

Thermal effects on behavior of juvenile walleye pollock (*Theragra chalcogramma*): implications for energetics and food web models

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Abstract: The behavioral responses of fishes to temperature variation have received little attention despite their direct implications to bioenergetics-based models of production and encounter-based models of food web dynamics. Behavioral characteristics of juvenile walleye pollock (*Theragra chalcogramma*), a pelagic marine zooplanktivore, were examined between 2 and 9 °C in large arenas. Routine swim speed, path sinuosity, and schooling cohesiveness of fish in small groups were described from overhead video observations. In a separate experiment, maximum swimming speeds were measured in a recirculating flume. Routine and maximum swimming speeds had contrasting responses to temperature demonstrating a behavioral rather than physiological regulation of activity level. Routine swim speed was 48% faster at 2 °C than at 9 °C. This result is inconsistent with the assumption of a constant activity multiplier for metabolism incorporated into most bioenergetics models of fish growth. Increased swim speed, along with the reduced path sinuosity observed at low temperatures, may reflect kinetic aspects of habitat selection. Group cohesion increased at low temperatures, with nearest neighbors averaging 32% closer at 2 °C than at 9 °C. These results demonstrate that representative models of energy flow through marine food webs depend on an improved understanding of the behavioral as well as physiological responses of fishes to thermal variation.

Résumé : On s'est peu intéressé aux réactions comportementales des poissons à la variation de température malgré leurs conséquences directes sur les modèles de production fondés sur la bioénergétique et sur les modèles de la dynamique des réseaux alimentaires basés sur les rencontres. Les caractéristiques du comportement de jeunes goberges de l'Alaska (*Theragra chalcogramma*), des poissons marins planctonophages pélagiques, ont pu être étudiées dans des grandes arènes entre 2 et 9 °C. Des observations vidéo en surplomb ont servi à décrire la vitesse de nage de routine, la sinuosité des trajets et la cohésion des bancs chez de petits groupes de poissons. Une expérience différente a permis de mesurer les vitesses maximales de nage dans un chenal à recirculation d'eau. La vitesse de nage de routine et la vitesse maximale réagissent différemment à la température, ce qui démontre qu'il existe une régulation comportementale du niveau d'activité plutôt qu'une régulation physiologique. La vitesse de nage de routine est de 48 % plus rapide à 2 °C qu'à 9 °C. Ce résultat ne s'accorde pas avec la présupposition de l'existence d'un multiplicateur constant d'activité pour le métabolisme que l'on incorpore dans la plupart des modèles bioénergétiques de croissance des poissons. La vitesse de nage accrue, de même que la sinuosité réduite des trajets, que l'on observe à températures basses, peuvent refléter les aspects cinétiques de la sélection de l'habitat. La cohésion des groupes augmente à basses températures et les voisins les plus proches sont en moyenne de 32 % plus près à 2 °C qu'à 9 °C. Ces résultats montrent que les modèles représentatifs du flux énergétique dans les réseaux alimentaires marins dépendent d'une compréhension améliorée des réactions comportementales en plus des réactions physiologiques des poissons à la variation thermique.

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Introduction

All organisms respond to changes in the environment with changes in behavior. Well-understood examples include functional responses to changes in prey availability and reducing risky foraging behavior in the presence of predators

(Milinski 1993). Temperature represents the most pervasive aspect of the environment affecting ectotherms and varies markedly on a variety of spatial and temporal scales. However, our understanding of the behavioral responses of marine fishes to temperature variation lags well behind our understanding of physiological responses. This has occurred despite the fact that behavior represents the link that allows (or prevents) physiological processes from scaling up to population- and ecosystem-level responses (Railsback 2001; Ovadia and Schmitz 2002).

While behavioral responses to thermal variation have not been thoroughly described for most fish species, routine (also called "volitional" or "voluntary") swimming speeds have been predicted to respond according to one of three general patterns. Swim speeds (and other measures of activity level) could parallel physiological processes, increasing

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with temperature within tolerance limits (Bennett 1990); as a component of behavioral thermoregulation, swim speed could increase with deviation from the preferred temperature (orthokinesis: Fraenkel and Gunn 1961); or fish could compensate for temperature variation, maintaining constant swim speeds across temperatures (Precht 1958). There is some support in the literature for each of these responses suggesting that such responses are specific to species or life history guild. Furthermore, largemouth bass (*Micropterus salmoides*) exhibit a combination of responses with activity levels remaining constant across a broad range of temperatures but declining at the lowest temperatures encountered (Lemons and Crawshaw 1985).

