Spatial variability in the somatic growth of pikeperch *Sander lucioperca*, an invasive piscivorous fish

Emma T. Nolan; J. Robert Britton

Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, BH12 5BB, United Kingdom

Running head: Growth of pikeperch

Corresponding author: Robert Britton, Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, BH12 5BB, United Kingdom.

rbritton@bournemouth.ac.uk

Abstract

Introduced fishes can develop invasive populations that impact native species and ecosystems. Understanding the population ecology of introduced species in their extended ranges and how this compares to their native ranges is therefore important for informing their management. Here, the age and somatic growth rates of the piscivorous freshwater fish pikeperch *Sander lucioperca* were analysed across their invasive and native ranges to determine their spatial patterns and drivers. Analyses were initially completed in their invaded range in central and western England. Populations varied spatially in their growth rates; they were slowest for a population in a narrow and shallow canal, and fastest in a large, impounded lowland river. A meta-analysis of parameters of the von Bertalanffy growth model then revealed that across their native and invasive ranges, their theoretical ultimate lengths (L_∞) and growth coefficients (K) were significantly related to latitude, but not longitude. Their relationships with latitude were non-linear, with higher values of L_∞ and lower values of K being evident towards their northerly and southerly range limits. Faster growth rates were evident in the middle of their range (45 to 55 °N), suggesting temperatures here were most optimal for growth, but were in a trade-off with reduced ultimate lengths. These spatial patterns suggest that whilst introduced *S. lucioperca* can colonise new waters across a wide area, the expression of their life history traits will vary spatially, with potential implications for how invasive populations establish and integrate into native fish communities.

Keywords: Climate change, Invasion, latitude-growth relationships, scale ageing, von Bertalanffy growth model, zander.

Introduction

Introductions of non-native fishes can potentially result in the establishment of sustainable populations that naturally disperse and invade (Cucherousset & Olden, 2011; Gozlan, Britton, Cowx, & Copp, 2010). Whilst only a small proportion of introduced fishes develop invasions, these fishes can have substantial impacts on native species (Gozlan, Andreou, et al., 2010; Gozlan, Britton, et al., 2010). For piscivorous fishes, impacts tend to be via predation with, for example, invasive largemouth bass *Micropterus salmoides* and peacock basses of the *Cichla* genus having deleterious impacts on native species richness and fish abundance (Gratwicke & Marshall, 2001; Pelicice & Agostinho, 2009). Managing the impact of invasive fishes in open systems is challenging (Britton, Gozlan, & Copp, 2011), so predictions that indicate whether an introduced species will develop an invasion are fundamental to their management (Copp et al., 2014, 2016). Spatial assessments of somatic growth rates assist these predictions (Britton, Harper, & Oyugi, 2010), especially as growth rates can be a strong proxy of other life history traits (Oyugi et al., 2011). The expression of life history traits can help to explain invasion patterns and processes for a number of non-native species (Olden, Poff, & Bestgen, 2006; Vila-Gispert, Alcaraz, & García-Berthou, 2005), particularly when related to abiotic parameters (Benejam, Alcaraz, Sasal, Simon-Levert, & García-Berthou, 2009). These patterns have also helped highlight the regions that are most vulnerable to invasion (Cucherousset et al., 2009; Ribeiro, Elvira, Collares-Pereira, & Moyle, 2008).

Pikeperch *Sander lucioperca* is a large-bodied piscivorous freshwater fish with a native range extending throughout much of Europe, from Germany in the West to Central Russia in the East (Maitland, 2004). The major driver of *S. lucioperca* introductions and translocations has been the diversification of fish assemblages to increase sport angling opportunities (Hickley & Chare, 2004).

Their popularity for angling has resulted in a series of regulated and unregulated releases across Western Europe, with their invasive range now including France, Spain, Portugal and Great Britain (Elvira & Almodóvar, 2001; Kopp et al., 2009; Ribeiro et al., 2009). In Britain, the first recorded *S. lucioperca* introduction was in 1878, when individuals of German origin were stocked into enclosed waters in the East of England (Copp, Wesley, Kovac, Ives, & Carter, 2003). Subsequent translocations to Eastern England occurred during the 1960s (Wheeler & Maitland, 1973) and it was these releases that lead to their establishment and invasion (Copp et al., 2003; Hickley, 1986; Linfield & Rickards, 1979). Reports of anglers capturing individuals from other catchments became widespread throughout the 1970s (Hickley, 1986; Wheeler, 1974), with self-sustaining populations now present throughout central and western England (Copp et al., 2003; Nunn, Bolland, Harvey, & Cowx, 2007; Smith, Leah, & Eaton, 1998).

Latitude can have a significant influence on the life history traits of freshwater fishes (Blanck & Lamouroux, 2007), mostly via spatial differences in temperature and light intensity (Heibo, Magnhagen, & Vøllestad, 2005; Rypel, 2012). Consequently, latitude is often used as an explanatory variable in assessments of life history trait variation over large spatial scales. This includes fishes in their European invasive range, where growth rates for invasive fishes tend to significantly decrease with increasing latitude (Benejam et al., 2009; Cucherousset et al., 2009). Although used less often, assessments in the longitudinal variability in growth rates can also provide insights into how growth varies spatially (Britton, Davies, & Pegg, 2013). For *S. lucioperca*, many studies have been completed on their life history traits, including growth rates (e.g. Ablak & Yilmaz, 2004; Argillier, Barral, & Irz, 2012; Błaszczyk, 2000; Copp et al., 2003; Ložys, 2004). However, these studies have been primarily associated with stock assessment and aquaculture (e.g. Balik, Çubuk, Özkök, & Uysal, 2004; Nyberg, Degerman, & Sers, 1996; Nyina-wamwiza, Xu, Blanchard, & Kestemont, 2005; Özvarol & İkİz, 2008).

