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Temperature effects on osmoregulatory physiology of juvenile anadromous fish

Introduction

The anadromous life history entails early development in fresh water followed by movement to the ocean and subsequent return to fresh water for spawning. In contrast to other euryhaline fish, in which movement from fresh water to sea water is often frequent, anadromy usually results in seasonal movement of juveniles from fresh water to sea water. For many (but not all) anadromous species seaward migration occurs only once in an individual's life. Some anadromous salmonids have evolved a preparatory adaptation (known as the parr–smolt transformation or smolting) in which salinity tolerance and other adaptations for ocean life develop at the time of seaward migration (McCormick & Saunders, 1987; Hoar, 1988). The relative 'strength' and developmental stage of the parr–smolt transformation varies widely among salmonids. Although smolting is by definition strictly a salmonid phenomenon, similar preparatory adaptations may exist in other anadromous species (Youson, 1980) but to date their presence has not been widely examined.

For most anadromous species seaward migration is highly seasonal, often spring or fall, at a time of rapid temperature change. Under these conditions temperature may be an important factor for determining the timing of development and migration, and may impose further physiological challenge to animals whose osmotic tolerances are being altered. Here we will review the known effects of temperature on the osmoregulatory physiology of anadromous fish with emphasis and speculation on aspects that may affect the survival and distribution of these important fish.

Anadromous salmonids

Smolt development

Most anadromous salmonids undergo a distinct transformation prior to migration from fresh water to the ocean. Behavioural and physical

changes are accompanied by a series of physiological and biochemical alterations that are crucial to the successful rapid entry of smolts to the marine environment. The parr–smolt transformation is mediated by hormonal changes in response to environmental stimuli. Among the hormones that have been found to participate in smolting are cortisol, thyroid hormones, growth hormone and prolactin (see review by Hoar, 1988). In response to spring hormonal changes there is a proliferation of chloride cells on the gill lamellae (Langdon & Thorpe, 1985; Richman *et al.*, 1987), which are involved in salt extrusion in sea water teleosts (Foskett & Scheffey, 1982). Na^+,K^+-ATPase, the primary enzyme for excretion of Na^+ and Cl^-, has been shown to be located in chloride cells (Karnaky *et al.*, 1976; McCormick, 1990). The specific activity of Na^+,K^+-ATPase increases during the parr–smolt transformation coincident with the onset of migration and the development of saltwater tolerance in several salmonid species (McCormick & Saunders, 1987).

Timing of the parr–smolt transformation is regulated by seasonal changes in environmental variables, especially cyclical variations in photoperiod and temperature. Early experiments demonstrated that photoperiod was the primary environmental factor controlling timing of the parr–smolt transformation (see reviews by Wedemeyer, Saunders & Clarke, 1980; Hoar, 1988). Seasonal changes in coloration and saltwater tolerance can be accelerated or delayed by manipulating photoperiod. Although photoperiod plays a pivotal role in the timing of smolting, there is also evidence that water temperature influences the timing and onset of smolting. For many salmonids the parr–smolt transformation is size dependent. Since temperature is an important factor in determining growth rates in salmonids it will directly affect the age at which smolting occurs. Temperature may also act directly as a cue for smolting and the onset of migration. We will examine evidence from the literature for these roles of temperature in affecting the initiation and timing of smolting in salmonids.

Temperature effects on growth

Achieving a minimum size appears to be necessary before smolting can occur (Clarke, Shelbourn & Brett, 1978; Thorpe *et al.*, 1980; Hoar, 1988). The minimum size for smolting is species-specific, and Clarke (1982) reported ranges from 10 g in coho salmon to greater than 50 g in steelhead trout. Growth is therefore important for smolt development, as higher water temperatures generally result in greater growth rates until an optimal temperature is exceeded (Brett, Shelbourn & Shoop, 1969).

The benefit of rearing in warmer water on smolt production has been clearly demonstrated for Atlantic salmon where considerable differences in growth rates result in a bimodal size distribution within populations (Thorpe, 1977; Thorpe *et al.*, 1980). The upper mode (UM) of the population exhibit a growth spurt in early autumn, while the lower mode (LM) of the population has a reduced appetite leading to lower growth rate and requires an additional year in fresh water before undergoing the parr–smolt transformation (Metcalfe & Thorpe, 1992). In general, the better the opportunity for growth in the spring and summer, the higher the percentage of fish that enter the UM and smolt the following spring (Thorpe, 1994).

An overall increase in water temperature of rivers due to global warming may benefit many stocks of fish due to greater growth opportunity. In northern latitudes increased growth will shorten the duration of river life and reduce mortality (Power & Power, 1994). Acceleration of growth and smolt production have already been documented in streams where water temperatures have increased due to removal of overhead cover (Holtby, 1988) or discharge of thermal effluent (Thorpe *et al.*, 1989). In southern latitudes, increases above optimal temperature for growth during the summer may lead to a decline in growth and smolt production. The consequence of decreased growth is longer river life, greater parr density and increased exposure to density-dependent mortality (Power & Power, 1994). Consequently, global warming will be beneficial if it brings the fish closer to its optimal temperature and deleterious if it raises temperature beyond the optimum.

