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ORIGINAL PAPER

# Thermal reaction norms for growth vary among cohorts of Pacific cod (*Gadus macrocephalus*)

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**Abstract** While much effort has been directed at determining the spatial scales of adaptation in thermal reaction norms for growth, it is widely assumed that these reaction norms have high temporal stability. Water temperatures in the Gulf of Alaska in 2007 were the coldest on record since the mid-1970s and we present evidence that the thermal reaction norm for growth of age-0 Pacific cod (*Gadus macrocephalus*) in this cohort differed significantly from two adjacent cohorts. In addition to exhibiting higher growth potential at low temperatures, the 2007 cohort had a higher mean vertebral count, consistent with the widespread thermal effect known as "Jordan's Rule." Variation among cohorts in these physiological and morphological traits suggests a persistent response to environmental history (epigenetic effect). Temperature-induced phenotypic plasticity in the reaction norm for growth has significant implications for using growth rates to evaluate habitat quality and illustrates the complex responses of fishes to climate variability.

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## Introduction

Temperature is a primary driver of all aspects of the physiology of ectotherms including growth potential. As such, the relationship between water temperature and potential growth rate ("temperature-dependence of growth" or "thermal reaction norm for growth") is considered a critical trait of species and populations and has been described for multiple life stages for a wide variety of marine and freshwater fishes. Ultimately, the responses of populations and communities to climate forcing represent the cumulative effects of a suite of physiological and behavioral responses to temperature and its interaction with other abiotic and biotic aspects of the environment (King et al. 1999; Rijnsdorp et al. 2009).

It is widely accepted that thermal reaction norms are evolved to maximize survival and fitness in prevailing thermal regimes (Huey and Kingsolver 1989; Angilletta et al. 2002; Salinas and Munch 2012). Over the past decade, there has been increased research attention devoted to describing the spatial scale at which thermal reaction norms are adapted to local climate regimes (Conover et al. 2006). A number of studies have shown local adaptation in temperature-dependent growth responses in fishes, frequently corresponding to latitudinal clines in temperatures and growing season length (reviewed by Conover et al. 2010). In addition, efforts to reconstruct historical dynamics of harvested species have led researchers to evaluate the temporal stability of reaction norms of growth and maturation to temperature over decades (Mollet et al. 2007). However, few studies have specifically evaluated the temporal stability of reaction norms to temperature under different climate regimes, and none have tested the assumption that growth rates measured for one cohort apply to subsequent cohorts.

Due to the confounding effects of prey availability, oxygen levels, social interactions, and selective mortality, it is difficult to resolve thermal reaction norms using field collections alone. Thermal reaction norms are more definitively described in the laboratory where other environmental factors can be controlled, isolating the influence of temperature. Homogeneous groups of organisms are reared across a range of temperatures under unrestricted foraging conditions. The relative performance in these treatments describes the thermal reaction norm for growth for the species, population, or experimental cross of interest. The resulting growth responses are then applied to a variety of ecological questions (King et al. 1999; Searcy et al. 2007; Freitas et al. 2007; Hurst et al. 2010a).

Pacific cod (*Gadus macrocephalus*) is a widespread marine species, occurring on continental shelves throughout the eastern and western North Pacific and Bering Sea. They are an important component of North Pacific and Bering Sea fisheries and food webs. Along the West Coast of the United States, landings of Pacific cod trail only those of Alaskan walleye pollock (*Theragra chalcogramma*; NMFS 2008). However, until recently, detailed information about thermal effects on Pacific cod biology was limited to the egg stage (Alderdice and Forrester 1971). Thermal effects on the behavior of Pacific cod larvae and juveniles have been examined by Hurst et al. (2009) and Davis and Ottmar (2009). Hurst et al. (2010b) described the interactive effects of temperature and body size on growth potential of larval and early post-settlement juveniles, and Laurel et al. (2011) described the interactive effects of temperature and prey availability on larval growth. However, none of the studies to date have considered the potential for variation among cohorts in their responses to thermal variation.

In this paper, we describe the thermal reaction norms for growth of juvenile Pacific cod from three naturally produced annual cohorts (2006–2008). Although not a part of the a priori study design, this period included a marked variation in thermal conditions in the Gulf of Alaska during the spawning and early developmental period of Pacific cod: the winter and spring of 2007 were the coldest on record since the mid-1970s (Janout et al. 2009). In addition, we describe variation among these cohorts in mean vertebral count (a trait known to vary inversely with incubation temperature in numerous fishes). Together, these results suggest temperature-induced phenotypic plasticity in the early life history extends to both physiological and morphological traits. These results have important implications for evaluating habitat quality in marine ecosystems and understanding the population responses to climate variability across a variety of spatial and temporal scales (Stillman 2003).

