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Population consequences of reproductive decisions

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Behaviour can be a key component of animal population ecology, yet the population consequences of behavioural decisions are poorly understood. We conducted a behavioural and demographic study of the bitterling *Rhodeus sericeus*, a freshwater fish that spawns in live unionid mussels. We used a population model incorporating game theory decisions and measurements of demographic parameters in order to provide predictions of population size among 13 populations of this fish. Our model predicted that the observed behavioural spawning decisions, while maximizing individual fitness, cause a significant 6% reduction in population size compared with randomly distributed spawnings. We discuss our findings in the context of the population consequences of adaptive behaviour.

Keywords: individual behaviour; population dynamics; bitterling; *Rhodeus sericeus*

1. INTRODUCTION

Behavioural ecology is founded on the principle that natural selection favours decisions that maximize the inclusive fitness of individuals (Hamilton 1972; Williams 1975; Krebs & Davies 1997). Yet the population consequences of this paradigm are not clear (Sutherland 1996; Fryxell & Lundberg 1998). An understanding of the behavioural basis of population ecology may increase the predictive power of population models and could extend their application to novel conditions (Hassell & May 1985; Parker 1985; Bernstein *et al*. 1988; Anholt 1997). For example, competition for resources between female red deer (*Cervus elaphus*) can cause reduced reproductive success and survival in subordinates, which could suppress the population size (Clutton-Brock & Albon 1985). Similarly, Gordon (1997) demonstrated that the proximity of neighbouring colonies of red harvester ants (*Pogonmyrmex barbatus*) influences the foraging patterns of colonies, with repercussions for food acquisition and colony growth.

Here we use the bitterling (*Rhodeus sericeus*), a species of freshwater fish, in order to explore the importance of behaviour to population dynamics. Bitterling are suitable for investigating the role of reproductive behaviour in population ecology because they use a spawning site that can be readily quantified, manipulated and assessed for quality. Males defend territories around freshwater mussels and attract females for spawning. Female bitterling insert a long ovipositor into the exhalant siphon of a mussel, depositing one to six eggs into the gills. During a spawning season, a female typically lays 100–300 eggs (Duyvené de Wit 1955; Wiepkema 1961; Nagata 1985). Mussels may contain eggs from many spawnings and many females (up to 257 embryos in the gills of a single mussel); thus, spawning by bitterling is analogous to superparasitism in parasitoids, whereby a clutch of eggs is deposited on a host that is already parasitized by a member of the same species (Godfray 1994). Male bitterling fertilize the eggs by releasing sperm at the inhalant siphon of the mussel so that water drawn in by the mussel carries the sperm to the eggs (Kanoh 1996). Embryonic development is completed in the mussel. Juvenile bitterling depart their host via its exhalant siphon after exhausting their yolk supply, which is a period of approximately four weeks (Aldridge 1999).

Four species of freshwater mussel (*Anodonta anatina*, *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus*) are used as spawning hosts by bitterling (Reynolds *et al*. 1997). Smith *et al*. (2000) used field experiments to show that female bitterling have highly significant preferences for spawning in *A. anatina*, *U. pictorum* and *U. tumidus* while avoiding spawning in *A. cygnea*. Female bitterling were further shown to avoid superparasitized mussels. The mortality rates of bitterling embryos in mussels have proved to be strongly density dependent and the strength of the density dependence varies significantly between mussel species, with the strongest density-dependent mortality of embryos in *A. cygnea*.

The fact that female preferences for mussels match the survival of their embryos in those mussels raises the possibility that oviposition choices by females have ramifications for population dynamics. Our aim in this study was to incorporate these behavioural preferences by female bitterling into a population model in order to investigate the significance of spawning decisions to bitterling population dynamics. We tested for the effects of varying spawning site availability and quality, predator density and refuge availability in order to quantify the relative contribution of behavioural decisions to bitterling demography.

