



THE ATRIUM, SOUTHERN GATE, CHICHESTER, WEST SUSSEX P019 8SQ

**\*\*\*IMMEDIATE RESPONSE REQUIRED\*\*\***

Your article may be published online via Wiley's EarlyView® service (<http://www.interscience.wiley.com/>) shortly after receipt of corrections. EarlyView® is Wiley's online publication of individual articles in full-text HTML and/or pdf format before release of the compiled print issue of the journal. Articles posted online in EarlyView® are peer-reviewed, copy-edited, author-corrected, and fully citable via the article DOI (for further information, visit [www.doi.org](http://www.doi.org)). EarlyView® means you benefit from the best of two worlds - fast online availability as well as traditional, issue-based archiving.

Please follow these instructions to avoid delay of publication

**READ PROOFS CAREFULLY**

- This will be your only chance to review these proofs. **Please note that once your corrected article is posted online, it is considered legally published, and cannot be removed from the Web site for further corrections.**
- Please note that the volume and page numbers shown on the proofs are for position only.

**ANSWER ALL QUERIES ON PROOFS** (Queries for you to answer are attached as the last page of your proof.)

- List all corrections and send back via e-mail to the production contact as detailed in the covering e-mail, or mark all corrections directly on the proofs and send the scanned copy via e-mail. Please do not send corrections by fax or in the post.

**CHECK FIGURES AND TABLES CAREFULLY**

- Check size, numbering, and orientation of figures.
- All images in the PDF are downsampled (reduced to lower resolution and file size) to facilitate Internet delivery. These images will appear at higher resolution and sharpness in the printed article.
- Review figure legends to ensure that they are complete.
- Check all tables. Review layout, title, and footnotes.

**COMPLETE CTA (if you have not already signed one)**

- Please send a scanned copy with your proofs and post your completed original form to the address detailed in the covering e-mail. **We cannot publish your paper until we receive the original signed form.**

**OFFPRINTS**

- 25 complimentary offprints of your article will be dispatched on publication. Please ensure that the correspondence address on your proofs is correct for dispatch of the offprints. If your delivery address has changed, please inform the production contact to the journal - details in the covering e-mail. Please allow six weeks for delivery.

**Additional reprint and journal issue purchases**

- Additional **paper reprints** (minimum quantity 100 copies) are available on publication to contributors. Quotations may be requested from [mailto:author\\_reprints@wiley.co.uk](mailto:author_reprints@wiley.co.uk). Orders for additional paper reprints may be placed in advance in order to ensure that they are fulfilled in a timely manner on publication of the article in question. Please note that offprints and reprints will be dispatched under separate cover.
- PDF files of individual articles may be purchased for personal use for \$25 via Wiley's Pay-Per-View service (see <http://www3.interscience.wiley.com/aboutus/ppv-articleselect.html>).
- Please note that regardless of the form in which they are acquired, reprints should not be resold, nor further disseminated in electronic or print form, nor deployed in part or in whole in any marketing, promotional or educational contexts without further discussion with Wiley. Permissions requests should be directed to <mailto:permreq@wiley.co.uk>
- Lead authors are cordially invited to remind their co-authors that the reprint opportunities detailed above are also available to them.
- If you wish to purchase print copies of the issue in which your article appears, please contact our Journals Fulfilment Department <mailto:cs-journals@wiley.co.uk> when you receive your complimentary offprints or when your article is published online in an issue. Please quote the Volume/Issue in which your article appears.



## AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS

*Aquatic Conserv. Mar. Freshw. Ecosyst.* **16**: 1–11 (2006)Published online in Wiley InterScience  
(www.interscience.wiley.com) DOI: 10.1002/aqc.809

## ***A case study on the population ecology of a topmouth gudgeon (*Pseudorasbora parva*) population in the UK and the implications for native fish communities***

J.R. BRITTON<sup>a,\*</sup>, G.D. DAVIES<sup>a</sup>, M. BRAZIER<sup>b</sup> and A.C. PINDER<sup>c</sup><sup>a</sup> National Fisheries Laboratory, Environment Agency, Brampton, Huntingdon, Cambridgeshire, UK<sup>b</sup> Environment Agency North Area, North West Region, Penrith, Cumbria<sup>c</sup> Centre for Ecology and Hydrology, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset, UK

## ABSTRACT

1. The topmouth gudgeon *Pseudorasbora parva* is a small Asian cyprinid species that has proved invasive throughout many European countries. Following an initial introduction into the wild in 1996, the species is now proving invasive in the UK, with at least 25 infested waters in England and Wales, of which 10 are known to have direct connection to a major river catchment.

2. To demonstrate the threat of *P. parva* to fisheries in the UK, a case study is presented on a lake located in the Lake District of England where the species was introduced in 2000. The species rapidly established a breeding population that, by 2003, was the dominant species in size classes < 70 mm. In 2004, they were the only species in the lake that produced young-of-the-year.

3. Individual *P. parva* adopted the reproductive tactics of early maturity, multiple spawning, male dominance and male nest guarding; sexual dimorphism was manifested in larger body size of males. These traits were in contrast to the resident, native species of the lake, including roach *Rutilus rutilus* and gudgeon *Gobio gobio*, which adopted traits of later maturity and single spawning.

4. This case study, therefore, revealed relatively rapid establishment of a *P. parva* population, their subsequent numerical dominance of the fish community, and the impediment of the recruitment of native fish. The implications for UK fisheries are concerning: should *P. parva* continue to disperse and individuals adopt similar traits as those in this case study, there may be few waters immune from their invasion, numerical dominance and subsequent impacts.

