Growth rates in two natural populations of *Gasterosteus aculeatus* in northwestern Spain: relationships with other life history parameters

E. San Miguel, R. Amaro, J. Castro, M. Hermida, C. Fernández

Abstract

Growth rates in two natural populations of Gasterosteus aculeatus *in north–western Spain: relationships with other life history parameters.* We analysed growth rates of two natural populations of the three–spined stickleback fish, *Gasterosteus aculeatus*, in Galicia (north–west of Spain) where it has a strictly annual life cycle. We used the von Bertalanffy growth model to estimate nonlinear function for length–at–age data sets. These European peripheral populations reach the highest growth rates (*k* of the von Bertalanffy model > 0.4 month^{-1}) known for this species. Instantaneous mortality rates and fecundity were computed using von Bertalanffy model parameters for each population. Mortality rates found in Galician populations were 2.0–2.3 higher times than those observed in general for Gasterosteidae. Combining both mortality and fertility, different intermediate fitness optima in each population were obtained for mature females. Overall, these differences in life history compared to other studied populations of sticklebacks can be interpreted as local adaptations to a Mediterranean climate type with high degree–days. Consequently, these populations at the edges of the species' range may have adapted to the unique environmental conditions and may be of interest in ecology and conservation.

Key words: Ontogenetic growth, Peripheral populations, Semelparous, Fitness, Natural mortality, Half–life, *Gasterosteus aculeatus*

Resumen

Tasas de crecimiento en dos poblaciones naturales de Gasterosteus aculeatus *en el noroeste de España: relación con otros parámetros vitales.* Se analizaron las tasas de crecimiento de dos poblaciones naturales de Galicia (noroeste de España) del pez espinoso *Gasterosteus aculeatus*, cuyo ciclo biológico es estrictamente anual. Para ello, se utilizó una función no lineal para conjuntos de datos de longitud por edad: el modelo de crecimiento de von Bertalanffy. Estas poblaciones europeas periféricas tienen las tasas de crecimiento más altas (k en el modelo de von Bertalanffy > 0,4 mes^{-1}, en promedio) conocidas para esta especie. A partir de los parámetros del modelo de von Bertalanffy, se calcularon las tasas de mortalidad instantánea y de fecundidad de cada población, y se observó que las tasas de mortalidad de las poblaciones gallegas son de 2 a 2,3 veces superiores a las observadas en general en Gasterosteidae. La combinación de la fertilidad y la mortalidad produjo diferentes valores óptimos intermedios de eficacia biológica para las hembras maduras de cada población. En términos generales, estas diferencias encontradas en rasgos vitales con respecto a otras poblaciones estudiadas de pez espinoso se pueden interpretar como adaptaciones locales a un clima de tipo mediterráneo con un valor alto de grados–día. Por tanto, estas poblaciones situadas en los límites de la zona de distribución de la especie pueden estar localmente adaptadas a condiciones ambientales muy específicas y pueden ser de interés en los ámbitos de la ecología y la conservación.

Palabras clave: Crecimiento ontogenético, Poblaciones periféricas, Semélparas, Eficacia biológica, Mortalidad natural, Vida media, *Gasterosteus aculeatus*

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Introduction

The Mediterranean region is a biodiversity hotspot for freshwater ecosystems, harbouring many species (many of them endemic) and genetically distinct lineages that are of conservation concern (Araguas et al., 2012; Sharda et al., 2018). One of these species is the three–spined stickleback *Gasterosteus aculeatus,* L. It is a small teleost fish and is a model organism in evolutionary biology and ethology (Bell and Foster, 1994; Mäkinen et al., 2006; Cresko et al., 2007; Mäkinen and Merilä, 2008). This fish is widely distributed throughout the northern hemisphere in latitudes ranging from 35º to 70ºN (Crivelli and Britton, 1987). The Iberian Peninsula is the southern limit in the East Atlantic Ocean (Fish-Base, 2019). The species lives in a variety of habitats (marine, streams, rivers, lakes), leading to a high level of phenotypic variation (Bell and Foster, 1994). Iberian Peninsula populations are mainly located in freshwaters habitats in Portugal and Galicia (a region in northwest Spain). In the rest of Spain, they are limited to fragmented populations (Doadrio, 2002).

The Galician populations of *G. aculeatus* have been evaluated on the basis of their morphometric and meristic characteristics by multivariate analysis (Fernández et al., 2000; Hermida et al., 2005a, 2005b). Heritabilities for some meristic characters have also been estimated in a natural population (Hermida et al., 2002). More recently, Pérez–Figueroa et al. (2015) obtained the first estimate of *Ne* / *Nc* (effective population size/population census) in Galician rivers using molecular markers. The genetic diversity (assessed by nuclear and mitochondrial markers) for local stickleback populations has also been discussed in relation to its phylogeography and conservation in the wider context of Ibero–Balearic populations (Vila et al., 2017).

Galician sticklebacks constitute peripheral populations and are in greater peril than central populations, like various other animal and plant species (Lesica and Allendorf, 1995; Guo et al., 2005). Lying at the southern edge of the species´ European range, they appear to be close to their physiological and reproductive limits, and have undergone local extinction in the recent past (Vila et al., 2017). *G. aculeatus* is currently classified as endangered under IUCN criteria in both Spain and Portugal (the two Iberian countries). In particular, in Spain the species is classified as vulnerable (Doadrio, 2002) and the local government of Galicia (Xunta de Galicia) includes it in its catalogue of threatened species (CATGEA, 2007).