2. METHODS

(a) *Study sites*

Field data were collected from 13 lakes in the south-east of the Czech Republic at the centre of the natural range of the bitterling in Europe (Kottelat 1997). The lakes were created 25–30 years ago (Jurajda 1995) and all contained bitterling and unionid mussels. The bitterling populations varied 90-fold between lakes and the mussel populations varied 500-fold. The lakes were isolated, with the fish in them representing discrete populations. The size of the lakes varied from 0.6 to 2.5 ha with a maximum water depth of *ca*. 2 m.

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The distance around the margin of every lake was measured to the nearest 1 m and each metre of lake margin was classed as either shallow sided with aquatic macrophytes or steep sided without macrophytes. The distance the macrophytes extended from the bank was measured to the nearest 1 cm at 30 m intervals and the water depth at that point measured to the nearest 1 cm. Juvenile bitterling were never found more than 2 m from the lake edge where marginal vegetation was absent (mean distance = 1.3 m and s.e. = 0.38 m). Thus, where vegetation was absent the water depth was measured at a distance of 2 m from the water's edge. By assuming a linear gradient in the lake margin, we were able to use these measurements to estimate the total volume of water of each habitat type available to juvenile bitterling in each lake. In those lakes with small and fractured areas of vegetated margin, a minimum of 10 m^3 of this habitat was assigned to the lake. The total surface area of every lake was estimated from 1:10 000 scale maps.

(b) ***Juvenile census***

The density of juvenile bitterling was assessed one to two times each month (May–September) each year from dipnet samples collected at 5 m intervals around the perimeter of each lake. The water volume sampled by the dipnets was estimated in field trials (18.7 l, s.e. = 0.66 l and $n = 50$) by attaching a 150-l plastic bag to the rim of the dipnet and measuring the volume of water in the bag to the nearest 100 ml.

The catchability of different juvenile bitterling size classes using a dipnet was tested by enclosing a 13.1 m^2 area of lake margin with a net and depleting juvenile bitterling with 25 sweeps in each of ten depletion 'runs'. A total of 327 juvenile bitterling were caught, ranging in size from 10 to 35 mm standard length (SL) (from the tip of the snout to the base of the tail fin). The fish were split into four size classes and the catchability between size classes was tested by analysis of covariance using the catch as the dependent variable and the cumulative catch as the covariate. There was no significant difference in the catch in each size class (ANCOVA $F_{3,35} = 0.12$ and $p = 0.947$) and the cumulative catch was a significant covariate (ANCOVA $F_{1,35} = 310.54$ and $p < 0.001$).

(c) ***Adult census***

We censused the bitterling populations by electrofishing each spring prior to annual spawning and in the autumn following spawning over a period of three years (1995–1997). Between eight and 17 measured stretches of lake bank were enclosed with nets, then the area inside was depleted in three fishing 'runs'. Electrofishing took place in water of between 0.5 and 1.5 m depth with a mean conductivity of 595 $\mathrm{mS\,cm^{-1}}$ (s.e. = 13.3 $\mathrm{mS\ cm^{-1}}$). The bitterling abundance within the netted areas was estimated using the generalized Zippin (1958) removal method. Estimates of the total bitterling population size were made by multiplying the estimates for the electrofished lake margin distances to the entire lake. Censuses of perch (*Perca fluviatilis*) were conducted in parallel with those for bitterling.

(d) ***Mussel census***

At least eight belt transects of 1 m^2 quadrats were used in each lake in order to estimate mussel abundance, size and species composition. Each quadrat was searched by hand by a diver. The efficiency of this method was verified by searching three times in each of three transects; in every case no additional mussels were located. There was no significant difference in the estimated abundance of mussels in seven lakes that were compared between 1995 and 1996 (Wilcoxon signed-ranks test, $T_+ = 0.169$, $n = 7$ and $p = 0.866$).

