

Allis shad adopts an efficient spawning tactic to optimise offspring survival

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Abstract The potential effects of global warming on the allis shad population were tested by combining a time series of spawning acts with expected thermal survival rates for embryos and larvae until 14 days post hatching. The yearly mean survival of spawn for each reproductive season was calculated and an index of reproductive efficiency based on this survival rate was proposed. The randomness of the spawning tactics was evaluated by shuffling the spawn acts time series. This approach was applied to the Gironde-Garonne-Dordogne (south-west France) population, which recently collapsed. The yearly mean thermal survival of spawn is slightly variable at approximately 55% over 2003–2012 despite fluctuating temperatures. An especially low survival (35%) was recorded for the last season (2013). For eight of the 11 reproductive seasons, the index of reproductive efficiency was high (> 80%) and largely above indices obtained by a random spawning tactic. Therefore shad are able to adopt an efficient spawning tactic to anticipate favourable thermal conditions for survival of their offspring. However, thermal behavioural rules still need to be expanded to understand the failures in their reproduction efficiency.

Keywords *Alosa alosa* · Spawning tactic · Behavioural plasticity · Temperature · Adaptation to environmental change

Introduction

Species are expected to display different responses to climate changes, including (i) physiological modifications, (ii) shifts in species distribution, (iii) changes in phenology and (iv) adaptation by genome evolution (Hughes 2000). The last point clearly results in genetic changes, whereas the other three responses are mainly based on mechanisms of phenotypic plasticity (Crozier et al. 2008). The phenotypic plasticity is the ability of an organism with a given genotype to change its phenotype in response to environmental changes (West-Eberhard 1989; Pigliucci 1996). Among plastic traits, behaviour plasticity plays a special role in evolution and adaptation. Behaviour is often the first adaptive response (West-Eberhard 1989): in such a mechanism, the individuals adapt to environmental variability by switching behaviours according to the environmental conditions (Stearns 1989).

Temperature is a main driver of metabolism and ontogenetic development for ectotherms and thereby indirectly influences the phenology and the life history traits (Angilletta et al. 2002; Brown et al. 2004). More specifically, the water temperature influences growth, development, feeding, reproduction, behaviour and distribution of fish (Golovanov 2013). Early life stages are particularly sensitive to temperature fluctuations and to

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the temporal variability of primary and secondary production because of their limited energetic storage and lower trophic levels (Houde 1989). Discharge may directly or indirectly impair the recruitment success. For example, May and June discharges explained 80–87% of recruitment variability in year-class strength of American shad in the Connecticut River between 1966 and 1980 (Crecco and Savoy 1987) and a stock-recruitment model including a discharge-dependent mortality rate has been proposed for this species (Lorda and Crecco 1987). Mechanistically, high flow may increase abrasion of eggs on hard substrate (Ulanowicz 1975; Stoll et al. 2010), transport embryos and larvae to unsuitable habitats of low food density and high predator abundance (Reichard and Jurajda 2004; Nack et al. 2015; Walton et al. 2017), increase turbidity which may interfere with the feeding ability (Mion et al. 1998), reduce water temperatures thereby delaying the development of eggs and larvae (Lorda and Crecco 1987). In this context, many species have developed spawning tactics to optimise their offspring survival in variable environmental conditions (Lambert 1990; Murua et al. 2003; Durham and Wilde 2006). Reproductive behaviour in freshwater is triggered by environmental cues such as water temperature and discharge (Quinn and Adams 1996). When spawners and offspring experience very similar environmental conditions because of a limited incubation period and limited eggs and larvae drift, Quinn and Adams (1996) postulated that adults should behaviourally adjust the spawning timing (or the migration timing in their study cases) to optimise the environmental conditions for offspring survival.

The allis shad (*Alosa alosa*), which is an anadromous species, was originally distributed from Norway to Morocco (Baglinière et al. 2000). Many shad populations have declined in the last several decades, which have resulted in a contraction of the species distribution (Lassalle et al. 2008). River fragmentation, pollution, habitat degradation and overfishing are more frequently cited causes of these declines (Taverny et al. 2000). Consequently, the species was listed as vulnerable in the Red List of Threatened Species of the International Union for Conservation of Nature and in many European conservation initiatives (Habitat Directive, Annexes II and V; OSPAR Convention, Annex V; Berne Convention, Annex III).