## Methods

### Temperature records

In the Gulf of Alaska, the winter and spring of 2007 were anomalously cold, being the coldest on record since the mid-1970s (Janout et al. 2009). Two sets of temperature records were used to illustrate interannual variation in water temperatures. Nearshore temperatures in the vicinity of the fish collection site were obtained from a logging station at 10.7 m depth in Trident Basin (57.782°N 152.389°W), on the northeast coast of Kodiak Island. In addition, offshore sea surface temperatures measured at 1 m below the surface were obtained from NOAA's National Ocean Buoy Data Center for station 46078 at Albatross Banks (56.074°N 152.572°W), 65 NM south of Kodiak Island. Both records provided a continuous record of hourly temperatures over the study period of January 1, 2006 through December 31, 2008, which were converted to daily averages for these analyses. Although we do not have detailed information on the spawning times of Pacific cod in the central Gulf of Alaska or specific spawning locations of fish recruiting to Kodiak Island nurseries, general observations indicate that spawning takes place over rocky substrates of 20–200 m depth between mid-March and mid-April (Dunn and Matarese 1987). Average temperatures from 15 March to 15 April were used to characterize interannual variation in thermal regime during the spawning period of Pacific cod in this region (Dunn and Matarese 1987).

### Growth rate experiments

Age-0 Pacific cod were captured from a Kodiak Island juvenile nursery (Anton Larsen Bay) in August 2006, August 2007, and July 2008 using a 36-m beach seine. Fish were maintained for at least 48 h at the Alaska Fisheries Science Center (AFSC) Kodiak Laboratory in ambient seawater prior to shipment to the AFSC Laboratory in Newport, Oregon. Fish were shipped overnight in insulated containers filled with seawater and oxygen. Prior to use in laboratory experiments, fish were maintained in 1-m-diameter round tanks with flow-through seawater maintained at 8–10 °C. During this acclimation period, fish were fed thawed krill and a gelatinized combination of squid, krill, herring, commercial fish food, amino acid supplements, and vitamins on alternate days.

Each experiment was initiated by assigning fish into size categories ($N = 3$) based on visual estimation in order to minimize the potential for intra-cohort cannibalism frequently observed in larval and juvenile gadids (Folkvord and Otterå 1993, Sogard and Olla 1994). Three groups of fish ($n = 7$–10) were assigned to each temperature treatment ($n = 4$; 12 tanks total for each cohort). Although size sorting resulted in significant differences in mean fish size among the tanks within temperature treatments, these differences were minor and the tanks were considered replicates for the analysis of cohort and temperature effects (Table 1). After establishment of experimental groups, temperatures were adjusted to treatment temperatures at a rate of <2 °C d$^{-1}$; fish were acclimated to the treatment temperature for 10–14 days prior to measuring growth rates. The 2006 and 2007 cohorts were tested at 2, 5, 9, and 13 °C, and the 2008 cohort was tested at 2, 5, 8, and 11 °C. Tank temperatures were checked twice daily and maintained within 1 °C of target temperatures (Table 1). Growth data from the 2008 cohort were included in a previous paper describing early ontogenetic patterns (Hurst et al. 2010b).

Experimental tanks for the 2006 and 2007 cohorts were 1 m in diameter and filled to a depth of 55 cm. Experimental tanks for the 2008 cohort were 66 × 45.7 cm, filled to a depth of 23.2 cm. The smaller tanks were used to test fish from the 2008 cohort, which were collected earlier in the growing season and tested at a smaller size (0.88 ± 0.30 g, compared to 5.76 ± 1.70 and 1.84 ± 0.68 g in for the 2006 and 2007 cohorts, respectively). The tanks were supplied with flow-through sea water (except that water in the 11 and 13 °C treatments was partially re-circulated through a heater). During the experiments, fish were fed thawed krill to apparent satiation once per day. In addition, a gelatinized combination of squid, krill, herring, commercial fish food, amino acid supplements, and vitamins was provided three times per week. Lights were maintained on a 12:12 h light:dark photoperiod for all experiments. Tanks were checked twice daily for mortalities which were removed, weighed, and measured.

Growth rates were estimated by weighing (wet mass $M_W$ to 0.01 g) and measuring (total length $L_T$ to 1 mm) all fish in the experiments three times at 10–21-day intervals depending on fish size and water temperature. Longer intervals were used for larger fish and in lower temperature treatments (Table 1). To minimize stress from repeated handling of small fish, wet masses for the 2008 cohort were measured only at the end of the experiment. $M_W$ of individual fish at earlier sampling points was estimated from regressions based on measures of fish collected and transported to the laboratory but not used in this experiment.