Copyright © 2006 John Wiley &amp; Sons, Ltd.

Received 30 January 2006; Accepted 10 August 2006

KEY WORDS: invasion; population ecology; maturity; multiple spawning; roach; gudgeon

\*Correspondence to: Dr Rob Britton, National Fisheries Laboratory, Bromholme Lane, Brampton, Huntingdon, Cambridgeshire PE28 4NE, UK. E-mail: robert.britton@environment-agency.gov.uk

## INTRODUCTION

The topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1842) has proved to be a highly invasive fish species across Europe following initial introduction in 1960 (Bianco, 1988; Wildekamp *et al.*, 1997). A small cyprinid species native to Japan, China, Korea and the River Amur basin, today it is widespread and locally abundant within favourable habitats throughout much of Europe and Russia, with populations also reported from Kazakhstan, Turkey and Algeria (Perdices and Doadrio, 1992; Wildekamp *et al.*, 1997). Although the species was first recorded in the wild in the UK in 1996 (Domaniewski and Wheeler, 1996), there were only four infested sites reported in 2002 (Gozlan *et al.*, 2002). However, distribution has since increased, with the species now present in at least 25 sites. A number of these are established populations in lakes with connection to major river catchments, providing a mechanism for fluvial dispersal (Pinder *et al.*, 2005). As *P. parva* has recently been found to be a vector of an emergent infectious disease (Gozlan *et al.*, 2005) and is classed as an international pest (Welcomme, 1992), their increased distribution raises concern over their potential to invade new habitats and exerts impacts on native fish communities in the UK.

In their natural range and expanded range of mainland Europe, the life history traits of topmouth gudgeon include batch spawning, nest guarding and early maturity (e.g. Bruton, 1986; Rosecchi *et al.*, 2001). In conjunction with broad environmental tolerance limits, these are traits that generally favour the ability of an invading fish species to succeed in colonizing new water bodies (Riccardi and Rasmussen, 1998; Pinder *et al.*, 2005). Indeed, the invasion success of *P. parva* has led them to be described as the most invasive fish in Europe (Gozlan *et al.*, 2005). However, despite their increased UK distribution, there are no data available from invaded waters adequately describing their population ecology, yet, these data are crucial in understanding *P. parva* invasion success in new waters in the UK following introduction and the subsequent consequences they may provoke. The aims of this case study are to document the establishment, population structure and reproduction of *P. parva* in an infested lake in the English Lake District and to relate these outputs to those of the resident species in the lake.

## MATERIALS AND METHODS

The *P. parva* population studied was present in a shallow lake (<2.5 m) of 2.2 ha in the Lake District (north-west England) at latitude 54° N (note: the name of the lake has been withheld for reasons of confidentiality). Summer water temperatures rarely rose above >20°C, with winter temperatures rarely falling below 0°C. Ice cover in winter was infrequent and rarely lasted for more than two consecutive days. Naturalized populations of roach *Rutilus rutilus* (L.) and gudgeon *Gobio gobio* (L.) were present in the lake, along with large (300 mm) common bream *Abramis brama* (L.), tench *Tinca tinca* (L.) and common carp *Cyprinus carpio* L., following introductions designed to enhance the lake's recreational, catch and release fishery. These will all be referred to as 'resident species' throughout the text.

Although their introduction was believed to have occurred in 2000, the presence of *P. parva* in the lake was only confirmed in October 2002 when anglers reported a new, unknown species being captured in the fishery, with a specimen submitted for identification (I.J. Winfield, pers. comm.). The lake was sampled in March 2003 using a 50-m seine net of mesh size 2.5 mm; in August 2004, using the same net, and a 1.5 m diameter micromesh drop net; and in February 2005, when point samples were taken using both electric fishing and a micromesh seine net. Samples were also available from a *P. parva* eradication exercise using chemical treatment that was initiated on 22 March 2005, during which the larger (250 mm) *C. carpio*, *T. tinca* and *A. brama* were all removed from the lake prior to the piscicide rotenone being applied. Full details of the rotenone application are available in Britton and Brazier (in press). Following the treatment,

1 samples of *P. parva*, *R. rutilus*, *G. gobio* and *A. brama* were taken back to the laboratory for analyses of life-  
history traits.  
3 In the laboratory, fork length (mm), weight (g), sex and gonad weight were measured for individual fish,  
with three scales and the operculum removed for ageing. Ages were determined by viewing the scales under  
5 a projecting microscope ( $\times 10$ ) and counting the number of annuli, with the age validated by examination  
of the opercula of 10% of the sample under a binocular microscope ( $\times 5$ ). Length at age was estimated by  
7 back-calculation (Francis, 1990), with  $L_{-\infty}$  (maximum theoretical length) of the von Bertalanffy growth  
model (von Bertalanffy, 1938) determined using the nonlinear method in the software Simply Growth  
9 (©Pisces Conservation Ltd). Gonado-somatic index ( $I_G$ ) was calculated by gonad weight/somatic weight,  
where somatic weight was total weight minus gonad weight. Age at maturity was calculated from the  
11 percentage of mature fish in each age class using the formula of DeMaster (1978). Length at maturity was  
determined using a modification of this formula, with 5-mm length intervals in place of age classes (Trippel  
13 and Harvey, 1987) and was represented graphically by fitting a logistic ogive to the proportion of sexually  
mature fish. Sex ratio was expressed as the relative proportion of mature female/male fish. Batch fecundity  
15 was determined by counting the number of ripening oocytes in the ovary, with the relationship between  
fecundity ( $F$ ) and fork length ( $L_F$ ) described by the logarithmic transformation of the power curve  $\log F =$   
17  $\log a + b \log L_F$ , where  $a$  and  $b$  are parameters (Bagenal and Braum, 1978). Fecundity at length estimates  
were then available from  $F = aL_F^b$ . During determination of individual fecundity, the diameters of 30  
19 ripened eggs were measured. Statistical analyses were calculated in MINITAB© and modal distribution of  
lengths at age 1 determined using decomposition assessment following Bhattacharya's method in FiSAT  
21 (FAO/ICLARM Stock Assessment Tools).

