Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Gadus macrocephalus*)

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Abstract—Pacific cod (*Gadus macrocephalus*) is an important component of fisheries and food webs in the North Pacific Ocean and Bering Sea. However, vital rates of early life stages of this species have yet to be described in detail. We determined the thermal sensitivity of growth rates of embryos, preflexion and postflexion larvae, and postsettlement juveniles. Growth rates (length and mass) at each ontogenetic stage were measured in three replicate tanks at four to five temperatures. Nonlinear regression was used to obtain parameters for independent stage-specific growth functions and a unified size- and temperature-dependent growth function. Specific growth rates increased with temperature at all stages and generally decreased with increases in body size. However, these analyses revealed a departure from a strict size-based allometry in growth patterns, as reduced growth rates were observed among preflexion larvae: the reduction in specific growth rate between embryos and free-swimming larvae was greater than expected based on body size differences. Growth reductions in the preflexion larvae appear to be associated with increased metabolic rates and the transition from endogenous to exogenous feeding. In future studies, experiments should be integrated across life transitions to more clearly define intrinsic ontogenetic and size-dependent growth patterns because these are critical for evaluations of spatial and temporal variation in habitat quality.

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Fluctuations in the distribution and abundance of marine species are highly influenced by climate-driven changes in ocean conditions (Perry et al., 2005). In the Gulf of Alaska and Bering Sea, oceanographic regimes linked to climate conditions (Hollowed et al., 2001; Peterson and Schwing, 2003) occur across a variety of time scales, from seasonal to multidecadal (Hunt and Stabeno, 2002). These climate cycles have been linked to major shifts in the composition of valuable groundfish communities (Anderson and Piatt, 1999). Imposed upon this variation is the potential for longer-term climate changes, such as the warming of surface waters and loss of sea ice (e.g., Hunt et al., 2002). Such warming trends have already been observed in the Gulf of Alaska (Royer and Grosch, 2006) and Bering Sea (Stabeno et al., 2007). The response of individual populations and entire communities to environmental forcing depends upon the physiological and behavioral traits of individual species and the cumulative set of trophic interactions between species (Freitas et al., 2007; Yatsu et al., 2008; Hurst et al., 2010).

Spatial and temporal variation in temperature and prey availability are considered to be primary drivers of growth and survival in early life stages of fishes and their influence on recruitment has been central to various generalized models of recruitment (see review by Cowen and Shaw, 2002). The oscillating control hypothesis (OCH) states that population production of groundfish in the Bering Sea is linked to climate-driven patterns of prey production: cold winters with extensive sea ice result in early, low-density blooms in cold water, resulting in reduced survival of larvae (Hunt and Stabeno, 2002). Evaluation of the OCH and predicting potential responses to future aspects of climate change require detailed information on the temperature-dependent vital rates of early life stages of fish (Kristiansen et al., 2007; Hollowed et al., 2009; Rijnsdorp et al., 2009).

Pacific cod (*Gadus macrocephalus*) is a widespread marine species 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. In recent years, U.S. landings of Pacific cod trail only those of Alaska walleye pollock (*Theragra chalcogramma*) and Atlantic and gulf menhaden (*Brevoortia tyrannus* and *B. patronus*) (NMFS, 2008). Between 2002 and 2006, U.S. landings of Pa-

Table 1

Summary of experiments conducted at the Alaska Fisheries Science Center laboratory in Newport, Oregon, where growth rates were determined for early life stages of Pacific cod (*Gadus macrocephalus*) collected from the central Gulf of Alaska.

Stage	Temperatures (°C)	Year	Experiment duration (dah=days after hatching)	Sample type	No of tanks	*n* fish
Eggs	0, 2, 4, 6, 8	2006	Fertilization to hatching	Measured at hatching	15	30/sample
Preflexion larvae	3, 8	2007	Hatching to 35 dah	Tank sample	6	10/sample
	2, 5, 8	2008	Hatching to 36 dah	Tank sample	9	10/sample
Postflexion larvae	2, 4, 8, 11	2007	50 to 105 dah	Tank sample	12	10/sample
Juveniles	2, 5, 8, 11	2008	approx. 132 to 150 dah	Serial measures	12	10/tank

cific cod averaged 28 times those of Atlantic cod (*Gadus morhua*).

Despite the pervasive influence of temperature on all aspects of biology and its potential linkage to recruitment patterns, there has been little examination of the thermal ecology of Pacific cod. The effects of temperature on the vertical distribution of larvae (Hurst et al., 2009) and juveniles (Davis and Ottmar, 2009) have been examined. Thermal effects on growth of Pacific cod has been examined in only the very early life stages: development rates of eggs and prefeeding larvae (Alderdice and Forrester, 1971; Laurel et al., 2008) have been examined across a wide range of temperatures. In addition, B. J. Laurel (unpubl. data) compared the effects of prey density on growth of preflexion larvae at two temperatures. However, these studies are insufficient to describe the functional response to temperature for larvae, and as of yet, no data exist for later larval stages or juveniles.