The Gironde Basin (south-west France) was previously the reference for the European allis shad population, i.e., large effectives and well documented (Martin

Vandembulcke 1999; Chanseau et al. 2004). However, the population recently collapsed (Rougier et al. 2012) and recruitment failure in continental waters is suspected. Juvenile abundance has markedly declined since 2000, and the adult abundance has only declined since 2005 (Rougier et al. 2012). A moratorium on fishing was enforced in 2008 without any clear signs of recovery since then (ICES 2014).

Allis shad is a semelparous species where sexual maturity is triggered by a size threshold around 55 cm (Rougier et al. 2015). Consequently, female age at maturity ranges between 4 and 6 years with a majority of the 5-year spawners (Cassou-Leins et al. 2000). The incubation duration for allis shad is less than 10 days long (Cassou-Leins and Cassou-Leins 1981; Jatteau et al. 2017). Therefore, this species is a good candidate to test the Quinn and Adams (1996) hypothesis. Shad spawners need specific environmental conditions to spawn. The temperature at the onset of spawning has been reported to be in the range of 15 to 20 °C (Roule 1922; Cassou-Leins and Cassou-Leins 1981; Boisneau et al. 1990). In Brittany, upstream spawning migration is stopped when temperature are below 10–11 °C (Mennesson-Boisneau et al. 2000; Acolas et al. 2006) and the reproduction activity itself is inhibited below 14 °C (Acolas et al. 2006). In the Gironde Estuary, only a few migrants were caught by commercial fishermen when the water temperature was lower than 11 °C (Rochard 2001) and no spawning occurred in this basin at temperatures below 12 °C (unpublished data). These thresholds vary with latitude (Cassou-Leins et al. 2000). The high discharges can also explain the limited success of the reproduction activity (Boisneau et al. 1990).

In addition to its role in spawning, temperature affects shad embryos and larvae survival (Crecco et al. 1983; Crecco and Savoy 1985; Savoy and Crecco 1988; Aprahamian and Aprahamian 2001). Recently, Jatteau et al. (2017) estimated a thermal survival curve for allis shad early life stages based on laboratory experiments. The optimal range, corresponding to a survival higher than 80% of the maximum survival, was between 16.6 °C and 24.8 °C, which was consistent with the results of Hundt et al. (2015b). The tolerance range, which corresponded to survival higher than 5% of the maximum survival, was between 10.3 °C and 29.9 °C.

The date of the egg laying is a phenotypically plastic trait. The proximate environmental cues that trigger laying are not necessarily the same environmental factors that influence subsequent offspring survival and

growth. Temperature, photoperiod and other environmental variables can serve as proximate cues if they predict the future via a correlation with environmental factors that determine the selection of the optimal laying tactic (Visser 2008). The laying date is affected by temperatures earlier than those influencing the juvenile mortality. Therefore, timing of the reproduction date is probably strongly selected by the close match between the offsprings' thermal sensitivity and the temperature conditions during embryogenesis and after hatching.

This study first describes the annual reproductive efforts exhibited by female allis shad and the expected survival of early stages based on Jatteau et al. (2017) curves and temperatures between 2003 and 2013. It then explores whether the reproductive activity influences early stage survival. The efficiency of allis shad reproduction for the 11 spawning seasons is compared to a random tactic (i.e. shuffled spawn acts time series). Finally, adaptation capacity of the species to address environmental fluctuations and the subsequent risk of population extirpation due to climate warming are discussed.

Method

Field data

The reproductive activities of allis shad in the Garonne River were obtained from the Lamagistère spawning ground, which was one of the most important spawning grounds (Fig. 1) (around 30% of the total activity; Gaillagot and Carry 2014). The reproductive activity was estimated as the daily number of spawning acts corresponding to fast, circular nocturnal movements of at least two side-by-side spawners at the water's surface (Roule 1923; Acolas et al. 2006). A detailed description of the protocol to count spawner acts was provided by Gaillagot and Carry (2014). Briefly, the evaluation of spawning acts was based on auditory survey which was performed one night out of two at the beginning and the end of the reproduction season and three nights out of four during the period of high activity. The counting of spawning acts took place between 2 am and 3 am, period corresponding to the peak of activity (Cassou-Leins et al. 2000). These figures were extrapolated to the all night with a nocturnal pattern regularly updated during the season. The missing nights were estimated by linear interpolation. The observation period is

defined as the period ranging from the first night to the last night of effective auditory survey. It includes nights with no reproduction activity. The spawning season was estimated as the period between the first and the last days when spawning acts were recorded.