## 23 RESULTS

### 25 Population establishment and abundance

27 The data from the March 2003 sample indicated that *P. parva* was already extremely abundant in the lake  
— despite being introduced less than 3 years earlier — with both juveniles and adults present, providing  
29 evidence that a breeding population had become established. In August 2004, a subsample of 450 fish  
<70 mm revealed *P. parva* dominance; the only other species recorded in the sample were *R. rutilus* ( $n = 2$ )  
31 and *G. gobio* ( $n = 1$ ). Although electric fishing point-samples in February 2005 revealed spatial variance in  
*P. parva* distribution, mean density was  $6.1 \pm 3.2 \text{ m}^{-2}$  (Table 1), with fish present between 11 and 61 mm.  
33 There were no other species recorded. The eradication exercise in March 2005 revealed some limitations of  
the previous sampling, as an increased abundance of *G. gobio*, *R. rutilus* and *Abramis brama* (L.) was  
35 recorded (Table 1). However, their combined abundance was only  $1.6 \text{ m}^{-2}$ , considerably below the  
estimates recorded for *P. parva* in the point samples (Table 1). This confirms the numerical dominance of  
37 *P. parva* in the fish community in 2004/05 and demonstrates the ability of the species to establish  
numerically dominant populations in UK waters rapidly following their introduction. There were no  
39 comparative data on fish abundance available for the period prior to *P. parva* introduction.

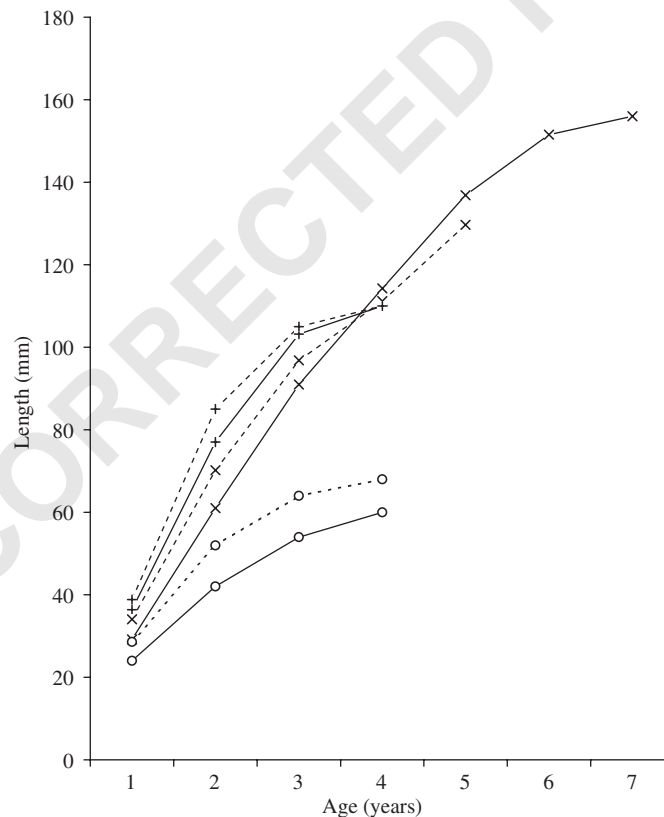
### 41 Population structure and growth

43 The eradication samples showed that *P. parva* attained lengths to 78 mm and age 4 years old, *G. gobio* to  
117 mm and 4 years old, *R. rutilus* to 157 mm and 7 years old and *A. brama* to 128 mm and 4 years old  
45 (Table 1). However, with the exception of *P. parva*, there were no young-of-the-year recorded (youngest fish  
age 2 years, length 55 mm). Furthermore, no *C. carpio* and *T. tinca* <250 mm were present, suggesting that  
47 these species had been unable to reproduce successfully and/or recruit in the lake following introduction, a  
common feature of these species in northern England owing to temperatures rarely being sufficient to

1 induce spawning. Because of low abundance of *A. brama* in the sample, no further analyses of their life-  
 3 history traits were recorded. The pre-maturation growth of *P. parva* was relatively fast, with a mean of 40%

5 Table 1. Life history traits of *Pseudorasbora parva*, *Rutilus rutilus* and *Gobio gobio* in the lake in NW England

	<i>P. parva</i>		<i>R. rutilus</i>		<i>G. gobio</i>	
	♀	♂	♀	♂	♀	♂
9 Mean density (m <sup>-2</sup> )	6.1 ± 3.2			< 1.6		
9 Proportion of maximum length produced in first year of life (%)	40	42	19	26	31	33
11 <i>L</i> <sub>-infinity</sub> (mm)	65	81	253	249	121	119
11 Sex ratio (F:M)	1:2.18		1:0.95		1:1.175	
13 Age at maturity (yr)	1.8	1.7	3.9	3.9	2.8	2.6
13 Mean egg size (mm)	0.65 ± 0.15		1.09 ± 0.14		0.68 ± 0.13	
15 Mean fecundity of fish at first reproduction	262		1671		1436	
15 Fecundity of fish of mean length	374		7771		2351	
15 Mean no. eggs per gram body weight	351		228		194	
17 Maximum fork length (mm)	59	78	164	148	109	117
17 Maximum age (yr)	4	4	7	6	4	4



