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Climate change and the “green” energy paradox: the consequences for twaite shad *Alosa fallax* from the River Severn, England

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Abstract

The River Severn, U.K., represents the northern limit of the known spawning distribution of twaite shad *Alosa fallax*. Temperature influences both the timing of the spawning migration into fresh water and spawning success in terms of year class strength. A stock recruitment model with a temperature component was used to estimate the effect of an increase in temperature predicted by climate change projections on population persistence and distribution. An increase of 1°C and 2°C above the current mean water summer (June – August) temperature of 17.8°C was estimated to result in a 3- and 6-fold increase in the population, respectively. Climate change is also predicted to result in an earlier commencement to their spawning migration into fresh water. The model was expanded to investigate the impact of any additional mortality that might arise from a tidal power barrage across the Severn Estuary. Turbine mortality was separated into two components; 1) juvenile (pre-maturation) on their outmigration during their first year and on their first return to the river to spawn and 2) post-maturation mortality on adults on the repeat spawning component of the population. Under current conditions decreasing pre-maturation and post-maturation survival by 8% is estimated to result in the stock becoming extinct. It is estimated that an increase in mean summer water temperature of 1°C would mean that survival pre and post-maturation would need to be reduced by ~10% before the stock becomes extinct. Therefore, climate change is likely to be beneficial to populations of *A. fallax* within U.K. rivers, increasing survival and thus, population persistence.

Key words: stock and recruitment; temperature.

INTRODUCTION

How species respond to climate change is largely unknown. Changes in distribution, phenology and abundance have been described (Hughes, 2000; Parmesan, 2006) and can have positive or negative consequences for the persistence of a species. Not surprisingly, commercially/economically important species and those species that are significantly below their reproductive potential have been of primary focus when attempting to understand responses to climate change.

As part of the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol, industrial nations agreed to reduce their greenhouse gas emissions by an average of 5% (compared to 1990 levels) by 2012 (Liverman, 2008). To achieve this, a reduction in energy consumption coupled with an increase in energy production from renewable sources is necessary (Mitchell, 2006). Renewable energy sources include wind, sunlight, geothermal heat, tides and rain. Such sources are considered as “green” energy sources as they are continually replenished (renewable) and, therefore, generally not considered to have an adverse impact on the environment. However, the process(es) required to harness some sources of renewable energy can have deleterious effects on the surrounding environment, e.g. wind farms affecting birds (Exo *et al.* 2003) and hydropower schemes impacting on fish (Schilt, 2007).

In the U.K., tidal power has the potential to produce at least 10% of the country’s electricity needs, of which 4.4% of the supply could come from a tidal power barrage across the Severn Estuary (SDC, 2007). Such a scheme would make a considerable contribution to the U.K. Government’s aspiration that 20% of the national electricity supply should come from renewable sources by 2020 (HMSO, 2007). However, the Severn estuary is subject to a number of national and international designations. It is classified as a Special Protection Area (SPA) for birds under the EU Birds Directive (Directive 2009/147/EC) and is a Special Area of Conservation (SAC) under the EC Habitats Directive (Council Directive 92/43/EEC) as are the rivers Wye and Usk which drain into the estuary. An initial assessment of the impact of a tidal barrage on the integrity of the SAC - a primary designation feature being twaite shad *Alosa fallax fallax* (Lacépède), indicated a risk of mortality sufficiently high to eradicate the stock (SDC, 2007). *A. fallax* has declined considerably in abundance throughout its geographic range (Baglinière & Elie, 2000; Aprahamian *et al.* 2003). For this reason, *A. fallax* has been listed under the international union for the conservation of nature (IUCN) World Red Data Book (IUCN, 2006), included in Appendix III of the Bern Convention (Anon., 1982) and incorporated into Annexes II and V of the EC Habitats Directive (Council Directive 92/43/EEC).

Throughout Europe there are several factors linked with the continued decline of *A. fallax* populations including; poor water quality (particularly in lower reaches and estuaries), habitat destruction as a result of flood defence and reengineering works or gravel extraction impacting on available spawning habitat (Aprahamian *et al.* 2003). However, perhaps the most significant impact is considered to be due to artificial barriers. Structures such as dams prevent adults from accessing spawning grounds and their impact may be exacerbated by overfishing as fish congregate and become easier to capture below obstructions (Baglinière & Elie, 2000).

In addition to those pressures, the possible impact of climate change must also be considered. In the U.K., self-sustaining populations of *A. fallax* are currently confined to rivers draining into the Bristol Channel of the west coast; rivers Severn, Wye, Usk and Tywi (Aprahamian & Aprahamian, 1990). These rivers represent the northern limit of the known spawning distribution of *A. fallax* (Aprahamian *et al.* 2003) in the U.K. Within these regions, the medium emissions scenario (U.K.CP09) predicts the central estimate of increase in mean summer air temperature to be 2.5°C by 2050, ranging from between 1.0°C and 4.6°C albeit with a wide range of uncertainty (Murphy *et al.* 2009).

The importance of temperature in regulating the behaviour and dynamics of alosine clupeids has been documented in several reviews (e.g., Baglinière *et al.* 2003, Limburg *et al.* 2003, Mettee & O'Neil, 2003, and Petersen *et al.* 2003). For *A. fallax* their distribution and abundance has been shown to be positively correlated with temperature (Lassalle *et al.* 2008, 2009). Spawning success varies between years with good recruitment associated with warm years (Holmes & Henderson, 1990; Aprahamian & Aprahamian, 2001). Similarly for *Alosa sapidissima* (Wilson), a positive correlation between year class strength (YCS – defined as a quantitative measure of abundance of a cohort) and two primary abiotic factors; flow and temperature (Marcy, 1976; Leggett, 1977; Crecco & Savoy, 1984), and secondarily related to the size of the spawning stock (Crecco *et al.* 1986) has been shown. Henderson & Brown (1985) also found that YCS for a landlocked population of *Alosa pseudoharengus* was determined by water temperature. Given the strong link between temperature and annual population success for several shad species, climate change is likely to play a major role in determining the persistence and distribution of *A. fallax* in U.K. rivers.

Alosa fallax is an anadromous species, entering the Severn Estuary in April to start the freshwater phase of their spawning migration (Aprahamian, 1981). The timing of their movement into the estuary appears related to temperature; peak immigration occurring at temperatures ranging between 10.6 and 12.3° C (Aprahamian, 1988). A close correlation between migration and temperature serves to minimise egg and larval mortality as well as increasing the probability of adult post-spawning survival (Leggett, 1985). Spawning occurs between May and July with June being the main month (Aprahamian, 1982). The juveniles are present in the estuary from July until they migrate seaward in the autumn (Claridge & Gardner, 1978; Aprahamian, 1988). A portion of the one-year-old fish re-enter the estuary in the spring before again migrating seaward in the autumn (Aprahamian, 1988).