(e) ***The models***

We used age-structured models in which the numbers of fish in age class i were the number in class $i-1$ multiplied by the survival rate. All parameter estimates affecting each transition probability in the model were derived from data collected in 1996 and 1997 only. The mortality rates of the fish in all populations were estimated by tracking age cohorts over a two-year period. The mean instantaneous mortality rates were estimated to be 0.93 (s.e. = 1.280) for the second summer and 0.07 (s.e. = 0.021) for the third summer; no bitterling were found to survive a fourth summer. Survival at other life stages was determined by density-dependent functions. The number of juveniles each year was determined by the female fecundity in each age class between one and three years multiplied by the number of females in each age class. Female size (L_t) was estimated each April using a Von Bertalanffy growth equation (Allen 1971) ($L_t = L_\infty(1 - \exp^{[-K(t-t_0)]})$), with parameters derived by age-calibrated, length–frequency analysis using FiSAT (Gayanilo & Pauly 1997): $L_\infty = 62$ mm, $t_0 = -0.7$ years and $K = 0.43$. The female fecundity was estimated from size using a size–fecundity relationship derived by dissecting the ovaries of 77 females prior to spawning and making direct counts of yolked oocytes. The relationship between size and fecundity took the form $F = aL^b$, where F is the fecundity and L is the fish SL in millimetres. The value fitted for parameter a in this model was 0.07 (s.e. = 0.012) and for parameter b was 2.165 (s.e. = 0.121) ($r^2 = 0.81$, $F_{1,75} = 318.33$ and $p < 0.001$). Resorption of oocytes was taken as negligible and bitterling were assumed to be batch spawners with determinate fecundity, such that breeding season fecundity is fixed at the start of spawning with oocyte number declining over the spawning season (Wootton 1998). Evidence for this assumption derives from a study by Solomon *et al.* (1984), which demonstrated determinate fecundity in the closely related *Rhodeus ocellatus*. A random subsample of 50 adult bitterling collected in October 1995 from eight populations showed no significant difference in the frequency of the sexes ($\chi^2 = 0.0$, d.f. = 1 and $p = 1$); thus, the sex ratio was taken as unity.

Based on Smith *et al.* (2000), we assumed that the eggs were distributed between mussels in the margins of the lakes in an ideal free way (Fretwell 1972), such that the distribution of eggs reflected the mussel abundance and ratio of the density-dependent mortality rate among species. Based on the release of juvenile bitterling from mussels, which lasted from late May to late July, we assumed the spawning season lasted two months. Aldridge (1999) showed the mean incubation period of bitterling embryos in mussels from the day of spawning to be 28 days. We fitted Hassell *et al.*'s (1976) model of density dependence $S = (1 + aN)^{-b}$ to data for density-dependent infection of bitterling by the parasitic anchorworm (*Lernaea cyprinacea*), where S is the number of bitterling surviving from October to April and N is the mean density of bitterling in the lake margins in October. The constant a is a scaling constant which, for a given value of b, determines the density at which the proportionate mortality reaches a fixed value (Bellows 1981); b is the strength of the density dependence. The values for a and b were 0.19 (s.e. = 0.235) and 0.61 (s.e. = 0.978), respectively ($r^2 = 0.50$). For the mortalities of the embryos in mussels we fitted data to the relationship $Z = aN^b$, where Z is the daily instantaneous mortality rate and N is the number of embryos in the mussels. The values of parameter b in the relationship were 0.038

(s.e. = 0.0087) ($r^2 = 0.33$, $F_{1,39} = 19.53$ and $p < 0.001$), 0.054 (s.e. = 0.0159) ($r^2 = 0.44$, $F_{1,15} = 11.57$ and $p = 0.004$), 0.035 (s.e. = 0.0063) ($r^2 = 0.53$, $F_{1,28} = 31.21$ and $p < 0.001$) and 0.044 (s.e. = 0.0051) ($r^2 = 0.70$, $F_{1,75} = 75.54$ and $p < 0.001$) for *A. anatina*, *A. cygnea*, *U. pictorum* and *U. tumidus*, respectively. Since the intercept of this model did not vary significantly from zero ($t_{120} = 1.56$ and $p = 0.123$), a common value of zero was used for a for all mussel species. In nursery habitat, the instantaneous juvenile mortality rates were derived from a multiple regression of the form $Z = a + b_1(\log_e \text{ juvenile bitterling density}) + b_2(\text{perch density})$. The values for a, b_1 and b_2 were 1.67 (s.e. = 0.829), 0.58 (s.e. = 0.113) and 0.164 (s.e. = 0.038), respectively. The fit of the model was significant ($r^2 = 0.58$, $F_{2,19} = 13.20$ and $p < 0.001$). The juvenile bitterling density and perch density were not significantly correlated ($r = 0.31$ and $p = 0.143$).