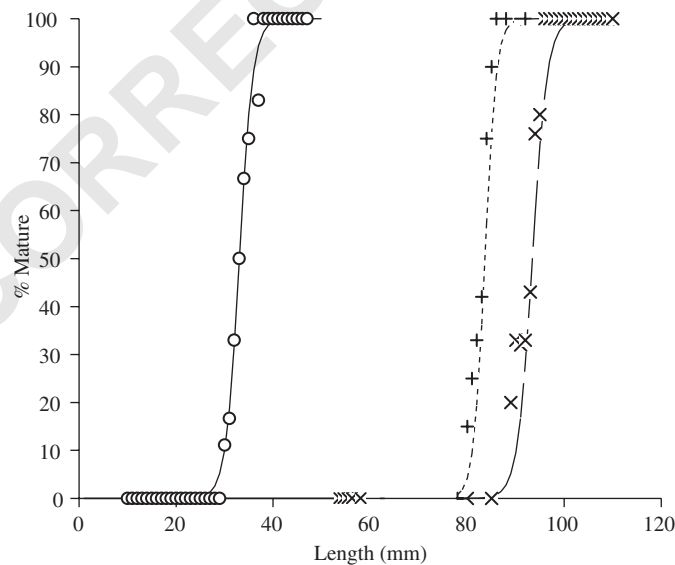
47 Figure 1. Mean length of age of female (solid lines) and male (dashed lines) *Pseudorasbora parva* (○), *Rutilus rutilus* (×) and *Gobio gobio* (+), March 2005 (standard error values have been omitted for reasons of data clarity).

1 (female) and 42% (male) of total growth achieved by age 1 (Table 1). This was followed by much lower  
 2 proportional growth increments following maturation (Figure 1). By contrast, *G. gobio* and *R. rutilus*  
 3 produced a lower relative proportion of growth in their first year of life, but achieved higher  $L_{\infty}$ ,  
 4 maximum lengths and ages than *P. parva* (Table 1, Figure 1).  
 5

## 7 Reproduction

9 The relatively high growth increment in the first year of life of *P. parva* facilitated individuals reaching  
 10 maturity at lengths > 36 mm during their second year of life (Table 1, Figure 2). By contrast, *G. gobio* and  
 11 *R. rutilus* matured at more advanced ages and lengths (Figure 2). There were considerable differences in the  
 12 sex ratios between the species, with *P. parva* dominated by males, but with ratios close to 1:1 in both *G.*  
 13 *gobio* and *R. rutilus* (Table 1). Female *P. parva* were only prevalent at size classes of 35 to 50 mm, males  
 14 were then the dominant sex at lengths above this (Figure 3). Only one female *P. parva* was present > 55 mm  
 15 (59 mm). By contrast, there was no significant difference in the lengths of male and female *G. gobio* and *R.*  
 16 *rutilus* (*t*-test, *df* 10, *P* > 0.05; Figure 3).  $I_G$  values for *P. parva* ranged between 0.037 and 0.127 (mean  
 17 0.089), *G. gobio* 0.055 and 0.078 (mean 0.065) and *R. rutilus* 0.101 and 0.176 (mean 0.136), indicating that  
 18 *P. parva* was investing a similar proportion of resources in gonad development as the resident species at the  
 19 time of sampling.

20 The mean fecundity of both an individual female at first maturity and of mean mature length was  
 21 comparatively low for *P. parva* compared with *G. gobio* and *R. rutilus*, although *P. parva* produced the  
 22 highest mean number of eggs per gram body weight (Table 1). The *P. parva* estimates also represented  
 23 batch fecundity only, rather than total fecundity. A large number of unripened eggs (<0.1 mm) were also  
 24 present in the ovary. This was not the case for *R. rutilus* or *G. gobio*, suggesting that multiple spawning  
 25 events only occurred in *P. parva*. This was supported by back-calculated lengths at age 1 that suggested  
 26 poly-modal lengths for *P. parva* but only single modes for *R. rutilus* and *G. gobio* (Figure 4). Modal  
 27 progression analysis (FAO/ICLARM Stock Assessment Tools) confirmed the presence of at least three



47 Figure 2. Maturity ogives showing length of maturity of *Pseudorasbora parva* (O), *Rutilus rutilus* (x) and *Gobio gobio* (+), March 2005.