The introduction of tidal barrages to generate energy can increase mortality rates for species that pass through the turbines as part of their migration (Stokesbury & Dadswell, 1991; Gibson & Daborn, 1995; Gibson & Myers, 2002). In the context of global warming and its ecological consequences (Hughes, 2000; Parmesan, 2006) temperature is expected to have a positive effect on the persistence of *A. fallax*, but in the Severn estuary any benefits that might arise from an increase in temperature (Holmes & Henderson, 1990; Aprahamian & Aprahamian, 2001) may be offset by an increase in mortality from the tidal barrage scheme. The aim of this study was two-fold; firstly, to quantify the change in population abundance that might arise from an increase in water temperature in line with current climate change predictions, and

secondly, what degree of additional mortality, as a result of barrage introduction, would be responsible for a decreasing population persistence under varying climate scenarios.

MATERIALS AND METHODS

STOCK

The adult population of *A. fallax* entering the Severn Estuary at the start of the freshwater phase of their spawning migration was sampled between 1979 and 1997. Counts of *A. fallax* were obtained from the catches of Atlantic salmon *Salmo salar* L. putcher net fishermen operating near Lydney on the Severn Estuary (51.689 N, 2.564 W) (Fig. 1) between 15th April and 15th August. The putcher rank consists of 650 conical shaped traps constructed from metal bar 6 mm in diameter, designed to sieve fish on both the flood and ebb tides, for details see Aprahamian (1981). Between 1979 and 1988 the size of the traps and their arrangement in the rank changed; after 1988 fishing effort was constant. The changes affected the size of the opening of the traps as opposed to the spacing of the bars and thus, their selectivity was considered not to be affected. The effect of the changes on fishing effort and the raising factors used to compare catches taken between 1979 and 1987 with those after 1987 are shown in Table 1. In 1982 no sampling was possible, as the putcher rank collapsed and for the years 1983 and 1984, no estimates of fishing effort were available. Sampling was conducted on a daily basis to ensure both tides were sampled, to avoid bias from variation in diurnal patterns of behaviour or catchability (Aprahamian, 1981).

Sampling was carried out between 15th April and 19th June, the main migration period through the estuary (Aprahamian, 1981). Samples of the catch or sub-samples (50 fish) of the catch if the number of fish caught exceeded 50, were taken in order to partition the run according to sex, age and spawning history. Age and spawning history were determined from analysis of scales (Baglinière *et al.* 2001). As the timing of the migration through the estuary differed between years (Aprahamian, 1988) the migration was divided up into eight periods (week) of between 13 / 14 tides and one of 18 tides. The latter was the first period and took account of the number of days required to install the putcher rank. The periods were ranked according to catch per unit effort (CPUE) and the top five periods used to calculate an index of the size of the spawning stock (mean catch per tide). This was because in some years no, or relatively few, samples were taken towards the end of the run. The proportion of the available tides sampled ranged from 5% to 67% (mean = 31% year⁻¹) and the number of fish aged ranged from 110 to 617 (mean 359 fish year⁻¹).

The CPUE (X) for each age class (i) was calculated separately for males and females as follows :

$$X_i = \sum_{j=1}^7 \sum_{k=1}^5 x_{ijk} 5^{-1} \quad (1)$$

Where:

x = mean catch of shad per tide of fish age i , spawning number j (spawning number 1 is a fish spawning for the first time or virgin spawner, spawning number 2 is a fish spawning for the second time it will have one spawning mark on its scale etc.) in period k .

To reduce the possibility of bias derived from sampling too few tides, the index was estimated using the change in abundance between successive age groups. Subjectively a value of 10% of the 127 tides available between 15th April and 19th June was taken as the threshold. In those years where < 10% of the tides were sampled (1979, 1982-1984), the index was calculated as follows:

$$\Delta_{ij} = \text{Log}_e (X_{ij(t)}) - \text{Log}_e (X_{ij(t+1)})$$

where :

Δ_{ij} = Instantaneous rate of change between successive age groups for fish of a particular age (i) and spawning number (j).

X_{ij} = the mean catch per tide for the five periods, of fish of a particular age (i) and spawning number (j).

t = year.

In 1979, CPUE was back calculated using the 1980 CPUE data and the instantaneous rate of change between the years 1980 and 1981. For the period between 1982 and 1984, the CPUE for fish age 6 years and older in 1982, 7 years and older in 1983 and for fish aged 8 years and older from 1984 were estimated from the 1981 CPUE data and the instantaneous rate of change between the years 1980 and 1981. The other age classes were back calculated from the 1985 CPUE data and the instantaneous rate of change between the years 1980 and 1981 and between 1985 and 1996. This was done to make allowance for any possible change in efficiency as a result of the change in construction material and because it provided the closest approximation to the age structure recorded in 1983 and 1984. Only samples where the number of fish from a particular age group and spawning number were ≥ 5 were used to estimate the instantaneous rate of change.

Selectivity (C_i) was estimated from the catch curve for each age group as follows:

$$C_i = e^{((\text{Log}_e X_{i+1} R_{i+1}) + S)} X_i^{-1}$$

where:

R = proportion of repeat spawners of age class i

S = instantaneous rate of spawning mortality (0.6651), derived from the catch curve.

The correction factors applied to each age were as follows: for age classes 3, 4 and 5 years a factor of 13.11, 3.64 and 1.81 was applied respectively, for age classes 6 to 10 years a value of 1.00 was used in each case.

An index of the total number of eggs deposition (E) in year t was calculated as follows:

$$E_t = \sum_{i=3}^{12} X_{i(t)} F_i C_i$$

Where the fecundity of age class i (F_i) is calculated as:

$$F_i = 34324I^{0.538} \quad (\text{Aprahamian, 1982})$$

Where:

I = age in years

RECRUITMENT

The CPUE at age 6 years (X_6) was used as a proxy for recruitment. Age at maturity can vary between cohorts by up to a year, however, in general > 98% of fish have matured (Aprahamian & Lester, 2001). For the 1974 and 1975 year classes and those between 1979 and 1991, the age 6 years CPUE was determined directly from catch data using equation 1. For the 1973 and for the 1976 to 1978 year classes, the index was estimated from the CPUE and the instantaneous rate of change as outlined above. The 1972 index was estimated from the number of 7 year old fish caught in 1979, assuming that 68% of fish age 6 years survive to age 7 years. The survival rate was determined from the relationship between the number of fish age 6 years caught in year t and the number of 7 year old fish caught in year $t+1$, for the 1973 to 1990 year classes (Aprahamian & Lester, 2001).