There has been much less focus on their spatial variability in growth parameters (Milardi, Lappalainen, Malinen, Vinni, & Ruuhijärvi, 2011; Pérez-Bote & Roso, 2012), and how their age range and somatic growth rates might vary across their native and invasive distributions. This is despite the ecological and management utility of these data for assisting invasion risk assessments across their invasive range (Copp et al., 2014, 2016).

Consequently, the aim here was to synthesise data on *S. lucioperca* somatic growth rates from across their native and invasive ranges via a combination of field study and literature review. To initially test how invasive *S. lucioperca* growth rates vary between populations at small spatial scales, a field study focused on invasive populations in central and western England. To then test how *S. lucioperca* growth rates vary across their native and invasive European ranges, a meta-analysis tested spatial patterns in their somatic growth rate parameters across their entire range. As per patterns for other invasive fishes (e.g. Benejam et al., 2009; Cucherousset et al., 2009), it was predicted that latitude would be a significant predictor of *S. lucioperca* growth rates, with decreased growth rates with increased latitude.

Methods

Field study sites

The field study was mainly focused on the River Severn basin in central and western England. In this basin, the distribution of *S. lucioperca* is restricted to the Warwickshire Avon (52.0874 N, 1.9481 W), the lower River Severn, generally below the city of Worcester (52.3664 N, 2.3043 W), and the Gloucester-Sharpness Canal that is connected to the Severn estuary at its downstream end (51.7249 N, 2.4733 W). In addition, the Grand Union Canal has hydrological connection with the Warwickshire

Avon and has invasive *S. lucioperca* present. An area of this canal close to its connection with Warwickshire Avon was thus also sampled (52.2287 N, -0.9159 W).

A common feature of these invaded waters is that they are heavily regulated for navigation; the Severn and Warwickshire Avon are impounded by navigation weirs, the Grand Union Canal comprises of series of locks to overcome changes in the gradient of the surrounding land and the Gloucester-Sharpness canal was constructed specially for navigation of goods into Gloucester docks. However, the waters differ considerably in their other features. The lower River Severn is up to 40 m in width, with depths to 8 m and is subject to regular winter spates when levels can increase by 5 m. The Warwickshire Avon is generally of widths to 25 m and depths to 4 m, and although also prone to floods in winter, these tend to be much less severe than the Severn. The Grand Union Canal is generally no more than 15 m in width with depths rarely exceeding 2 m, and flood events are rare, whilst the Gloucester-Sharpness canal is unusually broad and deep for a British canal, being approximately 25 m wide with depths to over 5 m. *Sander lucioperca* were confirmed as present in the Warwickshire Avon in 1976, the lower River Severn in 1980 and the Grand Union Canal in 1984 (Hickley, 1986; Nunn et al., 2007). There is no specific evidence over the timing of their introduction into the Gloucester-Sharpness canal or whether it was from a release by anglers or, perhaps more unlikely, natural dispersal via the Severn estuary, although mixohaline waters have been suggested as a potential dispersal route for *S. lucioperca* (Brown, Scott, & Wilson, 2007).

Growth data on these populations was then supplemented by data on the age and growth rates of *S. lucioperca* from the River Great Ouse system (52.3276 N, 0.1769 W). With a catchment area of approx. 8600 km^2, the River Great Ouse is one of the largest river basins in England and, in the area of sampling, consists of heavily modified, impounded and regulated river channel of 20 m width and depths to 2 m, with the flow regulated by numerous sluices for drainage and flood relief (Pinder, Marker, Mann, Bass, & Copp, 1997). The rationale for including *S. lucioperca* from here was that the fish of the Severn and Great Ouse system all originated from the same original stock that was introduced into Eastern England in 1878 (Copp et al., 2003). Thus, the inclusion of the Great Ouse data utilised fish of the same genetic lineage to the Severn and represented another population from an impounded and regulated river channel.

Field sample collection

The age and growth analyses were completed on data obtained from scales collected from *S. lucioperca*, as scales provide a consistent and reliable method for age and growth rate analyses (Britton, 2007). The habitat characteristics of the River Severn, Warwickshire Avon ('Lower Warwickshire Avon') and Gloucester Sharpness Canal (Table 1) meant their sampling for *S. lucioperca* using typical sampling methods were generally inefficient and/ or unfeasible (e.g. electric fishing, seine netting, fyke netting). Thus, scale sample collection was primarily via catch and release angling. This was facilitated by the Environment Agency, the inland fishery regulatory body of England, who established a network of anglers within the River Severn basin. Participating anglers recorded their catches and were trained in the collection of scale samples. Correspondingly, from 2014 to 2017, anglers collected scales (3 to 5 scales per fish from the area below the dorsal fin and above the lateral line) from captured *S. lucioperca*, with additional recording of the location, date of capture and fish fork length (FL, nearest mm). Additional scale samples were collected using seine netting techniques within off-channel boat marinas. For the Grand Union canal, scales were collected from *S. lucioperca* in April 2017 where sampling used boat mounted electric fishing. In addition, some data were available for *S. lucioperca* from an upstream site on the Warwickshire Avon, where electric fishing was completed in May 2000 (‘Middle Warwickshire Avon’; 52.1894 N, 1.7045 W). The Great Ouse fish were sampled by seine netting in August 2003 and 2005.

Age and growth determination from scales

Scales were aged on a projecting microscope (x10 to x48 magnification). Ages were determined by counting of annual growth marks (‘annuli’), where an annulus was identified as the transition between two uninterrupted zones of closely and widely spaced circuli. In order to minimise error in age estimations, a confidence scoring system was utilised. In this system, the age estimate was assigned a score of 1 or 2, where 1 indicated relatively high confidence (e.g. scales with clearly defined annuli and high certainty in the age estimate) and 2 indicated reduced confidence (e.g. scales were poorly defined annuli with high age estimate uncertainty). Scales which were assigned a score of 2 were excluded from subsequent analyses to minimise the probability of using data based on low ageing accuracy. Following their ageing, scales were measured for their scale radius and the distances from the scale focus to the first, second and last annulus. These measurements were converted to back-calculated lengths using the Fraser-Lee back-calculation equation (Francis, 1990):

where L_c is the fish body length at capture, S_i the mean scale length at annulus i, S_c the mean scale total length and c is the intercept from the regression of body length on mean scale length. Back calculated lengths enabled the growth increment between age 1 and 2 to be determined (interpreted as the ‘juvenile growth rate’) and the back calculated length at the last annulus (i.e. hatching date calculated as April according to Lappalainen, Dörner, & Wysujack, (2003) provided a length at age that was not biased by sampling date).