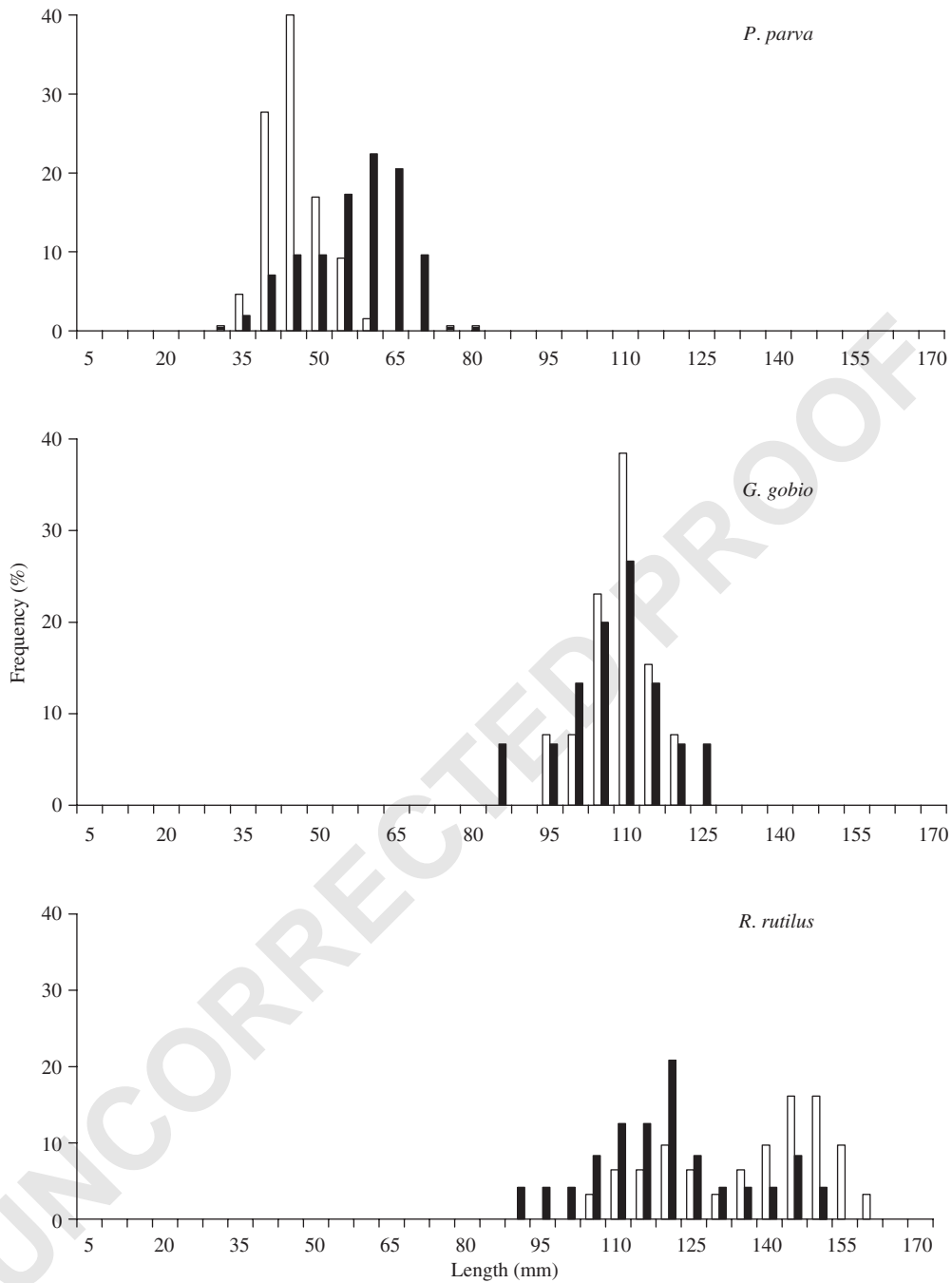


Figure 3. Proportion of males (■) and females (□) by length for *Pseudorasbora parva*, *Rutilus rutilus* and *Gobio gobio*, March 2005.