In addition to effects on swim speed, temperature may provide an ultimate or proximate cue for changes in other aspects of fish behavior. Effective behavioral thermoregulation in coastal or open oceans is thought to require responses in travel path (klinokinesis) as well as velocity (Fraenkel and Gunn 1961; Reynolds 1977; Neill 1979). Temperature-dependent shifts in the diel periodicity of activity in species using sheltering and crypsis as primary antipredator strategies appear to be linked to low foraging requirements at low temperatures (Fraser et al. 1993; Hurst and Duffy 2005). Little work has been done on the behavioral responses of continuously swimming pelagic fishes that use schooling as the primary antipredator tactic. Two studies examining thermal effects on schooling behavior (Griffith 1978; Weetman et al. 1998) found reduced group cohesion in threadfin shad (*Dorosoma petenense*) and guppy (*Poecilia reticulata*) schools at lower temperatures.

Walleye pollock (*Theragra chalcogramma*) are an integral component of North Pacific and Bering Sea food webs and support major regional fisheries (Livingston 1993). Juveniles inhabit the surface and subsurface waters of the Gulf of Alaska and Bering Sea where they encounter a broad range of temperatures. In addition to wintertime exposure to temperatures below 2 °C, the summertime persistence of a cold intermediate layer (~2 °C, surface waters up to 10 °C) over large portions of the eastern Bering Sea shelf creates significant spatial variation in temperature of juvenile walleye pollock habitat (Luchin et al. 1999). Walleye pollock can feed and maintain positive growth at temperatures as low as 2 °C (Smith et al. 1986), with maximum growth and consumption rates of juveniles estimated to occur near 10 °C (Ciannelli et al. 1998). Individuals can select preferred temperatures in experimental vertical gradients, with the preferred temperature varying with nutritional state (Sogard and Olla 1996). In addition, juveniles have considerably plastic patterns in schooling behavior, varying swim velocity and group cohesiveness in response to nutritional state, predator presence, and prey patchiness (Ryer and Olla 1995; Sogard and Olla 1996, 1997). Laboratory observations of the distributional and behavioral responses of walleye pollock to biotic and abiotic factors have been found to be robust when compared with field observations, even when operational scales differ (Olla et al. 1995, 1996). Hence, walleye pollock provide a useful model species for examination of thermal impacts on pelagic fishes and marine food webs.

In this paper, I explore the effects of temperature on both the capacity for and expression of swimming behavior of juvenile walleye pollock. Coordinated changes in swim speed,

swim path, and schooling cohesiveness are described by observing free-swimming groups of temperature-acclimated fish in large circular arenas. The thermal dependence of maximum swimming speed is used to discriminate swimming changes due to behavioral regulation versus physiological constraints. I describe how these behavioral responses conflict with our current understanding of fish behavior as incorporated into encounter- and bioenergetics-based models of ecosystems.

Materials and methods

Capture and holding

Age-0 walleye pollock, 10–20 mm total length (TL), were captured from nearshore waters of Puget Sound at Port Townsend, Washington, with a lighted lift net suspended from a dock. Fish were held for at least 24 h in ambient seawater prior to shipment to the National Marine Fisheries Service laboratory in Newport, Oregon. Prior to use in the experiment, fish were reared in groups in 61 or 122 cm diameter round tanks. All tanks were maintained at 9–10 °C with a photoperiod of 12 h light : 12 h dark. Initially, fish were fed daily a combination of thawed *Artemia* sp. and commercially available food. Later, feeding was reduced to three times per week and food changed to a gelatinized combination of squid, krill, herring, commercial food, amino acid supplements, and vitamins.

Routine swimming characteristics

Routine swimming characteristics (speed, path sinuosity, and group cohesiveness) of juvenile walleye pollock in small groups ($n = 6$ fish per group) were examined at three temperatures, 2, 5, and 9 °C, representing most of the range encountered by juveniles of this species in the Bering Sea and Gulf of Alaska (Bailey et al. 1999). To minimize tank effects on fish behavior, fish were tested at the smallest body sizes (<100 mm) in the largest arenas (2.9 m diameter) that still permitted consistent discrimination in video observations.

Fish were transferred to acclimation tanks (1 m diameter) and temperatures adjusted at a rate of 1 °C·day⁻¹ to achieve target treatment temperatures. Groups of >50 walleye pollock were acclimated to test temperatures for at least 2 months prior to testing. Sizes of fish used in trials averaged 82.4 mm TL, ranging from 63 to 103 mm, with fish in 2 °C trials averaging 7.2 mm shorter than fish in the 5 and 9 °C treatments owing to differential growth during the acclimation period (analysis of variance (ANOVA), $F_{[2,249]} = 22.22$, $p < 0.05$). For each trial, groups of six similarly sized fish (within group average length CV = 5.0) were captured from acclimation tanks, measured, and introduced into the experimental arenas. Fish were acclimated to the experimental arena for approximately 40 h prior to making observations. Fish were fed thawed *Artemia* sp. once while in experimental arenas at 1600 on the day prior to experimental observations (14.5 h prior to making observations). Lights in the experimental arenas were off from 1800 to 0600. Experimental observations were made between 0630 and 0800 to eliminate any potential disturbance from routine laboratory activities.