Any conservation measures aimed at protecting this species require understanding of life history strategies, meaning the evaluation of their life history traits, under natural conditions, if possible. Life history traits are of great interest, especially in this species, *G. aculeatus*, whose populations have evolved by finding many different ways to combine these traits to affect fitness (Bell and Foster, 1994; Baker et al., 2015). Given the climatic differences between the Iberian Peninsula and northern Europe, the southern limit populations are probably subject to different selective forces and will show adaptations not found in northern populations. For example, *G. aculeatus* is a strictly annual species

in Galicia (Fernández et al., 2000; Pérez–Figueroa et al., 2015): fish breed once in the year following their birth and die shortly after breeding (a semelparous life history), as many dead adults can be found among thousands of young fish. This annual cycle, which is usual in southern populations (Crivelli and Britton, 1987; Clavero et al., 2009), is exceptionally found in some European northern populations (Wootton et al., 2005).

Another topic of long interest in conservation and evolution of life history is the description of ontogenetic growth. Data on growth of *G. aculeatus* Iberian populations are scarce, but they are necessary to contribute to knowledge of their biology and to design effective conservation strategies in Galicia. One of the purposes of this study was to estimate growth parameters from length–at–age data obtained in natural conditions –in two Galician rivers– applying the von Bertalanffy growth function (VBGF) (Ricker, 1979).

Empirical studies in teleost fishes have demonstrated a significant connection between growth parameters and life history attributes such as natural mortality and fecundity (Wootton, 1979; Roff, 1984; Gunderson, 1997; Mangel, 2006). Thus, we combined our study on individual growth with the survival exponential distribution and fecundity to obtain lifetime reproductive output. In this way we could describe the lifetime expected reproductive success (ERS) or fitness as the product of survival and fecundity at maturity (Roff, 1984; Mangel, 2006). From this last function, we deduce that fitness will reach a maximum at an intermediate age at maturity (Roff, 1992, 2002) and it is relevant for comparative purposes among populations. In general terms, this work aims to increase our knowledge of the biology of semelparous populations of this species in the Iberian Peninsula with a view to establishing appropriate conservation strategies.

Material and methods

Study area and sampling collection

The samples used for this study come from two rivers (fig. 1): the Rato River (Rato 29T619547, 4761482; 2.8 km from Miño) and the Asma River (Asma; 29T601686, 4717706; 5.5 km from Miño). Both rivers are tributaries of the Miño River (the main Galician river), and are located, and isolated, upstream and downstream by the Belesar dam. Such isolation impedes movement of fishes and configures an important drainage area of Galicia (Pérez–Figueroa et al., 2015). The samples were collected monthly between May and November 1998 using hand nets with a mesh size of 2 mm, selecting specimens greater than 12 mm in length (from tip to tail). All samples were measured using a digital calliper to the nearest 0.01 mm, and then returned to the water. At all times, this work was carried out under the supervision of forest rangers from the autonomous government (Xunta de Galicia).

The annual cycle is usual in southern populations of *Gasterosteus aculeatus* (Clavero et al., 2009; Fernández et al., 2000; Pérez–Figueroa et al., 2015). Analysis of otoliths (unpublished data 2005, Asma River) revealed
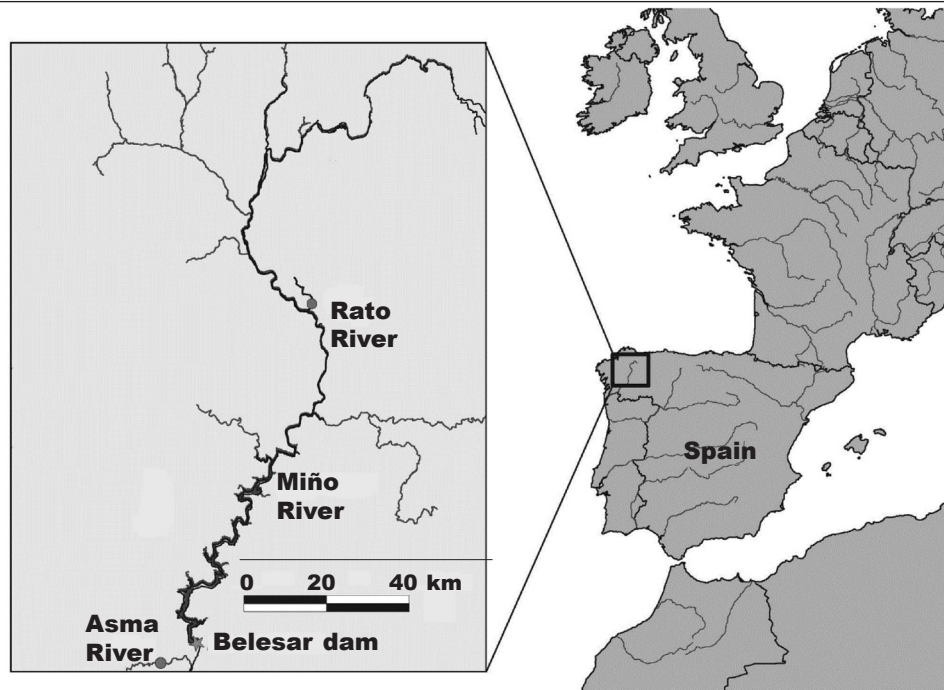
Fig. 1. Map of the Miño River basin and its location in Spain. Circles show the sampling points. The star represents the location of the Belesar dam that isolates the upstream basin.