In this article we describe the growth of early life stages of Pacific cod as a function of temperature and body size. Separate experiments were conducted with preflexion larvae, postflexion larvae, and postsettlement juveniles. From these experiments and published data on embryos, we determined the parameters for models of stage-specific growth and for an integrated model of size- and temperature-dependent growth. These functions will be used to evaluate the relative contributions of temperature and feeding conditions to observed variation in growth among wild Pacific cod (Folkvord, 2005; Hurst et al., 2010).

Materials and methods

We determined the thermal sensitivity of growth rates at three life stages: preflexion larvae, post-flexion larvae, and postsettlement juveniles (Table 1). Growth rates at each ontogenetic stage were measured in three replicate tanks at four to five temperatures, encompassing the range likely to be encountered by fish in the Gulf of Alaska and Bering Sea. Nonlinear regression was used to describe the relationship between growth rate and temperature at each developmental stage and to describe the combined effects of temperature and body size on growth rates of early life stages.

Preflexion larvae

Two experiments were conducted to describe the growth of Pacific cod larvae after hatching. In 2008, fish were reared at 2°, 5°, and 8°C to 36 days after hatching (dah). These data were combined with data on fish reared under identical conditions to 35 dah at 3°C and 8°C in 2007 (B. J. Laurel, unpubl. data). The 8°C treatment was conducted in both experiments to evaluate potential differences in overall growth rates between years.

Fish for the larval growth experiments were reared in the laboratory from eggs collected from spawning adults. Female and male Pacific cod were caught by commercial jigging gear from spawning grounds in Chiniak Bay, Kodiak Island, Alaska. The gametes were mixed and placed into 4-L incubation trays at 4°C. At 24 hours after fertilization, fertilized eggs were shipped in insulated containers to the Alaska Fisheries Science Center's (AFSC) laboratory facilities in Newport, Oregon. Eggs were transferred to flow-through 4-L plastic trays and incubated at 4°C. Hatching occurred 19–22 days after fertilization, after which larvae were transferred to larval rearing tanks.

Experimental rearing tanks were 100-L cylinders with conical bottoms and dark green walls. Water was supplied to the tanks at a rate of 250 mL/min. Weak upwelling circulation was maintained in the tank by positioning the in-flow at the bottom center of the tank and with light aeration. Light regime during larval rearing was maintained at 12:12 h light:dark; light was provided by overhead fluorescent bulbs at a level of 6.7 $\mu E/m^2 s$ at the water surface.

Larval growth experiments were initiated by stocking rearing tanks (maintained at the egg incubation temperature of 4°C) with 400 larvae which hatched over a 4-day period in the middle of the hatch cycle. The last day that newly hatched fish were stocked into rearing tanks is nominally referred to as experimental day 0. After the tanks were stocked with fish, tank temperatures were adjusted to treatment temperatures over 2 days. Larvae were reared on a combination of rotifers

(*Brachionus plicatilis*) enriched with Algamac 2000 (Aquafauna, Hawthorne, CA; Park et al., 2006) and microparticulate dry food (Otohime A, Marubeni Nisshin Feed Co., Tokyo). Rotifers were supplied at densities of 4 prey/mL twice daily and dry food was provided 2–3 times per day.

At periodic intervals, a subsample of 10 larvae was removed from each tank to determine the mean size of larvae in the tank. For the 2007 experiments, six samples were drawn at 7-d intervals (starting on day 0). For the 2008 experiments, all tanks were sampled on days 0, 10, 23, and 36. Sampled larvae were individually photographed under magnification and measured from calibrated digital photographs using ImagePro® (Media Cybernetics, Bethesda, MD) software. The morphometrics used in these analyses were standard length (L_S) and body depth of the myotome at the anus (D).

Dry weight of individual larvae was calculated using a two-step model with L_S and D developed from an independent collection of similar size Pacific cod larvae reared in the laboratory under identical conditions. These fish were individually photographed and dried on preweighed foil at 68°C for at least 24 hours before determination of dry mass (to 1.0 μg) with a microbalance. Fourty-four fish with L_S of 5 to 11 mm were sampled periodically over the first 45 dah. First, the body depth deviation (D_{Dev}) was calculated for each fish, reflecting variance in "condition" from the equation

$$D_{Dev} = D - 0.0873 \cdot e^{0.2164 \cdot L_S}. \quad (1)$$

Individual dry mass (M_D mg) was calculated from D_{Dev} and L_S from the equation

$$M_D = 0.0204 \cdot e^{0.3734 \cdot L_S} + (0.9685 \cdot D_{Dev} - 0.1113). \quad (2)$$

These equations explained 97.8% of the variation in dry mass of fish in the sample.

Growth rates were calculated for each replicate tank from the increase in mean size of fish in measured subsamples. Growth in length (g_L, mm/d) and mass (g_M, /d) were calculated from linear regression of mean length and ln-transformed mass against sampling date.