The model simulations began with 100 individuals in each age class and ran for 100 years. The trials showed that the final population size was independent of the initial population size after this period. During the simulations, we allowed all estimates of density dependence and mortality affecting each transition probability in the model to vary randomly by ± one 95% CI of the parameter estimates. One hundred predictions of population size were generated for each simulation in order to provide a prediction of the mean population size in October. Simulations in which populations declined to extinction were included in the estimates of the mean population size.

In order to investigate the importance of selected model components we compared the predictive power of the full model with others from which components were removed. To remove discrimination by bitterling among mussels according to the number of bitterling embryos already inside, we used a Poisson distribution of the eggs among mussels. To examine the importance of discrimination according to mussel species, we removed these choices such that all mussels received equivalent numbers of eggs from females.

3. RESULTS

(a) *Bitterling population dynamics*

The abundance of juveniles in each population in each year showed a similar pattern over time. There was a rapid increase in May as the juveniles were released from the mussels followed by an exponential decline in abundance as mortalities occurred. The mean date of peak abundance among all populations and years was 6 July (s.e. = 2.9 days). The magnitude of the peak abundance of juvenile bitterling varied significantly between populations within years (Kruskal–Wallis $H = 22.2$, d.f. = 12 and $p = 0.036$). There was no relationship between the peak abundance of juveniles and the abundance of perch or the extent of vegetated, marginal nursery areas (defined as water < 1 m deep with submerged, floating or emergent macrophytes). However, there was a highly significant relationship with mussel abundance and weaker relationship with lake area (figure 1 and table 1).

After emergence from their host mussel, juvenile bitterling spend their first summer among aquatic macrophytes in lake margins and recruit to the adult population in autumn. They may then survive for a further 18 months, reproducing at most twice during their lifetime. The abundance of juvenile bitterling at the end of their first summer was independent of lake size and the availability of marginal nursery habitat, but was significantly