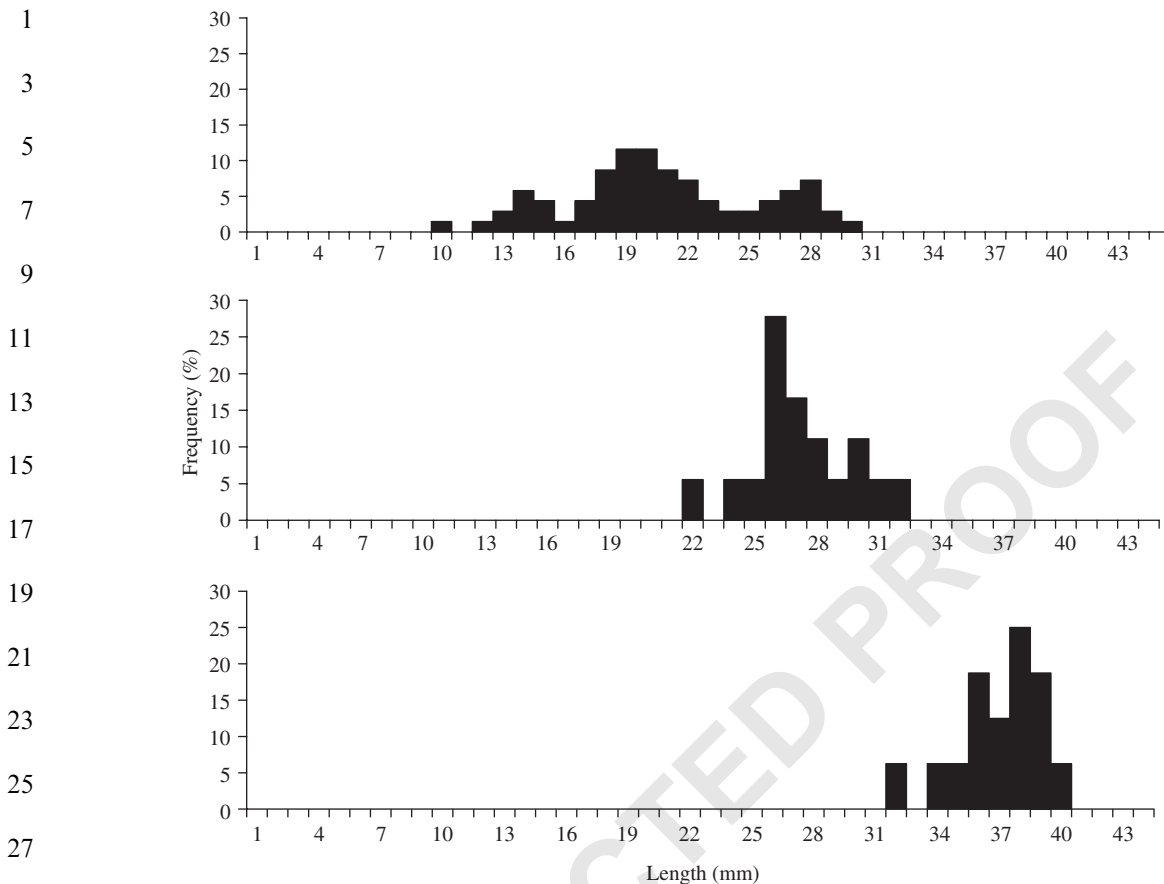


Figure 4. Back-calculated lengths at age 1 showing a poly-modal distribution for *Pseudorasbora parva* (top) and single modes in *Rutilus rutilus* (middle) and *Gobio gobio* (bottom).

modes with a separation index of  $>2$  for *P. parva* cohorts, with only a single mode for *R. rutilus* and *G. gobio*.

## DISCUSSION

In this case study, the reproductive behaviour of *P. parva* involved early maturity and multiple spawning that enabled effective early-life reproduction and, in conjunction with a limited lifespan, a high population turnover that appeared to promote their rapid establishment in the lake. This facilitated their invasion success and, within 4 years of their introduction, had assisted *P. parva* in becoming the numerically dominant species in the fish community. With the exception of sunbleak *Leucaspius delineatus* (Heckel), the suite of traits adopted by *P. parva* in this lake comprise a reproductive strategy that is unique to cyprinid species in Europe, yet is utilized by  $>50\%$  of established non-native fish species in the UK (Maitland, 2000).

Of ecological advantage to *P. parva* was their ability to use this suite of reproductive behaviours in an environment where the resident *R. rutilus* and *G. gobio* adopted traits of later maturity and spawning just



1 Table 2. Life history traits of the *Pseudorasbora parva* population in north-west England compared with two populations from  
 3 southern Europe (Rosecchi *et al.*, 1993, 2001)

3 Trait	Lake in NW England	Fumemorte Canal, S France	L. Mikri Prespa, NW Greece
5 Maximum fork length (mm)	78	92	80
Age at maturity (yr)	1.8	1	1
7 Proportion of mature fish at age 1 (%)	32	100	100
Mean length at maturity (mm)	38	76	51
9 Multiple <i>vs.</i> single spawning	Multiple	Multiple	Multiple
Batch fecundity ( $F_b$ ) relative to size ( $L_F$ )	$\ln F_b = 2.388$ $\ln L_F - 3.063$	$\ln F_b = 2.256$ $\ln L_F - 2.946$	$\ln F_b = 2.961$ $\ln L_F - 6.342$
11 Mean batch fecundity of fish at first reproduction	277	920	200
Maximum age (yr)	4	2	3

13

15

17 once in a breeding season (Table 2; Vila-Gispert and Moreno-Amich, 2002). This was despite other  
 19 populations of these species adopting some of the traits displayed by the *P. parva* population at different  
 21 latitudes and environmental variables (Vila-Gispert and Moreno-Amich, 2002). It was unlikely, however,  
 23 that these life-history traits had been solely responsible for *P. parva* colonization success. Factors including  
 25 niche availability, favourable habitat and the presence of few natural predators (for example, there were no  
 27 piscivorous fish present in the lake) were also likely to have been important factors in assisting colonization.

29 Although there was similarity between the traits utilized by the *P. parva* population in this lake and with  
 31 populations elsewhere in Europe, individuals in this population were slower-growing and matured later  
 33 (Table 2). Although the reasons for this can only be speculated upon, it may have been a response to the  
 35 latitude and temperate climate of the Lake District compared with southern Europe. This would have  
 37 resulted in a shorter growth season of lower mean temperatures, with these being an important determinant  
 39 of fish life-history traits (Cowx, 2001). However, as Katano and Maekawa (1997) demonstrated that growth  
 41 of female *P. parva* significantly decreases with increased density, the slower growth of *P. parva* in this lake  
 43 may have resulted from their abundance producing a high degree of intraspecific competition for resources  
 45 between individuals through density-dependent pressures. During their initial, explosive phase of invasion  
 47 following their introduction, individual *P. parva* may have all matured by age 1 and grown faster (similar to  
 the populations in southern Europe), with this no longer possible owing to the subsequent combination of  
 high population density and resultant limiting resources.