Mean daily water temperature data were recorded at the control station at the Golfech Dam fish pass located two kilometres upstream of the study site. Temperature was recorded every hour (automatic probe NKE S2 T) and averaged by day. Daily temperatures were grouped into five classes based on tolerance and optimal ranges proposed by Jatteau et al. (2017): below the minimum tolerance range (≤ 10.8 °C), between the minima of the tolerance and the optimal ranges (> 10.8 °C and ≤ 16.6 °C), within the optimal range (> 16.6 °C and ≤ 24.8 °C), between the maxima of the tolerance and optimal ranges (> 24.8 °C and ≤ 29.8 °C), and above the maximum tolerance range (> 29.8 °C). In 14 days, temperatures do not vary a lot so that for each spawning act, temperatures during the 14 days post hatch (dph) belong to two classes at most. In view of this, each spawning act was assigned to the worst class associated with the temperature between egg laying and 14 dph.

Thermal survival of recruitment (TSR)

The TSR evaluates the expected yearly mean spawn survival from fertilisation up to 14 dph and thus provides information on the reproductive success for different spawning seasons. The limit of 14 days corresponds to the duration of Jatteau et al. (2017) experiments of early stage survival.

The TSR index is based on the combination of experimental thermal survival curves and field measures of water temperature. The computation required four steps:

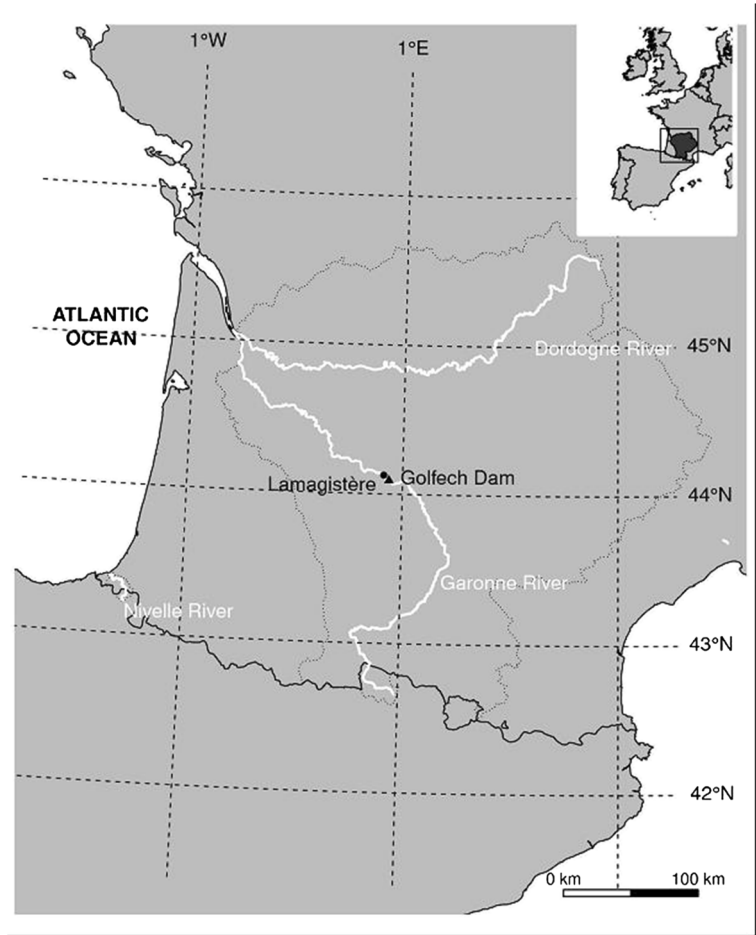
1. The computation of incubation duration $d(j)$ in days for the embryos spawned on day j .

Jatteau et al. (2017) found an exponential relationship between the incubation duration and the temperature, which is as follows:

$$d = 1124 T^{-1.83} \text{ or } dT^{1.83} = 1124$$

However, field temperatures are not constant and therefore it was necessary to modify the formula to account for daily temperature variability as observed in nature. The previous formula was modified to link the

Fig. 1 Location of the study site. Reproduction acts were recorded from the Lamagistère spawning ground (black point) on the Garonne River. Temperatures were monitored at the Golfech dam (black triangle). Thermal performance curve were estimated on shad from the Nivelle River by Jatteau et al. (2017)



incubation duration of the embryos spawn on the day j and the temperatures of the following days:

$$\sum_{i=0}^{d(j)-1} T(j+i)^{1.83} = 1124$$

where $T(i+j)$ denotes the temperature i days after spawning on day j .