Postflexion larvae

Growth rates of postflexion larvae were measured in a separate experiment applying similar procedures. Experiments were established with fish 50 dah, reared at 8°C under conditions similar to those described above for preflexion larval experiments. Given the variation in body size among cultured fish, each fish was assigned to one of three size categories on the basis of visual estimation. This sorting by size was done to minimize the potential for intracohort cannibalism frequently observed in larval and juvenile gadids (Folkvord and Otterå, 1993, Sogard and Olla, 1994). One group of 35–40 larvae from each size category was assigned to each temperature treatment (2°, 4°, 8°, 11°C). In addition, a sample of 15–20 fish from each size category was sacrificed to determine initial size distributions.

After establishment of experimental groups (day 0), temperatures were adjusted to target temperatures at a rate of 2°C per day. Larvae were offered particulate food three to four times per day, supplemented with enriched rotifers twice per day (first 20 d only). As fish grew, larger size particulate food (up to 620 μm) was included in daily feedings. A subsample (7–10 fish) was drawn from the 8°C and 11°C treatments on day 18 and from the 2°C and 4°C treatments on day 24. The experiments were ended and all surviving larvae were measured on day 32 for the 8°C and 11°C treatments and on day 45 for the 2°C and 4°C treatments. Lengths (L_S and L_T) of all sampled larvae were measured with digital calipers under a dissecting microscope and wet masses (M_W) were measured with a microbalance. Dry mass (M_D) of each larvae was determined after 48 hours in a drying oven at 50°C.

Growth rates were calculated from the increase in mean size of fish in measured subsamples. Growth in length (g_L, mm/d) and mass (g_M, /d) were calculated from linear regression of mean length and ln-transformed mass against sampling date.

Postsettlement juveniles

Age-0 Pacific cod were captured from Kodiak Island juvenile nurseries in July 2008 with a 36-m beach seine. Fish were maintained for at least 48 hours at the AFSC Kodiak Laboratory in ambient seawater before shipment to the AFSC's laboratory in Newport, Oregon. Fish were shipped overnight in insulated containers filled with seawater and oxygen. Before use in laboratory experiments, fish were maintained in 1-m diameter round tanks with flow-through seawater maintained at 8–10°C. Fish were fed thawed krill and commercially available pellets on alternating days.

The experiment was initiated by assigning fish-size categories based on visual estimation and stocking fish into experimental tanks. One tank of each size category (n=3) was assigned to each temperature treatment (n=4; 12 tanks total). After establishment of experimental groups, temperatures were adjusted to treatment temperatures (2°, 5°, 8°, and 11°C) and fish were acclimated to the treatment temperature for 10 days.

Experimental tanks were 66×45.7 cm, filled to a depth of 23.2 cm. During the experiment 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, and dead fish were removed, weighed, and measured.

Growth rates were estimated by measuring (L_T to 1 mm) all fish in the experiment three times at 10-d intervals. To minimize stress to small fish from repeated handling, wet masses were measured only at the end

of the experiment. Wet mass (M_W) of individual fish at earlier sampling points was estimated from regressions based on measurements of fish collected but not used in this experiment and the final experimental measurements.

Growth rates (g_L and g_M) of juvenile cod were determined by regression of the measurements of fish length and ln-transformed mass against sampling date. 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 experiment. Fish that died during the experiment were not included in statistical analyses.

Growth models

For each of the life stages examined (egg–embryos, preflexion larvae, postflexion larvae, juveniles), temperature-dependent growth functions were estimated for growth in length and mass. For consistency with the most commonly applied field measures of body size, growth rates of embryos and larvae were expressed in terms of L_S and M_D, and juvenile growth rates as L_T and M_W. Growth of postflexion larvae were expressed in both sets of measures.

For each life stage, a second-order polynomial function was fitted to describe the relationship between temperature and growth rate. For consistency in best-fit models, the second-order term was maintained, although it was not statistically significant in some cases. For these models, mean temperatures measured during the growth interval were applied, rather than experimental target temperatures. The mean growth rate measured in each replicate tank (n=3 per temperature) was used as the level of observation.

In addition to stage-specific models, an integrated model of size- and temperature-dependent growth (STDG) was developed (Folkvord, 2005). Data for the model were derived from the above experiments on larvae and juveniles and from previously published data on the hatching times and sizes as a function of temperature (Laurel et al., 2008). Despite representing easily identified discrete life stages with differing habitats, data on growth of embryos before hatching were included with posthatch data to clarify intrinsic patterns in potential growth rates through the early life stages. Growth rates of prehatch embryos were estimated from the size and age (days after fertilization) at hatching, assuming $M_{D=}$0.01 μg and $L_{S=}$0.0 mm at fertilization. In order to standardize measures across life stages, measured M_W for juveniles was converted to M_D and measured L_T was converted to L_S on the basis of measurements of similarly size fish (Hurst, unpubl. data).