Water depth in the 2.9 m diameter experimental arenas was restricted to 30 cm such that activity was largely con-

finned to the X - Y plane and could be described from a single overhead camera. Two arenas were maintained at each of the three test temperatures, and temperature treatments were run synchronously. Fourteen trials were conducted at each test temperature. Individual fish were reused within temperature treatments in the experiment, with at least 1 week between observations, and group membership was not maintained across trials. There were no temporal trends in any metric (i.e., replicate order not a significant factor in any analyses of swim speed, path, or group cohesiveness) indicative of biases associated with multiple observations of fish in the experiments.

The routine swimming speed of juvenile walleye pollock was described by digitizing the path of randomly chosen fish for 1 min at 5 min intervals throughout the observation period. The only criteria for selection of fish to be tracked was that the fish not be temporarily separated from the group such that the speed of the individual generally reflected that of the group. The average of 20 measurements of swimming speed during a trial was used as the level of observation in the analyses. Routine swimming speed ($\text{mm}\cdot\text{s}^{-1}$) was analyzed with analysis of covariance (ANCOVA) with temperature as the main effect and mean length of fish in the group as the covariate.

Path sinuosity was described by the area of the minimum convex polygon that contained an entire 1 min swim path. High path sinuosity (or high turning rate) is reflected in small polygon areas and straighter paths in larger polygon areas. Average swim path polygons during the 1 min observation periods occupied less than 25% of the total tank area, indicating that changes in path polygon areas reflected changes in path sinuosity, unconstrained by tank size. Owing to the inherent increase in area use with distance traveled in the 1 min sample, analysis of polygon area between temperature treatments was conducted with ANCOVA with path distance as the covariate. Path distance and polygon area were log-transformed prior to analysis. Trial replicate ($n = 14$) was treated as a random factor nested within temperature treatment.

The effect of temperature on schooling cohesiveness of walleye pollock was described through changes in nearest neighbor distances among fish in the group. Nearest neighbor distances were measured for each fish in the group from still frames at 5 min intervals between 0700 and 0800 ($n = 13$ per trial). Mean nearest neighbor values were averaged for each trial and compared between temperature treatments with ANCOVA. The potential for body size effects on nearest neighbor distances was evaluated by inclusion of mean fish length in each trial group as a covariate.

Maximum swimming speeds

Maximum swimming speeds (U_{crit}) of juvenile walleye pollock were tested at three temperatures, 2, 5, and 9 °C. Fish were transferred to temperature acclimation tanks (1 m diameter) and temperatures adjusted to test temperatures at a rate of 1 °C \cdot day $^{-1}$. Fish were acclimated to test temperature for at least 2 months prior to testing. During acclimation, feeding was reduced to two times per week to reduce growth differences between temperatures. Fish were offered food 22–26 h prior to measurement of swimming capacity. At least 27 fish were tested at each temperature with individual

fish used only once in swimming trials. Tested fish ranged from 67 to 143 mm TL and body size did not vary significantly among temperature treatments (ANOVA, $F_{[2,80]} = 0.249$, $p = 0.97$).

The test flume consisted of a header tank (1000 L) that fed directly into the test chambers. Three 5-hp, 1750-rpm pumps returned water from the water bath to the header tank at a maximum rate of 95 L \cdot s $^{-1}$. A baffle in the header tank prevented pump turbulence from being introduced into test chambers. A 38 cm cylinder containing three 15 cm diameter test chambers was attached directly to the header tank. The test chambers were 115 cm long and had 6.4 mm mesh nylon netting at the upstream and downstream ends. Water temperature in the flume was maintained within 0.1 °C of test temperature by recirculating water through a glycol-supplied heat exchanger. Flow velocities were continuously measured 5 cm downstream of swimming chambers with an electromagnetic flowmeter (Marsh-McBirney Flo-Mate model 2000). Velocities in the three parallel swimming chambers were generally within 10 mm \cdot s $^{-1}$ and were never observed to differ by more than 20 mm \cdot s $^{-1}$.

For each trial, individual fish were captured from acclimation tanks, measured (TL), and introduced into the swimming chambers. Fish were acclimated to the swimming chambers for 15 min at a flow velocity of 50 mm \cdot s $^{-1}$. Flow velocities were then increased by 50 mm \cdot s $^{-1}$ at 10 min intervals until the fish became exhausted. When exhausted, the downstream barrier was removed and the fish captured from the swimming chamber.