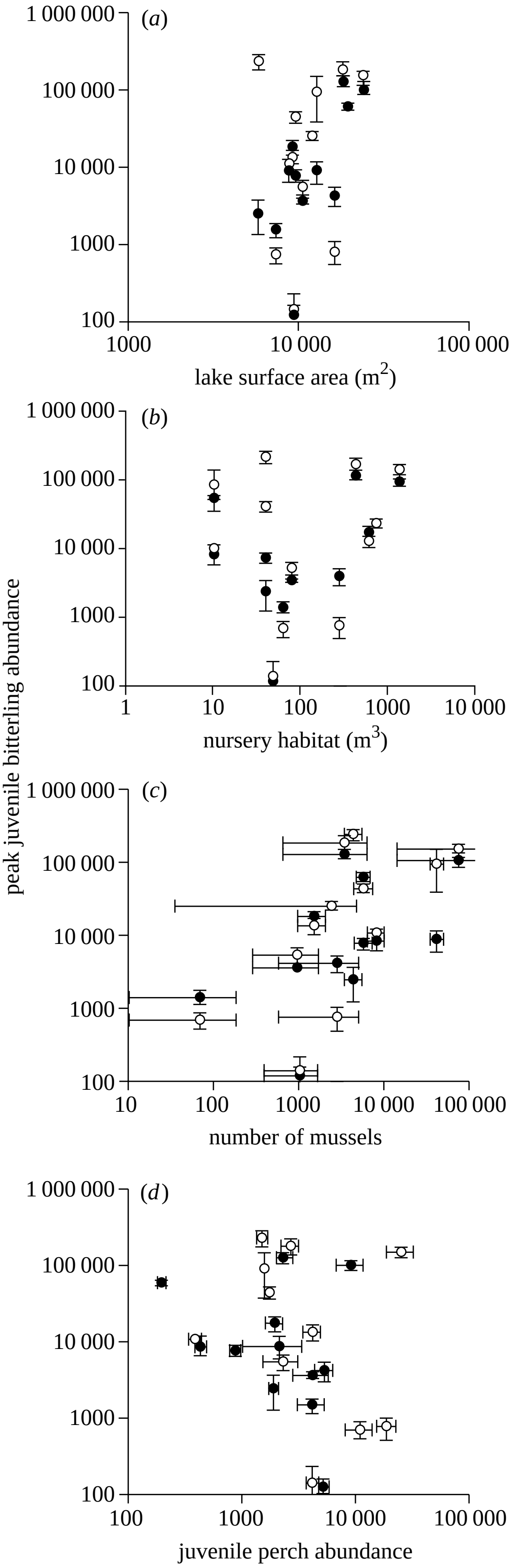

Figure 1. Relationship of the juvenile bitterling peak abundance from 1996 to 1997 with (a) lake surface area, (b) volume of nursery habitat, (c) mussel abundance and (d) peak abundance of perch. Each point represents a different population within years. Abundances were estimated for 1996 (open circles) and 1997 (filled circles). All axes are $\log_{10}$ transformed with estimates ± 1 s.e.

Table 1. *Results of the analysis of covariance of* log_{10} *peak juvenile bitterling abundance (d.f. = 1,23) and* log_{10} *bitterling recruitment strength (d.f. = 1,19) between 1996 and 1997*

covariate and year effects	peak juvenile abundance		recruitment strength	
	F	*p*	*F*	*p*
lake area (m^2)	4.85	0.039	0.74	0.401
year	0.60	0.447	0.13	0.721
perch abundance	1.10	0.307	6.19	0.023
year	0.59	0.452	0.12	0.731
nursery volume (m^3)	1.01	0.326	0.01	0.906
year	0.25	0.625	0.30	0.762
mussels in lake margin	12.10	0.002	5.23	0.035
year	0.68	0.420	0.30	0.591

dependent on the density of perch, the chief predator of juvenile bitterling and mussel abundance (figure 2 and table 1). After emergence from their host mussel the instantaneous mortality rate of juveniles until autumn, when they are in nursery areas, was shown by analysis of covariance, with bitterling density as the covariate, to be significant (log_{10} transformation, ANCOVA $F_{1,19} = 4.88$ and $p = 0.041$), with a weak effect of year (log_{10} transformation, ANCOVA $F_{1,19} = 3.67$ and $p = 0.070$) (figure 3*a*). There were significant correlations between the perch abundance in 1996 and 1997 and the amount of nursery habitat, though no other independent variables were significantly correlated (table 2).

The overwinter mortality in bitterling was density independent, though infection by anchorworm was correlated with the fish density (log_{10} transformation, $r_{1996} = 0.67$ and $r_{1997} = 0.96$) (figure 3*b*). During autumn surveys the mean prevalence of this parasite was 8.7% (s.e. = 4.42%) whereas this had declined to 3.9% (s.e. = 3.16%) in spring. Since this parasite is not believed to drop off the host and infections during winter are unlikely (Fryer 1982), this suggests a mortality rate of 56% (s.e. = 7.3%) among infected fish compared to 41% (s.e. = 7.3%) for uninfected fish (Wilcoxon signed-rank test, $Z = 1.83$, d.f. = 4 and $p = 0.068$). The survival of bitterling at all other life stages was density independent (figure 3*c*).

(b) *Model analysis*

A sensitivity analysis was conducted in which the model parameters were altered ±10% of the variance of the parameter estimates. The parameter sensitivities were compared using a sensitivity index ($S = \{[(R_a - R_n)/R_n]/[(P_a - P_n)/P_a]\}$), where R_a and R_n are the model responses to the altered and nominal parameters and P_a and P_n are the altered and nominal parameters, respectively (Haefner 1996). The results show a tendency for nonlinear responses to the parameter changes (table 3), with greatest sensitivity to changes in the parameters of the multiple regression of the juvenile bitterling mortality rate in relation to the density and perch abundance.