Growth rate analyses of scale data

The age and growth data from the scales were analysed in two ways. First, length-at-age data were fitted, using non-linear, least-squares regression, to the von Bertalanffy growth model, , where L_t is length at age t, L_∞ is the asymptotic length, K is the rate at which the curve approaches L_∞ and t_0 is the theoretical age of the fish at zero length. 95 % confidence limits for von Bertalanffy growth parameters were obtained by non-parametric bootstrap resampling over 10,000 iterations. This provided estimated values of L_∞, K and t_0.

Secondly, analysis of standardised growth residuals compared the *S. lucioperca* growth rates across the field sampling sites (other than the 'Middle Warwickshire Avon' where the juvenile growth data were not available). The analyses were completed using both lengths at the last annulus and the juvenile growth rate (Amat Trigo, Gutmann Roberts, & Britton, 2017; Beardsley & Britton, 2012). For the juvenile growth rate, the mean length increment (i.e. the back-calculated length difference between 1 and 2 years) across all populations was used to calculate the residuals, taken as the difference between the individual length increment of each fish and the mean length increment. For lengths at the last annulus, residuals were calculated using modelled length values, obtained by fitting the back-calculated length at last annulus to the von Bertalanffy growth model across all populations. The residual value of each individual fish was then calculated as the difference between its modelled and observed value. The standardized residual of each individual was determined and compared between populations using ANOVA, with type II sums of squares used to account for unbalanced data due to differences in sample sizes (Langsrud, 2003); Tukeys post-hoc tests were used to determine the significance of differences between the populations.

Growth rate comparisons across the ranges of Sander lucioperca

The von Bertalanffy growth model parameters of L_∞ and K for *S. lucioperca* within these field sites were then compared with data from other populations from across their native and invasive ranges, as gathered by literature review. This review was based on searches completed in Web of Science, and supplemented by Google Scholar, starting with search terms based on the species name ('pikeperch'; pike-perch'; 'zander'; '*Stizostedion lucioperca*'; '*Sander lucioperca*') in 'title' searches, and then using these within Boolean logic search terms with words including 'age', 'growth', 'von Bertalanffy', 'invasive', 'introduced', 'non-native', and their combinations. Searches were then completed using the same terms but searching for 'topic' to provide any additional material that would otherwise have been missed. These searches were then supplemented by data from Fishbase.org (Froese & Pauly, 2018). Across these studies, data were omitted where the values were considered unreliable or were deemed to be not biologically relevant (Supplementary information, table S1). These criteria were primarily where the value of L_∞ was considered very high or very low for the species in general, suggesting sampling had not been representative of the population (Živkov, Trichkova, & Raikova-Petrova, 1999), or had been subject to high harvest rates (i.e. an anthropogenic pressure that other populations had not been subjected to). Where von Bertalanffy growth model parameters were calculated based on standard or total length, these were converted to fork length using linear models from Copp et al. (2003) to enable comparisons to be consistent across studies. The relationship between the location of populations, as latitude and longitude, were then tested against L_∞ and K using linear and non-linear models, where regression statistics and the lowest value of Akaike's Information Criteria (AIC) were used in combination to select the best fitting model. All statistical analysis and graphical outputs were performed using R (Version 3.4.3; R Development Core Team 2017).

Results

Field study on growth parameters of invasive Sander lucioperca

There were 625 *S. lucioperca* aged in the field study, of which 472 were retained for analyses based on a confidence score of 1. These retained fish ranged in length between 74 and 770 mm, with individuals aged to 11 years old (Table 1). However, populations from the Grand Union Canal, the Gloucester-Sharpness canal and the 'Middle Warwickshire Avon', were only present in samples to 8 years old (Table 1; Table S2). For the data combined across all populations, L_∞ was 996 mm and K was 0.13. Across the populations, mean L_∞ values ranged from 753 to 980 mm, and K between 0.12 and 0.22 (Table 1, Fig. 1). However, there was considerable overlap in the 95 % confidence limits of these growth parameters across the populations, suggesting differences between these populations were not significant.

Analysis of standardised growth residuals revealed significant differences between these populations in both their juvenile growth rates (ANOVA: $F_{4,347} = 45.01$, $P < 0.01$; Fig. 2a) and lengths at the last annulus (ANOVA: $F_{5,434} = 16.97$, $P < 0.01$; Fig. 2b). For juvenile growth rates, Tukey post-hoc tests revealed that significant differences were due to slower growth in the Grand Union Canal population compared to all other populations ($P < 0.01$) and faster growth in the River Great Ouse compared to all other populations ($P < 0.01$). For length at the last annulus, Tukey post-hoc tests showed that significant differences were due to faster growth in length at last annulus on the River Severn population to those of the Grand Union Canal, the River Great Ouse ($P < 0.01$) and the middle Warwickshire Avon ($P < 0.05$). The Grand Union Canal also showed slowest growth across all populations and significant differences with the Gloucester-Sharpness Cana, the River Severn ($P < 0.01$) and the River Great Ouse ($P < 0.05$).

Spatial variability in Sander lucioperca growth rates

Literature review provided 34 studies with data on the von Bertalanffy growth parameters of *S. lucioperca,* of which 22 were retained for further analysis (Supplementary information, Table S1). The analysis also included data from the 6 invasive populations from the field study.