Temperature effects on smolting

Warmer rearing temperatures during the late winter and spring have been demonstrated to advance the timing of the parr–smolt transformation in coho salmon (Zaugg & McLain, 1976) and Atlantic salmon (Solbakken, Hansen & Stefansson, 1994). We have used data from a number of studies on Atlantic salmon to model the date at which peak gill Na^+,K^+-ATPase activity is observed as a function of mean water temperature and plotted this relationship in Fig. 1a. Data were included from experiments that maintained fixed or ambient (seasonally changing) temperature regimes and natural or simulated natural photoperiod. Warmer rearing temperature significantly advanced the date of peak gill Na^+,K^+-ATPase activity, with an estimated 5 week difference in peak levels when mean daily temperature is increased from 2 to 10 °C. Another approach to examining the role that temperature plays on increasing development rate of smolting is to plot maximal gill Na^+,K^+-ATPase activity as a function of degree days, the accumulated
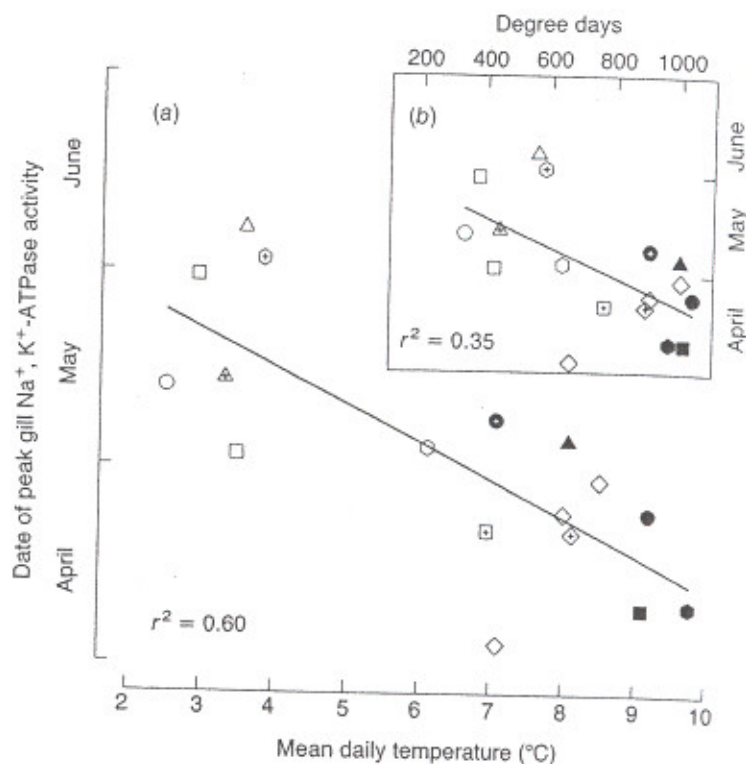
Fig. 1. (a) Effect of mean water temperature on the date of maximal Na+,K+-ATPase activity in Atlantic salmon smolts. Mean water temperature was calculated from 1 January to the peak of Na+,K+-ATPase activity. Data for this analysis included studies conducted at ambient (seasonally changing) and constant temperatures. (b) The cumulative degree days experienced until maximal Na+,K+-ATPase activity for the same data as shown in (a). Degree days are calculated as the additive daily temperatures experienced since 1 January to the peak in gill Na+,K+-ATPase activity measured in each study. First order regression lines are shown on each plot. Symbols represent the following studies and conditions: Atlantic salmon reared at ambient (increasing) temperature (⬦, Boeuf & Prunet, 1985); ambient temperature (◇, Boeuf *et al.*, 1985); ambient temperature (△, Duston *et al.*, 1991); 6–8 °C (◓, McCormick *et al.*, 1987); 10 °C from 9 January (●) or ambient temperature (○, S. McCormick *et al.*, unpublished data); 10 °C from early January (■), ambient temperature (□) or ambient temperature advanced 6 weeks (⊡, S. McCormick, unpublished data); ambient temperature (⊕, Olsen *et al.*, 1993); and ambient temperature (○) or 12 °C from 6 February (●, Solbakken *et al.*, 1994).

daily temperature in degrees Celsius (Fig. 1*b*). If smolting was strictly temperature dependent, degree days to the peak in gill Na^+,K^+-ATPase activity would be constant and independent of date. From this relationship, however, it is clear that at warmer temperatures more degree days are required to achieve an advance in timing of peak gill Na^+,K^+-ATPase activity. This limited capacity of temperature to accelerate smolting supports previous work indicating that photoperiod is the primary environmental factor driving the parr–smolt transformation.