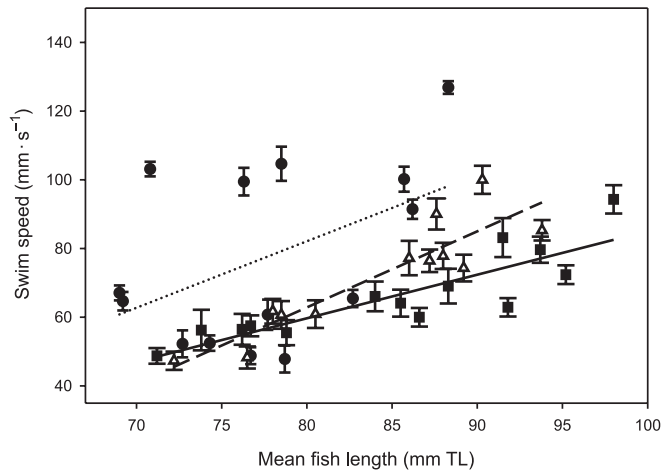
Maximum swimming velocities were calculated according to the equation $U_{\text{crit}} = V + vT/t$, where V is the highest speed maintained for a full time interval, v is the velocity increment (50 mm \cdot s $^{-1}$), t is the time interval (10 min), and T is the amount of time spent at the fatigue velocity (Brett 1964). The U_{crit} velocities were not corrected for blocking effects, as the cross-sectional area of the fish was less than 2% of the swimming chamber. Differences in critical swimming velocities between temperature treatments were analyzed using ANCOVA with temperature as the main effect and body length as the covariate.

Results

Routine swimming speed

Routine swimming speed of juvenile walleye pollock in small groups was a function of both water temperature and body size (Fig. 1). Swimming speeds increased with mean body length of fish in the group (covariate effect, $F_{[1,38]} = 23.21$, $p < 0.001$). Routine swimming speeds decreased with increasing temperature between 2 and 9 °C (ANCOVA, $F_{[2,38]} = 5.56$, $p = 0.008$). For a common fish length of 80 mm TL, routine swimming speed decreased 32% from 82.4 mm \cdot s $^{-1}$ at 2 °C to 55.5 mm \cdot s $^{-1}$ at 9 °C. There was a nonsignificant interaction effect between fish length and temperature on swim speed (homogeneity of slopes, $F_{[2,36]} = 2.70$, $p = 0.08$). There was also a trend for increased variation among trials at low temperatures (homogeneity of variances, $F_{[2,39]} = 2.91$, $p = 0.06$).

Fig. 1. Routine swimming speeds of juvenile walleye pollock (*Theragra chalcogramma*) as a function of body size and temperature. Each point is the mean (\pm SE) of 20 measurements of swim speed over 1 min of individuals randomly selected from the group at 5 min intervals plotted against the mean length of fish in the group. Circles and dotted line, 2 °C; triangles and dashed line, 5 °C; squares and solid line, 9 °C. Regression lines shown are calculated separately for each temperature, but slopes did not differ significantly.



Path sinuosity

Swim path sinuosity of juvenile walleye pollock increased with water temperature. The area of the smallest polygon that contained a 1 min swim path decreased with increasing temperature (ANCOVA with distance traveled as covariate, $F_{[2,39]} = 7.69$, $p = 0.002$) (Fig. 2). Within temperature treatment, there was also a significant effect of replicate trial (ANCOVA, $F_{[39,797]} = 7.94$, $p < 0.001$). This variation among trials within temperature treatment was not correlated with the size of fish in the trial (ANCOVA, $F_{[1,38]} = 0.6468$, $p = 0.426$).

Schooling behavior

Group cohesiveness in the six-member walleye pollock groups was higher at the lower temperatures tested. Distances to nearest neighbors were on average 32% lower at 2 °C than at 9 °C (18.7 versus 27.3 mm; ANOVA $F_{[2,39]} = 36.08$, $p < 0.001$) (Fig. 3). In addition to the temperature effect, there was a significant effect of trial replicate within temperature (ANOVA, $F_{[39,504]} = 6.75$, $p < 0.001$). There was a nonsignificant trend toward groups with larger members maintaining closer neighbors (test of length as a covariate, $F_{[1,38]} = 2.99$, $p = 0.092$) and there was no interactive effect of fish size with temperature on nearest neighbor distances (homogeneity of slopes, $F_{[2,36]} = 0.90$, $p = 0.414$).

Maximum swimming speed

Water temperature had a significant positive effect ($p < 0.001$) on U_{crit} values of juvenile walleye pollock (Fig. 4). Maximum swimming speed increased with body length at all temperatures ($p < 0.001$). For a given size of 100 mm TL, maximum swim speed increased from 259 mm · s⁻¹ at 2 °C to 349 mm · s⁻¹ at 9 °C. There was no significant interaction ef-

Fig. 2. Mean area of polygon occupied by juvenile walleye pollock (*Theragra chalcogramma*) during 1 min of routine swimming. Each point is the adjusted mean (\pm SE) polygon area measured during 14 trials corrected to a standard path length with ANCOVA across temperatures.