In this experiment, the relationship between ln-transformed mass and measurement time was approximately linear, and specific growth rates (SGR) were determined by regressing the measurements of ln-mass against measurement date for each fish. Growth rates were not corrected for variation in initial size among tanks as there was no significant relationship between tank mean fish size and tank mean growth rate (expressed as deviations from combined and cohort-specific temperature-dependent curves; $r^2 < 0.025$; $p > 0.35$). In lieu of marking the 7–10 individual fish in each tank, we assumed that size rank was maintained within each replicate tank during the

**Table 1** Summary of growth experiments conducted at the Alaska Fisheries Science Center laboratory in Newport, Oregon, with age-0 Pacific cod (*Gadus macrocephalus*) collected from the central Gulf of Alaska

| Cohort | Tank style | Experiment duration, days | Nominal temperature, °C | Actual temperature, °C (SD) | *R*1 mean mass, g (SD) | *R*2 mean mass, g (SD) | *R*3 mean mass, g (SD) |
|---|---|---|---|---|---|---|---|
| 2006 | 1-m diam | 64 | 2 | 2.3 (0.5) | 3.46 (0.21) | 4.31 (0.43) | 6.79 (0.38) |
| | 1-m diam | 64 | 5 | 4.8 (0.6) | 5.05 (0.38) | 5.54 (0.38) | 7.97 (0.67) |
| | 1-m diam | 43 | 9 | 8.4 (0.3) | 4.70 (0.41) | 5.73 (0.34) | 7.93 (0.48) |
| | 1-m diam | 43 | 13 | 12.4 (0.4) | 4.92 (0.19) | 5.52 (0.22) | 7.23 (0.39) |
| 2007 | 1-m diam | 42 | 2 | 2.3 (0.4) | 1.47 (0.08) | 1.52 (0.11) | 2.65 (0.17) |
| | 1-m diam | 42 | 5 | 5.1 (0.4) | 1.34 (0.10) | 1.89 (0.08) | 2.79 (0.18) |
| | 1-m diam | 30 | 9 | 9.1 (0.6) | 1.26 (0.16) | 1.74 (0.10) | 2.59 (0.17) |
| | 1-m diam | 30 | 13 | 13.0 (0.5) | 1.18 (0.13) | 1.39 (0.12) | 2.06 (0.09) |
| 2008 | 66 × 45.7 cm | 17 | 2 | 2.4 (0.5) | 0.51 (0.02) | 0.89 (0.09) | 1.06 (0.08) |
| | 66 × 45.7 cm | 17 | 5 | 5.2 (0.7) | 0.64 (0.03) | 0.84 (0.12) | 0.95 (0.07) |
| | 66 × 45.7 cm | 17 | 8 | 8.2 (0.7) | 0.68 (0.06) | 0.96 (0.15) | 1.05 (0.10) |
| | 66 × 45.7 cm | 17 | 11 | 11.2 (0.6) | 0.69 (0.04) | 1.04 (0.09) | 1.16 (0.08) |

Replicates (*R*1, *R*2, *R*3) are ordered by increasing mean fish mass at the start of the experiment

experiment. However, because the individual fish within each tank cannot be considered independent observations, for all analyses, we used the mean growth rate observed in each tank ($N = 36$) as the level of observation. In general, fish that died at any point during the experiment were excluded from calculations determining growth rate for the tank. However, this would have precluded obtaining any growth rate estimates for the 13 °C treatment of the 2007 cohort. Therefore, we included data from the first 2 weeks of the experiment for two of the three replicate tanks where over half of the fish survived until day 14.

For each cohort, we modeled the temperature-dependence of growth with a second-order polynomial. We used the mean temperatures measured during the growth interval in these analyses, rather than the nominal treatment temperatures. To determine the factors that contributed to growth variation across the three experiments, we examined models with and without a cohort ($C$) main effect and interactions between cohort and the linear ($T$) and second-order ($T^2$) temperature terms (van Doorslaer and Stocks 2005) and used AIC to determine which model(s) best described the data (Burnham and Anderson 2002). The presence of cohort-specific variation in thermal reaction norm for growth was indicated by models including cohort x temperature (linear or second-order) interactions performing better (lower AIC scores) than models without these interaction terms. The effects identified for inclusion based on AIC model scores were subsequently evaluated for statistical significance with traditional $F$ tests.

### Vertebral counts

Age-0 Pacific cod were captured from two nearshore nurseries (Anton Larsen Bay and Cook's Bay) in July and August 2006, 2007, and 2008. Fish were captured with a 36-m beach seine and held on ice prior to freezing in the laboratory. The fish used for vertebral counts ($N = 81$–$169$ for each cohort) were collected from the same areas at the same times as those transported to the laboratory for growth experiments, but were not the same individuals used in the growth experiments.

For X-ray analysis, fish were thawed and preserved in 95 % ethanol. Fish were X-rayed in groups in a cabinet X-ray machine (Faxitron MX-20). Plates were exposed for 180 s at 19 kVp. Finished plates were examined under a dissecting microscope with transmitted light. For each fish, three independent vertebral counts were made by the same reader on different days. If a discrepancy existed between counts, a fourth count was made, and the fish was included in the data set only if three of the four counts agreed. Vertebral counts did not include the urostyle. Standard length ($L_S$) of each fish was measured from X-rays using digital calipers.