Although increases in rearing temperature will accelerate smolt development, an upper temperature exists for successful smolting. This range, however, differs from that for growth. Rearing temperatures of 17.5 °C in sockeye salmon impaired smolt development, whereas a lower temperature (10 °C) resulted in higher seawater tolerance (Clarke *et al.*, 1978). Steelhead trout reared at 6.5 or 10 °C showed a 2-fold increase in gill Na^+,K^+-ATPase activity in March, whereas, fish reared at 15 or 20 °C showed no increase in gill Na^+,K^+-ATPase activity (Adams, Zaugg & McLain, 1973). However, in Atlantic and coho salmon, higher temperatures (16–20 °C) resulted in normal increases in gill Na^+,K^+-ATPase activity, but these decreased rapidly after the peak (Johnston & Saunders, 1981; Zaugg & McLain, 1976) (see section on Loss of smolt characteristics). The temperatures found to suppress smolting in these species are near or less than the optimum temperature for growth (Fig. 2). Different temperature optima exist for development of seawater tolerance and for growth. This does not necessarily indicate a 'conflict' between the two as smolting is a winter/spring phenomenon and temperatures for optimal growth will occur later in the year.

Seasonal changes in temperature as a stimulus for smolting

Increasing day-length, in combination with increasing temperature, is a stronger stimulus to smolting than each alone, as shown by increases in gill Na^+,K^+-ATPase activity (Muir *et al.*, 1994) and migration rate (Wagner, 1974; Muir *et al.*, 1994). Photoperiod manipulation at constant temperature, however, still produces smolts (see Hoar, 1988), indicating that seasonal changes in temperature are not crucial. In the absence of a photoperiod stimulus, the evidence for temperature directly stimulating smolting is equivocal. There was no significant effect on smolting in sockeye reared under increasing (7–13 °C), constant (10 °C) or decreasing (13–7 °C) temperature regimes (Clarke *et al.*, 1978). Temperature raised in February from 5 to 12 °C resulted in earlier development of saltwater tolerance in Atlantic salmon compared with controls held at ambient water temperature (5–6 °C) (Solbakken *et al.*, 1994).
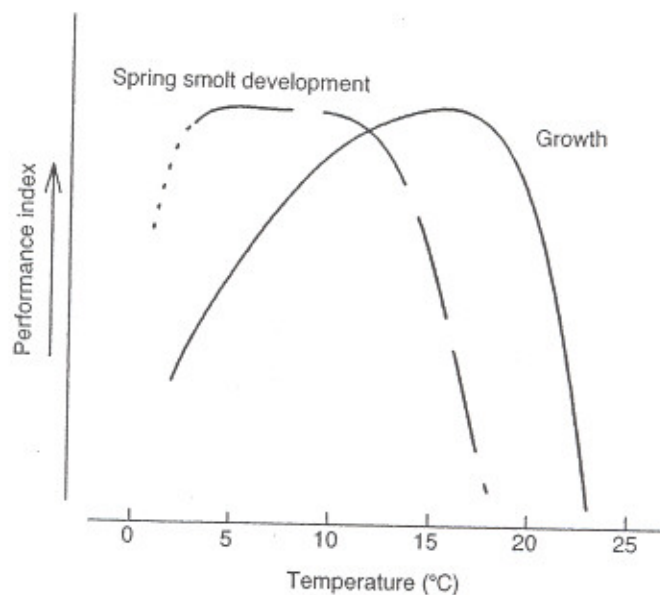
Fig. 2. A theoretical relationship between water temperature, smolt development and growth. The growth curve was modified from that of Brett *et al.* (1969) and is typical for salmonids. An optimal temperature for growth exists, but is greater than the optimal temperature for smolting. At temperatures that favour smolt development, an increase in temperature will accelerate the parr–smolt transformation as shown in Fig. 1. At temperatures where smolt development is impaired, peak gill Na^+,K^+-ATPase activity levels and saltwater tolerance are reduced or occur only transiently.

McCormick *et al.* (1987, 1989) found that exposure to continuous light inhibited the increase in salinity tolerance and gill Na^+,K^+-ATPase activity that normally occur in the spring. In these studies, water temperature during the spring remained constant (6–8 °C). In contrast, Atlantic salmon reared in constant light with seasonally changing water temperature that increased rapidly in late May (2–12 °C) showed typical smolt characteristics, with marked silvering, sea water tolerance and high Na^+,K^+-ATPase activity (Staurnes, Sigholt & Gulseth, 1994). These limited studies indicate that water temperature may be a cue for development of saltwater tolerance in juvenile Atlantic salmon in the absence of a photoperiod stimulus.

Temperature may also play an important role in stimulating behavioural changes associated with smolting. In Atlantic salmon, the start of migration has been found to be controlled by a combination of rate of increase in temperature and absolute temperature in the river during the spring (Jonsson & Ruud-Hansen, 1985). Timing of chinook salmon migration is related to water temperature, with 7 °C appearing to be a thermal threshold for migration (Raymond, 1979). Temperature may not be the only factor stimulating downstream movement of smolts, as river discharge is linked to migration of Atlantic salmon (Solomon, 1978) and steelhead trout (Raymond, 1979).

Although winter temperatures are unlikely to exceed an upper thermal limit for successful smolting, temperatures high enough to impair smolting may be reached in the spring. Water temperatures above 12 °C in steelhead (Adams *et al.*, 1973) and 17 °C in sockeye (Clarke *et al.*, 1978) are detrimental for smolting due to suppressed increases in gill Na^+,K^+-ATPase activity and impaired development of salinity tolerance. If global warming causes an overall 2 °C increase in temperature or shifts the spring increase in temperature to an earlier date, the onset of smolting may be advanced. Conducting experiments where temperature increases earlier or is moderately elevated above ambient river temperature (e.g. 2 °C) throughout the winter and spring is essential to understand fully impacts of global warming on physiological changes related to the parr–smolt transformation in juvenile salmonids.