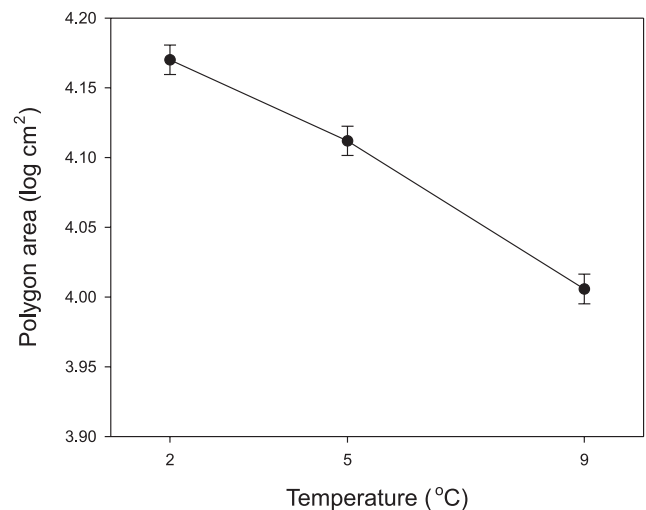
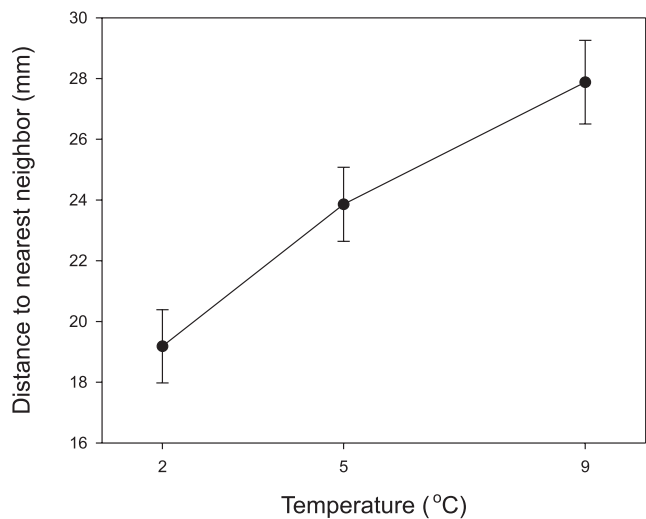


Fig. 3. Nearest neighbor distances of juvenile walleye pollock (*Theragra chalcogramma*) in six-member groups. Points represent the mean (\pm SE) of average measures within a trial. Twelve measurement points per trial, 14 trials per temperature.

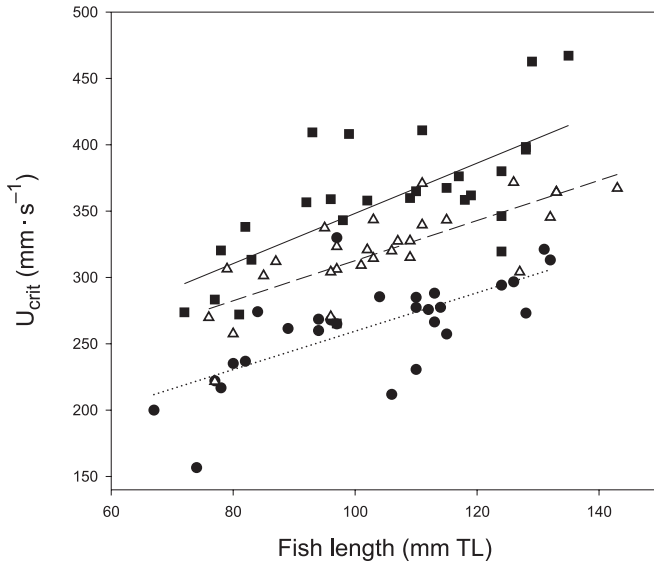


fect between temperature and body size on swimming speed ($p = 0.390$).

Discussion

Juvenile walleye pollock responded to variation in water temperature with changes in characteristics of their routine swimming behavior. These responses reflect life history adaptation to a variable environment in which temperature directly affects physiological processes and serves as a proximate cue for changes in other environmental factors (Reynolds 1977; Komers 1997). Walleye pollock increased routine swim speed, reduced path sinuosity, and reduced the distance among fish in a group at lower temperatures. In ad-

Fig. 4. Maximum (critical) swimming speeds (U_{crit}) of juvenile walleye pollock (*Theragra chalcogramma*) measured in a recirculating swimming flume. Points are U_{crit} values of individual fish plotted against fish length. Circles and dotted line, 2 °C; triangles and dashed line, 5 °C; squares and solid line, 9 °C. Regression lines shown are calculated separately for each temperature, but slopes did not differ significantly.