Quantitative monthly sampling of juvenile *A. fallax* has been carried out at Hinkley Point 'B' Nuclear Power Station (Fig.1) since October 1980 (except during 1986) (P. Henderson, Pisces Conservation Ltd., U.K.). Sampling dates were chosen to coincide with intermediate range tides in the spring-neap cycle. Sampling was standardised, so that on each visit six consecutive samples were collected over a 1 hr period using plastic baskets covered with 6 mm mesh and positioned to collect all the debris washed from two of the four drum screen which filter the cooling water entering the power station. The debris was sorted and the number of *A. fallax* captured per hour recorded and the standard length of the fish measured. The method is selective towards juvenile fish with the majority of *A. fallax* caught being of age 0+ (Holmes & Henderson, 1990).

For the 1992 to 1996 year classes the recruitment of age 6 year old *A. fallax* was estimated from the relationship between the number of juvenile *A. fallax* caught at Hinkley Point 'B' Nuclear Power Station between 1st June in year t and 31st May in year $t+1$, and the CPUE index of 6 year old female shad caught in the putcher fishery in year $t+6$ (Aprahamian & Aprahamian, 2001).

STOCK - RECRUITMENT

Stock recruitment was modelled using the Ricker relationship (Ricker, 1954).

$$E_{6(t+6)} = aE_t e^{-bE_t}$$

Where;

E_t = the number of eggs deposited in year t (stock)

$E_{6(t+6)}$ = the number of eggs deposited by fish age 6 years in year t+6 (recruits).

a = egg survival at low density

b = index of density dependence

Water temperature is strongly correlated with spawning success, explaining 77% of the variability (Aprahamian & Aprahamian, 2001). Changes in temperature, therefore, have the potential to greatly affect the number of shad returning to a river. Under existing (baseline) climate scenarios, inter-annual success can be highly variable, whereby temperatures can be sufficiently low to be detrimental to recruitment or alternatively, high enough to support population persistence (Aprahamian & Aprahamian, 2001). In order to assess the role of temperature in recruitment success and the potential for climate change to offset any increased rates of mortality associated with the introduction of tidal power turbines, recruitment success under baseline and climate scenarios were modelled. Uncertainty was inbuilt within the model by incorporating a stochastic temperature function (equation 2; referred to as T herein) based on daily water temperature data obtained from Oldbury Nuclear Power Station between 1972 and 1996. After Aprahamian & Aprahamian (2001), the number of eggs deposited by each cohort at age 6 years was determined as follows:

$$\text{Log}_e X_6 = 0.851T - 13.341 \quad (2)$$

Where:

T = mean daily water temperature ($^{\circ}\text{C}$) between June and August inclusive.

Three temperature scenarios were modelled: baseline, climate scenario 1 and climate scenario 2. The baseline scenario, reflective of present day conditions, incorporated mean (\pm S.D.) June-August water temperature data of $17.8 \pm 0.97^{\circ}\text{C}$ from between 1972-1996. Climate scenarios were based on medium emission predictions (U.K.CP09) and adopted a 1 and 2°C average temperature increase for scenario 1 ($18.8 \pm 0.97^{\circ}\text{C}$) and 2 ($19.8 \pm 0.97^{\circ}\text{C}$) respectively. As the variation in mean temperature cannot be predicted in climate scenarios, the variation surrounding mean baseline data was applied. For the purposes of the model, temperatures were independently modelled for time step (i.e. $t = 1$ year). As follows:

$$E_{6t} + e^{(\text{Log}_e X_{6t} + ((T_t - 17.8)0.85))} F_6$$

Where:

T_t = mean daily water June – August temperature in year t .

The total number of eggs deposited over the lifetime of a particular cohort (Y) in year t was estimated as follows:

$$Y_t = \sum_{i=5}^3 (e^{((\text{Log}_e X_{i+1} R_{i+1}) + S)}) F_i + a(e^{(\text{log}_e E_t + ((T_t - 17.8) 0.85))}) e^{-bE_t} + \sum_{i=7}^{12} (e^{((\text{Log}_e X_{i-1}) - S)}) F_i \quad (3)$$

MODEL SIMULATIONS

Baseline and climate scenario models were run in conjunction with Markov Chain Monte Carlo (MCMC) simulations (PopTools, CSIRO, Australia). Mean, variance and confidence limits were derived for each scenario and turbine mortality combination using 1000 iterations.

ENVIRONMENTAL DATA

Water temperature data were obtained from a variety of Environment Agency sources and the mean June – August temperature was calculated for the most downstream site in a river system. Time periods differed among rivers, as such direct comparison between systems was not possible. The data were used to provide an approximation as to the magnitude of the shift in latitude of the critical temperature needed for the persistence of *A. fallax* as a result of a 1°C and 2°C warming scenario.

RESULTS

STOCK RECRUITMENT

The relationship between stock, measured as the number of eggs deposited in year n and the number of recruits measured as the number of eggs produced by females age 6 years in year $n+6$ [Fig. 2(a)] and when the estimate of recruits has been standardised using temperature as an explanatory variable [Fig. 2(b)], indicates that there is a weak density dependent relationship and that stock explains a small proportion of the variability in recruitment measured 6 years later. The relationship can be described by the equation:

$$E_{6(t+6)} = 0.299 E_t e^{(-2.589 \cdot 10^{-7} \cdot E_t)} \quad (r^2 = 0.132; P = 0.1266),$$

with lower and upper 95% confidence intervals for a of 0.1463 – 0.6099 and for b of $-4.181 \cdot 10^{-7}$ – $-9.977 \cdot 10^{-8}$, respectively.

It is evident from Fig. 2 that the stock does not produce enough recruits from a single age-class spawning once to enable the population to persist.

POPULATION PERSISTENCE IN RELATION TO TEMPERATURE

Alosa fallax in the Severn are multiple spawners and summation of the total number of eggs produced by a particular cohort over its life time indicates that in years when temperatures are elevated, a greater number of eggs were produced (E_y) than were deposited (E_t) (Fig. 3). The relationship (with 95% confidence intervals in brackets) can be described by the equation:

$$E_y \cdot E_t^{-1} = -68.5(\pm 39.3) + 56.0(\pm 31.6) \text{Log}_{10} T$$

($r^2 = 0.674$; $P = 0.004$).

Where:

$$E_y = \sum_{i=3}^{12} X_{i(y)} F_i C_i$$

The relationship indicated that the equilibrium temperature is in the region of 17.4°C.

EFFECT OF TEMPERATURE ON LIFETIME FECUNDITY

A temperature component was fitted to the stock recruitment relationship (equation 3) and the effect on lifetime fecundity computed for baseline and climate scenarios (Fig. 4). The model indicates that at a mean baseline temperature of 17.8°C, the population is able to persist whereby replacement is achieved (Fig. 4). However, annual recruitment success is highly variable among years, with population persistence not possible in colder years. Under climate scenario 1, the model suggests an increase in water temperature of 1°C would be sufficient to support population persistence in all but the coldest years and result in on average, a 3.6 fold increase in the population (Fig. 4); a predicted increase in line with observed data (Fig. 3).