Loss of smolt characteristics

Increases in salinity tolerance that occur during smolting are known to be reversible; fish that are maintained in fresh water beyond the period of normal spring migration lose their elevated capacity for hypo-osmoregulation and growth in sea water (Folmar *et al.*, 1982; McCormick & Saunders, 1987; Hoar, 1988). Although exhaustive studies on the environmental factors that might affect loss of smolt characteristics have not been conducted, studies to date clearly indicate that higher temperatures will increase the rate at which these characters are lost. Zaugg and McLain (1976) found that coho salmon previously reared at 6 or 10 °C experienced increasingly rapid losses of gill Na^+,K^+-ATPase activity upon exposure to higher temperatures (15 or 20 °C). Juvenile steelhead exposed to 13 °C for 20 days at the peak of smolting had lower gill Na^+,K^+-ATPase and reduced migratory behaviour compared with fish maintained at 6 °C (Zaugg & Wagner, 1973). Photoperiod can also influence this process: exposure of masu

salmon to short photoperiod increased the number of fish showing morphological indications of loss of smolt characteristics (Kurokawa, 1990).

Recent studies have found that as in Pacific salmon, Atlantic salmon respond to elevated temperatures with reductions in salinity tolerance and gill Na^+,K^+-ATPase activity (Duston, Saunders & Knox, 1991; S. McCormick, M. O'Dea & J. Carey, unpublished data). Figure 3 presents a summary of these data, demonstrating a relationship between degree days experienced by smolts and loss of gill Na^+,K^+-ATPase activity. Treatment groups in these studies included constant temperature (10, 13 and 16 °C) and ambient conditions (seasonal change in water temperature) under which temperature increased rapidly in spring. This analysis indicates that after the peak in gill Na^+,K^+-ATPase activity there is a period of stability (around 100 degree days) followed by a period of rapid decline. There is no indication from this analysis that changes experienced under ambient temperatures were qualitatively different than constant temperature, nor does it appear that higher temperatures have a greater effect than that predicted by degree days.

Research on Atlantic salmon reared in the wild indicates that loss of smolt characteristics also occurs under some conditions in naturally migrating smolts. As part of a restoration programme in northeastern USA, Atlantic salmon have been stocked into tributaries as fry where they remain for 2–3 years before migrating as smolts. In the Connecticut River, near the historical southern distribution of Atlantic salmon, smolts generally migrate in the mainstem of the river from early May to early June. Migrating smolts captured early in May at a dam bypass facility 198 km from the ocean had high salinity tolerance and gill Na^+,K^+-ATPase activity (S. McCormick *et al.*, unpublished data). Fish sampled in late May had significant reductions in both salinity tolerance and gill Na^+,K^+-ATPase activity. Earlier reductions in gill Na^+,K^+-ATPase occurred in 1993 when river temperatures were warmer relative to the migratory period in 1994. In addition, fish captured in early May and maintained in river water under laboratory conditions exhibited a period of stable salinity tolerance and gill Na^+,K^+-ATPase followed by a decline. As in studies on laboratory and hatchery fish, this decline is correlated with the degree days experienced by these fish (Fig. 3). Because these declines in salinity tolerance and gill Na^+,K^+-ATPase activity were detected 198 km from the mouth of the Connecticut River, it seems likely that further losses would occur in the time required to complete migration to the ocean (probably a minimum of 7 days). Reductions in physiological smolt characters may result in decreased survival, growth and swimming performance in sea
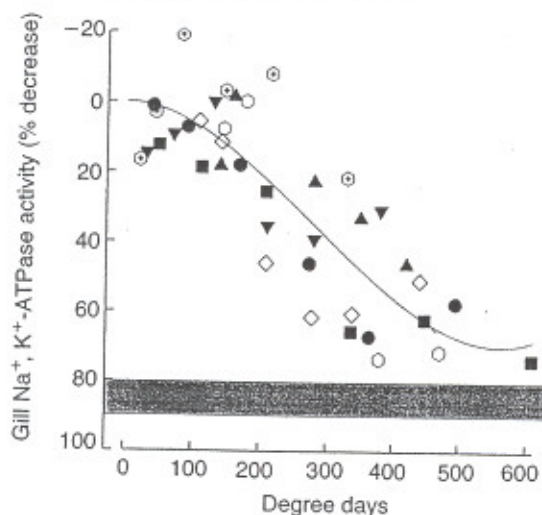
Fig. 3. Effect of degree days experienced on loss of gill Na$^+$,K$^+$-ATPase activity in Atlantic salmon smolts. Percentage loss of gill Na$^+$,K$^+$-ATPase activity is calculated as percentage change from peak levels between 20 April and 3 May. Degree days are calculated as the additive daily temperature experienced since peak gill Na$^+$,K$^+$-ATPase levels. Symbols represent the following conditions: laboratory-reared Atlantic salmon (Duston *et al.*, 1991) at 16°C (■), 13°C (●), 10°C (▼) and ambient (increasing) temperature (⊕); laboratory-reared Atlantic salmon (S. McCormick, unpublished data) at 10°C (▲) and ambient temperature (○) and Atlantic salmon reared in the wild, captured early in migration and maintained at ambient temperature (◇). Shaded bar represents levels of gill Na$^+$,K$^+$-ATPase typical of parr with low salinity tolerance. Line is a third-order regression forced to go through the origin, $r^2 = 0.70$.

water, increased predator susceptibility and reduced migratory behaviour (McCormick & Saunders, 1987; Hoar, 1988).