Differences in mean vertebral counts among Pacific cod cohorts were tested with ANOVA. Preliminary analyses indicated no effect of month of capture ($p = 0.549$) or sampling site ($p = 0.747$) on mean vertebral count within cohort.

## Results

### Temperature records

Water temperatures in the central Gulf of Alaska varied significantly among the years associated with the examined cohorts of Pacific cod (Fig. 1). The winter and spring of 2007 were significantly colder than those of 2006 and 2008. For example, over the period 15 March to 15 April, generally corresponding to the spawning period of Pacific cod, temperatures recorded at 10 m depth in Trident Basin averaged 1.71 °C in 2007, compared to 3.73 and 3.38 °C in 2006 and 2008, respectively. This interannual variation in temperature was not localized to nearshore Kodiak Island waters: similar patterns among years were seen in the record of sea surface temperatures at Albatross Banks, 65 NM south of Kodiak Island. Furthermore, longer-term records of sea surface temperature in the central Gulf of Alaska (GAK1 mooring) indicated that the winter and spring of 2007 were the coldest on record since the mid-1970s (Janout et al. 2009).

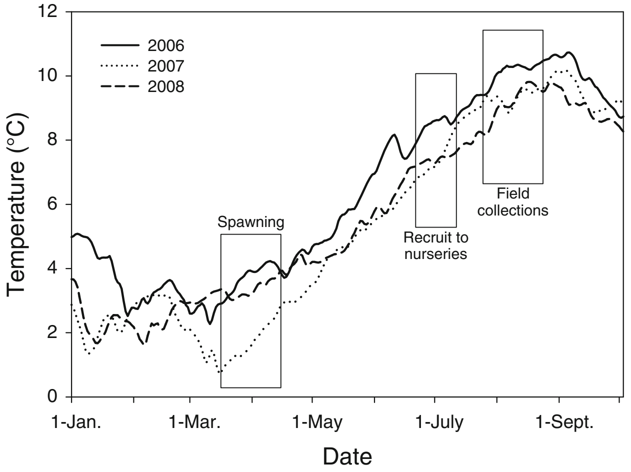

**Fig. 1** Temperature records from Kodiak Island, Alaska 2006–2008. Curves are 3-day running averages of water temperature measured at 10.7 m depth in Trident Basin, northeast coast of Kodiak Island, Alaska. *Boxes* indicate approximate times of Pacific cod spawning, recruitment of juveniles to nearshore nursery grounds, and field collections for growth rate experiments and vertebral counts

### Cohort growth responses

Pacific cod from the three cohorts displayed significantly different growth and mortality responses to temperature in laboratory trials (Fig. 2). Of the three cohorts tested, the 2007 cohort had the highest growth rates at the two lower temperatures (ANOVA $F_{[2,12]} = 7.774$, $p = 0.007$). However, these higher growth rates did not extend to the warmer temperatures tested, and the 2007 cohort had low survival in the highest temperature (13 °C) treatment. These results contrast the reaction norms observed for fish from the 2006 and 2008 cohorts. These cohorts had lower growth rates at 2 °C, but growth rates increased more rapidly with temperature up to 11–13 °C. In the 2006 and 2008 cohorts, there were no indications of elevated mortality at the highest temperatures tested. Growth rates were most variable in the 2008 cohort, when fish were tested at the smallest sizes.

Using AIC for model selection to describe growth rates confirmed that the temperature-dependence of growth differed among Pacific cod cohorts. The models that provided the best fit to the data included an interaction between cohort and either the linear or second-order temperature terms (Table 2). The model with a cohort main effect and interactions with both temperature terms had a lower residual error but higher AIC score indicating that the model was over-parameterized, likely due to the colinearity between temperature and temperature$^2$. All models that did not include an interaction between cohort and temperature had higher AIC scores. Overall, the two best models, accounting together for 76 % of the Akaike weights, included direct cohort and temperature effects as well as a cohort–temperature interaction. Additional support for the model selection results based on AIC is provided by the fact that all terms included in the best performing models were statistically significant based on traditional $F$ tests.

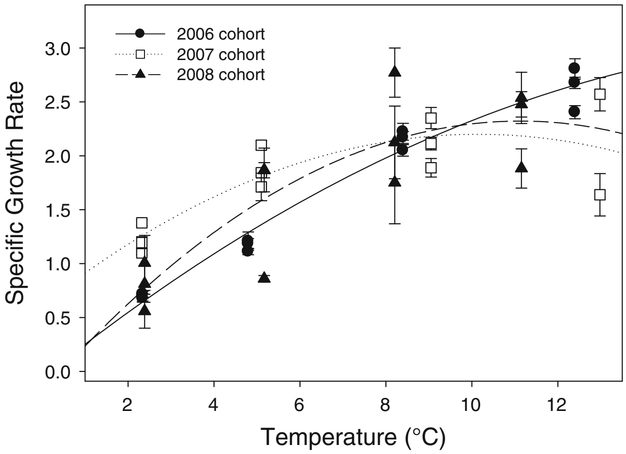

**Fig. 2** Cohort-specific thermal reaction norms for growth of juvenile Pacific cod (*Gadus macrocephalus*) collected from Kodiak Island, Alaska. Points are mean growth rates (±SE) of the 7–10 fish in each replicate tank plotted against treatment temperature. *Error bars* represent standard errors of growth rates among individuals within each tank, but analyses are conducted only on tank mean growth rates. *Curves* are second-order polynomial fits to growth data for each cohort: circles and solid line, 2006 cohort; squares and dotted line, 2007 cohort; triangles and dashed line, 2008 cohort