Across these 22 populations, L_∞ ranged between 709 and 1116 mm and K between 0.03 and 0.24 (Supplementary information, Table S1). The L_∞ and K parameters derived for the six invasive populations from England sat within these data, with their values towards the higher values of K and lower values of L_∞. However, von Bertalanffy growth parameter estimates were only retained from three of the English populations within the field study through application of the criteria used to exclude literature values from the meta-analysis (*cf.* Table S1). This resulted in the data from the lower Warwickshire Avon, the Grand Union Canal and the Gloucester-Sharpness Canal not being included in the analysis. For the 25 retained populations, the relationship between L_∞ and K was significant, with decreasing values of K as L_∞ increased (linear regression: $R^2 = 0.19$, $F_{1,23} = 5.56$, $P = 0.02$, Fig. 3). The relationships between latitude and both L_∞ and K were best described by non-linear regression (AIC; Table 2) and revealed significant U-shaped relationships ($P = 0.05$ and $P < 0.001$ respectively). There were higher values of L_∞ and lower values of K at the either end of their latitudinal range (Fig. 4). The relationships of longitude with both L_∞ and K were non-significant ($P > 0.05$; Table 2; Fig. 4).

Discussion

Across their entire range, the results suggested *S. lucioperca* were rarely present in samples above the age of 10 years and L_∞ only exceeded 900 mm in a small number of populations. Spatially, there was variation in von Bertalanffy growth parameters across their entire range, with this at least partially explained by the influence of latitude. This spatial variation in von Bertalanffy growth parameters was less apparent in the field study that was completed at a smaller spatial scale. However, the standardized residuals of juvenile growth rates and length at the last annulus indicated some significant differences in growth rates between populations, even at this reduced spatial scale, suggesting factors other than latitude were also important determinants of *S. lucioperca* growth rates.

It was predicted that latitude would have a significant influence on the growth of *S. lucioperca*, with growth rates decreasing as latitude increases, given that this is a common spatial pattern for many freshwater fishes in the northern hemisphere (Blanck & Lamouroux, 2007; Cucherousset et al., 2009; Heibo et al., 2005), and previous studies have shown fast growth rates in some southern *S. lucioperca* populations (Lappalainen et al., 2003). Whilst there was a significant relationship between both von Bertalanffy growth parameters and latitude, AIC values indicated that the best fitting models were both non-linear, with this contrary to the prediction. Instead, the models indicated U-shaped relationships between the parameters, whereby populations were comprised of individuals of larger body sizes with slower growth rates towards their northerly and southerly limits. These non-linear relationships were likely to have resulted from the population growth rates having a non-linear relationship with environmental factors (Lappalainen, Tarkan, & Harrod, 2008), especially water temperature. This is because water temperatures tend to strongly correlate with latitude, and the strong influence of temperature on fish growth rates is well established (Magnuson, Crowder, & Medvick, 1979). Thus, the increases in *K* (growth coefficient) that were apparent from approximately 45 to 55 °N might be linked to water temperatures in these areas providing more optimum thermal conditions for faster and efficient growth rates. Indeed, some increases in water temperature have positive effects on *S. lucioperca* growth, with the number of degree days over 10°C increasing their annual length increments (Buijse & Houthuijzen, 1992; Lappalainen et al., 2005; Lappalainen, Milardi, Nyberg, & Venäläinen, 2009; Ložys, 2004). However, faster growth rates tend to generally limit ultimate body sizes due to the influence of, for example, the earlier onset of sexual maturity that diverts energy from somatic growth to reproduction (Ložys, 2004), so potentially explaining the trade-off of higher *K* values but lower ultimate lengths at 45 to 55 °N.

At higher latitudes, freshwater fish populations often show slower growth and larger asymptotic lengths (Blanck & Lamouroux, 2007), and thus the results of the relationships of L_∞ and *K* with latitude outside of 45 to 55 °N were consistent with this. For example, the slower growth rates that were apparent towards the southerly limits of their range might relate to sub-optimal, warm summer temperatures that prevented their efficient growth, and thus depressed the values of *K* (Lappalainen et al., 2008). There might have also been a genetic component in the spatial growth patterns of *S. lucioperca*, given that significant population genetic variation has been detected across their range (Eschbach et al., 2014). This could not, however, be tested here.

Density dependent factors could also have been influencing the growth rates of these *S. lucioperca* populations, with this potentially related to differences in prey availability. In other piscivorous fishes, growth rates were 1.3 times faster at low population densities than high densities in immature walleye *Sander vitreus* (Venturelli, Lester, Marshall, & Shuter, 2010). However, Haugen et al. (2007) revealed conflicting interactions between density-dependent and density-independent factors affecting the growth of pike, *Esox lucius* a large-bodied piscivorous species. Variation in the annual growth rates of a 0+ *S. lucioperca* population has been explained by the higher availability of prey species in warmer years (Mooij, Lammens, & Densen, 1994). The onset of piscivory in *S. lucioperca* can also influence juvenile growth rates (Buijse & Houthuijzen, 1992), with the realised lengths of piscivorous fishes early in life generally being an important determinant of their ultimate sizes (Mittelbach & Persson, 1998). Additionally, *S. lucioperca* express faster growth rates in eutrophic waters (Argillier et al., 2012), with Keskinen & Marjomäki (2003) revealing *S. lucioperca* growth was positively correlated with total phosphorus and turbidity, and negatively with size of the water body. In our study, there were some significant differences apparent in juvenile growth rates in the field component. It can thus be hypothesised that differences in the growth rates between the Grand Union Canal and the River Great Ouse to all other populations were at least partially related to differences in prey availability, the physical characteristics of the water body and the onset of obligate piscivory between these populations. However, it was beyond the scope of this study to decouple the relative influences of these factors on *S. lucioperca* growth rates. It was also possible that sample year affected the juvenile growth rates of these populations via, for example, differences in prey availability and temperature. Additionally, these samples were obtained by different sampling methods, increasing the risk of some sampling bias in fish through selective sampling. Thus, the interpretation of these field data warrant some caution due to these issues.