Under climate scenario 2, the model indicates that a 2°C increase in average water temperature to 19.8°C would see the population increase by on average, a factor of 6.3 and recruitment is predicted to be successful in all years (Fig. 4).

EFFECT OF TEMPERATURE ON TIMING OF FRESHWATER PHASE OF SPAWNING MIGRATION.

Aprahamian (1988) reported that peak immigration into the estuary occurred at temperatures ranging between 10.6 and 12.3°C, at between 119 – 134 days after

January 1st (Fig. 5). An increase in water temperature of 1 and 2°C would result in the peak of the run occurring 6 - 10 days and between 16 – 17 days earlier, respectively (Fig. 5).

EFFECT OF TEMPERATURE ON DISTRIBUTION

A long term average mean June – August daily water temperature in excess of 17.5°C is suggested for a population of *A. fallax* to persist (Fig. 3 and 4). Data on river temperature from the lower reaches were limited with little consistency in the time period available among river systems. Nevertheless, the data suggest that an increase in average water summer temperature of 1°C would result in habitat becoming suitable in terms of the temperature regime in large west coast rivers such as the rivers Dee (latitude 53.1892° N) (15.9°C, 1979-1999) and the Eden (latitude 54.9723° N) (16.5°C, 1997-2007). For some of the small flashy (a river that responds quickly to an increase in rainfall) rivers intermediate in latitude between the Eden and the Dee (e.g. the River Kent (latitude 54.2424° N; 15.9°C, 2005-2007)), a 2°C rise in water temperature would be required to ensure a suitable thermal regime.

On the east coast, the rivers Thames (latitude 51.4771° N) and Ouse (latitude 53.6971° N) (18.3°C, 1979-1999; 17.8°C, 1999-2009, respectively) already have a thermal regime similar to that of the River Severn. However, even a 2°C rise would not extend suitable habitat as far north as the River Tyne (latitude 54.9888° N) (15.0°C, 1995-2009).

IMPACT OF ADDITIONAL MORATALITY – PERSISTENCE Vs EXTINCTION.

A tidal power barrage has the potential to impact on 1) fish spawning for the first time (includes juveniles (age 0+) on their outmigration in their first autumn and adults on their return to the river to spawn for the first time at between 2 and 6 years old (Aprahamian & Aprahamian, 2001)) and 2) repeat spawners, currently ~50% of the spawning population are repeat spawners with fish making up to 7 spawnings (Aprahamian *et al.* 2003).

The impact of additional mortality prior to spawning for the first time suggests that an average increase of 50% (juvenile) and 90% (adults) on current mortality rates would result in the population becoming extinct under the current temperature regime (Fig. 6). However, the natural fluctuations in climatic conditions in any given year result in population extinction occurring when turbine mortality rates are between 0 and 60% and, 0 and >90% for juvenile and adult shad (based on 95% CI), respectively (Fig. 6). If average summer water temperatures were to increase by 1°C (18.8°C) or 2°C (19.8°C), then the estimated average mortality rates required for population extinction are ~60% and 70% (juvenile) and ~95% (adults) for each climate scenario, respectively (Fig. 6). Using a precautionary approach and adopting the worst-case for both climate scenarios (lower 95% CI), the model indicates that maximum additional turbine mortality should not exceed 10% and 50% (juvenile) and, 10% and 90% (adults) for 18.8 and 19.8°C climate scenarios (Fig. 6).

DISCUSSION

The forecast increase in temperature (Murphy *et al.* 2009) is predicted to benefit populations of *A. fallax* in the U.K. and is consistent with the findings of Lassalle *et al.* (2008, 2009) and Holmes & Henderson (1990). An increase in temperature of 1 - 2°C is expected to modify the timing of the spawning migration by *A. fallax* into fresh water, bringing this transition forward by between 6 - 17 days, and is consistent with observations in other species of shad e.g., *A. sapidissima* from the Colombia River, U.S.A. (Quinn & Adams, 1996). Warming may also result in the earlier outmigration of the juveniles in the autumn (Boisneau *et al.* 2008). Similar changes in life-cycle timing have also been observed in other fish species (Perry *et al.* 2005; Southward *et al.* 2004), birds (Crick *et al.* 1997; Crick & Sparks, 1999) and amphibians (Beebee, 1995).

In order for *A. fallax* to persist, a long-term summer average water temperature exceeding 17.5°C is needed. In regions northward of the Severn estuary, river temperatures seldom exceed this threshold delineating the northern distribution of *A. fallax*. Under the predicted climate scenarios, the environment is predicted to warm sufficiently to increase the northern distribution range of *A. fallax* in the U.K.. A 1°C rise in temperature is predicted to increase the northern range of *A. fallax* by 150 km beyond its existing northerly limit and possibly up to 350 km could be achieved. Such an increase is in line with predictions for other species (Hughes, 2000). However, the extent of any range increase is likely to be constrained by local factors such as river size (volume) and available habitat.

Alosa fallax is regarded as a lusitanian (warm temperate) species and abundance is predicted to increase with a 1-2°C rise in temperature by a factor of 3.6 and 6.3, respectively. The mechanism by which temperature may be acting to control the population is likely to be through its effect on hatching success and/or growth rate. For *Alosa alosa* Linnaeus, temperatures below 16°C result in larval mortality at the egg stage (Hoestlandt, 1958). At temperatures between 16°C and 18°C, larval condition is poor resulting in difficulty emerging from the egg (Cassou-Leins & Cassou-Leins, 1981), optimum temperature for the survival of eggs and larvae being in the region of 20°C (Charles & Jatteau, unpublished data, Cemagref, Bordeaux, France). When temperatures increase, growth may be faster, such that 0+ fish are vulnerable to predation from aquatic invertebrates for a shorter period of time (Mann, 1991) and thus, enhancing population persistence.

Temperature may also effect food production, with primary production greater in warmer years. Year class strength in *A. sapidissima* has been shown to be positively correlated with zooplankton density evidenced by an increase in the percentage of larval shad (<13 mm) with food in their guts (Crecco & Savoy, 1987). The similarity in the coefficient of variation in year class strength between the study of Aprahamian & Aprahamian (2001) and that of Henderson & Seaby (1999) support the conclusion that the mechanism operates during the first four months before the fish migrate seaward in the autumn (Claridge & Gardner, 1978; Aprahamian, 1988).

The weak relationship between stock size and recruitment suggests that the population is regulated by mainly thorough abiotic processes, specifically temperature. Similar reports have been made for *A. sapidissima* on the Connecticut River, U.S.A. (Crecco *et al.* 1986) and for the landlocked population of *A.*

pseudoharengus in Lake Huron, North America (Henderson & Brown, 1985). In these studies, density-dependent factors of recruitment without the influence of climatic factors removed, accounted for between 5 and 7% of the variation in recruitment in Lake Huron (Henderson & Brown, 1985) and approximately 2% on the Connecticut River, U.S.A. (Crecco *et al.* 1986). In contrast, strong density-dependent regulation is evident in semelparous populations of *A. alosa* in the Loire, France (C. Mennesson-Boisneau, unpublished data, University of Tours, France) and in the Gironde, France (Martin-Vandembulcke, 1999).