The incubation duration (rounded down to the next whole number) was then calculated by solving the following inequality:

$$d(j) = \max(k) \mid \sum_{i=0}^{k-1} T(j+i)^{1.83} < 1124$$

where k is the number of days since fertilisation.

2. The computation of expected cumulative embryo survival $S_{CUMembryo}(j)$ for embryos spawn on day j .

Jatteau et al. (2017) used a logistic regression with a cubic polynomial of temperature to assess the embryo survival from :spawning to hatching

$$S_{CUMembryo} = \frac{1}{(1 + e^{-1.24 + 1.127T - 7.83 \times 10^{-2}T^2 - 6.11 \times 10^{-4}T^3})}$$

which produced a daily survival by assuming a constant survival rate over the incubation period:

$$S_{embryo} = \frac{1}{(1 + e^{-1.24 + 1.127T - 7.83 \times 10^{-2}T^2 - 6.11 \times 10^{-4}T^3})^{1124T^{-1.83}}}$$

Considering the variable temperatures during the incubation phase, the expected embryo survival from spawning to hatching for embryos spawn on day j became:

$$S_{CUMembryo}(j) = \sum_{i=0}^{d(j)-1} \frac{1}{(1 + e^{-1.24 + 1.127T(j+i) - 7.83 \times 10^{-2}T(j+i)^2 - 6.11 \times 10^{-4}T(j+i)^3})^{1124T(j+i)^{-1.83}}}$$

3. The computation of the expected larvae cumulative survival $S_{CUMlarvae}(j)$ over 14 days after the hatch for larvae issued from the spawn of day j .

This computation was performed with the Jatteau et al. (2017) formula applied with temperatures of the 14 days following the hatch.

$$S_{CUMlarvae}(j) = \sum_{i=d(j)}^{d(j)+13} e^{(1.85-5.13 \times 10^{-1} T(j+i)+1.02 \times 10^{-2} T(j+i)^2+7.01 \times 10^{-5} T(j+i)^3)}$$

4. Computation of the $TSR(k)$ as the weighted mean of expected embryo survival and expected 14 dph larvae cumulative survival using the daily number of spawns $Nspawn_k(j)$ over spawning season k ,

$$TSR(k) = \frac{\sum_{j=1}^{n_k} Nspawn_k(j) S_{CUMembryo}(j) S_{CUMlarvae}(j)}{\sum_{j=1}^{n_k} Nspawn_k(j)}$$

where n_k is the number of days in the reproduction season k .

$TSR(k)$ can be simply interpreted as the average expected survival of all eggs laid during the season k .

Randomness of the reproduction behaviour and an index of reproduction efficiency (I_{TSR})

$TSR_{min}(k)$ and $TSR_{max}(k)$ correspond to the minimum and maximum values that $TSR(k)$ can take during season k . These values are calculated with a time series of the spawning acts number and embryo-larval survival sorted into the opposite (one increasing and one decreasing) and the same (both increasing) orders. The former corresponds to the highest number of spawns associated with the dates of the worst survival and the latter to the highest numbers of spawn associated with the dates of best survival.

To test the randomness of the reproduction behaviour, the distribution of the $TSR(k)$ is calculated by shuffling the spawn act time series for a spawning season k 10,000 times. This illustrates the value of TSR irrespective of the date of spawning but with the same distribution of the reproduction activity. The quantiles 0.025 and 0.975 define the range of $TSR(k)$ corresponding to a random reproduction activity.

Based on these previous indicators, the efficiency of the reproduction activity relative to the expected thermal survival of the young stages for season k was evaluated

with an index ranging from 0 and 1 and was calculated as follows:

$$I_{TSR}(k) = \frac{(TSR(k)-TSR_{min}(k))}{(TSR_{max}(k)-TSR_{min}(k))}$$

The distribution of $TSR(k)$ based on shuffling the spawning acts series was used to calculate the distribution of I_{TSR} and to similarly test the randomness of the reproduction behaviour.

To sum up, TSR assesses whether survival was good (high TSR) in a specific year while I_{TSR} assesses whether fishes could have done better (low I_{TSR}) with a more appropriate spawning tactic.

Results

The four strongest reproduction activities occurred during the first several seasons, which were then followed by two years (2007 and 2008) of low activity. Then, the number of reproduction acts increased until 2011. The last two seasons (2012 and 2013) were again very low (Fig. 2).