In the field component of this study, the age and growth rate data were derived only from scales. This was because *S. lucioperca* is now considered a recreationally important fishery resource in most invaded waters in England (Hickley & Chare, 2004), with catch-and-release angling almost universally utilised by anglers. This is despite legislation that controls the distribution of the species in England (Hickley & Chare, 2004), with some evidence suggesting significant ecological impacts on native fish communities following their introduction (Fickling & Lee, 1983; Hickley, 1986; Smith et al., 1998). The use of scales in ageing studies can be problematic, especially in older fishes where the aggregation of annuli on the scale edge can result in ageing errors, with these usually being under-estimations of age (Amat Trigo et al., 2017; Britton et al., 2013). Nevertheless, in a comparative study on the use of calcified structures for age determination in *S. lucioperca* from Turkey, Bostanci (2008) found that scales were typically clear and straight forward to interpret, with the only exception being scales collected from large, long-lived individual fish. Scales were also used as a reliable ageing method for British populations of *S. lucioperca* by Copp et al. (2003) and Britton (2007). The use of the confidence scoring system in ageing the scales should have also increased the reliability of the data used in analyses, with those scales that were difficult to age with high certainty not being used. It should be noted that the scales aged with high uncertainty were not just those from large, slow growing fish, but include scales from smaller fish, where the annuli on the scales were too indistinct to enable a reliable age estimate. There was also no bias in the rejected scale data with respect to the population or the sampling method.

The use of literature review to compile a meta-analysis of *S. lucioperca* growth data enabled the study to look at growth patterns across a large spatial area. Similar approaches have been recently used for invasive fishes such as roach *Rutilus rutilus* (Tarkan & Vilizzi, 2015) and carp *Cyprinus carpio* (Vilizzi & Copp, 2017). Whilst effective at describing growth over environmental gradients and large spatial areas, differences in how data were collected and/ or analysed between the studies also potentially introduces some discrepancies into analyses. For example, in our study, standard, fork and total length were all used in the reporting of L_∞, and so all values were converted to fork length to enable reliable comparisons. In doing so, however, they might have slightly affected the relationship of L_∞ versus K, given K values could not be altered in same manner. However, the adjusted difference in lengths was relatively minor (generally < 20 mm) and so did not have a material effect of the relationship of L_∞ versus K. In addition, there are a number of analytical methods to derive von Bertalanffy growth parameters from length at age data, such as use of two or three parameter growth models that can result in different estimates (Pardo et al., 2013). However, these analytical issues could not be easily controlled in our meta-analysis and, thus, it was assumed that the published values were accurate for the sampled fish.

The increasing water temperatures that are generally predicted to occur via climate change will potentially have profound impacts on water resources and river ecosystems (Johnson et al., 2009; Wilby et al., 2006). As a result, there will be major changes in freshwater fish distribution and community structure (Graham & Harrod, 2009; Ruiz-Navarro, Gillingham, & Britton, 2016a). Ecological impacts of freshwater invaders are likely to be enhanced with this warming, such as through altered competitive interactions and increased predation pressure on native species (Rahel & Olden, 2008). However, predicting the response of specific invaders to warming is inherently difficult due to these being influenced through complex direct and indirect effects (Britton, Cucherousset, Davies, Godard, & Copp, 2010; Kuczynski, Legendre, & Grenouillet, 2018). For example, in temperate freshwaters, it is likely that all fishes (plus other taxa) will respond to warming by altering their distributions, life history traits and phenology (Comte & Grenouillet, 2013; Ruiz-Navarro et al., 2016a; Ruiz-Navarro, Gillingham, & Britton, 2016b). This is likely to lead to range changes and altered population abundances (Ruiz-Navarro et al., 2016b). For *S. lucioperca* to invade temperate regions, low water temperatures are not considered a constraint due to them being primarily a cold-water species capable of reproducing at relatively low temperatures. Indeed, the temperate climate of England has not prevented population establishment and invasion in the last 50 years (Hickley, 1986; Copp et al., 2003). Thus, it is unlikely that climate change will have a substantial influence on their ability to invade new temperate regions, unless the warming results in temperatures that are too high for their survival. However, given the significant relationships between latitude and their von Bertalanffy growth parameters, then it is likely that as warming proceeds then the impact for *S. lucioperca* is likely to be through altered growth rates. In England, for example, it is likely that their ultimate lengths will reduce and growth rates increase, and potentially result in more abundant populations comprised of smaller individuals. This is in line with predictions for a number of native fishes (Ruiz-Navarro et al., 2016b).

In summary, this meta-analysis of the von Bertalanffy growth parameters of *S. lucioperca* suggested that whilst their introductions can result in invasive populations within a wide spatial area and in climates that range from temperate to Mediterranean, the expression of their life history traits will vary considerably. Growth rates will be faster in their mid-range (approximately 45 to 55 °N) than at their northerly and southerly range limits, most likely due to the influence of temperature, although it is acknowledged that other factors will influence their growth at the population level, such as prey availability. These results highlight the extent to which their growth data varies spatially and can be applied to their invasion management by providing a more robust basis for risk assessments that utilise data on their life history traits.

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Table 1. Samples size, length and age range and Von Bertalanffy growth parameters estimates for invasive *Sander lucioperca* in England, values in parentheses represent the 95% confidence limits of each parameter estimate.

River	N	Length (mm)	Age (years)	*L*∞	*K*	t0
Gloucester-Sharpness Canal	18	345-660	2 - 8	980 (679, 2509)	0.13 (0.03, 0.36)	-1.10 (-3.94, 0.65)
Grand Union Canal	129	169-551	2 - 6	820 (598, 1726)	0.18 (0.05, 0.34)	-0.08 (-0.75, 0.46)
Lower Warwickshire Avon	26	90-695	0 - 11	870 (713, 1143)	0.16 (0.10, 0.25)	-0.82 (-1.23, -0.46)
Middle Warwickshire Avon	35	142-650	1 - 7	753 (676, 904))	0.22 (0.15, 0.30)	-0.08 (-0.54, 0.23)
Great Ouse	70	110-760	1 - 10	853 (725, 1138)	0.19 (0.11, 0.28)	-0.27 (-0.73, 0.03)
Severn	181	74-770	0 - 10	874 (806, 964)	0.18 (0.15, 0.21)	-0.43 (-0.62, -0.26)

Table 2. Linear and non-linear (2^{nd} order polynomial) regression statistics for the relationship between von Bertalanffy growth parameters $L\infty$ and K versus latitude and longitude. *significant at $P \leq 0.05$; **significant at $P \leq 0.01$.