The integrated STDG model was initially fitted with generalized additive models (GAM) to examine the potential effects of nonlinear interactions between mass and temperature on growth. These nonlinear, nonparametric regression techniques do not require *a priori* assumptions on the shape of the relationship between the dependent and independent variables. After evaluation of potential interactions based on evaluation of the generalized cross validation (GCV), a parametric model formulation was selected that best represented patterns in the growth data. Final models were fitted with parametric nonlinear regression in Statistica (vers. 6.0, StatSoft, Tulsa, OK). This approach was undertaken separately to provide STDG models for growth expressed in mass (M_D) and length (L_S).

Results

Preflexion larvae

Mean size of larvae at hatch was slightly larger in the 2007 experiment than in the 2008 experiment (L_S 5.16 vs. 4.90 mm; $F_{[1,60]}$=45.4, P<0.001). However, there was no significant difference among years in growth rates of preflexion larvae reared at 8°C (g_L $F_{[1,4]}$=1.52, P=0.237; g_M $F_{[1,4]}$=3.90, P=0.119), therefore data from the two experiments were combined to describe the effect of temperature on growth rate. In addition, there were no differences in growth rates among replicate tanks at a given temperature (tested as the interaction between day and tank on mean size, all P>0.05).

Growth in length and mass of Pacific cod larvae was significantly affected by rearing temperatures across the range examined (Fig. 1; g_M $F_{[3,11]}$=30.0, P<0.001; g_L ($F_{[3,11]}$=59.4, P<0.001). After 35 days, fish reared at 8°C were 2.6 times larger than fish reared at 2°C (M_D 0.271 vs. 0.104 mg). Growth rates were fitted as a second-order function of temperature (Table 2).

Postflexion larvae

The sorting of fish by size before the establishment of experimental groups produced significant differences in initial sizes of experimental fish (group mean L_S 14.02 to 16.10 mm; P=0.004). Differences among size groups within temperature treatment were generally maintained throughout the experiment but growth rates were slightly higher in the small-size groups than the in large-size groups. The effect of size group was significant for growth expressed as g_M ($F_{[2,6]}$=15.7, P=0.004) but not for g_L ($F_{[2,6]}$=1.78, P=0.248).

Growth in length and mass of postflexion Pacific cod larvae was significantly affected by rearing temperatures across the range examined (Fig. 2; g_M $F_{[3,6]}$=34.3, P<0.001; g_L ($F_{[3,6]}$=63.0, P<0.001). Growth rates (for g_M and g_L) at 11°C averaged 2.2 and 3.0 times, respectively those observed at 3°C in similar size treatments. Growth rates were described as a second-order function of temperature (Table 2).

Juveniles

Sorting of fish by size before the experiment resulted in significant differences in initial size among replicates within temperature treatments (L_T $F_{[8,83]}$=9.46,

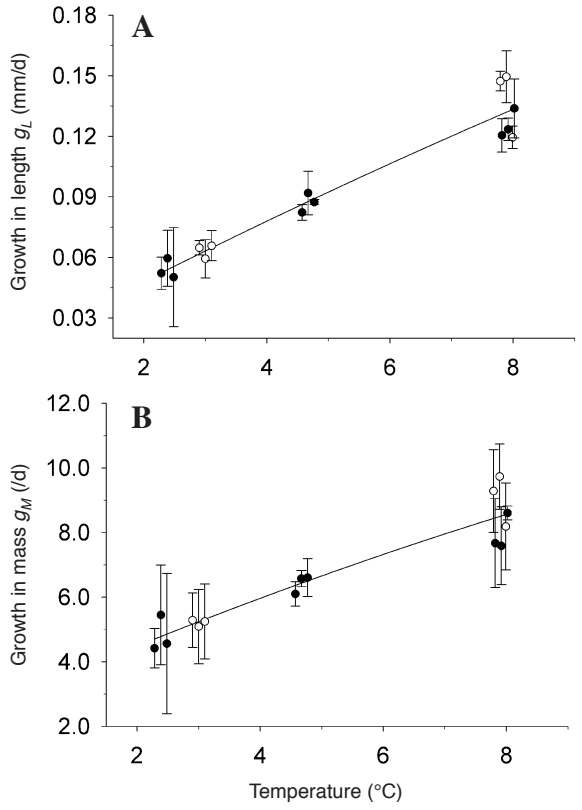

Figure 1

Temperature-dependent growth rates of preflexion larval Pacific cod (*Gadus macrocephalus*) in (**A**) standard length and (**B**) dry mass. Fish used in experiments were the offspring of spawning adults collected in the central Gulf of Alaska in April 2007 (open symbols) and 2008 (filled symbols). Values are the mean growth rates (±standard error) for three replicate tanks at four temperatures. Overlapping points are displaced horizontally for clarity.