Figure 3 details the correspondence between spawning acts and the expected cumulative survival up to 14 dph. The survival time series resembles dome-shaped curves with high values located mainly between mid-May and mid-June. Most spawning acts were recorded during day associated with high values of juvenile survival (conversely, few spawning acts occurred during days associated with low survival; Fig. 3). The start of the reproduction season usually fluctuates between the end of April and the first days of May, but an early beginning was observed in the last three years. The spawning seasons were finished between mid-June and mid-July with no obvious trend.

The proportion of spawning acts assigned to the worst class associated with the temperature

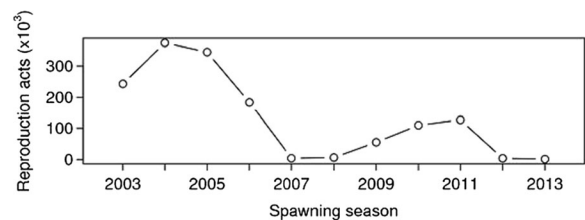


Fig. 2 Evolution of the total number of reproduction acts according to the 11 studied reproduction seasons

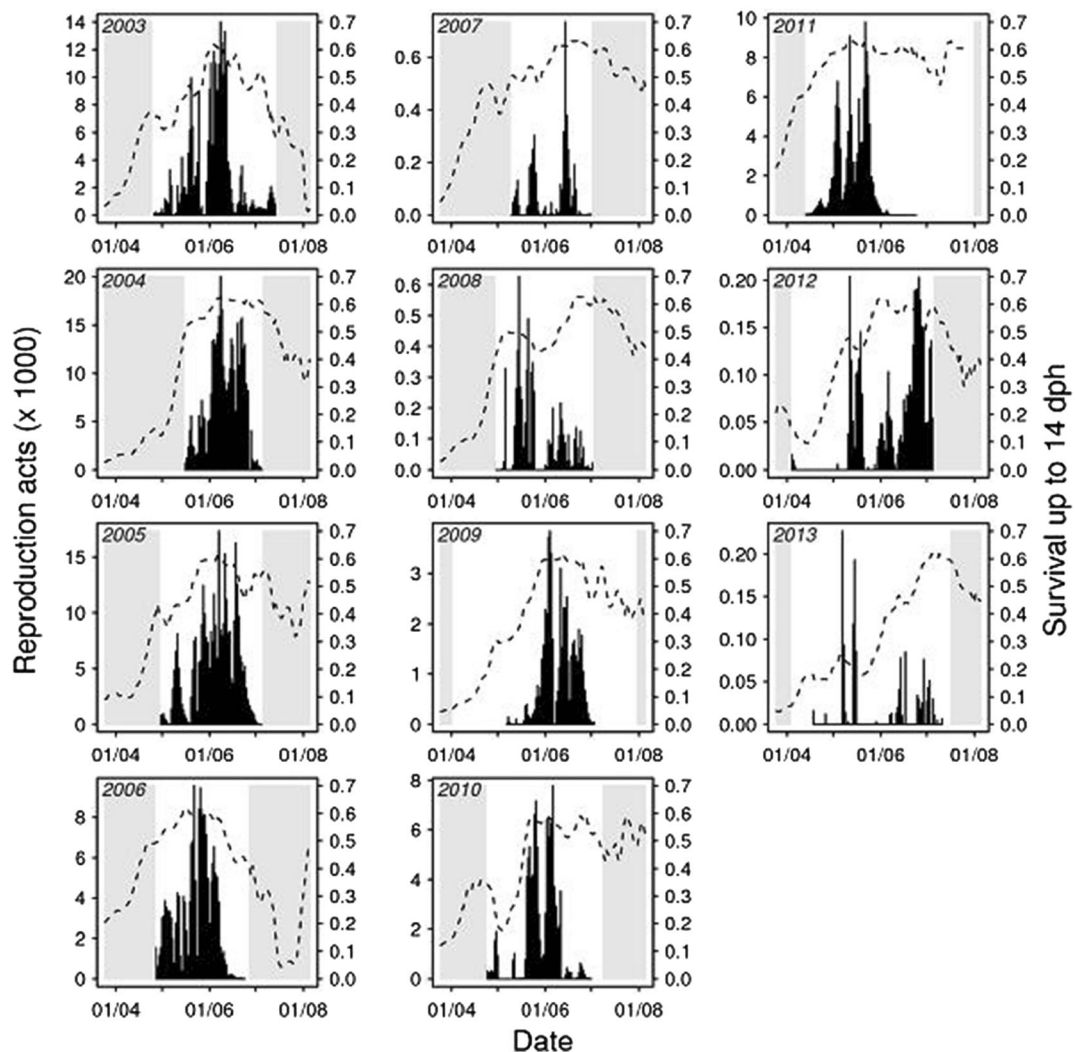


Fig. 3 Evolution of the spawning acts number (bar) and the survival from embryos up to 14 dph (dotted line) for the 2003–2013 seasons. The x axis labels correspond to the day and the