The model predicted an increase in the population size with increasing mussel abundance for lakes with large nursery areas, but a smaller effect as populations become limited by low nursery availability (figure 4*a*). A high predator density was predicted to reduce the population

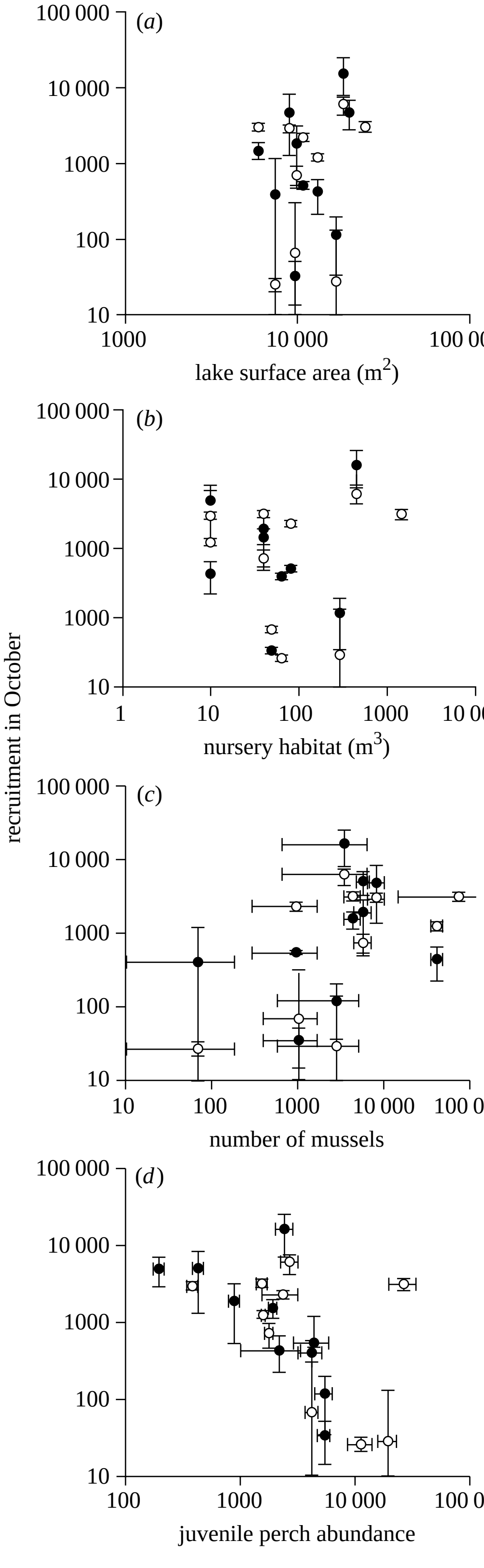

Figure 2. Relationship of the bitterling recruitment in October from 1996 to 1997 with (*a*) lake surface area, (*b*) volume of nursery habitat, (*c*) mussel abundance and (*d*) peak abundance of perch. Each point represents a different population within years. Abundances were estimated for 1996 (open circles) and 1997 (filled circles). All axes are log_{10} transformed with estimates ±1 s.e.