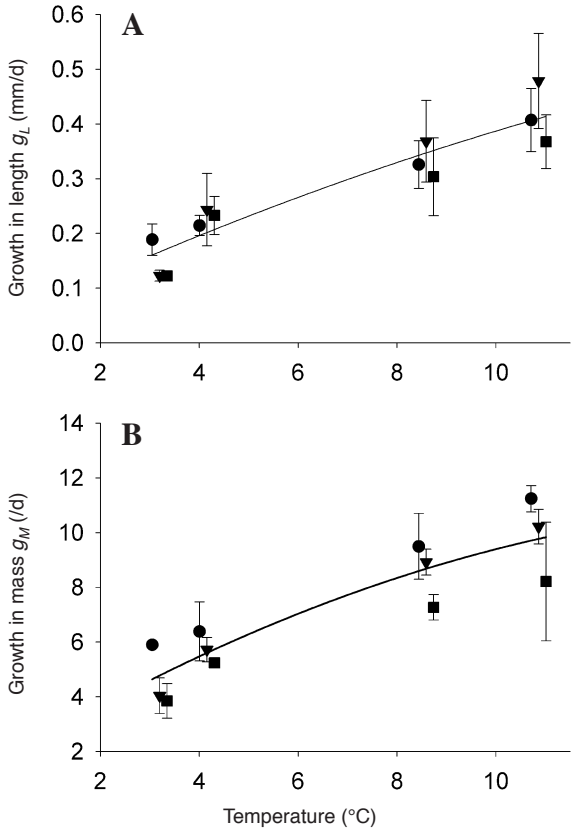

Figure 2

Temperature-dependent growth rates of postflexion larval Pacific cod (*Gadus macrocephalus*) in (**A**) standard length and (**B**) dry mass. Fish used in the experiment were the offspring of spawning adults collected in the central Gulf of Alaska in April 2007. Values are the mean growth rates (±standard error) for three replicate tanks at four temperatures. Symbols represent groups based on initial size sorting of larvae (circle: small; triangle: medium; square: large). Overlapping points are displaced horizontally for clarity.

$P<0.001$). Differential growth during the temperature acclimation period resulted in slight differences in initial sizes among temperature treatments (treatment mean L_T range: 48.8–51.8 mm; $F_{[3,83]}=2.70$, $P=0.051$). Although there were significant differences in growth rates among tanks within temperature treatments, these were not consistent across size groups, resulting in a significant interaction between temperature and size group (g_M $F_{[6,60]}=2.23$, $P=0.052$; g_L: $F_{[6,60]}=2.34$, $P=0.042$).

Growth in length and mass of juvenile Pacific cod was significantly affected by rearing temperatures across the range examined (Fig. 3; g_M $F_{[3,6]}=59.3$, $P<0.001$; g_L ($F_{[3,6]}=26.7$, $P<0.001$). Growth rates at 11°C averaged 2.9 and 3.7 times (g_M and g_L, respectively) greater than those observed at 2°C in similar size treatments. Best-fit functions describing growth as a second-order function of temperature are shown in Table 2.

General growth model

Models of growth rates of early life stages of Pacific cod indicated a discontinuity from strict allometric scaling during the early larval stage. Growth rates of preflexion larvae were lower than predicted based on a purely ontogenetic model incorporating growth-rate data from embryos to settled juveniles. Therefore, two-stage models were developed to describe growth in the egg stage separately from the posthatch, free-swimming stages. Although growth was a function of both temperature and body size, it was effectively modeled as the product of independent functions of temperature and body size. There were no significant interactions in the sense that the parameters of the temperature-dependence function were not themselves a function of body size. Therefore, embryonic and free-swimming stages shared a single

Table 2

Stage-specific growth models for early life stages of Gulf of Alaska Pacific cod (*Gadus macrocephalus*). Models describe growth in mass (g_M) and length (g_L) as a function of temperature (T) for each stage. r^2 is the coefficient of determination.

Stage		Growth functions	r^2
Eggs–embryos	temperature range: 0–8°C		
	dry weight (μg)	$g_M = 3.807 + 1.493 \cdot T - 0.032 \cdot T^2$	0.929
	standard length (mm)	$g_L = 0.104 + 0.024 \cdot T - 0.00002 \cdot T^2$	0.939
Preflexion larvae	temperature range: 2–11°C		
	dry weight (μg)	$g_M = 2.990 + 0.772 \cdot T - 0.077 \cdot T^2$	0.897
	standard length (mm)	$g_L = 0.179 + 0.015 \cdot \mathrm{T} - 0.0001 \cdot T^2$	0.941
Postflexion larvae	temperature range: 3–11°C		
	dry weight (g)	$g_M = 1.652 + 1.059 \cdot T - 0.028 \cdot T^2$	0.830
	wet weight (g)	$g_M = 0.531 + 0.857 \cdot T - 0.024 \cdot T^2$	0.897
	standard length (mm)	$g_L = 0.034 + 0.043 \cdot T - 0.0008 \cdot T^2$	0.882
	total length (mm)	$g_L = 0.044 + 0.019 \cdot T - 0.001 \cdot T^2$	0.889
Juveniles	temperature range: 2–12°C		
	wet weight (g)	$g_M = -0.998 + 0.579 \cdot T - 0.022 \cdot T^2$	0.826
	total length (mm)	$g_L = -0.081 + 0.079 \cdot T - 0.003 \cdot T^2$	0.762

temperature-dependence function, differing only in elevation through ontogeny (Fig. 4).