If scenarios of global warming which predict increases in river temperatures of 2°C are realized, temperature-related loss of smolt characteristics will have a negative impact on Atlantic salmon populations. Figure 3 indicates that Atlantic salmon have a period of 100–200 degree days in which to migrate without loss of gill Na$^+$,K$^+$-ATPase activity; a 2°C increase in average river temperature would decrease this period by 10–20%. Temperature increases greater than 2°C may occur through earlier and more rapid increases in spring temperature that may

accompany global warming (Hengeveld, 1990), resulting in even shorter periods for downstream migration. Although loss of smolt characters may be partly compensated by earlier migration from tributaries (since temperature appears to act as a migratory cue; Jonsson & Ruud-Hansen, 1985), the mainstems of rivers are likely to be more significantly affected by increases in air temperature (Meisner, 1990). Fish in long river systems may be more susceptible to loss of smolt characteristics due to inherently longer periods of migration. Other factors such as changes in food availability, growth rate, loss of rearing habitat and overall smolt production (Meisner, 1990; Mangel, 1994) must enter into overall considerations of the effects of global warming on anadromous salmonid populations.

Anadromous clupeids

Though details differ between species and geographic locations, the anadromous clupeids all possess a common life history in which spawning occurs in spring or early summer, larvae and juveniles grow for 1–6 months in rivers, lakes or estuaries and then migrate to the ocean in summer or autumn. In contrast to salmonids, little is known of the ontogeny of salinity tolerance in these species or even basic aspects of osmoregulatory physiology.

We have undertaken a preliminary investigation of the alewife (*Alosa pseudoharengus*) to examine survival and the response of gill Na^+, K^+-ATPase activity to changes in salinity and temperature. Juvenile alewives were collected from Lake Utopia, New Brunswick, Canada in September and maintained in 1 m diameter tanks with flow-through sea water (24–33 ppt) with seasonally varying temperature (13 °C in September, 5 °C in January). Between January and April fish were acclimated to 5 or 20 °C in either fresh water or sea water (28–30 ppt) over a period of one week. After 4–8 weeks, gill samples were taken and gill Na^+, K^+-ATPase activity was measured as outlined by McCormick *et al.* (1987). There were no mortalities except for fish acclimated to fresh water at 5 °C in which two of 10 fish died in the first week of exposure to 'full' fresh water. For alewives at 20 °C, gill Na^+, K^+-ATPase activity was approximately 4-fold higher for fish in sea water than those in fresh water (Table 1). Results were similar whether the activity was assayed at 5 or 20 °C. In contrast, fish acclimated to 5 °C had gill Na^+, K^+-ATPase activity in fresh water that was almost as high as fish in sea water. Gill Na^+, K^+-ATPase was 3-fold higher for alewives at 5 °C in fresh water than for those at 20 °C in fresh water. Higher levels of gill Na^+, K^+-ATPase in cold-acclimated freshwater fish have been described previously for pupfish (*Cyprinodon salinus*), roach

Table 1. *Gill Na$^+$,K$^+$-ATPase activity in freshwater- and seawater-adapted alewife acclimated to 5 or 20 °C.* Crude homogenates were assayed at both 5 and 20 °C. Values are mean ± SE (*n* = 6–8 in each group). For each assay temperature, two-way ANOVA indicated a significant effect of salinity (*P* < 0.001), no effect of temperature (*P* > 0.1), but a significant interaction (*P* < 0.01). *, significant difference from the freshwater, 20 °C group (*P* < 0.05, Student–Newman–Keuls test).

		Na$^+$,K$^+$-ATPase activity	
	Acclimation temperature	Fresh water	Sea water
Assay temperature 20 °C	20 °C	7.3 ±1.6	27.2*±1.5
	5 °C	18.9*±0.8	22.5*±3.5
Assay temperature 5 °C	20 °C	1.0 ±0.3	5.2*±0.4
	5 °C	3.0*±0.1	4.4*±0.7

(*Rutilus rutilus*) and Arctic char (*Salvelinus alpinus*) (Stuenkel & Hillyard, 1980; Schwarzbaum, Wieser & Niederstatter, 1991), but this response does not occur in all species (Paxton & Umminger, 1983). Higher gill Na$^+$,K$^+$-ATPase following cold acclimation may compensate for the lower transport capacity of enzymes at low temperatures (Q$_{10}$ effect). Absence of increased gill Na$^+$,K$^+$-ATPase following cold acclimation of some species may reflect their ability to affect ion transport by other mechanisms such as membrane fluidity and ion permeabilities (Schwarzbaum, Wieser & Cossins, 1992). This may also explain why gill Na$^+$,K$^+$-ATPase does not increase in alewives following cold acclimation in sea water.