Fig. 1. Mapa de la cuenca del río Miño y su situación en España. Los círculos indican los puntos de muestreo. La estrella indica la situación del embalse de Belesar, que aísla la cuenca superior.

that more than 97 % of reproductive adults collected in May or June (with more than 46 mm of standard length) are born in the previous year (age 1+), while fishes between 21 and 25 mm are born in the current year (age 0+). Thus, most fishes captured for our analysis in the two rivers from May to November were cohorts born in 1998, i.e., they belonged to the same generation.

Growth parameters, natural mortality, fecundity and expected reproductive success

The length–at–age data were employed to fit the von Bertalanffy growth function nonlinear model, hereafter referred to as VBGF, which has the form:

$$L_t = L_\infty (1 - e^{-k(t - t0)}) \qquad (1)$$

where L_t is length (in mm) at age t (in months); L_∞ is the asymptotic length (theoretical final length); k is the growth rate (month^{-1}); and t_0 is a constant to improve the fit and it generally takes very small values.

We also note that the rate constant k has units of reciprocal time and is difficult to interpret. It describes the speed at which the maximum size (asymptotic size) is reached; for example (assuming $t_0 = 0$), when $k = 0.5$, an individual attains 90% of its asymptotic length in 4.6 months; while if $k = 0.3$, it takes 7.6 months to reach this percentage.

Natural mortality (m), which is closely related to the growth parameters, and especially to the parameter k of semelparous organisms, can be expressed as (Roff, 1984; Mangel, 2006):

$$m = (3k) / (e^{kT} - 1) \qquad (2)$$

where T is the age at maturity (about 12 months for Galician stickleback populations).

On the other hand, supposing that survival to age t is given by the exponential distribution

$$l(t) = e^{-mt} \qquad (3)$$

where the natural mortality rate is fixed, and that the organism (female) matures at age t; and that fecundity is given by:

$$f(t) = a (L_t)^b \qquad (4)$$

where a and b are allometric parameters.

Combining both expressions (survival (3) and fecundity (4)), we can now define fitness or lifetime expected reproductive success as

$$R(t) = l(t) \ f(t) \qquad (5)$$

Due to legal regulations in Galicia, no more than

Table1. Number (*N*) of sticklebacks (total length) measured monthly in the Asma and Rato rivers; mean values ($\overline{X}$) and their standard errors (SE).

Tabla 1. Número (N) de ejemplares de pez espinoso medidos (longitud total) cada mes en los ríos Asma y Rato; valores medios ($\overline{X}$) y sus errores estándar.

Population		May	June	July	August	September	October	November
Asma	N	21	45	21	50	50	50	50
	$\overline{X}$	17.64	23.71)	39.54	46.20	46.50	46.67	47.00
		(0.40)	(0.35)	(1.13)	(0.07)	(0.05)	(0.07)	(0.07)
Rato	N	20	27	39	22	27	50	37
	$\overline{X}$	16.3	21.76	34.69	38.58	40.98	46.32	46.54
		(0.45)	(0.46)	(0.31)	(1.01)	(0.66)	(0.08)	(0.10)

Table 2. Parameter estimates for a von Bertalanffy growth function (VBGF) for each population. Values in parentheses are approximate lower and upper bounds for 95% confidence intervals.

Tabla 2. Estimaciones de los parámetros de la función de crecimiento de von Bertalanffy (VBGF) para cada población. Los valores entre paréntesis son los límites aproximados superior e inferior para intervalos de confianza del 95%.

	r^2 (%)	t_0	k	L_∞
Asma	90.00	0.37 (0.25–0.48)	0.52 (0.46–0.57)	50.33 (49.16–51.49)
Rato	92.53	−0.03 (−0.21–0.15)	0.32 (0.27–0.36)	53.16 (50.74–55.58)

two or three females can be collected per river. We thus trapped 28 females throughout the breeding season (May to early August) from ten tributaries of the Miño basin (including Asma and Rato rivers). The ovaries were dissected and all oocytes were counted. Fecundity ranged from 39 to 148 eggs, depending on the size (total length) of the female.

All model parameters and their standard errors (*SE*) were estimated using non–linear regression analysis by means of the GraphPad Prism version 4.0 for Windows (GraphPad Software, La Jolla California USA, www.graphpad.com).

Results

Table 1 shows the growth data in length of the cohorts born in 1998 by seven monthly sampling. Table 2 shows the growth parameters and confidence intervals estimated using the von Bertalanffy model.

By averaging r^2 values, we obtained 91%, which indicates good performance of the model, i.e. VBGF accounted for 91% of the variance in total length exhibited by these populations. The estimates of t_0 were very small, ranging from –0.03 to 0.37 months.