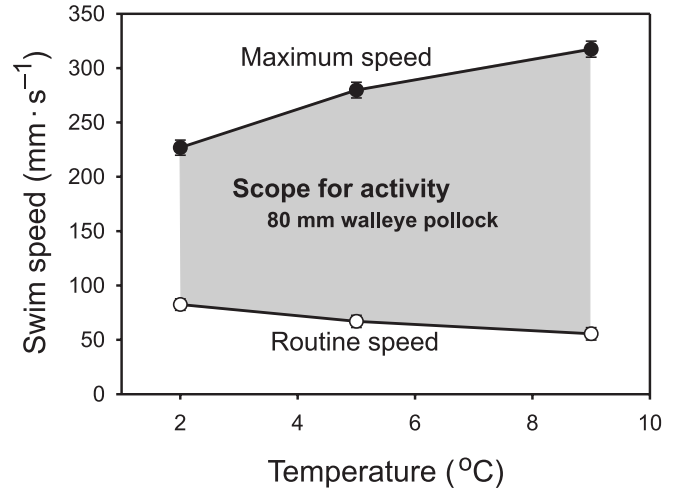
dition to reflecting mechanisms of habitat selection, behavioral characteristics play major roles in determining an organism's encounter rate with predators and prey and may affect the fate of an individual following a predator encounter. Hence, behavioral responses need to be incorporated into models of fish energetics as well as food web dynamics.

The experiments presented here were conducted to isolate the effects of temperature on behavioral traits (routine speed, path, and group cohesion) known to also vary in response to factors such as hunger level and predator presence (Johansson and Leonardsson 1998). Several studies have documented such effects in walleye pollock (Sogard and Olla 1997; Ryer and Olla 1998). In this experiment, routine swimming characteristics were examined in fish that were not actively foraging. Fish had been fed 14.5 h prior to making observations at all temperatures to minimize the differences in hunger level across treatments. However, it remains possible that differences among treatments attributed to temperature variation could be due to slight differences in nutritional state. A set of preliminary observations made at 2 and 10 °C on the fourth day postfeeding produced results similar to those reported here (T.P. Hurst, unpublished data), suggesting a generality of the temperature response.

Scope for activity

Routine volitional swim speed and maximum swimming performance exhibited markedly contrasting patterns in thermal sensitivity in juvenile walleye pollock. The increase in maximum swimming speed with temperature in juvenile walleye pollock is similar to the pattern observed in other ectotherms (Bennett 1990; Hurst and Conover 2001; O'Steen and Bennett 2003). This increased performance at higher temperatures is also consistent with other physiologi-

Fig. 5. Scope for activity of an 80 mm juvenile walleye pollock (*Theragra chalcogramma*) as a function of temperature. Scope for activity is expressed as the difference between maximum swimming speed measured in a recirculating flume and routine swim speed measured in 2.9 m diameter arenas.



cal processes (growth, metabolism, and digestion) in walleye pollock (Smith et al. 1986, 1989; Sogard and Olla 2000). Such thermal dependencies of physiological processes demonstrate that the contrasting pattern observed in routine swim speeds of juvenile pollock is not due to a physiological constraint. Rather, the changes in volitional swimming speed reflect a behavioral regulation of activity levels in the face of changing physiological capacity (O'Steen and Bennett 2003).

Scope for activity represents the degree to which an animal may increase activity levels beyond those routinely expressed or the difference between maximum physiological performance and routine activity (Irschick and Garland 2001). The scope for activity increased markedly with temperature in juvenile walleye pollock owing to the differences in thermal sensitivity of routine and maximum swimming speed (U_{crit}) (Fig. 5). Based on the laboratory experiments presented here, routine swimming activity (of an 80 mm TL walleye pollock) comprised 36% of maximum capacity at 2 °C but only 17% of maximum at 9 °C.

Swim speed and path

Observations of the effects of temperature on routine activity levels of fish vary markedly across species (Lemons and Crawshaw 1985; Hurst and Duffy 2005). Spontaneous activity of largemouth bass was constant across a wide range of temperatures but was reduced at the lowest temperatures encountered (Lemons and Crawshaw 1985). Hurst and Duffy (2005) observed a decrease in daytime, but not nighttime, activity of northern rock sole (*Lepidopsetta polyxystra*). The complexity and diversity of such responses demonstrate that activity does not routinely respond to thermal variation in parallel with physiological processes. Responses are species specific and need to be evaluated and interpreted in a broader life history context (O'Steen and Bennett 2003).