month (dd/mm) in the reproduction season. The white rectangles correspond to the observation window of the spawning activity (effective auditory survey)

between egg laying and 14 dph was plotted for each season in Fig. 4. Exposure to low temperatures (below the minimum of the optimal range) affected a higher proportion of spawning acts, particularly in 2008, 2010 and 2013, than exposures to high temperatures (above the maximum of the optimal range).

TSR remained stable at approximately 55% of the survival except for the 2013 season when an especially low survival (35%) was recorded (Fig. 5a). For eight of the 11 studied seasons, the efficiency of reproduction is higher than the one obtained by random reproduction activity (Fig. 5b). In these cases, the efficiency is higher than 80%.

Discussion

Interest of cumulative mortality from 14-dph larvae, TSR and I_{TSR}

This work corresponds to the first application of thermal performance curves of embryos and larvae (Jatteau et al. 2017) to field temperatures according to the seasonal time series of reproduction acts. It was possible to estimate the global efficiency of allis shad reproduction in terms of offspring survival for 11 spawning seasons in the Garonne River. This study also offers the possibility to test whether the laying tactic exhibited by this species optimises the survival of its early development stages as

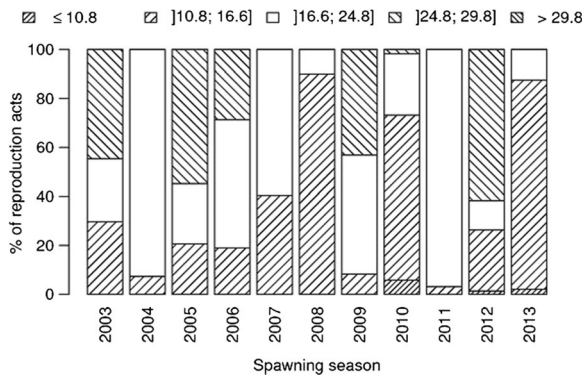


Fig. 4 Evolution according to spawning season of the proportion of spawning acts assigned to the worst class associated with the temperature between egg laying and 14 dph. The class limits are based on tolerance and optimal thermal ranges of Jatteau et al. (2017)

postulated by Quinn and Adams (1996) for species with a close temporal and spatial connection between the environments experienced by spawners and their progeny. More generally, it provides insights on the adaptive abilities of allis shad in response to climate warming.

TSR assumptions

The computation of the TSR relies on several assumptions.

- 1) Jatteau et al. (2017) estimated survival curves on shad from the Nivelle River (Fig. 1), whereas the field data used in this application were collected from the Garonne River, which is approximately

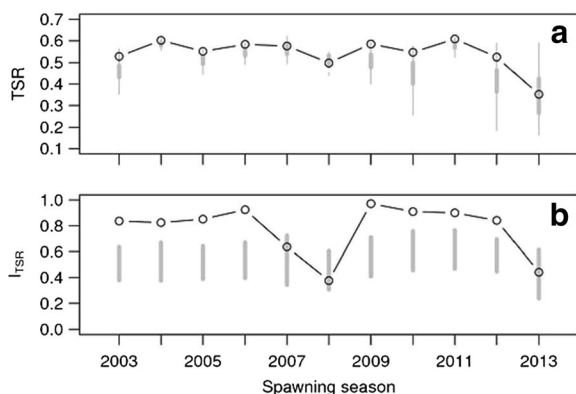


Fig. 5 Evolution of (a) the thermal survival of recruitment (*TSR*) and (b) the reproductive efficiency (I_{TSR}) according to the spawning seasons (thin vertical segments indicate the difference between the minimum and maximum of *TSR*, thick segments indicate the range corresponding to a 95% distribution of *TSR* or I_{TSR} for random reproduction behaviour)

250 km away. The possible local differences in thermal tolerances are implicitly neglected. First, Hundt et al. (2015b) found similar optimal thermal ranges for fish from the Garonne River. This putative local adaptation to temperature is impaired by straying between the catchments in the Bay of Biscay though individuals from the Nivelle Catchment displayed a higher level of genetic differentiation (Martin et al. 2015). Moreover, the Nivelle River displays less suitable thermal conditions for early stage survival than the Garonne River (Jatteau et al. 2017).