This parameter can therefore be confidently set to zero with very little effect on the model's performance. The estimates of *k* showed a marked difference when their confidence intervals were compared, and the Asma population showed the highest *k* value (0.52 month^{-1}). However, a similar comparison for L_∞ values did not show a significant difference between the studied rivers. Figure 2 shows the representative VBGF curves resulting from all these parameters. As age increases the relative differences in size also decrease for populations with different growth functions.

The instantaneous rate of mortality for each population, obtained by the expression (2), were 0.19 and 0.21 for Asma and Rato rivers, respectively. We applied these values to compute the probability of survival (e^{-mt}) in both populations as described by predicted survival curves in figure 3 (red lines), assuming constant *m* values throughout the life of mature females. Both curves showed a similar appearance: survivorship dropped precipitously in early sexual maturity until a certain age was reached, at which moment the rate of decline was substantially reduced.

The allometric parameters (*a* and *b*) related to fecundity (fig. 4) took the values 2.7×10^{-4} (SE = 5.4×10^{-4}) and 3.2 (SE = 0.5), respectively (with
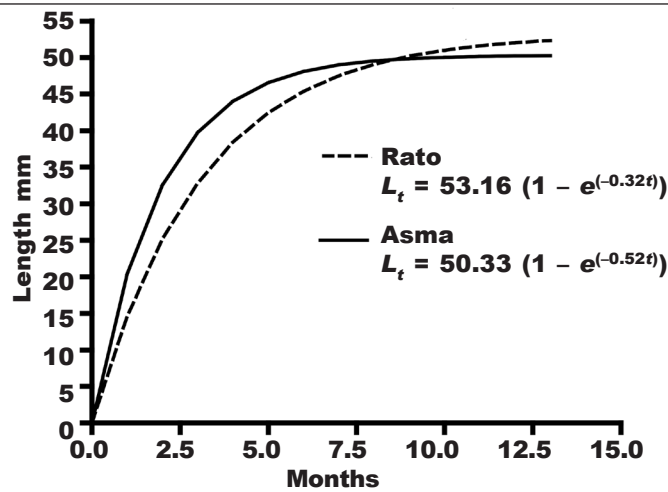
Fig. 2. Estimates of von Bertalanffy growth curves for natural populations of *Gasterosteus aculeatus* from the Asma and Rato rivers.

Fig. 2. Curvas de crecimiento de von Betalanffy estimadas para poblaciones naturales de Gasterosteus aculeatus *de los ríos Asma y Rato.*
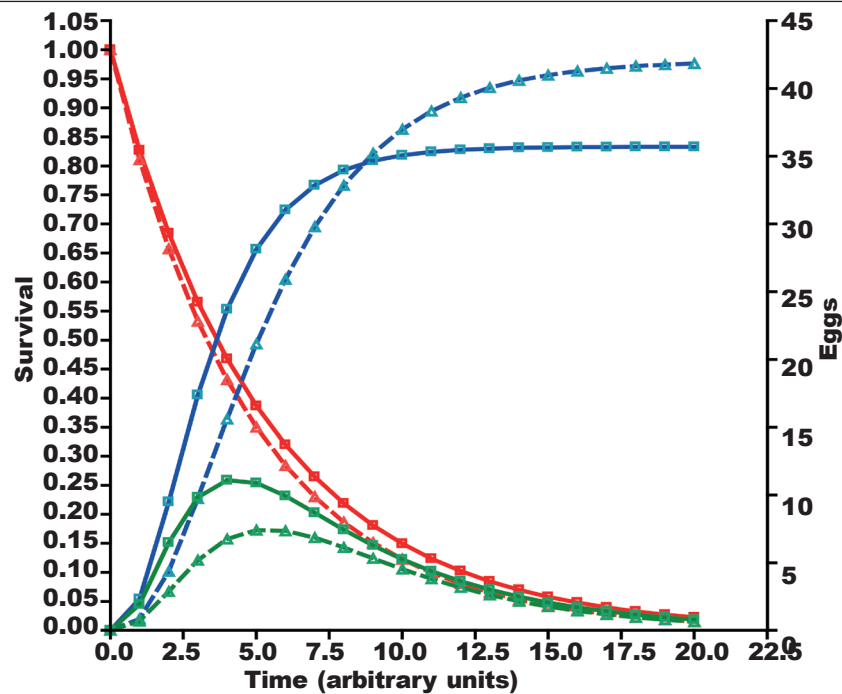

Fig. 3. Probability of mature females surviving (e^{-mt}, red lines) to reproduce (assuming a constant mortality rate), expected fecundity ($a(L_t)^b$, blue lines) and expected reproductive success (green lines) defined by $e^{-mt}a(L_t)^b$, as a function of age at maturity, in two (Galician) semelparous populations of *Gasterosteus aculeatus*. (Asma River, continuous line; Rato River, dashed line).