Growth rates of Pacific cod through the early life stages were described by the equations

$$g_L = \begin{cases} 0.076 + 0.029 \cdot T - 0.00002 \cdot T^2 & \text{if stage = embyro} \\ \dfrac{0.076 + 0.029 \cdot T - 0.00002 \cdot T^2}{1 - 0.059 / e^{L_S^{0.0758}}} & \text{if stage > embryo} \end{cases} \quad (3)$$

and

$$g_M = \begin{cases} (0.454 + 1.610 \cdot T - 0.069 \cdot T^2) \cdot \\ e^{-6.725 \cdot M_D} + 3.705 & \text{if stage = embryo} \\ (0.454 + 1.610 \cdot T - 0.069 \cdot T^2) \cdot \\ e^{-6.725 \cdot M_D} & \text{if stage > embryo} \end{cases} \quad (4)$$

These equations explained over 88% of the observed variance in growth rates of Pacific cod embryos to post-settlement juveniles (g_M r=0.969; g_L r=0.940). Analysis of residuals from these models indicated greater variance at higher growth rates (small body sizes and higher temperatures), but there were no trends in residuals in relation to experimental temperature or body size that would indicate significant departures from the model.

Discussion

Temperature is the dominant regulator of growth in early life stages of fishes. In this study we examined the ontogenic pattern in growth rate for early life stages of Pacific cod. We demonstrated a deviation from strict allometric scaling, wherein growth rates after hatching are lower than those predicted by body size allometry. We determined parameters for temperature-dependent growth functions in length and mass for specific life stages and for a unified STDG function. These measures of growth potential can be used to evaluate the biotic and abiotic factors regulating the growth and survival of early life stages of Pacific cod in the wild (Folkvord, 2005; Hurst et al., 2010).

Experiments

Because these experiments were conducted across a range of life stages, many aspects of our experimental method had to be adapted for each specific experiment, such as tank volume, prey type, and fish density. However, the most significant differences in method between egg–larval and juvenile experiments were the level of observation and source of fish. To estimate growth rates of embryos and larvae, subsamples of fish were drawn from a large tank population to determine mean size at a specific age (Otterlei et al., 1999; Monk et al., 2008). Change in mean size at age was then used to determine growth rate in each replicate tank. With this approach, there is the potential for size-selective mortality in the experiments to affect estimates of mean growth rates. Such size-selective mortality is most commonly assumed to be the result of predation (including cannibalism in single species culture). However, such an effect is unlikely to have occurred in these experiments: postflexion larvae were sorted by size before growth experiments specifically to avoid potential cannibalism, and we saw no evidence of cannibalism in the experiment (no larvae in samples with fish in their stomachs). Because juvenile fish could be handled, they were measured and returned to the tank and subsequently remeasured, providing

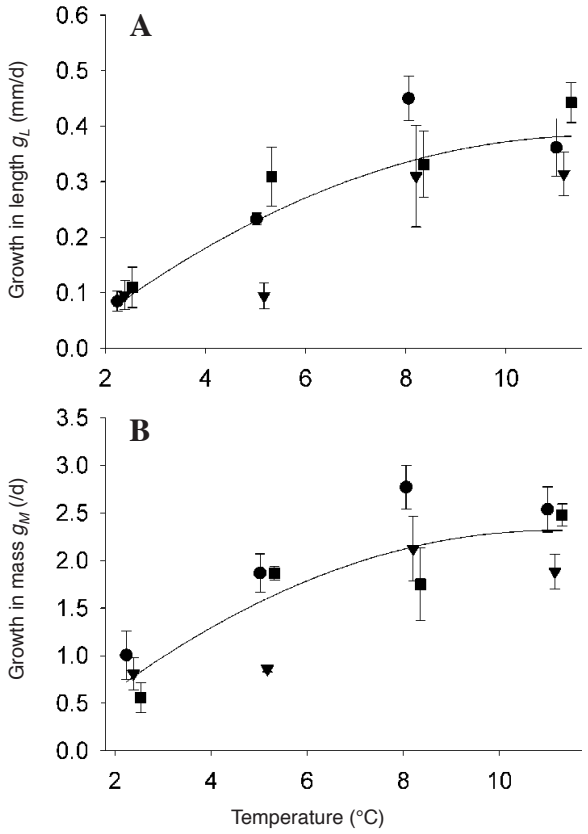

Figure 3

Temperature-dependent growth rates of postsettlement juvenile Pacific cod (*Gadus macrocephalus*) in (**A**) total length and (**B**) wet mass. Fish used in the experiment were collected from nearshore nursery areas at Kodiak Island, Alaska in July 2008. Values are the mean growth rates (± standard error) for three replicate tanks at four temperatures. Symbols represent groups based on initial size sorting of fish (circle: small; triangle: medium; square: large). Overlapping points are displaced horizontally for clarity.

growth trajectories for individual fish. These individual growth rates were then averaged to estimate mean growth rates of fish in each tank (Hurst and Abookire, 2006; Wijekoon et al., 2009).