The mortality of alewives in fresh water at cold temperatures is consistent with the findings of Stanley and Colby (1971) in which fresh water alewives exposed to 3 °C experienced greater loss of plasma and muscle sodium than fish at higher temperatures. Alewives at 3 °C in sea water also experienced ionic perturbations (high levels of plasma and muscle sodium). These authors noted that ion regulation was not significantly affected by temperatures up to 31 °C in either fresh water or sea water, indicating that in their normal geographic range osmotic tolerances of alewives are not likely to be negatively affected by global warming.

We have also examined the development of hypo-osmoregulatory ability in another anadromous clupeid, the American shad (*Alosa sapidissima*), an abundant species indigenous to the eastern coast of

the United States and Canada. The autumn emigration of juvenile shad peaks when declining river temperatures reach 14–9 °C (Leggett & Whitney, 1972; O'Leary & Kynard, 1986). These temperature-related behaviours may reflect a preference pattern due in part to physiological constraints as mortality of shad occurs at temperatures below 4 °C (J. Zydlewski & S. McCormick, unpublished data).

Information on the ontogeny of salinity tolerance of young American shad has been sparse and conflicting. Leim (1924) reported that shad eggs are able to hatch and survive through the yolk-sac larva stage in brackish water but are unable to develop in salinities significantly greater than isosmotic. Tagatz (1961) reported high mortality of juvenile shad (5.6–7.9 cm fork length) in isothermal direct transfers to 33 ppt sea water at 21 °C, and complete mortality when accompanied by a decrease in temperature to 13 and 7 °C. Due to this apparent lack of hypo-osmoregulatory ability, analogies were drawn between development of salinity tolerance in shad and the salmonid parr–smolt transformation. Although Chittenden (1973) found 100% survival in isothermal (17 °C) salinity transfers of juvenile shad (4.4–6.1 cm), these fish were transported in 5 ppt sea water, arguably allowing acclimation. Recent work in our laboratory has shown that tolerance of young shad to sea water develops long before the migratory period in the Connecticut River (Zydlewski & McCormick, 1996). In this study young shad were reared from eggs and subjected to direct transfers from 0 ppt fresh water to 35 ppt sea water at approximately 10 day intervals. Development of tolerance to full strength sea water was found to be coincident with the completion of the larval–juvenile metamorphosis (3–5 weeks after hatching). This period of development is characterized by the formation of gill filaments. Salinity tolerance developed 3 months prior to the peak of migration. While gill Na^+,K^+-ATPase activity is initially low in fish with good hypo-osmoregulatory ability, exposure of juvenile shad to sea water elicits an increase in gill Na^+,K^+-ATPase activity (Zydlewski & McCormick, 1996).

The ability to hypo-osmoregulate early in their development is consistent with their variable life history, as the adults may spawn within tidal influence hence exposing the young to elevated salinities well before their seaward migration. Early development of hypo-osmoregulatory ability possibly augments fresh water nursery areas during years of high juvenile populations (Crecco, Savoy & Gunn, 1983). Early migration in some rivers may reflect a 'spread the risk' migration strategy. The fact remains, however, that most young shad utilize fresh water habitat as a nursery ground and are required to

integrate developmental and/or environmental information for a success-ful autumn seaward migration.

One significant physiological change observed in migrating juvenile shad is a loss of hyperosmoregulatory ability. During the course of migration plasma chloride levels decline more than 20%, from 113 mM to less than 90 mM over a 5 week period, coincident with the decline in river temperatures (J. Zydlewski & S. McCormick, unpublished data). Juvenile shad held in fresh water and subjected to a decline in temperature corresponding to that of the river also exhibited decreases in plasma chloride, falling from 117 mM to 38 mM over 2 months. Juvenile shad cease feeding between 13 and 12 °C and high mortality was observed as temperature declined further. Plasma chloride levels and survival of shad maintained in fresh water at 23–24 °C also decrease, but the rate of decline is lower than in shad in cooler, ambient fresh water. High mortality of shad maintained in fresh water (16–20 °C) past the migratory period has also been observed by Howey (1985). It seems likely that high mortalities in these studies were caused by loss of hyper-osmoregulatory ability. Shad acclimated to 32 ppt sea water do not exhibit perturbations in plasma chloride at either constant (23–24 °C) or decreasing temperatures, and no mortality was observed in either seawater group until temperatures fell below 4 °C in the declining temperature group.

Pre-migratory young shad in the Connecticut River maintain rela-tively low levels of gill Na^+,K^+-ATPase, and there is up to a 3-fold increase in enzyme activity during migration (J. Zydlewski & S. McCor-mick, unpublished data). This increase is probably not related to salinity tolerance (as measured by survival after a 35 ppt sea water challenge) which developed earlier, though we cannot rule out the possibility that there are further, undetected increases in salinity tolerance during migration. Increased gill Na^+,K^+-ATPase activity during migration may be related to decreasing hyper-osmoregulatory ability or cold acclim-ation. The rate of increase in gill Na^+,K^+-ATPase, like the decline in plasma chloride, is also hastened by declining water temperature in fresh water.