In several species, marked increases in swimming speed were observed in response to declining temperatures and interpreted as an acute avoidance response (Sogard and Olla

1998). It does not appear that the higher swimming speeds of walleye pollock at 2 °C reflect such an acute avoidance response. Exposure to temperatures below 2 °C is a common aspect of the life history of walleye pollock and fish are able to maintain feeding and growth at these temperatures (Smith et al. 1986). In the present experiment, fish had been acclimated to test temperatures for at least 2 months with no ill effects. In fact, when exposed to rapid reductions in temperature (from 12 to 3 °C in 4 h), walleye pollock responded with a decrease in activity level (Sogard and Olla 1998).

Rather, the higher volitional swimming speed at lower temperatures may reflect an orthokinetic component (increased speed with departure from preferred conditions) of behavioral thermoregulation or a more general search strategy for thermally optimal habitats (Magnuson et al. 1979; Neill 1979). Reynolds and Casterlin (1979) referred to an "activity well" at the preferred temperature with activity levels increasing with increasing temperature deviation (Humston et al. 2000). Higher swimming speeds increase the probability of detecting thermal gradients in the environment. Correspondingly, the variability in swim paths observed in walleye pollock is consistent with a klinokinetic response (increased turning rates in preferred conditions) to temperature variation (Humston et al. 2000). Swim path sinuosity decreased significantly with temperature, further enhancing the probability of detection of positive thermal gradients (Bell 1991). In conjunction, the associated changes in speed and path may be representative of a gradient between an extensive searching pattern at low temperatures (for thermal cues) and an intensive searching pattern at warmer temperatures (for prey resources).

The interpretation of the swim path and speed changes in walleye pollock as components of behavioral thermoregulation assumes that the preferred temperature for this life stage is near or above 9 °C. Final preferendum experiments have not been performed, but laboratory experiments demonstrate ability for behavioral thermoregulation in walleye pollock. When placed in experimental gradients, age-0 walleye pollock selected warmer surface waters (8–9 °C) unless maintained on submaintenance rations (Sogard and Olla 1996) and age-2 walleye pollock selected temperatures above 10° independent of feeding history (Duffy-Anderson et al. 2003). In the wild, juvenile walleye pollock generally remain above the thermocline when foraging conditions are sufficient (Bailey 1989; Swartzman et al. 1994). Distribution relative to horizontal thermal gradients is less clear for juvenile walleye pollock because of their widespread distribution and the interactions with other physical and biological features but appears to be generally consistent with a preference for warmer waters. While age-0 walleye pollock have been observed at temperatures below 2 °C even in summer (Tang et al. 1996), they were most abundant in warmer waters of the western Gulf of Alaska (>8 °C at 50 m; Wilson et al. 1996) and the Aleutian Basin (7–9 °C surface and >4 °C at 100 m; Tang et al. 1996).

Schooling behavior

In both captivity and the wild, juvenile walleye pollock form dense, but not highly polarized, schools. The organization of fish into schools or shoals is considered the primary mechanism of predator defense in small pelagic fishes, po-

tentially reducing both the rates of predator encounter and risk of capture following an encounter (Pitcher and Parrish 1993). Schooling may also allow fish to forage more efficiently on patchily distributed resources but resulting in increased competition when prey patches are encountered (Eggers 1976; Robinson 1995). School cohesiveness has been demonstrated to vary in response to the relative pressures imposed by predation risk and hunger level (Ryer and Olla 1995, 1998; Sogard and Olla 1997).

The use of small groups (six fish) in these experiments is consistent with previous experiments and is required by the need to locate and track individuals within the group. While nearest neighbor distances may also vary with group size, the experiments presented here successfully isolated the effect of temperature on group cohesiveness in walleye pollock. The marginal costs and benefits of changing interindividual distances within a school have not been explicitly measured but are generally assumed to reflect a trade-off between higher survival of predator encounters in tight schools and higher feeding rates in looser schools (Pitcher and Parrish 1993). The reduction in energetic requirements at low temperatures may allow walleye pollock to enhance antipredator strategies in an environment where the penalty in terms of foraging is minimal. Alternatively, or in addition, the reduction in nearest neighbor distances may also reflect the need to enhance the schooling aspect of predator evasion in a low-temperature environment where physiological constraints limit maximum escape velocities (Abrahams 2006) or predators are more abundant (Bailey 1989). In balancing the relative risks of starvation and predation, the schooling responses of pelagic walleye pollock to temperature variation may be functionally analogous to the change in diel rhythm of sheltering and cryptic species (Fraser et al. 1993; Hurst and Duffy 2005).