For experiments with eggs and larvae, we used the offspring of field-caught spawning adults. In each year of experiments, gametes from one or two females were mixed with those of three to five males. Juvenile fish used in experiments were naturally produced and captured after recruitment to juvenile nearshore habitats. Therefore, the genetic diversity among experimental juveniles was significantly greater than that found in experimental eggs and larvae. This difference in potential genetic contributions to growth rates is not expected to have a significant influence on the overall growth patterns described here because maternal and genetic effects on growth have been shown to be small in relation to environmental factors such as temperature (Benoît and Pepin, 1999; Green and McCormick, 2005) and prey availability (Clemmesen et al., 2003).

Ontogenetic patterns of growth

By combining results across life stages, we clarified ontogenetic patterns in growth and length. With the exception of a departure during the preflexion stage, growth patterns followed expected size-dependent allometric patterns throughout much of the early development (Elliott and Hurley, 1995). Growth in mass (g_M) decreased with increases in body size (Wootton, 1990) and growth in length (g_L) was constant across life stages. Although the constancy of g_L across a range of body sizes in early life stages has been noted in other studies (Jones, 2002; Sigourney et al., 2008), those experiments have not generally included the presettlement egg and larval stages incorporated here. Interestingly, in Pacific cod, the general pattern of across-stage similarity in g_L extended from the egg–embryo stage into the juvenile stage.

There was a significant departure from the expected ontogenetic pattern in the preflexion larval period, most clearly observable in the g_L results. Measured g_L among preflexion larvae averaged only 41% of the rates measured for embryos, postflexion larvae, and settled juveniles. Although less readily apparent, a similar departure was observed in mass growth as the decline in g_M between the egg–embryo and preflexion larval stages was greater than expected from allometric patterns accounting for the observed differences in body size. In several studies on the growth of first-feeding gadids, higher growth rates were reported for fish reared on copepods than on cultured rotifers (Conceicao et al., 2010). Unfortunately, technical limitations preclude rearing sufficient quantities of copepods for use in experiments such as ours. For our study, larval Pacific cod were reared on essential-fatty-acid–enriched rotifers, as the best of the practicable prey alternatives. Therefore, it is possible that growth rates of preflexion larvae are under-estimates of maximum potential growth at this stage. However, the effect of prey type is insufficient to completely explain the significantly lower growth rate observed at this stage when compared to other stages. Further, similar observations of reduced growth rates of fishes in the early posthatch phase have been observed in several other studies. Experiments in which growth of haddock (*Melanogrammus aeglefinus*; Martell et al., 2005) was tracked through the egg–larva transition revealed a similar reduction in growth associated with hatching. A similar pattern is apparent in Atlantic cod, but without measurements of embryonic growth rates, the magnitude of decline at hatching could not be determined (Otterlei et al., 1999; Folkvord, 2005). However, these studies document a period of increasing growth rates after hatching, followed by growth rate declines along allometric expectations, indicating a similar overall pattern.

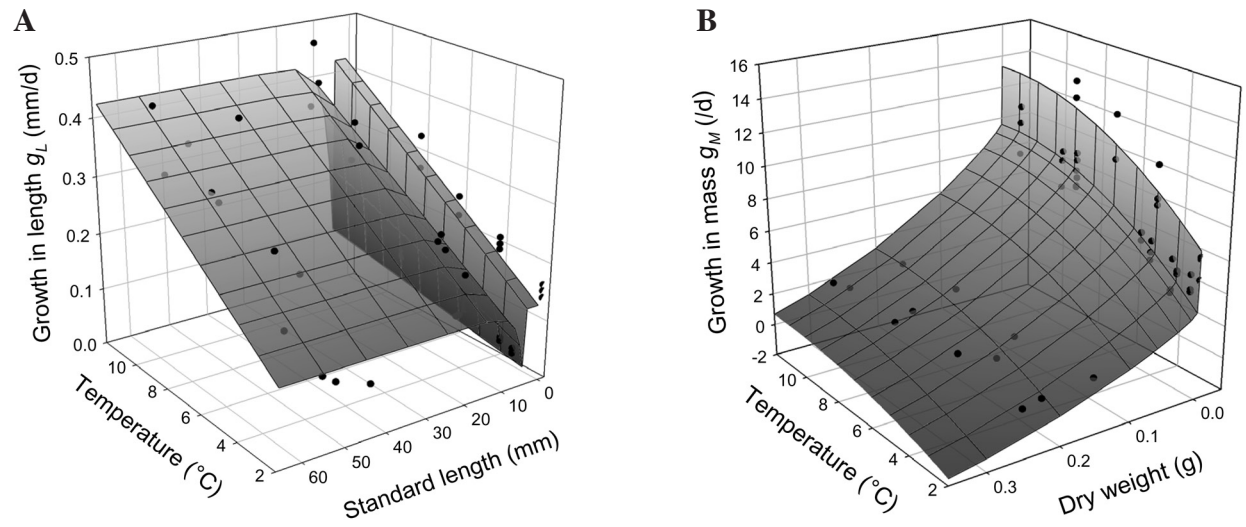

Figure 4

Size- and temperature-dependent growth rates of early life stages of Pacific cod (*Gadus macrocephalus*) from the central Gulf of Alaska in (**A**) standard length and (**B**) dry mass. Points are the tank mean growth rates measured in laboratory experiments. Surfaces are best-fit descriptions of growth rates. Parameter values are presented in Equations 3 and 4.