Both alewives and shad appear to have increased mortality at tem-peratures below 4 °C in both fresh water and sea water. Shad lose their capacity to regulate ions in fresh water at the end of the migratory period even at high temperatures, and cannot be reintroduced into fresh water from sea water after the migratory period. This is not the case for alewives, which can be reintroduced into fresh water after the migratory period. This difference in loss of hypo-osmoregulatory ability may explain why only one population of non-anadromous, freshwater

shad has been reported (in California, outside its native range; Lambert *et al.*, 1980), whereas non-anadromous populations of alewives are relatively common. The loss of hypo-osmoregulatory ability in shad has a partial parallel in smolting salmonids in which greater rates of sodium exchange have been reported for smolts in fresh water (Primmett *et al.*, 1988). Although most studies indicate that smolts do not lose their capacity to regulate ions in fresh water during migration (McCormick & Saunders, 1987), they may expend more energy counter-acting increased ion effluxes in fresh water and maintaining mechanisms for ion regulation in both fresh water and sea water. Whether physio-logically constraining as occurs in shad, or energetically demanding as potentially occurs in salmon, this osmoregulatory conflict of anadromy may be more widespread than currently appreciated.

A perturbation in the annual temperature regime may cause conflict-ing messages for the physiological processes of migration in juvenile clupeids. If the physiological changes discussed above are linked to migratory behaviour, as is likely, an increase in global temperature would extend the length of time during which juvenile shad may reside in fresh water by delaying migration. If the summer growing season currently limits the northern distribution of shad, temperature pertur-bation could result in northern range expansion. In currently populated rivers, a delay of migration could result in a larger average size of migrants, which might be beneficial to survival. Although the impact of increased temperature on food resources and predators is difficult to predict, from a strictly physiological viewpoint global warming may have positive effects on anadromous clupeids by allowing northern range expansion and increased growth opportunities in fresh water.

Other anadromous fishes

Lamprey

Many species of lamprey, including the sea lamprey (*Petromyzon marinus*), European river lamprey (*Lampetra fluviatilis*) and Australian lamprey (*Mordacia mordax*), are anadromous. Marine adults enter fresh water to spawn, and the eggs hatch into benthic, filter-feeding ammocoete larvae. These larvae remain in fresh water for 3–7 years until metamorphosing into juveniles. Metamorphosis is highly synchron-ized within populations and is marked by morphological and physiologi-cal changes (Purvis, 1980; Potter, 1980) followed by migration to the ocean. The main cue for seaward migration is water flow; consequently the migration is not precisely timed and may be protracted through the autumn into the next spring (Potter, 1970).

Lamprey metamorphosis is size dependent. Warmer rearing temperatures, except where optimal temperatures are exceeded, accelerate growth of ammocoetes and lower the mean age of metamorphosis (Potter, 1980). Low temperatures inhibit metamorphosis in ammocoetes of similar size and age. The proportion of metamorphosing sea lamprey is 11-fold higher in ammocoetes reared at 20–21 °C versus 7–11 °C from July to September (Purvis, 1980). Increased spring temperature appears to be an important cue for metamorphosis. Elevated winter temperatures (22–25 vs 15 °C) advance the transformation 4–5 weeks in Australian lamprey (Potter, 1970). The rate of temperature change and increasing day length may also be important cues for metamorphosis (Potter & Beamish, 1977; Eddy, 1969).

Sea water tolerance develops upon completion of metamorphosis (Morris, 1980; Beamish, 1980). This leads to the supposition that the factors that modify the timing and incidence of metamorphosis should also affect osmoregulatory performance; however, the relevant studies have not been done. Similar to the situation in teleosts, the gills, gut and kidney of lamprey are important organs of osmoregulation (Beamish, 1980; Youson, 1980). Mitochondrion-rich chloride cells are present in the gills of metamorphosed sea lamprey, and these cells enlarge and gill Na^+,K^+-ATPase activity increases after sea water acclimation. Studies on the effects of temperature on these and other osmoregulatory parameters are required to characterize adequately the effect of temperature on osmoregulation.

Elevated temperatures, as might occur from global warming, are likely to influence metamorphosis in three major ways. Increased growth will lower the mean age of ammocoetes at metamorphosis except where thermal growth optima are exceeded. Elevated temperatures would also increase the proportion of metamorphosing individuals in higher latitudes. Both of these effects would shorten river residence time of ammocoetes, and shift the species ranges to higher latitudes. Additionally, earlier rising spring temperatures will advance the timing of metamorphosis. Assuming the development of hypo-osmoregulatory ability is linked to metamorphosis, this would allow for earlier seaward emigration.

Sturgeon

The shortnose (*Acipenser brevirostrum*), Atlantic (*A. oxyrhynchus*) and white sturgeon (*A. transmontanus*) are anadromous, using seawater habitat to different degrees. In general, juvenile sturgeon migrate seaward over a period of years (Vladykov & Greeley, 1963). Atlantic sturgeon may

remain 1–6 years in fresh and brackish water before migrating to the ocean for an extended period of time (Smith, 1985). The riverine movements of young sturgeon are linked to temperature and include seasonal use of estuarine habitat, but the patterns are quite complex and poorly understood. A general effect of global warming might be a change in the use of the estuarine environment by juveniles.