The reproductive behaviours of invading species are often crucial to their colonization success, especially  
 where available niches are already occupied by resident species (Gozlan *et al.*, 2003a). In the case study, the  
 reproductive traits utilized by *P. parva* appeared to facilitate colonization and ensured successful spawning  
 in 2004 when reproductive and/or recruitment failure was apparent in the resident species. The causes of  
 this failure may have been climatic, for temperature is a key determinant of reproductive and recruitment  
 success in cyprinid species (Mills and Mann, 1985; Nunn *et al.*, 2003; Britton *et al.*, 2004). This appears  
 unlikely, however, given that *P. parva* young-of-the-year were abundant in the lake and the temperatures  
 required to initiate spawning in these species are similar. It was more likely a result of high interspecific  
 competition, with the high abundance of *P. parva* in length ranges < 50 mm (including the 0+, 1+ and 2+  
 age classes) producing intense competition with the 0-group resident fish for resources. This is because  
 recorded impacts of invading *P. parva* on endemic species include egg depredation, facultative parasitism  
 and effects of intense interspecific competition (Libosvářský *et al.*, 1990; Rosecchi *et al.*, 1993; Xie *et al.*,  
 2001). Alternatively, it may have been due to spawning inhibition of the resident species resulting from the  
 transmission from *P. parva* of an obligate intracellular eukaryote pathogen, similar to the lethal rosette  
 agent *Sphaerothecum destruens* (Gozlan *et al.*, 2005). Transmission of this pathogen from *P. parva* to

1 *L. delineatus* resulted in a 96% decline in the *L. delineatus* population over three seasons owing to spawning  
inhibition (Gozlan *et al.*, 2005). However, work is continuing to ascertain whether *P. parva* in this  
3 population were carriers and whether cyprinid fish native to England are susceptible to the impact of the  
pathogen (R. Gozlan, pers. comm.).

5 Further divergence was observed between the reproductive traits of *P. parva* and the resident species in  
sex ratios and sexual dimorphism. Unlike the resident species, the sex ratio of *P. parva* was biased towards  
7 males (Table 1), with the population at lengths > 55 mm male-dominated; as females were only prevalent at  
lengths of between 35 and 50 mm, sexual dimorphism was manifested in larger male body sizes (Figure 3).  
9 This is a common feature of *P. parva* populations and relates to their adoption of nest guarding as a  
reproductive behaviour, as they are a species that typically exhibits paternal care of young in order to  
11 promote egg survival (Adamek and Siddiqui, 1997). The phenotypic characteristics of male nest-guarders  
typically include large body sizes. In nest-guarding species such as stickleback, *Gasterosteus aculeatus* L.,  
13 these characters are important qualities for dominance and aggression, facilitating defence of the nest  
(Downhower and Brown, 1980; Rowland, 1989; McKinnon, 1996; Katano and Maekawa, 1997; Gozlan  
15 *et al.*, 2003b). As such, male body size enables females to discriminate between individuals during mate  
choice, with the larger males being more desirable (Maekawa *et al.*, 1996). In addition, the larger, more  
17 aggressive *P. parva* males are able to acquire more favourable substrates for spawning than smaller males  
(Konishi and Takata, 2004). A further advantage of the presence of large *P. parva* males is that females may  
19 regulate their fecundity according to the male body sizes present (Katano and Maekawa, 1997). In  
experimental studies, females increased their fecundity when large males were present; when small males  
21 only were present, fecundity was suppressed (Katano and Maekawa, 1997).

This case study has revealed that following *P. parva* introduction, a dramatic shift in the species  
23 composition and community structure of the lake occurred after only 4 years. In combination with the  
increasing distribution of *P. parva* and their presence in lakes that provide significant opportunities for  
25 fluvial dispersal (Pinder *et al.*, 2005), it implies that other fish communities in the UK of similar habitat and  
community structure are threatened by their introduction. If the native fish communities of the UK are to  
27 be protected from the invasion of this species, then preventative actions should include prohibiting *P. parva*  
introduction into new waters and their dispersal from invaded waters. Their elimination from infested  
29 waters that threaten to provide a pathway for fluvial dispersal will also minimize distribution, and options  
for this include eradication programmes similar to that completed on this lake, as this appears to have been  
31 successful (Britton and Brazier, in press). Otherwise, *P. parva* will become an alien species that will have to  
be accepted as a permanent addition to the fish fauna of the UK.

## ACKNOWLEDGEMENTS

37 The authors wish to thank the staff of the Environment Agency for their assistance in providing the samples for  
analysis, the Windermere, Ambleside and District Angling Association for their cooperation, and Ian Winfield for  
39 information on the initial recording of topmouth gudgeon in the lake. The views expressed are those of the authors and  
not their parent organizations.

## REFERENCES

- 45 Adamek Z, Siddiqui MA. 1997. Reproduction parameters in a natural population of topmouth gudgeon *Pseudorasbora*  
*parva* and its consequence and food characteristics with respect to sexual dissimilarities. *Polish Archives of*  
*Hydrobiology* **44**: 145–152.
- 47 Bianco PG. 1988. Occurrence of the Asiatic gobionid *Pseudorasbora parva* Temminck and Schlegel in south-eastern  
Europe. *Journal of Fish Biology* **32**: 973–974.