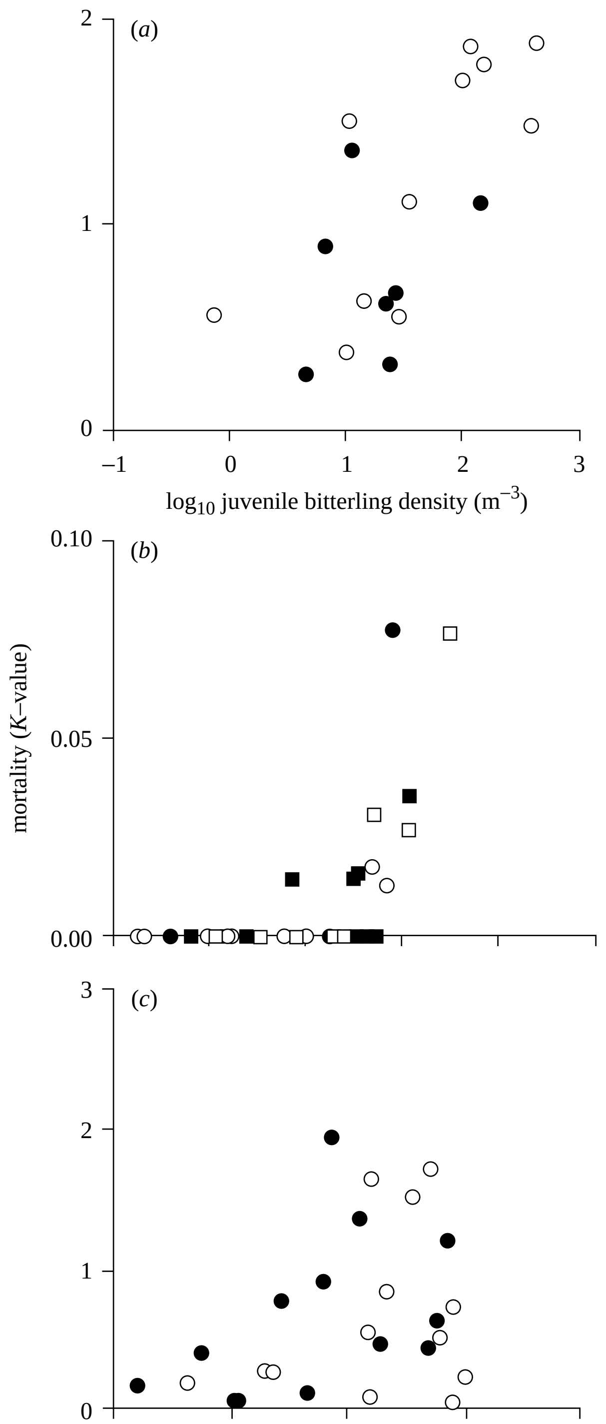

Figure 3. Density-dependent and -independent mortality at different life stages of the bitterling. The densities are $\log_{10}$ transformed. (*a*) Density-dependent mortality of juvenile bitterling in nursery habitat. Each point represents a different population within years. Abundances were estimated for 1996 (open circles) and 1997 (filled circles). The K-value $= \log_{10 a_x} - \log_{10 a_{x-1}}$, where a is the abundance at time x. (*b*) Estimates of the density-dependent mortality of adult bitterling due to infection by *L. cyprinacea*. Estimates for April 1996 (open circles), October 1996 (open squares), April 1997 (filled circles) and October 1997 (filled squares). (*c*) Density-independent mortality of adult bitterling. Each point represents a different population within stages. Mortalities were estimated for the first winter (open circles), second summer (shaded circles) and second winter (filled circles).

size at low nursery availability and high mussel abundance (figure 4*b*,*c*). At high nursery availability, the impact of predators is offset by access to refuges and the population size is predicted to be limited by density-dependent survival of the embryos in mussels.

(c) *Model validation*

We compared the model predictions of the mean October population sizes in 1995 for each study lake with the observed population sizes from the population censuses (figure 5). Both the precision ($\log_{10}$ transformation, correlation $r = 0.85$) and accuracy of the model (slope of fit, $b = 0.94$) revealed a close match between the mean observed and predicted population sizes. A plot of the residuals against fitted values showed no trend and none deviated significantly from normality (Kolmogorov–Smirnov (KS) test, $D = 0.22$ and $p > 0.15$). Embryo mortality estimates and behavioural choices were derived from laboratory experiments and from field studies in a lake that was not used to test the model (Smith *et al.* 2000). The transition probabilities in the model, which are dependent on the mortality rates and fecundity estimates, are independent of the estimates of population size used to test the model.

