), July size at capture (JulySL), and August size at capture (AugSL).

the warmest year in the study (2005) suggests that a consistently positive relationship with temperature does not always occur across all ontogenetic stages and covariation in temperatures within a year may not explain episodes of declined growth.

The concentration of juvenile stages in spatially limited nursery areas has prompted frequent consideration of density-dependent food limitation in many flatfish species (Beverton, 1995). We found no evidence for this hypothesis as there were no significant relationships between fish densities and otolith-derived growth rates. This is consistent with previous studies on juvenile NRS that reported no evidence for density-dependent effects on growth based on cohort means (Hurst et al., 2010). While conclusions vary, numerous other studies have also found that variation in growth rates of juvenile flatfishes is primarily driven by factors other than intraspecific competition (van der Veer et al., 1990; Sogard et al., 2001; Nash et al., 2007). Although prey availability could be more variable later in life, the carrying capacity of nurseries in the Gulf of Alaska may not be a limiting factor on post-settlement processes.

Site differences in both body size and growth rates were more commonly observed in August than in July or the immediate post-metamorphic period. Similarities during July sampling are potentially associated with larvae settling into the two nurseries that have experienced similar environmental conditions in the coastal ocean prior to settlement. In addition, July sampling occurred in the early post-settlement period. While differences in body size in August reflect the accumulation of growth differences among sites, the direct observation of differences in otolith-derived growth rates confirms the diverging conditions for growth. As in previous studies, Holiday Beach generally supported the fastest growth rates and largest age-0 fish (Hurst and Abookire, 2006; Hurst et al., 2010), but the fastest observed growth rates occurred at Pillar Creek in August 2005. Interestingly, the primary difference in growth conditions between nurseries does not appear to be water temperature as the sites were consistently within 0.5 °C of each other. Instead, the spatial growth variation suggests that summer nursery habitat conditions may be fairly dynamic, although this site variation appears to be consistently less than the observed interannual

variation.

#### 4.2. Carry-over effects of traits across pre- and post-settlement stages

Carry-over effects in which earlier growth or development influence post-settlement stages have been proposed for some species (e.g. Vigliola and Meekan, 2002; McCormick and Hoey, 2004; Smith and Shima, 2011). In their simplest form, body size variation generated during one life stage is “carried over” to the next stage with size differences persisting over time. In this study, we observed evidence for this type of carry-over effect with July sizes being positively correlated with the size and date of metamorphosis. Similarly, size in August was related to size at metamorphosis, date of metamorphosis and post-metamorphic growth. It is worth noting that capture size in July and August were not correlated with growth just prior to capture. While this recent growth did not appear to reinforce size differences generated in earlier stages, it was insufficient to override the previously-established patterns. Given the fact that NRS display a relatively small range in size at metamorphosis compared to other early life history size traits (Fig. 8), evidence of carry-over effects related to size at metamorphosis suggest that even small advantages at this critical life history event can have lasting impacts throughout the growing season.

More complex forms of carry-over effects are indicated when performance traits (e.g. growth rates) are influenced by the performance or environment experienced during a previous life stage. When related to thermal history, these are commonly considered effects of “acclimatization” and have been well documented in laboratory studies (Green and McCormick, 2005; Hurst et al., 2012; Burton and Metcalfe, 2014). Unfortunately, in the wild, these types of carry-over effects are difficult to distinguish due to patterns of temporal autocorrelation in environmental conditions. For example, the strong correlation observed between post-metamorphic and July recent growth rates could be due to such environmental covariation. However, the fact that July recent

growth rates had weak negative correlations with field temperatures suggests the possibility of a carry-over benefit of growth rate itself from the metamorphic to nursery stages, and may be contributing to this observed pattern. A negative correlation (not significant after Bonferroni adjustment) between larval growth rates and post-settlement growth rates suggests the possibility of compensatory growth between life history stages. Compensatory growth is a unique type of carry-over effect which has been observed in laboratory studies of larval and juvenile growth in flatfishes (Chambers et al., 1988; Bertram et al., 1993).