- 1 Bagenal TB, Braum E. 1978. Eggs and early life history. In *Methods for the Assessment of Fish Production in Fresh Waters*, 3rd edn, Bagenal TB (ed.). IBP Handbook No. 3, Blackwell Scientific Publications: Oxford; 165–178.
- 3 Britton JR, Axford SA, Cowx IG, Frear PA. 2004. Overview of recruitment patterns of roach *Rutilus rutilus* L. between 1969 and 2001 in the rivers of England and their influence on population abundance. *Ecohydrology and Hydrobiology* **4**: 91–102.
- 5 Britton JR, Brazier M. In press. Eradicating the invasive topmouth gudgeon, *Pseudorasbora parva*, from a recreational fishery in Northern England. *Fisheries Management and Ecology*.
- 7 Bruton MN. 1986. Life history styles of invasive fishes in Southern Africa. In *Ecology and Management of Biological Invasions in Southern Africa*, MacDonald AW, Kruger FJ, Ferrar AA (eds). Oxford University Press: New York; 201–208.
- 9 Cowx IG. 2001. Factors influencing coarse fish populations in rivers. Environment Agency RandD Publication 18, The Stationery Office, London.
- 11 DeMaster DP. 1978. Calculation of average age of sexual maturity in marine mammals. *Journal of the Fisheries Research Board of Canada* **35**: 912–915.
- 13 Domaniewski J, Wheeler A. 1996. The topmouth gudgeon has arrived. *Fish* **43**: 40.
- Downhower JF, Brown L. 1980. Mate preference of female mottled sculpins, *Cottus bairdi*. *Animal Behaviour* **28**: 728–734.
- 15 Francis RICC. 1990. Back-calculation of fish length: a critical review. *Journal of Fish Biology* **36**: 883–902.
- 17 Gozlan RE, Pinder AC, Shelley J. 2002. Occurrence of the Asiatic cyprinid *Pseudorasbora parva* in England. *Journal of Fish Biology* **61**: 298–300.
- Gozlan RE, Flower CJ, Pinder AC. 2003a. Reproductive success in male sunbleak, a recent invasive fish species in the U.K. *Journal of Fish Biology* **63** Suppl. A: 131–143.
- 19 Gozlan RE, Pinder AC, Durand AC, Bass JC. 2003b. Could the small size of *Leucaspius delineatus* be an ecological advantage in invading British watercourses. *Folia Zoologica* **52**: 99–108.
- 21 Gozlan RE, St-Hilaire S, Feist SW, Martin P, Kent ML. 2005. An emergent infectious disease threatens European fish biodiversity. *Nature* **435**: 1046.
- 23 Katano O, Maekawa K. 1997. Reproductive regulation in the female Japanese minnow *Pseudorasbora parva* Cyprinidae. *Environmental Biology of Fishes* **49**: 197–205.
- 25 Konishi M, Takata K. 2004. Size-dependent male-male competition for a spawning substrate between *Pseudorasbora parva* and *Pseudorasbora pumila*. *Ichthyological Research* **51**: 184–187.
- 27 Libosvářský C, Baruš CV, Sterba O. 1990. Facultative parasitism of *Pseudorasbora parva* Pisces. *Folia Zoologica* **39**: 355–360.
- 29 Maekawa K, Iguchi K, Katano O. 1996. Reproductive success in male Japanese minnows *Pseudorasbora parva*: observations under experimental conditions. *Ichthyological Research* **53**: 257–266.
- Maitland PS. 2000. *Guide to Freshwater Fish in Britain and Europe*. Hamlyn: London.
- 31 McKinnon JS. 1996. Red colouration and male parental behaviour in the threespine stickleback. *Journal of Fish Biology* **49**: 1030–1033.
- 33 Mills CA, Mann RHK. 1985. Environmentally induced fluctuations in year class strength and their implications for management. *Journal of Fish Biology* **27** Suppl. A: 209–226.
- Nunn AD, Cowx IG, Frear P, Harvey JP. 2003. Is water temperature an adequate predictor of recruitment success in coarse fish populations in lowland rivers? *Freshwater Biology* **48**: 579–588.
- 35 Perdices A, Doadrio I. 1992. Presence of the Asiatic Cyprinid *Pseudorasbora parva* Schlegel 1842 in inland Italian waters. *Rivista di Idrobiologia* **29**: 461–467.
- 37 Pinder AC, Gozlan RE, Britton JR. 2005. Dispersal of the invasive topmouth gudgeon *Pseudorasbora parva* in the UK: a vector for an emergent infectious disease. *Fisheries Management and Ecology* **12**: 411–414.
- 39 Ricardi A, Rasmussen JB. 1998. Perspectives: predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1759–1765.
- Rosecchi E, Crivelli A, Catsadorakis G. 1993. The establishment and impact of *Pseudorasbora parva*, an exotic fish species introduced into Lake Mikri Prespa north-western Greece. *Aquatic Conservation: Marine and Freshwater Ecosystems* **3**: 223–231.
- 43 Rosecchi E, Thomas F, Catsadorakis G. 2001. Can life history traits predict the fate of introduced species? A case study on two cyprinid fishes in Southern France. *Freshwater Biology* **46**: 845–853.
- 45 Rowland WJ. 1989. The effects of body size, aggression and nuptial conditions on competition for territories in male three-spine sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* **37**: 282–289.
- 47 Trippel EA, Harvey HH. 1987. Reproductive responses of five white sucker *Catostomus commersoni* populations in relation to lake acidity. *Canadian Journal of Fisheries and Aquatic Sciences* **44**: 1018–1023.

- 1 Vila-Gispert A, Moreno-Amich R. 2002. Life history patterns of 25 fish species from European freshwater fish  
communities. *Environmental Biology of Fishes* **65**: 387–400.
- 3 Von Bertalanffy L. 1938. A quantitative theory of organic growth. *Human Biology* **10**: 181–243.
- 5 Welcomme RL. 1992. A history of international introductions of inland aquatic species. *ICES Marine Science Symposia*  
**194**: 3–14.
- 7 Wildekamp RH, Van Neer W, Kucuk F, Unlusayin M. 1997. First record of eastern Asiatic gobionid fish  
*Pseudorasbora parva* from the Asiatic part of Turkey. *Journal of Fish Biology* **51**: 858–861.
- 9 Xie Y, Zhenyu L, Gregg WP, Dianmo L. 2001. Invasive species in China: an overview. *Biodiversity and Conservation* **10**:  
1317–1341.

9

11

13

15

17

19

21

23

25

27

29

31

33

35

37

39

41

43

45

47