There is at present little information on the levels of turbine-induced mortality that might be experienced by *A. fallax* in a tidal environment. Several factors arising from passage through a barrage have been attributed to juvenile and adult alosine mortality and include pressure effects, blade strike and shear effects (Dadswell & Rulifson, 1994). Dadswell & Rulifson (1994) citing the studies of Hogans & Melvin (1985) and Hogans (1987), reported mean (\pm 95% CI) mortality levels of $46.3 \pm 34.7\%$ and $21.3 \pm 15.2\%$, at a tidal turbine in the Annapolis river estuary, Canada, during 1985 and 1986, for adult *A. sapidissima*. The difference in mortality rate between the two studies was attributed to an increase in turbine efficiency and reduced handling stress (Dadswell & Rulifson, 1994).

Subsequently, Dadswell & Rulifson (1994) and Gibson & Myers (2002) used net capture rates to investigate juvenile mortality (0+ juveniles). Dadswell & Rulifson (1994) reported an overall mortality rate of 54.4% for *A. sapidissima*. However, trials in 1999 assessing turbine mortality for age 0+ *A. sapidissima*, *Alosa aestivalis* (Mitchill) and *A. pseudoharengus* indicated overall mean mortality rates (\pm 95% CI) of 23.4% (6.1-58.8), 8.1% (3.5-17.2) and 7.7% (1.5-31.4), respectively for a single passage (Gibson & Myers, 2002). Differences in turbine mortality estimates between studies were attributed to the duration the nets were deployed (Gibson & Myers, 2002).

Unpublished experimental studies have been used to predict injury rates for juvenile (70 mm) alosines during a Severn Tidal Power generating cycle. Overall mortality was estimated at 53%; the majority of which was attributed to shear effects (48%) and the remaining mortality to blade strike (4.9%) (*A. Turnpenny*, unpublished data, Turnpenny Horsfield Associates Ltd., U.K.). In contrast, a study at Annapolis Royal tidal power project (Nova Scotia, Canada) suggested that the main injuries to juvenile alosines were due to pressure effects (54.4%), with shear (1.2%) and mechanical effects (3.4%) secondary, 41% had no signs of damage (Stokesbury & Dadswell, 1991). It is unclear as to the exact mechanism which causes juvenile mortality, however, irrespective of the mechanism, it is clear that turbine mortality has the potential to greatly affect fish survival during passage through a tidal barrage turbine.

In estuaries, fish move in and out with the tide, so there is the possibility that they may make repeated passages through the turbines, which is in contrast with in-river structures where a single passage is assumed. However, nothing is known about the routes taken by the adult and juvenile *A. fallax* in the outer Severn estuary. Variation in catch between flood and ebb tide suggests that pre-spawning adults tend to use the flood tide in the main channel to facilitate upstream progress, and the ebb tide to reduce displacement from the stem. A movement inshore would reduce the risk

of passing through generating turbines, assuming fish pass facilities were placed close to the shore. Post-spawning fish are not, however, caught in any number in the fishery which operates close to the bank, indicating that seaward movement may be facilitated by swimming in the main channel on the ebb tide.

Aprahamian (1988) showed the impact of additional mortality on the mature stock of the Severn *A. fallax* population to be a decline in mean weight and in the number of spawnings. The indications from this study are that the populations in the River Severn and presumably also in the rivers Wye, Usk and Tywi are barely able to sustain themselves under current climate conditions and an iteroparous life history is essential for *A. fallax* to maintain a self-supporting population. Leggett (1976, 1977) and Gibson & Myers (2003) concluded a similar requirement for *A. sapidissima* and *A. pseudoharengus* populations close to their northern limits in North America. If 0+ *A. fallax* are as vulnerable to turbine mortality as *A. sapidissima* with a mortality rate of between 23.4 – 46.3% for a single passage, then an increase in mortality of ~30% is likely. At this level of mortality, it is predicted that the population would no longer be able to persist, even if climate temperatures were to increase by 1°C. A warming of 2°C would enable *A. fallax* to sustain the additional mortality from a single passage. Although the population would be larger and more resilient due to greater annual recruitment success, it would effectively only take two passages through the turbine before the population was no longer self-sustaining. However, if *A. fallax* responds in a similar way to *A. aestivalis* and *A. pseudoharengus* where turbine mortality rates are considerably lower, then it is possible that greater number of *A. fallax* will successfully pass through the turbines to support population persistence.

The increase in temperature that is forecasted to occur as a result of global warming is predicted to benefit the populations of *A. fallax* in the U.K.. However, the consequence of a tidal barrage across the estuary of the River Severn, to reduce the production of greenhouse gases will, most likely eliminate a self-sustaining population in this river. However, the impact on the populations in the rivers Wye and Usk will be dependent on the specific scheme chosen. The increase in temperature will mean that rivers further north may have an acceptable thermal regime which would enable a population of *A. fallax* to persist should a sufficient number of *A. fallax* disperse to those areas. However, to offset the possible impact of a tidal barrage, the rate of warming would ideally need to proceed the development of a barrage in order for populations to develop, although founder fish originating from French and Irish populations may establish new populations. Certainly, *A. fallax* has been reported as far north as the Solway Firth (latitude 54.8877° N), but as yet there is no evidence of a spawning population in its rivers (Aprahamian & Aprahamian, 1990). Thus, a paradox exists between trying to reduce the impact of greenhouse gas emissions and the possible local extinction of an internationally considered rare and endangered species.

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Table I. Change in the effective fishing effort of the putcher rank over the period 1979 - 1997, together with the raising factors used to adjust the catch to the effort deployed between 1988 and 1997.

Year	Effective fishing effort (arbitrary units)	Raising factor
1979	293	2.35
1980	384	1.79
1981	475	1.45
1985-1986	585	1.18
1987	586	1.17
1988-1997	689	1.00

Figure legends

Fig. 1. The Bristol Channel and lower River Severn, U.K. Sampling was carried out near Lydney for adults during the freshwater phase of their spawning migration and at Hinkley Point Power Station for juvenile *Alosa fallax*.

Fig. 2. (a) The relationship between the index of eggs produced at age 6 in year $t+6$ in relation to the index of eggs deposited in year t by the spawning stock and (b) the index of eggs produced at age 6 in year $t+6$ standardised to a temperature of 17.8°C in relation to the index of eggs deposited in year t by the spawning stock. The stock-recruit relationship for (b) is shown by the solid line with the 95% confidence intervals shown by the dotted lines.

Fig.3. The relationship between the ratio of recruits, the total number of eggs produced by a particular cohort over its life time (E_y) and the stock, the total number of eggs deposited that gave rise to that cohort (E_t) and mean water temperature between July and August in their first year in fresh water. Dotted line indicates 95% confidence intervals. Solid horizontal line indicates where the number of recruits equals spawning stock from which they were derived.