Implications for bioenergetics models

Applications of bioenergetics-based models have increased steadily in fisheries ecology. A long-recognized weakness of such models is the scarcity of detailed information on the behavior and activity levels of fish in situ (Boisclair and Leggett 1989; Rennie et al. 2005). In practice, the basal (or resting) metabolic rates of fish are measured in the laboratory and a multiplier is used to convert basal rates to rates of fish exhibiting "routine" activity levels in the wild. These "activity multipliers" are based on the investigator's intuition or determined through "solving" for the activity parameter to best fit the model to one set of laboratory or field data. The activity multiplier generally ranges from 1 to 3. Even in cases where metabolic rates have been measured across a range of swimming speeds, knowledge of swimming speeds exhibited in the wild, necessary for their application, is frequently lacking.

To date, most researchers have used a single activity multiplier across a the range of environmental conditions explored in a given application. However, several studies have demonstrated that behavioral responses to the environment conditions have important energetic consequences (Briggs and Post 1997; Hölker and Breckling 2002). A constant activity multiplier does not reflect a constant routine swim speed across temperatures. Rather, it implies that the energy expended on activity increases with temperature in parallel

with basal metabolic rate, implicitly assuming that routine swim speed increases with temperature (Briggs and Post 1997). For juvenile walleye pollock, Ciannelli et al. (1998, 2004) assumed an activity multiplier of 2.0, but the present experiments suggest the need for an activity multiplier that varies with water temperature.

A complete description of the bioenergetics of walleye pollock requires measurement of swimming metabolic rates as well as field validation of routine swim speeds. However, the available data are used to illustrate the significance of the observed patterns in routine swim speed on the activity multiplier (calculated for a 4.0 g, 80 mm TL walleye pollock). Temperature-dependent basal metabolic rates increase from 13.42 to 25.06 $\mu\text{g O}_2\cdot\text{min}^{-1}$ between 2 and 9 °C. To basal metabolic rates are added the costs of swimming to achieve routine metabolic rates. For this example, the cost of swimming is based on an assumption that the activity multiplier of 2.0 is accurate at 9 °C. Therefore, the isolated cost of routine swimming (i.e., excluding basal metabolism) at the observed speed of 93.1 $\text{mm}\cdot\text{s}^{-1}$ is 25.06 $\mu\text{g O}_2\cdot\text{min}^{-1}$. Measurements of the cost of transport have indicated that the energy required to move a fish at a specific velocity is generally constant across temperatures (Rome 1986). Therefore, the cost of swimming at 93.1 $\text{mm}\cdot\text{s}^{-1}$ at 2 °C would similarly be 25.06 $\mu\text{g O}_2\cdot\text{min}^{-1}$. However, routine swimming of this size walleye pollock was observed to be 48% faster at 2 °C than at 9 °C. Assuming that swimming costs increase linearly with velocity (likely to be true across speeds not requiring a gait change: Rome 1986), the isolated cost of activity for a walleye pollock at 2 °C would be 37.08 $\mu\text{g O}_2\cdot\text{min}^{-1}$. When added to the basal metabolic rate, this results in a total metabolic rate of 50.51 $\mu\text{g O}_2\cdot\text{min}^{-1}$, corresponding to an activity multiplier of 3.8. Hence, current models may be markedly underestimating the metabolic expenses and energetic requirements for growth of juvenile walleye pollock and species with similar thermal responses at low temperatures.

Implications for predator–prey encounter models

The behavioral responses of animals to environmental variation also have implications for food web models based on encounter rates between predators and their prey (Beauchamp et al. 1999). The increased routine swim velocity and straighter swim paths observed at low temperatures would be expected to increase encounter rates between walleye pollock and their predators. This effect would be most significant for encounters with slow-moving ambush predators (Petersen and DeAngelis 2000). Interestingly, while swim patterns would be expected to increase encounter rates at low temperatures, the observed schooling behaviors might serve to reduce encounters or increase survival following an encounter. Predator encounter rates reduce as the interfish distances and areal extent of the group decline. The reduction of distances between fish may also enhance the effectiveness of group responses when faced with an attack (Pitcher and Parrish 1993). The effect that environmental conditions, including temperature, have on the outcomes of predator–prey encounters is an area of study in need of clarification. Ultimately, a full understanding of the thermal effects on predator–prey encounter models requires incorpo-

ration of behavioral responses in both predator and prey and how they influence both encounters and outcomes.

Understanding individual and group behavior is a critical step in the approach of scaling up physiological factors to population- and community-level responses and one that has not received adequate attention. Juvenile walleye pollock responded to thermal variation by altering several aspects of routine behavior including swim speed, path, and school cohesiveness. These responses have major implications for our understanding of energy flows in the environment and do not conform to common assumptions based on physiological responses. It is unlikely that the thermal responses observed in juvenile walleye pollock, a semipelagic, subarctic zooplanktivore, will apply uniformly to species across a variety of thermal and foraging guilds. Future work should document species-specific behavioral responses that would allow the identification of broader patterns at work in structuring marine food webs.

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