- 2) Survival models of embryos or larvae that were calibrated at a constant temperature are applied to the fluctuating temperatures in the natural conditions. This assumption does not take into account the possible acclimation (Moss 1970; Reynolds 1978), which will lead to an overestimation of the survival.
- 3) Mean daily temperatures mask fluctuations throughout the day (Wehrly et al. 2009) and variations at the microhabitat scale. More extreme conditions may be experienced by the fish, and, thus, the survival calculation may also be inflated.
- 4) The egg number per spawning act is assumed to be constant throughout the reproductive season. Shad are fractional spawners with batch fecundity that is highly variable between individuals (Olney and McBride 2003; Hyle et al. 2014). However, even if the variability of the batch fecundity during a batch sequence for an individual or the evolution of the batch fecundity along the reproduction season are suspected (Chambers and Leggett 1996), no information is available for the allis shad.

Accepting these assumptions, the TSR can be used to explore direct consequences of temperature on the off-spring survival in the Garonne River.

Effect of cold temperatures

The TSR indicated that the most affected years in regard to spawning were not those with high temperatures. Indeed, the highest mortality obtained for 2013 coincided with a high proportion of spawning acts affected by extremely low temperatures (Figs. 4 and 5a). The slightly high mortality obtained for 2003, 2008 and 2012 also coincided with low temperatures, although to a lesser extent. Similar temperature optimal ranges for American

and allis shad early stages allow comparison between the two species (Jatteau et al. 2017). Higher mortality with lower temperatures was also reported for the American shad (Nack et al. 2015). This result is in agreement with the more numerous reports in the literature of death due to low temperatures than those attributed to heat (see Beiting et al. 2000 for a review).

Effect of warm temperatures

Increased larval survival of *A. sapidissima* was associated with higher water temperature (Crecco and Savoy 1985). Likewise, Ross et al. (1993) did not observe a reduction in American shad larval density during field sampling between 26 and 27 °C. Individuals in the embryonic stage rarely (or never) encounter a temperature higher than 25 °C because the spawning period is early in the season (Cassou-Leins et al. 2000) and because the potential future spawners can be blocked or die before spawning, which was suspected during the 2003 heat wave (Travade and Carry 2008). Nevertheless, older larvae could potentially be affected by higher temperatures and low levels of oxygen. Preliminary laboratory experiments for three-month-old juveniles have shown high sensitivity to hypoxia at 25 °C (Jatteau and Fraty 2012). These conditions were occasionally recorded during the summer migration of allis shad in the Gironde Estuary (Lanoux et al. 2013). Even with their higher tolerance, the negative impact of warm temperature risks to be exacerbated by climate change in the future.

Stability in survival

A clear survival sensibility to temperature was experimentally shown for allis shad until 14 dph (Jatteau et al. 2017). Surprisingly, the present estimations of TSR suggest that the mean survival only fluctuated between 50% and 61% between 2003 and 2012 and dropped to 35% only in 2013 (Fig. 5a). This relative stability cannot be explained by a lack of temperature changes (Fig. 4). Seasons 2004 and 2011 can be considered suitable with more than 90% of the reproduction within the optimal temperatures when seasons 2003, 2005 and 2010 are unfavourable with only 25% of the reproduction acts within the optimal range. The objective of this work was not to discuss all the possible causes of the collapse (see Rougier et al. 2012 for a review) but the present result confirms that the unfavourable thermal conditions, at least for fish up to 14 dph, were probably

not responsible for the recruitment failures. Nevertheless, an explanation of the population decline may be explored in the survival of older juveniles, possibly affected by the extreme thermal and oxic conditions in mud plug during estuarine migration. Alternatively, this result may suggest that allis shad adapted its spawning tactic to be able to mitigate the negative effects of extreme temperatures.