Studies on the ontogeny of seawater tolerance in sturgeon are limited. Survival of white sturgeon (0.4–56 g) in 15 ppt sea water increases with size, but even the largest juveniles tested show ion perturbations and no survival in 25 ppt sea water (McEnroe & Cech, 1985). It is not clear whether sturgeon develop hypo-osmoregulatory ability during a distinct phase of development or if osmotic tolerance develops evenly with increasing size. Studies which delineate the ontogeny of salinity and thermal tolerances (and preferences) of juvenile sturgeon are required before the impact of global warming on sturgeon juveniles can be predicted.

Striped bass

Striped bass (*Morone saxatilis*) is a commercially and recreationally important anadromous fish indigenous to the Atlantic coast of North America. Adults spawn in fresh and brackish water along the coast at 10–25 °C in the spring. Larval development is temperature sensitive, with an optimum for hatching and survival occurring at 18 °C and malformations occurring above 24 °C (Doroshev, 1970). Optimal salinity for larval survival is 2–3 ppt (Kane, Bennett & May, 1990). Salinity tolerance develops early (5 day old striped bass survive in 20 ppt sea water) and is relatively insensitive to temperature (Otwell & Merriner, 1975). However, significant mortalities occur if transfer to sea water is accompanied by a large change in temperature, either an increase or decrease. Juveniles (50–100 g) acclimated to sea water maintain plasma ions close to that of freshwater controls, and gill Na^+,K^+-ATPase activity is unaffected by seawater acclimation (Madsen *et al.*, 1994).

Extreme temperature changes are more detrimental to young striped bass than are salinity changes. The ability to hypo-osmoregulate appears to be affected only when increases in salinity are accompanied by considerable temperature changes and mortalities in these situations probably reflect thermal tolerance limits. While global warming may affect striped bass, the effect is not likely to be through osmoregulatory abilities.

Summary and projections

There are clear differences in the effect of temperature change on osmoregulatory physiology in different families of anadromous fish.

and it can be presumed that responses are likely to be species specific. The possibility that adaptations related to thermal physiology and behaviour may even be population specific is particularly important to consider for anadromous fishes in which reproductive isolation may occur. For these reasons it is difficult to make generalized statements about responses of anadromous fish to global warming. It will be important to examine and consider each species to determine precisely the impact of temperature change in the aquatic environment.

The effects of increased temperature and altered seasonality on anadromous salmonids will be complex. The number of smolts may be increased through greater growth opportunities in fresh water, but there will be a complex relationship between higher growth rates (more smolts) and lethal summer temperatures (fewer smolts). Although photoperiod is the primary factor regulating the timing of smolting, higher temperatures will result in earlier development of salinity toler-ance. In addition, higher temperatures also result in more rapid losses of salinity tolerance and gill Na^+,K^+-ATPase activity, and these losses are directly related to the degree days experienced by downstream migrants. Temperature-related loss of smolt characteristics will have a negative impact on Atlantic salmon populations by shortening the period for successful downstream migration. Overall, the negative impacts of temperature on anadromous salmonids will be greatest in the southern range of their distribution; positive effects may occur in their northern range.

In spite of recent research, less is known of the osmoregulatory physiology of anadromous clupeids than that of salmonids. In American shad, high salinity tolerance develops at the time of larval–juvenile metamorphosis (July), several months before the peak of downstream migration (October). At the end of the migratory period ion losses occur in laboratory-reared and wild fish, coincident with increased gill Na^+,K^+-ATPase activity. Ion losses are delayed in fish maintained at elevated (summer) temperature, indicating that higher autumn tempera-tures will permit a longer period of fresh water residence for shad. Currently there is too little known about other anadromous species to predict the effects of global warming on osmoregulatory physiology. More research is needed on all aspects of the development of salinity tolerance and changes that occur during migration.

It would appear that global warming may have its greatest and most complex effect on anadromous salmonids. This may be the result of their longer period of residence in fresh water and complex developmen-tal changes, but may also reflect our greater knowledge of this group of fish. In spite of this knowledge, there are several areas that require more research for salmonids and all anadromous species. Information

on the physiological changes that occur in anadromous fish under different thermal regimes in nature are necessary to confirm and extend laboratory studies. Connecting physiological responses with behavioural changes (such as migratory speed) and overall survival and return rates will increase our understanding of the environmental factors that limit migratory fish populations.

Unfortunately for anadromous fish populations, global warming is not the only anthropogenic source of environmental perturbation. Obstacles to migration such as dams and water diversions not only present a physical hindrance to migration but can alter water temperatures (and other aspects of water quality). The effects of global warming on water temperatures may be exacerbated in rivers with dams, and delays in migration imposed by dams may increase the detrimental effects of high temperature in both juvenile and adult fish. Pollution effects may also be greater at higher temperatures. Predicting the effects of global warming will necessitate incorporation of many environmental changes, both natural and manmade.

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