Fig. 4. The relationship between the number of recruits produced over a life-time and stock size in relation to temperature. Data are mean \pm 95% CL for baseline (17.8°C) and climate change scenarios (18.8°C and 19.8°C).

Fig. 5. Mean daily temperature recorded at Olbury Nuclear Power Station between 1976-1990, from January 1st (dotted line), solid line 1976-1990 mean $+1^{\circ}\text{C}$ and dashed line 1976-1990 mean $+2^{\circ}\text{C}$. Horizontal lines represent 10.6 and 12.3°C , the temperature range over which peak migration into fresh water occurs (Arahamian, 1988).

Fig. 6. Impact of turbine mortality on proportional abundance (mean \pm 95% CL) of juvenile and adult *A. fallax* under baseline (17.8°C) and climate scenarios (18.8°C and 19.8°C). Confidence limits were derived from Monte Carlo simulations ($n=1000$).

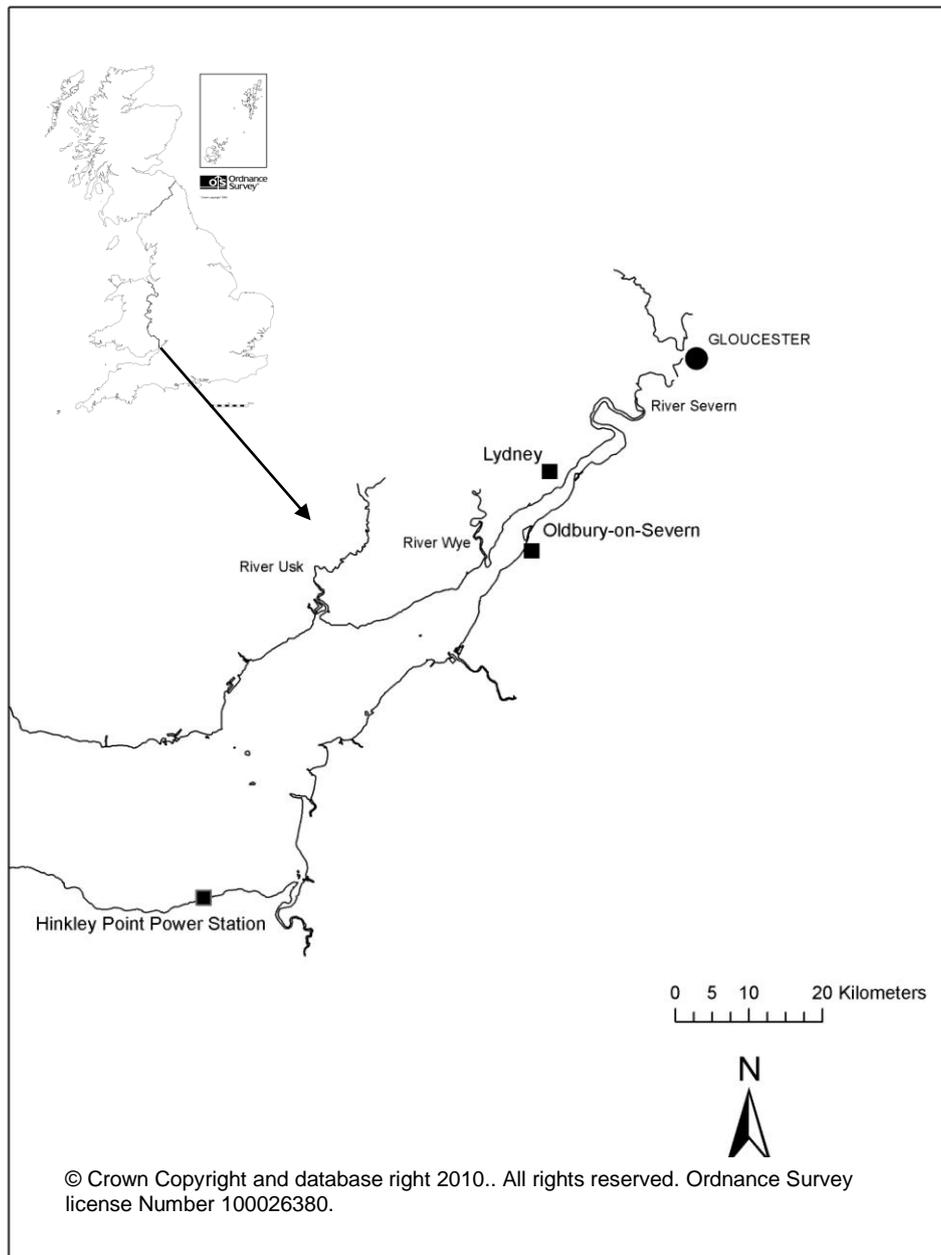


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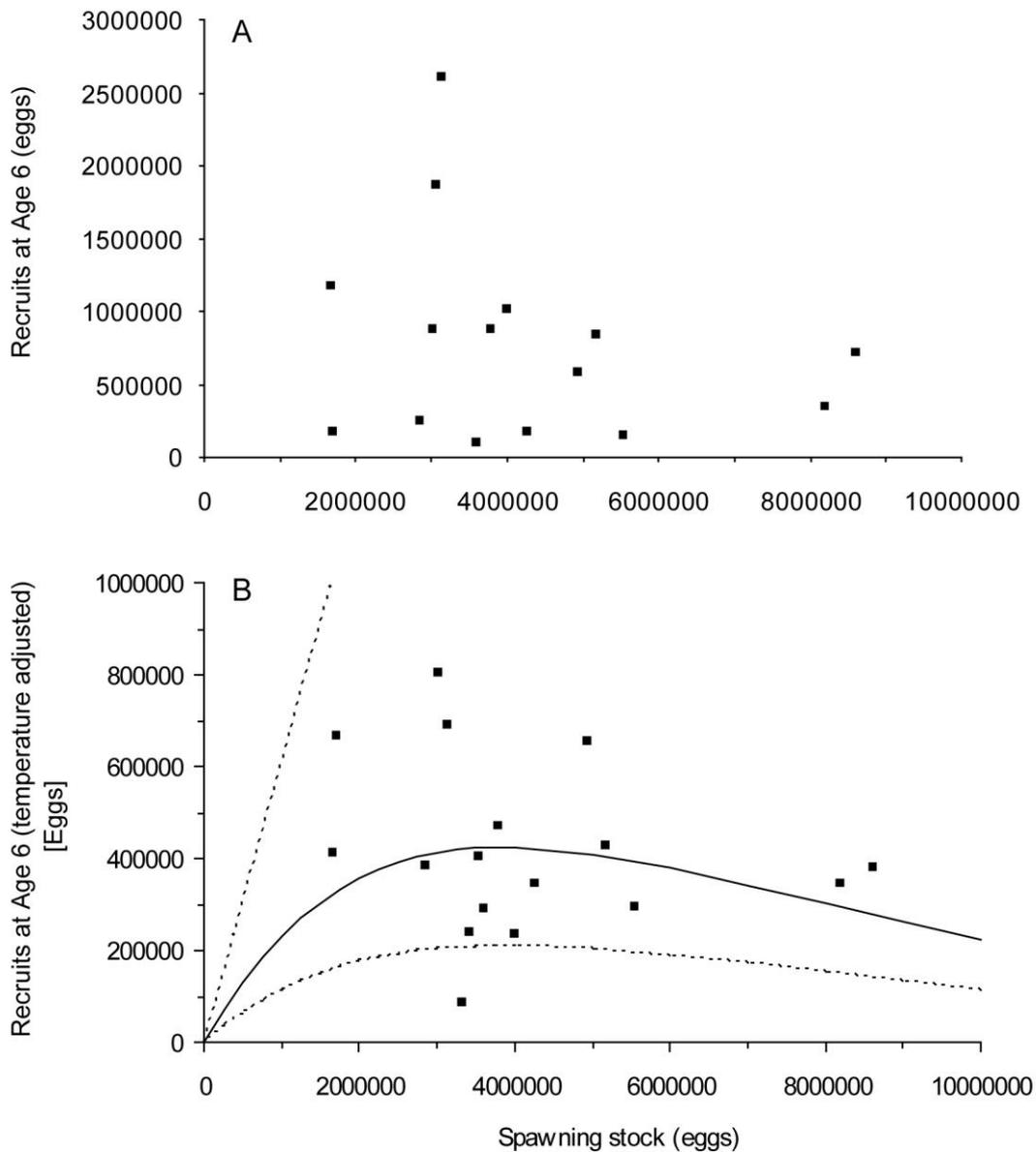