Relationship	Model	R^2	F	P	AIC
Latitude *vs*. L_∞	Linear	0.01	$_{(1,23)}$ 1.23	0.28	310.61
	Non-linear	0.16	$_{(2, 22)}$ 3.36	0.05*	307.25
Longitude *vs*. L_∞	Linear	0.04	$_{(1,23)}$ 2.07	0.16	309.76
	Non-linear	0.08	$_{(2, 22)}$ 2.13	0.14	309.50
Latitude *vs*. K	Linear	0.29	$_{(1,23)}$ 10.71	0.01**	-77.85
	Non-linear	0.43	$_{(2, 22)}$ 10.06	< 0.01**	-82.84
Longitude *vs*. K	Linear	-0.01	$_{(1,23)}$ 0.99	0.33	-69.34
	Non-linear	0.07	$_{(2, 22)}$ 1.87	0.18	-70.24

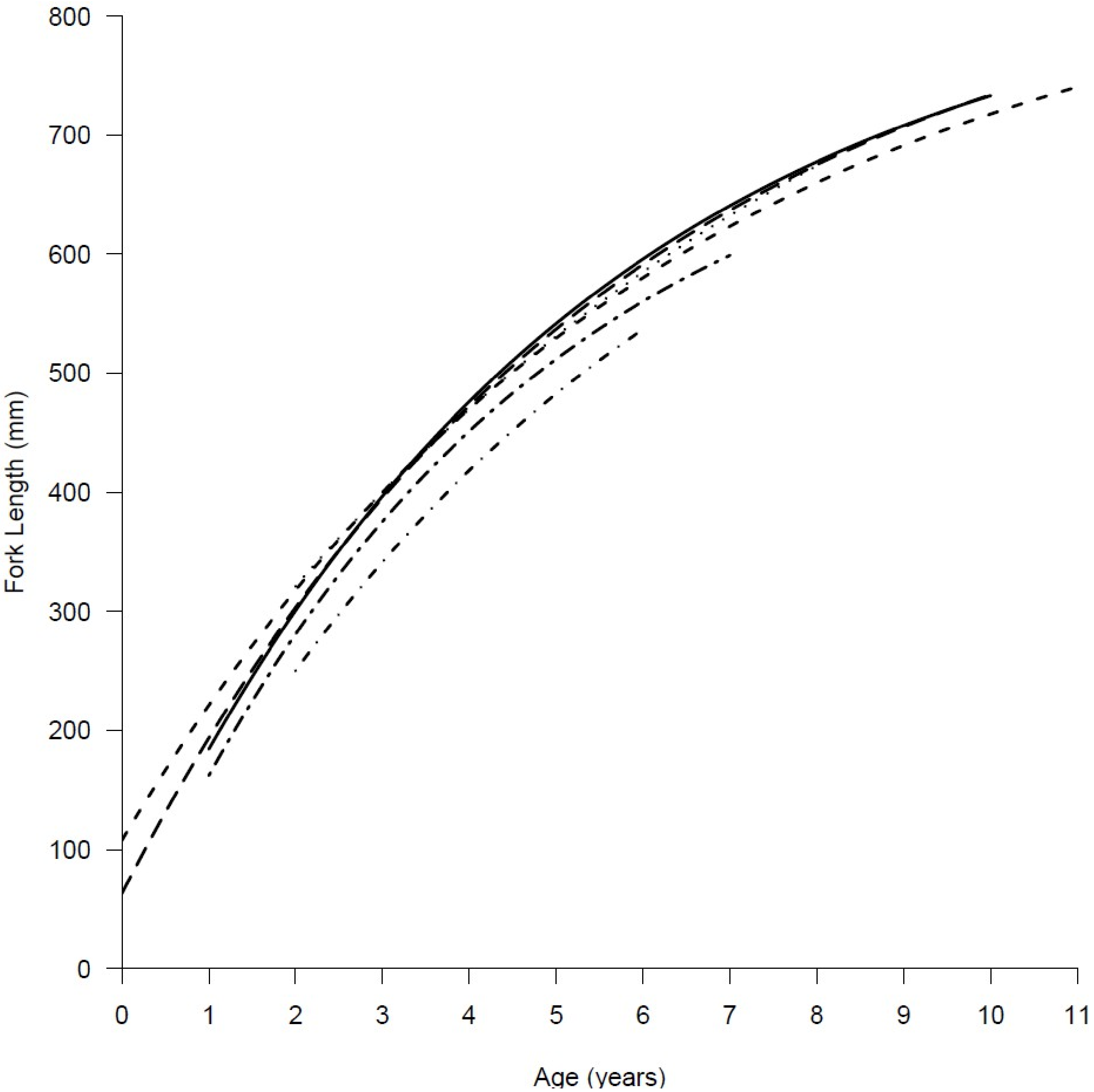
Figure captions

Figure 1. Fitted von Bertalanffy growth curve for populations of *Sander lucioperca* at sites in England including the Gloucester-Sharpness canal (dotted line), the Grand Union canal (dot-dash line), the lower Warwickshire Avon (dashed line), the middle Warwickshire Avon (two dash line) the River Great Ouse (solid line) and the river Severn (long dash line).