This reduction in growth during the egg–larva transition appears to be the result of increased metabolic expenditures associated with swimming in posthatch larvae and possibly a reduction in energy available for growth associated with the transition from reliance on endogenous energy stores to exogenous feeding (Torres et al., 1996; Yúfera and Darias, 2007). In Pacific cod, yolk reserves are depleted 3–12 dah, depending on water temperature (Laurel et al., 2008) and stomach fullness increased through the first 28 dah (B. J. Laurel, unpubl. data). The increase in growth rates after the preflexion transitional feeding stage coincides with the onset of diel vertical migrations (Hurst et al., 2009) and increased responsiveness to prey (Colton and Hurst, 2010) among postflexion Pacific cod larvae. The negative departure from an allometrically defined growth pattern after hatching indicates that the first-feeding stage represents a "critical period" in the early life history of Pacific cod and that the consequences for recruitment of this low growth may be greater at low temperatures (Kamler, 1992; Houde, 1996). In addition to inclusion of embryo measurements into larval studies, future studies with other species should encompass other major life history and habitat transitions, such as metamorphosis and settlement in flatfishes (Christensen and Korsgaard, 1999; Neuman et al., 2001) in order to clarify the physiological basis of growth patterns and to determine parameters for growth models.

Based on exploration of model structures for a unified STDG for early life stages of Pacific cod, a two-stage model was developed. The first stage described growth in the egg stage as a direct function of water temperature. The second stage described growth in posthatch fish as a function of water temperature and fish size. In addition to providing the best fit to experimental data, this formulation is logically consistent with the life history. Explicit discrimination between life stages coincides with hatching, whereas the function provides a continuous growth surface for all free-swimming stages. This stage-independent model for posthatch fish provides more realistic growth trajectories in modeling applications where fish are tracked over multiple stages.

Applications of growth models

By quantitatively accounting for the influence of temperature variation, laboratory-determined growth rates are being increasingly used to evaluate factors regulating growth rates of fishes in the wild (Folkvord, 2005; Rakocinski et al., 2006; Hurst et al., 2009). In these analyses, "realized growth" expresses observed growth in the field as a fraction of the potential growth at the encountered field temperatures (Hurst and Abookire, 2006), with field growth rates estimated from changes in mean size, otolith increment measures, or biochemical measures (RNA:DNA). In these studies it is important to recognize that growth rates of individuals are determined by both genetic and environmental factors. Growth models from laboratory experiments generally describe mean growth of a representative population under optimal foraging conditions, which should not be mistaken for the maximum growth rates that would be observed for the fastest growing individual. Therefore, field growth rates should be similarly expressed as a population mean rather than at the individual level. Realized growth rates near 100% indicate that growth rates in the population are directly limited by ambient

temperature variation. In studies of juvenile flatfishes, this temperature regulation of growth has been referred to as the "maximum growth/optimal food condition" hypothesis (Karikiri et al., 1991; van der Veer and Witte, 1993). Conversely, realized growth rates significantly below 100% indicate that growth is regulated by nonthermal environmental factors such as light regime or prey availability (Buckley et al. 2006; Kristiansen et al., 2007; Hurst et al., 2009).

Unfortunately, many studies of growth rates in fishes are conducted over a limited size range and usually within a single life stage. Therefore, these data have limited application where growth rates of wild fish are tracked over longer time periods or through early life history stage transitions. For example, in evaluating the mechanisms responsible for variation in survival and recruitment, it is critical to determine whether growth reductions among wild fish are due to inherent physiologically based patterns (as appears in post-hatch gadids) or are imposed by an unfavorable growth environment (Jones, 2002). In another application of laboratory data to field studies, the back-calculation of hatch dates from estimated temperature-dependent growth rates (Lanksbury et al., 2007) could be biased if ontogenetic patterns in growth variation are not accounted for.

Conclusion

Growth variation in early life stages can result in body-size variation that persists over time and has significant implications for the survival and recruitment of marine fish larvae (Houde, 1996; Jones, 2002). Successful evaluation of the biotic and abiotic factors regulating this underlying variation in growth requires detailed information on the size- and temperature-dependency of potential growth throughout the early life history. Identifying the intrinsic patterns in growth-rate allometry and reductions among preflexion larval Pacific cod was based on the integration of experimental data on embryos and larvae,—stages generally considered in isolation from each other. We suggest that data on embryos be routinely incorporated with larval data to clarify ontogenetic and temperature-dependent growth patterns in the early life history stages of fish.

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