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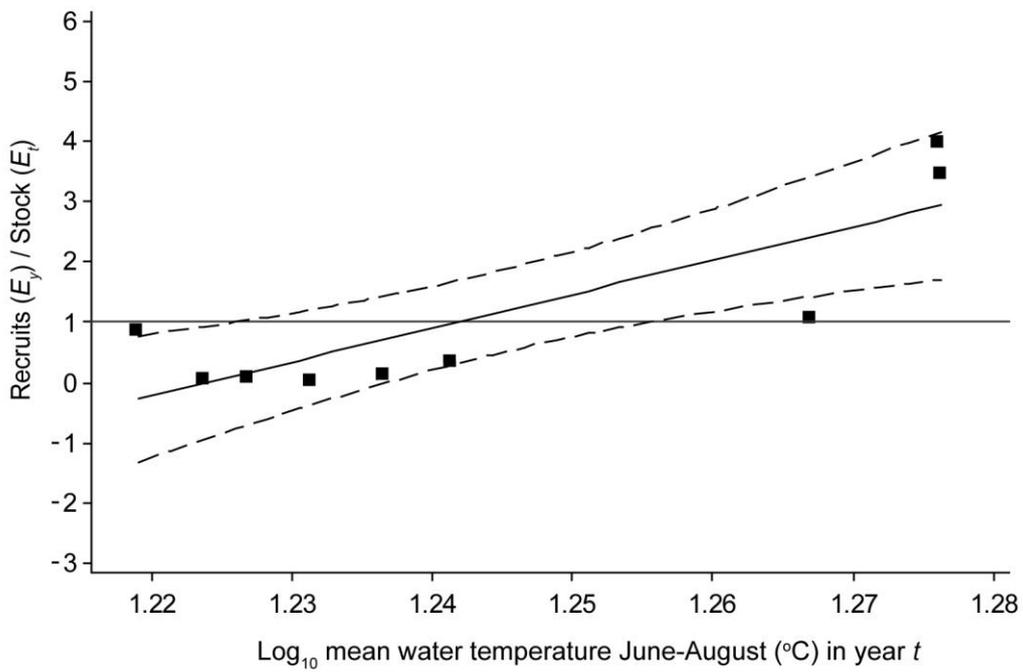


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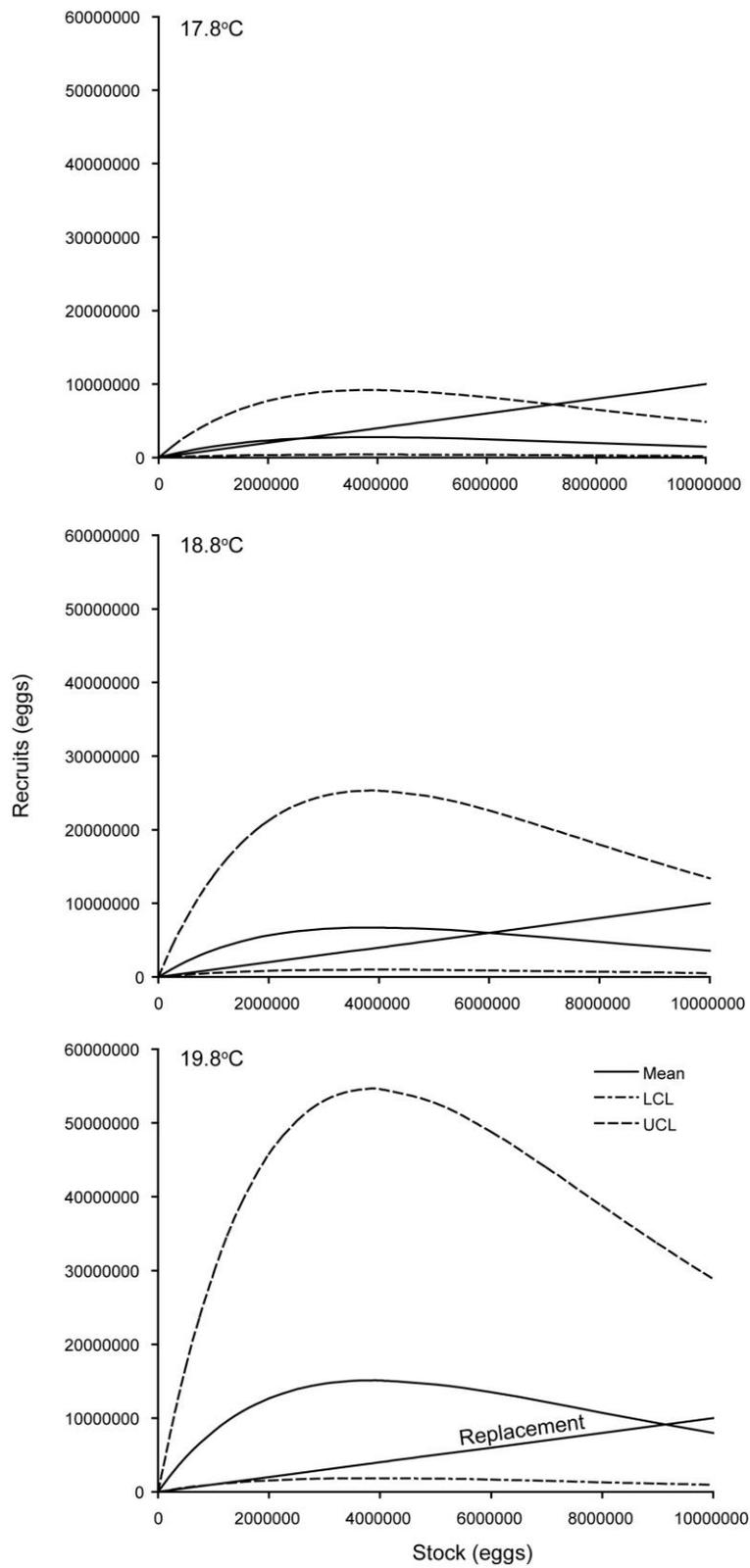