Figure 2. Mean standardised growth residuals for (a) juvenile growth rate; and (b) length at last annulus for the Gloucester-Sharpness canal (GSC), Grand Union Canal (GUC), the lower Warwickshire Avon (L. Avon), the middle Warwickshire Avon (M. Avon), the river Great Ouse (Ouse) and the river Severn (Severn). Error bars represent the upper and lower 95% confidence limits.

Figure 3. Relationship of $L\infty$ (as fork length) and K of the von Bertalanffy growth model for populations of *Sander lucioperca*, where the solid line is the significant relationship between the variables according to linear regression, filled circles represent values extracted from literature whilst open circles represent values from invasive populations in England derived in this study.

Figure 4. Relationships of latitude and longitude with $L\infty$ (as fork length) and K of the von Bertalanffy growth model for *Sander lucioperca*. The solid line represents the significant relationship between the variables according to polynomial regression (2nd order), filled circles represent values extracted from literature whilst open circles represent values from invasive populations in England derived in this study and retained in the meta-analysis.



Fork Length (mm)
800
700
600
500
400
300
200
100
0
0
1
2
3
4
5
6
7
8
9
10
11
Age (years)

677 Figure 1.

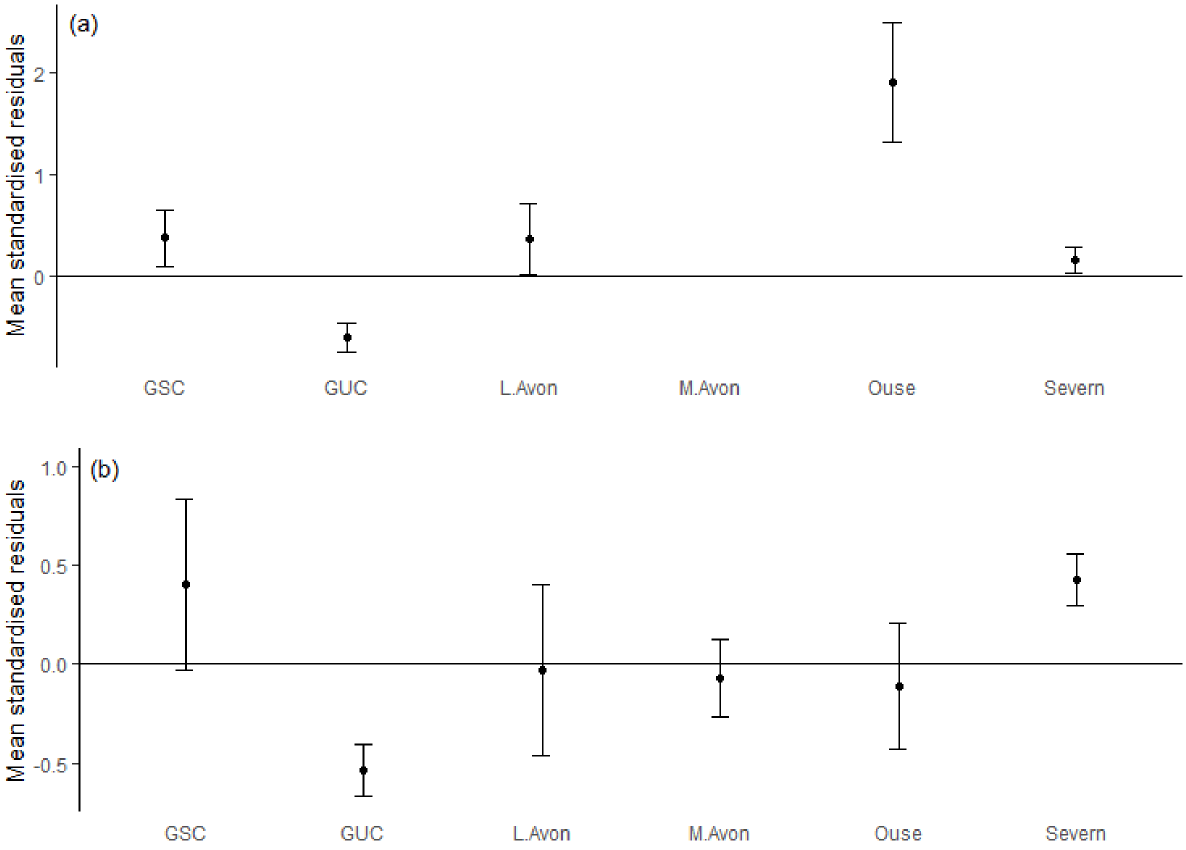

(a)
Mean standardised residuals
2
1
0
GSC
GUC
L.Avon
M.Avon
Ouse
Severn
(b)
Mean standardised residuals
1.0
0.5
0.0
-0.5
GSC
GUC
L.Avon
M.Avon
Ouse
Severn

Figure 2.