In general, mortality was low in most tanks and treatments over the course of the three experiments. To account for differences in experimental durations between temperature treatments, daily mortality patterns were converted to 30-day survival fractions for each tank. Over all years and treatments, 30-day survival averaged 82 %. Mortality rates in the 13 °C treatment of the 2007 cohort were significantly higher than those observed in all other treatments (post hoc LSD test, $p < 0.01$; Fig. 3). Half of the fish in the three replicate tanks died during the first 10 days of the experiment. After day 20, the remaining fish from the three replicates were pooled into a single tank, and two new groups of fish were acclimated to 13 °C and reared in the available experimental tanks. These additional groups experienced similarly high mortality patterns. The only other treatment with clustered mortality was the 5 °C treatment of the 2008 cohort. There was no relationship between tank mortality rate and estimated growth rates (based on deviations from cohort-specific and pooled-cohort growth models).

Given the differences in relative performance at different temperatures, we hereafter refer to the 2007 cohort (highest growth rates at low temperatures and poor survival at high temperatures) as the “cold-adapted” cohort and the 2006 and 2008 cohorts as “warm-adapted” cohorts.

### Vertebral counts

Vertebral counts of age-0 Pacific cod collected from Kodiak Island, Alaska, ranged from 50 to 56, with counts of 54 and 55 vertebrae being most common. Mean vertebral counts differed significantly among cohorts (Fig. 4; ANOVA $F_{[2,381]} = 6.268$, $p = 0.002$). Post hoc LSD tests indicated that mean vertebral count was significantly higher ($p < 0.05$) in the 2007 cohort than in the 2006 and 2008 cohorts. Mean vertebral count in the 2006 cohort was slightly but not significantly higher than in the 2008 cohort ($p = 0.105$). There was no significant correlation between vertebral count and $L_S$ within any cohort ($r < 0.15$, $p > 0.20$) or when fish were pooled across cohorts ($r = -0.05$, $p = 0.368$).

## Discussion

Experiments with juvenile Pacific cod collected from a single locale over three consecutive cohorts revealed

**Table 2** Results of model selection for temperature effects and cohort interactions on growth rates of juvenile Pacific cod (*Gadus macrocephalus*) collected from Kodiak Island Alaska

| Factors included | Terms | $k$[a] | RSS[b] | AIC[c] | $w$[d] |
|---|---|---|---|---|---|
| Full model | $I$, $C$, $T$, $T^2$, $C*T$, $C*T^2$ | 9 | 2.481 | 49.809 | 0.087 |
| Cohort, cohort* linear temp interaction | $I$, $C$, $T$, $T^2$, $C*T$ | 7 | 2.568 | 47.003 | 0.353 |
| Cohort, cohort* squared temp interaction | $I$, $C$, $T$, $T^2$, $C*T^2$ | 7 | 2.545 | 46.688 | 0.413 |
| Both cohort interactions but no cohort main effect | $I$, $T$, $T^2$, $C*T$, $C*T^2$ | 7 | 2.727 | 49.116 | 0.123 |
| Cohort* squared temp interaction, no cohort main | $I$, $T$, $T^2$, $C*T^2$ | 5 | 3.695 | 55.746 | 0.004 |
| Cohort* temp interaction, no cohort main | $I$, $T$, $T^2$, $C*T$ | 5 | 3.856 | 57.233 | 0.002 |
| Cohort term, but no interactions | $I$, $C$, $T$, $T^2$ | 5 | 3.698 | 55.772 | 0.004 |
| Null model—no cohort or interaction terms | $I$, $T$, $T^2$ | 3 | 3.880 | 53.452 | 0.014 |

The table shows all 8 tested models. Growth was modeled as a second-order function of temperature with single intercept ($I$), cohort-specific intercepts ($C$), and interactions between cohort and the linear ($T$), and second-order ($T^2$) temperature terms

[a] $k$ is number of parameters

[b] *RSS* residual sum of squared deviations from model

[c] *AIC* Akaike information criteria

[d] $w$ Akaike model weight (normalized relative likelihood)