#### 4.3. Selective mortality during the early post-settlement period

In this study, hatch size and the timing of metamorphosis were significantly different between July “settlers” and August “survivors”, suggesting that interconnections between life history stages could play an important role in post-settlement survival of NRS. This is not to suggest that mortality during the juvenile nursery phase is directly linked to hatch size, a trait expressed several months prior. Rather it suggests that survival during the juvenile phase is associated with a suite of related traits (including hatch size) expressed during early life (Meekan and Fortier, 1996; Meekan et al., 2006; D’Alessandro et al., 2013). Therefore, selective mortality of individuals may be attributed to a carry-over effect related to hatch size that operates across life history stages (Gagliano et al., 2007a). As described above, statistically significant correlations between size at hatch and subsequent post-metamorphic growth or size metrics were not observed. As a result, it is not clear which NRS trait(s) could be responsible for the apparent selection related to size at hatch, but we hypothesize that it may be associated with some inherent physiological trait such as metabolic performance or efficiency (Bochdansky et al., 2005; Garrido et al., 2015). Survival advantages associated with hatch size could also be related to maternal effects; that is, maternal condition prior to spawning influences offspring survival and fitness (Chambers et al., 1989; Riveiro et al., 2000; McCormick, 2006).

We also observed evidence for selection between July settlers and August survivors related to timing of metamorphosis, which suggests that mortality rate can vary with phenology, although the direction of that selection varied across years. Studies on selective mortality in other species have demonstrated variation in the intensity and direction of trait-mediated survival, often attributed to temperature influences (Gagliano et al., 2007b; Rankin and Sponaugle, 2011; Grorud-Colvert and Sponaugle, 2011). In this study, the pattern of selection on metamorphosis timing was not consistent across years or thermal regimes. We observed selection for earlier metamorphosis dates in 2009 and 2010, but a reversal of that pattern in 2007. As nursery grounds presumably maximize growth potential for juvenile fish (Gibson, 1994), individuals that metamorphose and settle earlier may be able to take advantage of a longer growing season when thermal conditions are favorable. However, in the Gulf of Alaska, 2007 was the coldest year observed in the past 25 years, potentially exposing earlier settlers to unfavorable thermal conditions resulting in survival advantages that favored later dates of metamorphosis.

Interestingly, there were no significant differences in growth histories between July settlers and August survivors. This suggests that during the early post-settlement period from July to August there was no selection related to growth rates exhibited in earlier life history stages or that such selection was not strong enough to detect here. The lack of significant differences between growth metrics of settlers and survivors does not, however, imply that growth selection does not occur in earlier life stages. Our approach of examining survivors and inferring pre-settlement traits from otoliths of those survivors means that selection that occurred in

early life history stages would not be detected. A more comprehensive approach would, for example, entail repeated sampling of the cohort during both pre- and post-metamorphic life history stages to identify selection in both stages. However, environmental conditions and logistical constraints make this an unlikely option for Gulf of Alaska species. Our sampling strategy was based on collections of early life history stages that we could be reasonably confident of capturing the same “population” over time. In addition, all cohort tracking studies are subject to the possibility of continued immigration to, or emigration from the nursery area between sampling periods. However, in our case, this potential is limited by the nearshore habitat use of this species and presence of geographical barriers (headlands and deep waters) between coastal embayments (Hurst and Abookire, 2006).

Overall, interannual variation in post-settlement growth metrics of NRS juveniles was best explained by the cumulative effect of temperatures from the late-larval to juvenile nursery period. Interannual variation in growth during the post-settlement period was greater than variation between nursery sites, and there was no evidence for density-dependent regulation of growth within nurseries. These observations suggest regional coherence in post-settlement growth dynamics, although it is plausible that spatial variation may occur at larger spatial scales. The positive role of larval temperatures on post-metamorphic and recent nursery growth suggests that thermal conditions experienced as larvae may influence post-settlement growth processes. We detected evidence for post-settlement selection related to hatch size and the timing of metamorphosis, although the patterns of selection varied across years. The observation that the warmest (2005) and coldest (2007) years of the study stood out as having distinctive patterns of trait variation across ontogeny and selection on hatch size and metamorphosis timing, respectively, suggests that indirect effects of temperature or other habitat or parental factors play a significant role in growth dynamics and patterns of survival during the post-settlement period. In addition, it implies that selective mortality during the juvenile nursery phase will likely be shaped by climate change. A better understanding of the environmental drivers of growth and mechanisms regulating the direction and strength of selective mortality across variable environmental conditions is needed to predict the responses of NRS and other fishery species in the Gulf of Alaska to future temperature variation.

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## Appendix

Table A.1

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

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

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.

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