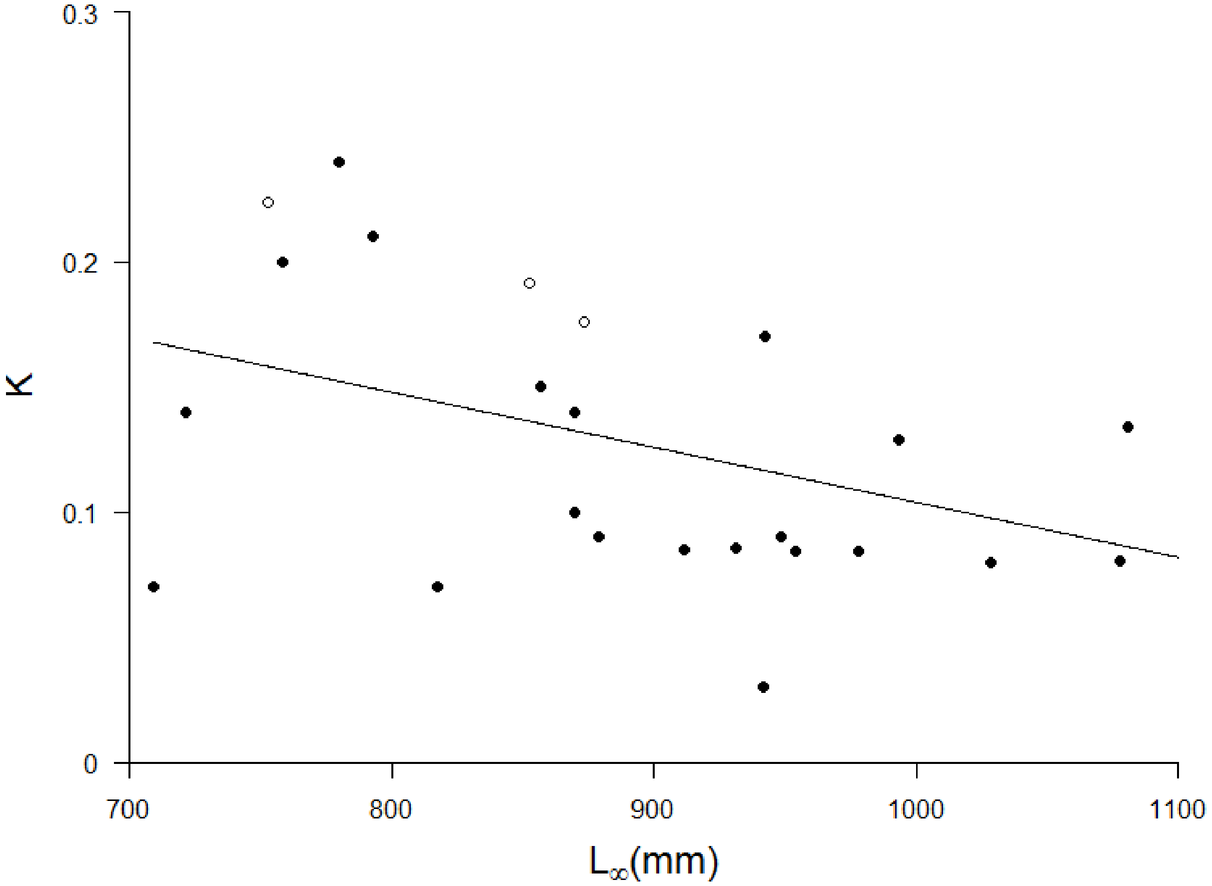


Figure 3.

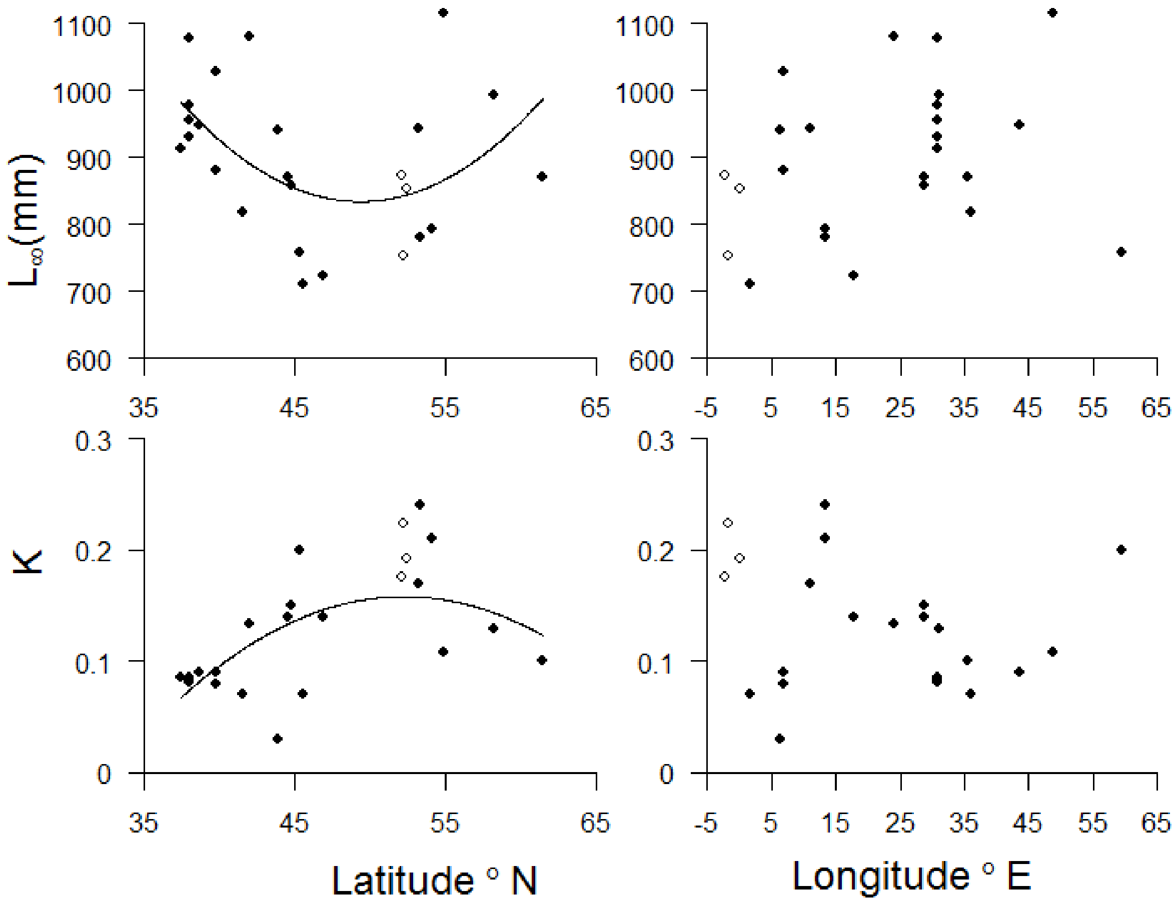

L∞(mm)
1100
1000
900
800
700
600
K
0.3
0.2
0.1
0
35
45
55
65
-5
5
15
25
35
45
55
65
Latitude ° N
Longitude ° E

Figure 4.