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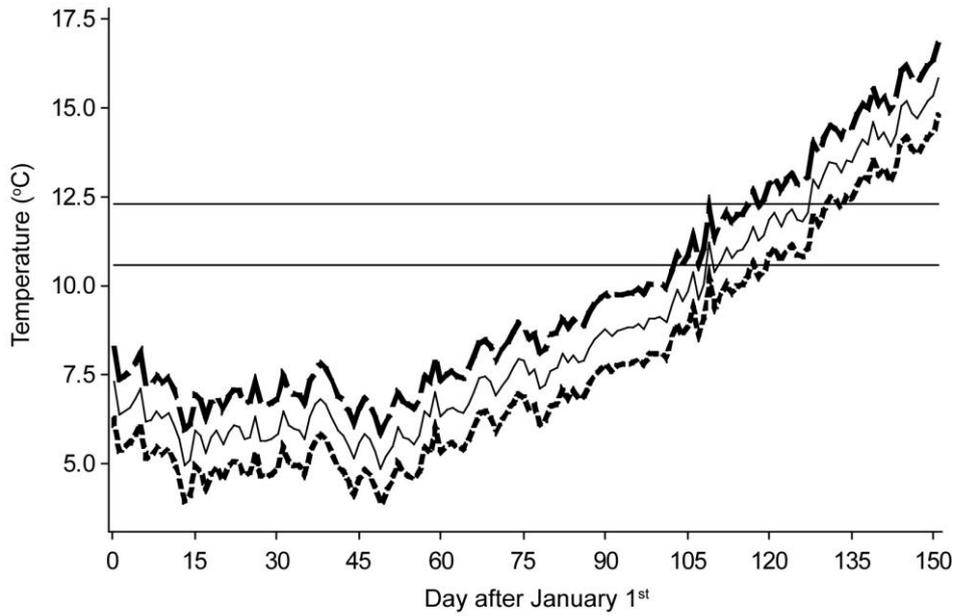


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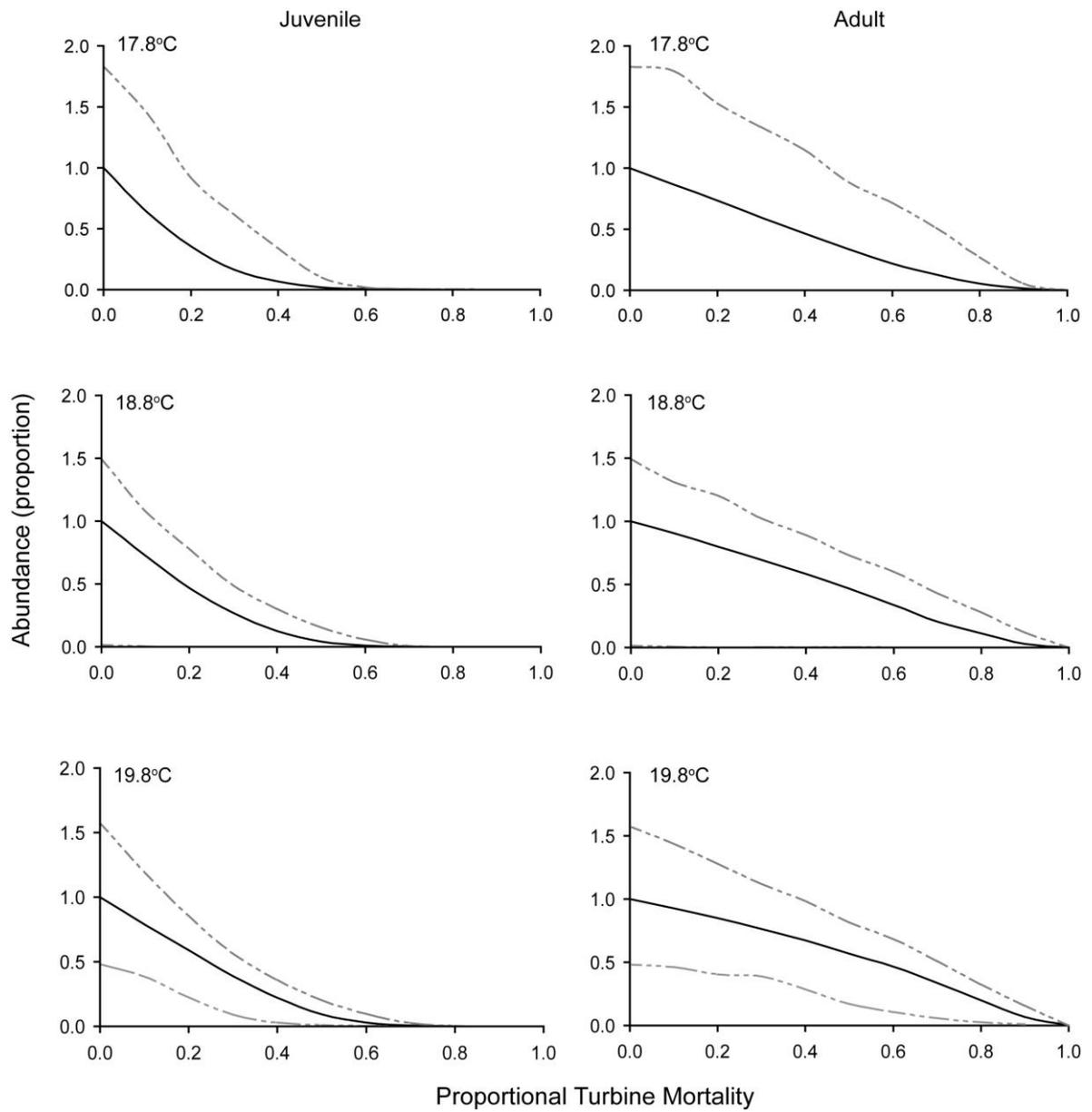


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