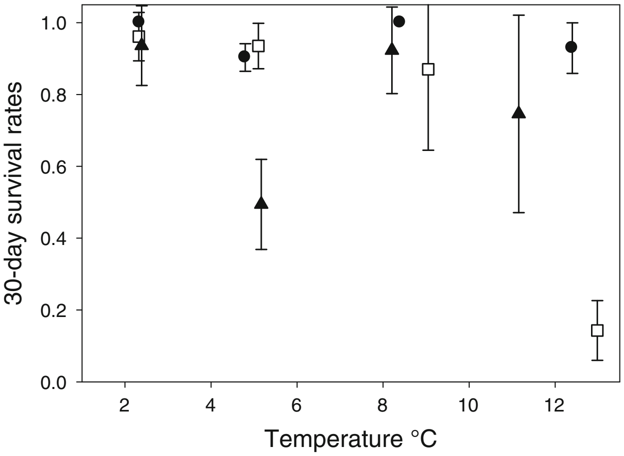

**Fig. 3** Survival rates of juvenile Pacific cod (*Gadus macrocephalus*) in laboratory experiments examining thermal effects on growth potential. Due to differing experimental periods among cohorts, survival rates are presented as estimated fraction surviving 30 days of experimental rearing. Points are mean 30-day survival rates (±SD) in each treatment plotted against treatment temperature; circles, 2006 cohort; squares, 2007 cohort; triangles, 2008 cohort

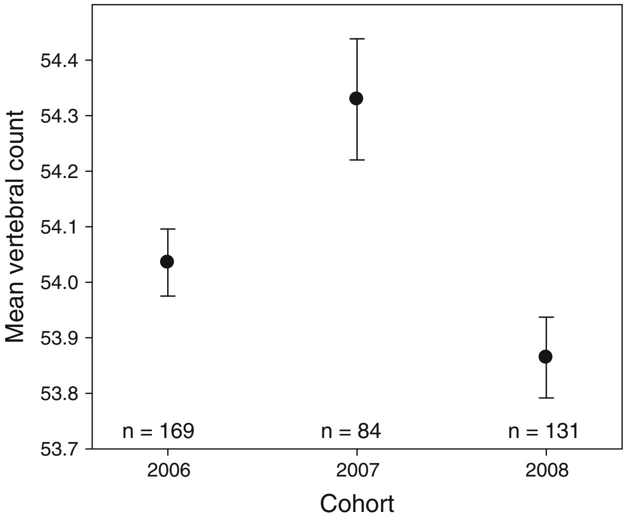

**Fig. 4** Mean vertebral counts (±1 SE) of age-0 Pacific cod (*Gadus macrocephalus*) collected from Kodiak Island, Alaska, from three naturally produced cohorts

intercohort variation in the thermal reaction norm for growth. The cold winter and spring of 2007 appeared to produce a cohort consisting of fish whose temperature-dependent growth rates suggest a "cold-adapted" phenotype. Although the mechanism responsible for this variation could not be confirmed, the observed variation in vertebral counts suggests that a persistent response to thermal history during early development could be responsible.

## Experimental considerations

As there is no way to conduct synoptic experiments testing for physiological differences among cohorts, the possibility that these results are due to some unmeasured aspect of the experimental environment cannot be unequivocally eliminated. However, we believe that these results are robust to such effects. Every effort was made to maintain standardized experimental protocols across the 3 years of experiments. Fish were captured from the same locations using the same gear and transported to the laboratory using similar procedures. In the laboratory, fish were acclimated in the same tanks and received the same food on the same schedules. Of the three experiments, applied protocols diverged most for the 2008 cohort when fish were tested at a smaller size in smaller tanks. However, these differences are unlikely to have a significant impact on the overall conclusions of cohort-specific variation in thermal reaction norms as the 2008 cohort was intermediate in growth response to temperature. Artifacts such as unobserved stress would be expected to impact all temperature treatments in parallel rather than inducing significant cohort x temperature interactions.

Vertebral counts of fishes have long been applied as a diagnostic character to delineate populations, with variation due, at least in part, to environmental influences (Ihssen et al. 1981). Numerous studies have demonstrated phenotypic plasticity in response to temperature variation in early development with lower temperatures resulting in higher mean vertebral counts (Fowler 1970; Lindsey 1988). While phenotypic plasticity in vertebral count has not been experimentally confirmed in Pacific cod, it has been demonstrated in the closely related Atlantic cod (*Gadus morhua*; Løken and Pedersen 1996), and the present data strongly suggest that it occurs in Pacific cod: mean vertebral count in the 2007 cohort of Pacific cod was significantly higher than in the other cohorts, consistent with the expected response to low temperature (Lindsey 1988). Although the mean vertebral counts differed by less than 1 between cohorts, this difference was statistically significant and similar in magnitude to the differences observed among cohorts of Atlantic cod (Brander 1979; Swain et al. 2001). The observed variation in mean vertebral count demonstrates that fish in the three cohorts contained intrinsic phenotypic differences. Further, the phenotypic covariance in multiple traits with links to the environment suggests a common environmental influence (Travis et al. 1999).