Fig. 3. Probabilidad de supervivencia (e^{-mt}*, líneas rojas) hasta la reproducción en hembras maduras (suponiendo una tasa de mortalidad constante), fecundidad esperada (*$a(L_t)^b$*, líneas azules), y eficacia biológica esperada (líneas verdes) definida por* $e^{-mt}a(L_t)^b$ *en función de la edad de madurez de dos poblaciones semélparas de* Gasterosteus aculeatus *en Galicia (río Asma, línea contínua; río Rato, línea discontinua).*
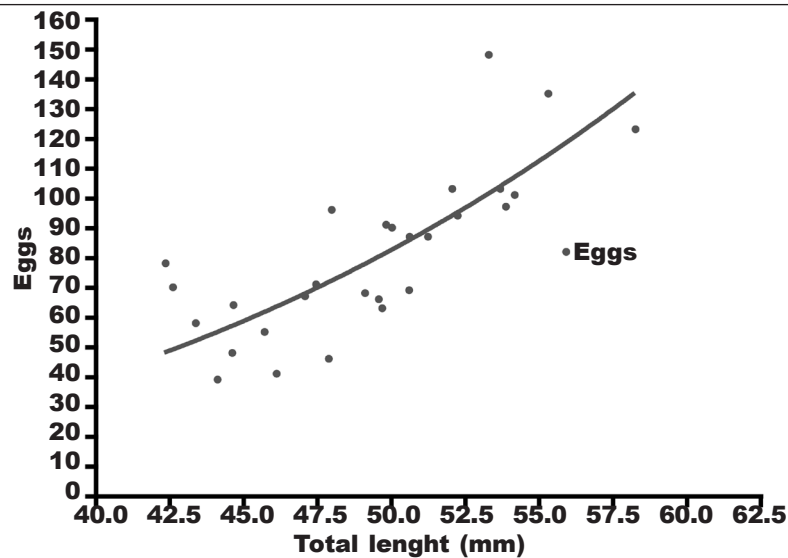
Fig. 4. Scatter diagram showing a typical (allometric) relationship between fecundity and total fish length from *Gasterosteus aculeatus* in the Miño basin.

Fig. 4. Diagrama de dispersión en el que se muestra una relación típica (alométrica) entre la fecundidad y la longitud total de hembras de Gasterosteus aculeatus *de la cuenca del Miño.*

$r^2 = 0.62$). As many empirical studies in fish species have shown that value of allometric *b* parameter is about 3 (Gunderson, 1997; Mangel, 2006; Roff, 1984), this value was used in the subsequent analysis.

After applying the expressions (3) and (4), we obtained expected fecundities and reproductive success (expression (5)) as functions of age at maturity for females (see fig. 3). At first, fecundities increased with age and then remained stable. With respect to fitness, both populations showed a maximum at an intermediate age but at different moments. This value was slightly higher for the Asma population (green lines in fig. 3).

Discussion

In a wide sense, the reproductive lifespan in a semelparous species is restricted to a single breeding season, even if age at maturity does not occur until after several years of development, such as in Pacific salmon species (Wootton and Smith, 2015). Life spans (and age at maturity) of *G. aculeatus* have been reported in many studies using otoliths, spines annuli, annual rings on the operculum and length–frequency plots (Bell and Foster, 1994; Yershov and Sukhotin, 2015). These studies comprise natural populations with different lifestyles (marine, stream dwelling, anadromous, lacustrine; revisions by Jones and Hynes, 1950; Wootton, 1984; Bell and Foster, 1994; Yershov and Sukhotin, 2015; FishBase, 2019). In general terms, their findings have concluded that this fish lives for a maximum of 1 to 5 years. Labo-

ratory populations can reach 5 years, and Reimchen (1992) reported an exceptional large–bodied natural population that attained eight years. Wootton (1984) suggested a gradual change (a north–south cline) as populations at higher latitudes are more long–lived, but his hypothesis did not reach statistical significance because some high–latitude populations are also short–lived (Giles, 1987). The Galician populations fit this geographical trend, so that a strictly annual cycle can be established as in other populations of sticklebacks at similar latitudes in Spain and France (Crivelli and Britton, 1987; Clavero et al., 2009). The length of time that an organism lives can have a relevant effect on other life history traits such as fecundity and survival.

Values on mortality rates and growth rates on *G. aculeatus* and nearby species (Gasterosteidae such as *Apeltes quadracus*, *Pungitius pungitius*, and *Spinachia spinachia*) reported to date are expressed in years[−1] (table 3). For comparative with our results, we divided these values by 12. Estimates of mortality (the exponential coefficient of mortality) and growth rates (and therefore $L_∞$) in natural conditions are usually hard to obtain. We found only 12 estimates for *k* and 3 for *m* (most of them for unsexed populations), considering *G. aculeatus* and other related closely species (FishBase, 2019; Yershov and Sukhotin, 2015; Roff, 1984; Pauly, 1980: Beverton and Holt, 1959). These estimates (table 3) varied from 0.048 to 0.280 and between 0.075 and 0.120 for *k* and *m*, respectively. Therefore, our estimates for Galician populations of sticklebacks are the largest reported so far. However, asymptotic values for Asma and Rato populations

Table 3. Estimates of growth rate (*k*) and instantaneous mortality (*m*) taken across a number of studies on Gasterosteids (FishBase, 2019).