I_{TSR} assumptions

For the sake of simplicity, computation of the randomness in I_{TSR} does not integrate any constraints in the seasonal distribution of the reproductive act number that may be induced by environmental conditions, internal fish states or interactions between individuals. A more comprehensive but more complex approach based on migrating and spawning behavioural rules (Jonsson and Jonsson 2009) should exceed this limitation. Data on timing of the arrival at the spawning grounds, evolution of the spawner density on the spawning grounds and variability of the spawning interval will be required but not easily available. Interannual variation in migratory timing is correlated with river temperature, i.e., colder temperatures delay migration while warmer temperatures advance it (Leggett and Whitney 1972; Quinn and Adams 1996). River discharge also influences the river temperature (Acolas et al. 2004). These relationships will have indirect consequences on the young stages of survival. On average, a female shad copulates from two to 10 times in a season (Olney and McBride 2003; Acolas et al. 2004, 2006; Hyle et al. 2014) with a 2–3 day spawning interval (Olney and McBride 2003; Hyle et al. 2014). This variability induces differences in the residency times on the spawning grounds and thus differences related to environmental conditions that the spawners experience.

Spawning tactics

The I_{TSR} evolution clearly showed that allis shad exhibits a spawning tactic that is more efficient than a simple random tactic in eight seasons among the 11 that were studied (Fig. 5b). This is in accordance with Quinn and Adams (1996) who predicted that shad would employ plasticity to respond to river conditions because of the short-time interval between adult migration timing and larval emergence. For example, the females can anticipate the conditions that their offspring will

experience a few days later by starting spawning when the temperature is still under the optimal range but increasing.

The 3 seasons with a suboptimal spawning tactic (2007, 2008 and 2013) are similar to cases of low spawning activity. This could be explained by a lack of breeding synchrony due to less social facilitation (Clayton 1978; Ochi 1986). Nevertheless, this mechanism is not the only one because in 2012, the abundance was also very low but I_{TSR} was high (Figs. 2 and 5b). Furthermore, cold temperatures can explain spawning tactic failures in 2008 and 2013 (Fig. 4). However the cold 2010 season was not associated with a low spawning efficiency. Discharge is also suspected of playing a role in spawning tactic failures (Acolas et al. 2006). The 2008 and 2013 seasons showed low I_{TSR} (Fig. 5b) and recorded floods during the spawning period (www.hydro.eaufrance.fr). However, the high discharge peaks observed in 2010 and 2012 were not reflected in the poor efficiencies of the spawning tactic. Consequently, underlying thermal behavioural rules still need to be expanded to clearly understand the failures in the reproduction efficiency.

Adaptation and shift distribution

Modelling studies of allis shad distribution suggests a preference of warm water for this species (Béguer et al. 2007) and predicted a northward shift in future climate change scenarios (Lassalle and Rochard 2009; Lassalle et al. 2009). Field observations reported the first signs of a natural recolonisation of the Seine River watershed (Belliard et al. 2009), which may herald this northern movement. Movement to the northern basins will likely be facilitated if the temperatures continue to increase during the spawning season (Rougier et al. 2015). The present results indicate that allis shad in the early stages of development are not strongly constrained by high temperatures because of suitable thermal tolerance of the early stages and the efficient egg laying tactic of the spawners.

However, even though it is unlikely in the near future, increasing temperatures could impair the efficiency of the spawning tactic (dramatic declines of TSR and I_{TSR}) and lead to a possible maladaptive response to climate change (Kennedy and Crozier 2010; Crozier and Hutchings 2014). In this case, behavioural plasticity alone will not be sufficient to allow a shift in shad distribution, and hence, genetic evolution in the

reaction norm will be needed to face ongoing global warming (Visser 2008).

Management perspectives

From a management perspective, TSR can be used to predict recruitment survival and anticipate when anthropogenic mortalities (fishing, pumping, etc.) should be reduced to strengthening the weak cohorts. The TSR could be easily used in a report card similar to that for the shad population in Gironde (Collin and Rochard 2012). It can also help to explain the efficiency variability of a stocking programme similar to the one implemented in the Rhine (Hundt et al. 2015a) and to optimise the release procedure. In the medium term, a higher frequency of low I_{TSR} will provide information concerning the risk of maladaptation of the spawning tactic to new environmental conditions and then the need to reinforce population protection.

Conclusion

A combined analysis of reproduction activity and fluctuations of expected embryo-larval mortality due to temperature confirms Quinn and Adams' (1996) hypothesis that shad selection favours an efficient spawning tactic to anticipate favourable thermal conditions for the survival of their offspring. Underlying behavioural rules still need to be explicitly formulated. New environmental conditions induced by ongoing climate change will challenge this behavioural plasticity. In the case of maladaptation coupled with no genetic evolution, the shift of shad distribution would be undermined.

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