## Causes of variation

It is important to note that the variation in thermal reaction norms for growth was documented in fish sampled from naturally produced cohorts. Laboratory experimentation testing fish across a range of temperatures was required to describe the reaction norm of a cohort, but the differences observed among cohorts were not experimentally generated (as in Salinas and Munch 2012). Further, the variation observed among Pacific cod cohorts differs from the types of maternal and incubation effects on embryonic and larval development commonly described in fishes (Green 2008; Burt et al. 2011). While such responses can have persistent effects, influencing later life stages, they generally apply equally across environments (but see Green and McCormick 2005, Janhunen et al. 2010). From a statistical view, they induce variation in elevation of the thermal reaction norms for growth, not change the shape of the reaction norm as indicated by the significant cohort by temperature interactions observed here. The variation in thermal reaction norms for growth among cohorts results from one of the two general mechanisms: phenotypic plasticity or genetic variation (Hutchings et al. 2007). The available evidence supports the former, but unequivocally differentiating between the two general mechanisms would require multi-generational laboratory experiments and a more detailed understanding of patterns of genetic variation in this species.

In addition to direct effects on development and growth rates, environmental exposure in the early life stages can induce irreversible changes in morphology and physiology, sometimes referred to as “non-genetic adaptations.” Among the most widely recognized of these in fishes are temperature-dependent sex determination, which has been documented in a number of coastal marine fishes (Conover 1984; Ospina-Álvarez and Piferrer 2008), and the effect of temperature on muscle fiber development (Martell and Kieffer 2007; Johnston et al. 2009). In addition, exposure to a specific environment during early development can produce persistent, but potentially reversible, physiological adjustments usually referred to as “acclimation” or “acclimatization” (McNab 2002). The effect of temperature variation during the larval stage on temperature tolerance in juveniles (Travis et al. 1999; Schaefer and Ryan 2006) is an example of this phenomenon. In both reversible and irreversible cases, these effects represent a form of phenotypic plasticity resulting from changes in gene expression (Schulte 2004; Kingsolver et al. 2004). In the current example, exposure to low temperatures in the egg and/or larval stages could have triggered a specific expression of the gene complex optimizing physiological performance at low temperatures with the trade-off of reduced performance at high temperatures (Munch and Conover 2003; Schulte 2004) as reflected in the variable thermal reaction norms.

If these patterns represent a form of developmental phenotypic plasticity, further work will be required to determine whether the response is induced during incubation following fertilization or prior to fertilization during oocyte development (“transgenerational plasticity”). Transgenerational plasticity (Youngson and Whitelaw 2008) is a specific type of maternal effect in which the environment experienced by the parents (not the parents’ genotype) determines the phenotype expressed by their offspring. To date, most studies of maternal effects in fishes have not explicitly differentiated the genetic/environmental influences on offspring characteristics (Burt et al. 2011). Although thermal transgenerational plasticity has only rarely been documented in fishes (but see Bashey 2006, Salinas and Munch 2012), it is fairly common in plants and some invertebrates, where it has been shown to influence population dynamics (Plaistow and Benton 2009). Importantly, the thermal environment experienced by the parents has been shown to influence vertebral counts in some species (Dentry and Lindsey 1978, Swain and Lindsey 1986). Further, recent experimental evidence confirms the presence of thermal transgenerational plasticity in a marine fish producing similar responses in reaction norms for growth as those observed among cohorts of Pacific cod (Salinas and Munch 2012).

Alternatively, if there are genetic differences behind the thermal responses and vertebral count variation of the cohorts, they could be the result of unrecognized fine-scale genetic variation in the spawning population (Swain and Frank 2000). Pacific cod recruiting to Kodiak Island embayments could be the progeny of parents with different genetically determined responses to temperature variation. In such a case, interannual variation in larval transport pathways could impact the genetic makeup of the cohort recruiting to a specific location (Weingartner et al. 2009). The available data on neutral genetic markers in Pacific cod indicate a much larger spatial scale of genetic variation (Cunningham et al. 2009), but there are currently no data on patterns of variation in the genes linked to key physiological processes. Interannual differences in genotype of a recruiting cohort could also be the result of a selective event occurring between spawning and recruitment to the nursery area. In cold years, the cohort would be dominated by individuals that are genetically predetermined to exhibit strong performance at low temperatures. Unfortunately, evaluating these potential genetic factors would require a level of detailed information on both neutral genetic markers and trait genes not available for this species.

## "Cold-adapted" and "warm-adapted" cohorts

For Gulf of Alaska Pacific cod, the data presented here suggest that environmental conditions during the egg or larval stage influence at least two aspects of phenotype, resulting in the production of cohorts of fish with "cold-adapted" or "warm-adapted" phenotypes. A "cold-adapted" cohort is one with higher mean vertebral counts, higher growth performance at low temperatures, and lower growth performance at high temperatures than a "warm-adapted" cohort, and vice versa.