*Tabla 3. Estimaciones de la tasa de crecimiento (*k*) y de la mortalidad instantánea (*m*) según varios estudios sobre gasterosteidos (FishBase, 2019).*

Species	*k* (1/*y*)	*m* (1/*y*)	Sex	Location	Latitude
G. aculeatus	0.57		M	Kandalaksha (RUS)	67º 09'
G. aculeatus	0.67		F	Kandalaksha (RUS)	67º 09'
G. aculeatus	1.79			Kiel Bay (GER)	54º 31'
G. aculeatus	0.64	0.9		Chesire (UK)	53º 14'
G. aculeatus	2.32			Ooster Schelde (NED)	52º 30'
G. aculeatus	2.4		F	Roscoff (FR)	48º 44'
G. aculeatus	4.2		M	Roscoff (FR)	48º 44'
G. aculeatus	1.78			Navarro River (USA)	39º 09
G. aculeatus	1.77			Navarro River (USA)	39º 02'
G. aculeatus	2.09			Navarro River (USA)	39º 11'
Apeltes quadracus	0.84	1.4	F	Chesapeake Bay (USA)	38º 19'
Apeltes quadracus	1.5		M	Chesapeake Bay (USA)	38º 19'
Pungitius pungitius	1.6	1.1		Chesire (UK)	53º 14'
Spinachia spinachia	1.78			Kiel Bay (GER)	54º 31'

are intermediate among those found in FishBase for Gasterosteidae after applying VBGF. Estimates of *m* here presented were obtained by the expression (1), that is, *m* is *k* dependent [more theoretical evidence for this can be found in Charnov (1993), Mangel (2006), Roff et al. (2006), and Hamel (2015)]. Furthermore, based on independent estimates of *k* and *m* in natural populations of hundreds of fish species, Pauly (1980) found a significant correlation between the two parameters, suggesting that *k* is a good predictor of *m* [for example, high *k* values correspond to high *m* values (Hamel, 2015)]. Thus, our *k* values may be sufficient to obtain a rough (approximate) estimate of *m*, and confirming that high mortality rates will in general be associated with low ages at first reproduction (Roff, 1984; Mangel, 2006).

Values *m* and *k* are also related to mean environmental temperature (Pauly, 1980). Ziuganov et al. (2010) recorded water temperatures in the Arctic region (1,750–1,850 degree–days) and Galicia (4,750–5,000 degree–days). The growth rate of Galician populations of *G. aculeatus* was at least 6–10 higher times than those of Artic populations (Yershov and Sukhotin, 2015), and mortality constants found in Galician populations were 2.0–2.3 times higher than those observed in general for Gasterosteidae (Roff, 1984). With higher mean annual temperatures in the south, the increment in metabolic rate would tend to increase growth rate.

Natural mortality, as defined in the literature, is made up by all possible causes of death except for fishing. These can include, for example, mortality caused solely by disease, by old age, or by both, or mortality proportional only to the number of potential predators. Causal (direct) and non–causal relationships between mortality and temperature in fish have been proposed. For example: temperature determines *m* via *k* increasing physiological mortality by aging; fishes living at higher temperatures have more chances to have encounters with predators (Charnov, 1993). We cannot specifically assign mortality to any of the aforementioned causes, and several of them may be acting at the same time on Asma and Rato stickleback populations.

Therefore, our Iberian (Galician) populations may have adapted to local conditions within the European population context of *G. aculeatus*. These local populations are also peripheral populations of *G. aculeatus*. In ecology, central (core) and peripheral populations are key components to be considered. Peripheral populations are essential in terms of species biogeography, evolution and conservation (Lesica and Allendorf, 1995). Peripheral populations in natural conditions exist under different environmental conditions and are distinct from core populations. Thus, marginalized populations at the edge of the species distribution range must be integral parts of the conservation efforts for global biodiversity (Johannesson and André, 2006). Asma and Rato populations may represent particular genetic (Hermida et al., 2002; Vila et al., 2017) and phenotypic (Fernández et al., 2000;

Hermida et al., 2005b) adjustments to their environments, and variations in growth and mortality rates here reported with respect to northern populations can enhance their conservation value.

Expression (4) predicts fitness in adult females of a semelparous organism (most species of fish are iteroparous) using two pieces of information: probability of survival to reproduce decrease with a constant mortality rate (e^{-mt}) and the assumption that fecundity is a power function of length. Mathematical models making these assumptions accounted for more than 80 % of the variation in natural populations of lizards, salamanders, and fish (Stearns and Koella, 1986; Stearns and Hoekstra, 2005). Thus, age at maturity appears to be adjusted to different intermediate fitness optima in each population (fig. 3), that is, the peaks of the curves are linked to specific age at maturity. The age at maturity in this mathematical model is the age at which the survival fecundity curve has a turning point or peak, that is, up until this age the product survival fecundity increases while after this age it decreases. Age at maturity and fitness are plastic traits that can respond to natural selection because they can vary among close related species, among populations within species, and among individuals within populations.

It is widely accepted that global climate change (warming or cooling) is impacting on marine and freshwater fish and will continue to do so (Moss, 2010). Most data on climate–induced effects have been obtained for commercially relevant species, while those that are not targeted by fisheries have received less attention. Non–commercial short–lived species are of special interest because climate–induced effects on their populations could be more clearly recognized than in exploited species (Yershov and Sukhotin, 2015). Data trends show climate change effects ranging from fish growth, digestion physiology and performance in marine and freshwater ecosystems: the literature is replete with studies on increased growth rates at elevated temperatures between and within fish species (Mazumder et al., 2015). As ectotherms fish cannot thermoregulate physiologically, but only behaviourally by moving to areas with appropriate temperatures, even a small increase in temperature may thus put them at high risk of extinction (Tewksbury et al., 2008). Cross–comparisons of fish populations in similar systems in South America and Europe and within Europe have shown that lower–latitude fish species are often not only individually smaller but also grow faster, mature earlier, have shorter life spans and allocate less energy to reproduction than species at higher latitudes (Jeppesen et al., 2012). As we have indicated there is a relationship between m and environmental temperature, but m is also connected to the half–life of our female cohorts. Half–life is a statistic used by demographers to measure the time it takes for half of a cohort of organisms to die: the equation used to calculate the time taken by the population to decrease to half its initial size is $t = \ln 0.5/m$ (Gotelli, 2008), and applying our estimates of instantaneous mortality rates the half–lives are about 3.6 and 3.3 months (Asma and Rato populations respectively). Climate–induced variation (elevated or low temperatures) in life history

traits (such as mortality) will have consequences in expected reproductive success, and therefore there will be a relevant probability of local extinctions. In Gasterosteids it is difficult to find experiments on a link between climate and populations dynamics, but it has been shown that modestly rising temperatures result in fewer males (*G. aculeatus*) making nests, and less time spent tending the nests (by fanning oxygenated water through them) by those that make them. As a result, fewer young are produced with more than a 2 °C rise in temperature over current values (Moss, 2010). Studies are needed to predict future effects, and highly resilient species, such as the three–spined stickleback, provide indications of what might happen to less robust species.

Acknowledgements

References

Araguas, R., Vidal, O., Pla, C., Sanz, N., 2012. High genetic diversity of the endangered Iberian three–spined stickleback (*Gasterosteus aculeatus*) at the Mediterranean edge of its range. *Freshwater Biology* 57: 143–154.

Baker, J., Wund, M., Heins, D., King, R., Reyes, M., Foster, S., 2015. Life–history plasticity in female threespine stickleback. *Heredity,* 115: 322–334.

Bell, M., Foster, S., 1994. *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press, New York.

Beverton, R. J. H., Holt, S. J., 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: *CIBA Foundation colloquia on ageing: the lifespan of animals,* vol 5: 142–180 (G. E. W. Wolstenholme, M. O'Connor, Eds.). J & A Churchill Ltd., London.

CATGEA, 2007. *Catálogo galego de especies ameazadas*. Xunta de Galicia (Decreto 88/2007 de abril). DOG 89, 7409.

Charnov, E., 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford University Press, Oxford.

Clavero, M., Pou–Rovira, Q., Zamora, L., 2009. Biology and habitat use of three–spined stickleback (*Gasterosteus aculeatus*) in intermittent Mediterranean streams. *Ecology of Freshwater Fish*, 18: 550–559.

Cresko, W., McGuigan, K., Phillips, P., Postlethwait, J., 2007. Studies on threespine stickleback developmental evolution: progress and promise. *Genetica*, 129: 105–126.

Crivelli, A., Britton, R., 1987. Life history adaptations of

Gasterosteus aculeatus in a Mediterranean wetland. *Environmental Biology of Fishes,* 18(2): 109–125.

Doadrio, I., 2002. *Atlas y Libro Rojo de los Peces Continentales de España*. CSIC. Ministerio de Medio Ambiente, Madrid.

Fernández, C., Hermida, M., Amaro, R., San Miguel, E., 2000. Lateral plate variation in Galician stickleback populations in the rivers Mino and Limia, NW Spain. *Behaviour*, 137: 965–979.

FishBase, 2019. Growth parameters for Gasterosteidae. Available from http://www.fishbase.se/popdyn/PopGrowthList_family.php?id=2420&genusname=Gasterosteus&speciesname=aculeatus&fc [accessed on 29 May 2019].

Giles, N., 1987. Population Biology of the three–spined sticklebacks, *Gasterosteus aculeatus*, in Scotland. *Journal of Zoology*, 212: 255–265.

Gotelli, N. J., 2008. *A Primer of Ecology*. Sinauer Associates, Massachusetts.

Gunderson, D., 1997. Trade–off between reproductive effort and adult survival in oviparous and viviparous fishes. *Canadian Journal of Fisheries and Aquatic Sciences,* 54: 990–998.

Guo, Q., Taper, M., Schoenberger, M., Brandle, J., 2005. Spatial temporal population dynamics across species range: from center to margin. *Oikos,* 108:47–57.

Hamel, O., 2015. A method for calculating a meta–analytical prior for the natural mortality rate using multiple life history correlates. *ICES Journal of Marine Science,* 72(1): 62–69.

Hermida, M., Fernández, C., Amaro, R., San Miguel, E., 2002. Heritability and 'evolvability' of meristic characters in a natural population of *Gasterosteus aculeatus*. *Canadian Journal of Zoology,* 80: 532–541.

– 2005a. Geographical and temporal FA variation in threespine stickleback populations from Galicia (NW Spain). *Evolutionary Ecology,* 19: 517–532.

– 2005b. Morphometric and meristic variation in Galician threespine stickleback populations, northwest Spain. *Environmental Biology of Fishes,* 73: 189–200.