Temperature variation in the environment includes a significant temporal auto-correlation. Due to the nature of large-scale climate and weather patterns, a cold winter is likely to be followed by colder than average spring and summer conditions. Hurst et al. (2010a) demonstrated this temporal autocorrelation in Kodiak Island embayments and explored the implications for assessing growth performance of juvenile northern rock sole (*Lepidopsetta polyxystra*). Given this temporal autocorrelation in the environment, the selective advantage of phenotypic plasticity in thermal reaction norm for growth is readily apparent. Individuals from a "cold-adapted" cohort produced in a cold spawning season would have higher growth rates at the anticipated lower temperatures in the subsequent growing season. Conversely, a warm spawning season would produce a "warm-adapted" cohort that would be able to take advantage of the growth opportunities of a subsequent warm growing season. Variation in body size generated early in life can persist in the population with subsequent implications for size-dependent mortality (Imsland et al. 2007). Similar evolutionary arguments have been made to explain the widespread variation in vertebral count in response to incubation temperature (McDowall 2008). The effect of vertebral count on survival has been demonstrated in both laboratory and field studies (Swain and Lindsey 1984, van der Veer et al. 2000). They suggested that higher vertebral counts result in greater body flexibility and improved swimming performance of larvae and small juvenile fish in low-temperature waters with higher viscosity, enhancing predator escape behavior.

## Implications

To the best of our knowledge, the variation among cohorts from the same location in thermal reaction norms for growth observed for juvenile Pacific cod has not been described for any other fish species. The lack of recognition of such variation likely stems from a general belief that physiological traits in a population are static, at least over time scales less than several generations. Once a temperature-dependent growth function is described for a particular population, it is typically assumed that the thermal reaction norm for growth is a static trait of the population. Therefore, there is as yet little opportunity to evaluate whether variation in reaction norms for growth is widespread among coastal marine fishes. However, recognition of persistent effects of early life history environmental conditions (Imsland et al. 2006; Mollet et al. 2007) and the documentation of thermal transgenerational plasticity in growth (Salinas and Munch 2012) suggest that the effect on growth rates may not be unusual.

The occurrence of inter-cohort variation in thermal reaction norms for growth has several significant implications for studies of growth variation, regardless of the specific mechanism generating the variation. First, it is possible that this variation could be mistaken for another source of variation. For example, studies of local adaptation in thermal reaction norm are frequently conducted by capturing naturally produced organisms for subsequent rearing in "common garden" experiments (Dutil et al. 2008; Harrald et al. 2010). Apparent differences between populations could be due to independent (non-synchronized) environmental variation arising in each of the tested source populations. To minimize this risk, it is important for common garden experiments to use organisms reared in a common environment, preferably for a complete generation prior to experimentation (Conover et al. 2010; Harrald et al. 2010). While this may not be practicable for long-lived marine species, at a minimum, the parents from all tested populations should be reared at the same temperatures to eliminate potential pre-fertilization environmental effects (Wijekoon et al. 2009).

A second implication of these results affects the use of laboratory-determined growth rates to evaluate habitat quality and determine factors regulating growth in the field. In these applications, observed growth rates in the field are compared to maximum growth potential at the temperatures encountered in the field (Zijlstra et al. 1982; Rakocinski et al. 2006; Hurst et al. 2010a). If growth rates are near the maximum predicted, it is assumed that temperatures limit further increases in growth (Folkvord 2005; Hurst and Abookire 2006). Conversely, if growth rates are significantly below the predicted maximum, it is frequently assumed that growth is limited by prey availability (Clemmesen et al. 2003) or the presence of some other limiting factor (Buckley et al. 2006; Ryer and Hurst 2008). The results presented here suggest that in some cases, these analyses could be confounded by variation in thermal reaction norms for growth among cohorts which could bias estimates of growth potential.

## Conclusion

Thermal variation has a significant influence on the growth dynamics of fishes and other ectotherms and is assumed to be a primary mechanism by which climate variation is translated into variation in population productivity. However, expressed growth rates are influenced by a variety of environmental factors including prey availability, habitat type, social interactions, and predation threat. Growth has also been shown to be a function of an individual's growth (Ali et al. 2003), nutritional (Imsland et al. 2006), and thermal history (Nicieza and Metcalfe 1997; Hurst et al. 2005). The variation in thermal reaction norms described here for juvenile Pacific cod may be a common life history adaptation for organisms living in variable environments. Early life stage growth rates have a marked influence on the survival and recruitment of fishes because of the size-dependent patterns of mortality (Sogard 1997). Water temperature is frequently considered to be a primary driver of this early growth variation. However, there are many examples where growth rates were not directly related to ambient temperature variation or growth variation was less than expected based on temperature variation (Power and Attrill 2007; Gunnarsson et al. 2010). Variation in the thermal reaction norm for growth could buffer the effects of interannual variation in temperature on growth rates of juvenile organisms. Further understanding of the range of physiological responses to temperature variation will improve our understanding of population and community dynamics under potential future environments.

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