Jeppesen, E. Mehner, T., Winfield. I., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmkist, H., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandström, A., Blanco. S., Kangur, A., Ragnarsson, H., Tarvainen, M., Ventelä, A., Søndergaard, M., Lauridsen, T., Meerhoff, M., 2012. Impacts of climate warming on the long–term dynamics of key fish species in 24 European lakes. *Hydrobiologia*, 694: 1–39.

Johannesson, K., André, C., 2006. Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Molecular Ecology,* 15(8): 2013–2029.

Jones, J., Hynes, H., 1950. The age and growth of *Gasterosteus aculeatus*, *Pigosteus pungitius* and *Spinachia vulgaris*, as shown by their otoliths. *Journal of Animal Ecology,* 19(1): 59–73.

Lesica, P., Allendorf, F., 1995. When are peripheral populations valuable for conservation? *Conservation Biology,* 9: 753–760.

Mäkinen, H., Cano, J. M., Merilä, J., 2006. Genetic relationships among marine and freshwater populations of the European three–spined stickleback (*Gasterosteus aculeatus*) revealed by microsatellites. *Molecular Ecology,* 15: 1519–1534.

Mäkinen, H., Merilä, J., 2008. Mitochondrial DNA phylogeography of the three–spined stickleback (*Gasterosteus aculeatus*) in Europe–Evidence for multiple glacial refugia. *Molecular Phylogenetics and Evolution,* 46(1): 167–182.

Mangel, M., 2006. *The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology*. Cambridge University Press, Cambridge.

Mazunder, S. K., De, M., Mazlan, A. G., Zaidi, C. C., Rahim, S. M., Simon, K. D., 2015. Impact of global climate change on fish growth, digestion and physiological status: developing a hypothesis for cause and effect relationships. *Journal of Water and Climate Change*, 6(2): 200–226.

Moss, B., 2010. *Ecology of Freshwaters: A View for the Twenty–First Century*. John Wiley & Sons Ltd., Chichester.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer,* 39(3): 175–192.

Pérez–Figueroa, A., Fernández, C., Amaro, R., Hermida, M., San Miguel, E., 2015. Population structure and effective/census population size ratio in threatened three–spined stickleback populations from an isolated river basin in northwest Spain. *Genetica,* 143(4): 403–411.

Reimchen, T., 1992. Extended longevity in a large–bodied *Gasterosteus* population. *Canadian Field–Naturalist,* 106: 122–125.

Ricker, W. E., 1979. Growth rates and models. In: *Fish physiology, VIII: Bioenergetics and growth*: 677–743 (W. S. Hoar, D. J. Randall, J. R. Brett, Eds). Academic Press, New York.

Roff, D., 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 989–1000.

– 1992. *The Evolution of Life History: Theory and Analysis*. Chapman and Hall, New York.

– 2002. *Life History Evolution*. Sinauer Associates, Sunderland, MA.

Roff, D., Heibo, E., Vollestad, L., 2006. The importance of growth and mortality costs in the evolution of the optimal life history. *Journal of Evolutionary Biology,* 19(6): 1920–1930.

Sharda, S., Argenti, E., Lucek, K., 2018. On the status of threespine stickleback (*Gasterosteus aculeatus*, Linnaeus 1758) in Lake Bracciano, *Italy. Fishes,* 3(17): 1–6.

Stearns, S., Hoekstra, R., 2005. Life history and sex allocations. In*: Evolution, an Introduction*. Oxford University Press, Hampshire.

Stearns, S., Koella, J., 1986. The evolution of phenotypic plasticity in life history traits: predictions of reaction norms for age and size at maturity. *Evolution,* 40(5): 893–913.

Tewksbury, J., Huey, R., Deutsch, C., 2008. Putting the

heat on tropical animals. *Science*, 320: 1296–1297.

Vila, M., Hermida, M., Fernández, C., Perea, S., Doadrio, I., Amaro, R., San Miguel, E., 2017. Phylogeography and Conservation Genetics of the Ibero–Balearic Three–Spined Stickleback (*Gasterosteus aculeatus*) (online). *Plos One*, 12(1): e0170685, Doi:10.1371/journal.pone.0170685.

Wootton, R. J., 1979. Energy costs of production and environmental determinants of fecundity in teleost fishes. *Symposia of the Zoological Society of London,* 44: 133–159.

– 1984. *A Functional Biology of Stickleba*cks. Croom Helm, London and Sidney.

Wootton, R., Adams, C., Attrill, M., 2005. Empirical Modelling of the Population Dynamics of a Small Population of the Threespine Stickleback, *Gasterosteus aculeatus*. *Environmental Biology of Fishes,* 74:151–161.

Wootton, R. J., Smith, C., 2015. *Reproductive Biology of Teleost Fishes*. John Wiley & Sons, Chichester.

Yershov, P., Sukhotin, A., 2015. Age and growth of marine three–spined stickleback in the White Sea 50 years after a population collapse. *Polar Biology,* 38(11): 1813–1823.

Ziuganov, V., San Miguel, E., Neves, R., Longa, A., Fernández, C., Amaro, R., Beletsky, V., Popkovitz, E., Kaliuzhin, S., Johnson, T., 2000. Life span variation of the freshwater pearl shell: A model species for testing longevity mechanisms in animals. *Ambio,* 29(2): 102–105.