A comparison of the predicted population size between the years 1995 and 1997 with the observed population size as a covariate showed that the model predictions were not significantly different between years ($\log_{10}$ transformation, ANCOVA $F_{2,26} = 0.78$ and $p = 0.471$), while the observed population size was a significant covariate ($\log_{10}$ transformation, ANCOVA $F_{1,26} = 66.86$ and $p < 0.001$). Thus, the relationship between the observed and predicted population sizes did not differ significantly between years. The absence of a significant year effect is because neither the mussel abundance nor the amount of nursery habitat varied over the course of the study. In 1998 the mussel abundance and the amount of nursery habitat changed in several populations due to flooding. The model accurately predicted subsequent changes in the bitterling population size at these sites (C. Smith, J. D. Reynolds, W. J. Sutherland and P. Jurajda, unpublished data).

(d) *Behavioural contribution to the population size*

We used the model to explore the relative importance of behavioural choices to bitterling population dynamics by removing selected components from the full model, then testing the predictions of that model against those of the full model (figure 6 and table 4). A model that excluded preferences by female bitterling for superparasitized mussels predicted population sizes significantly larger than the full model by 6% (figure 6*a* and table 4). Discrimination by adult bitterling among mussel species proved non-significant, predicting population sizes only 1% larger than the full model (figure 6*b* and table 4). The removal of other, non-behavioural parameters from the model had varying effects on the predictive power of the model. The removal of anchorworm was predicted to have a negligible effect on the population size (figure 6*c* and table 4), whereas the removal of predators would significantly increase the population size by 23% (figure 6*d* and table 4) and removal of the nursery areas would result in significant reductions in the population size of 48% (figure 6*e* and table 4). The residuals plots for each model

Table 2. *Correlation matrix for independent variables used to explain* $\log_{10}$ *peak bitterling abundance and* $\log_{10}$ *recruitment*

(Significance level of correlations in parentheses.)

	lake area	mussel abundance	nursery volume
mussel abundance	0.53 (0.063)	—	—
nursery volume	0.35 (0.245)	−0.03 (0.931)	—
perch abundance$_{1996}$	0.50 (0.117)	−0.13 (0.702)	0.73 (0.010)
perch abundance$_{1997}$	0.07 (0.833)	−0.21 (0.521)	0.71 (0.010)

Table 3. *Sensitivity of bitterling population model to model parameters*

(For calculations see the text. The sensitivity values correspond to a 10% increase (+) and decrease (−) in the variance of parameter estimates.)

	sensitivity	
parameter	+	−
juvenile mortality b_2	1.62	1.67
juvenile mortality a	1.65	1.53
juvenile mortality b_1	1.02	1.02
U. pictorum density dependence	0.66	0.67
A. anatina density dependence	0.49	0.53
U. tumidus density dependence	0.31	0.31
fecundity	0.24	0.20
mortality during second summer	0.26	0.17
A. cygnea density dependence	0.14	0.16
L. cyprinacea density dependence	0.03	0.03
mortality during third summer	0.02	0.02

exhibited no marked trends as a function of the fitted values and none deviated significantly from normality (KS test, $p > 0.05$).

4. DISCUSSION

The model incorporating field and laboratory data concerning bitterling behaviour, reproductive output and mortality produced a good fit to the population sizes in our 13 study lakes in 1995 (figure 5). The model allows quantification of the importance of reproductive behaviour for population size and suggests that, whereas discrimination by bitterling among mussel species as hosts for their young has a minor effect on population size; discrimination against mussels containing embryos may reduce populations by 6% compared with random spawning (table 4). This is because a random (Poisson) distribution of eggs among mussels would lead to enhanced survival of embryos in those mussels receiving few spawnings, ultimately resulting in better recruitment. This result accords with the paradigm that the behaviours of individuals are selected in order to maximize their individual lifetime reproductive success, not the long-term interests of the population. However, more specifically, a distribution of eggs among mussels that minimizes the individual mortality of embryos, based on an ideal free distribution, may reduce population sizes in comparison with a population of bitterling which distributed their eggs randomly.

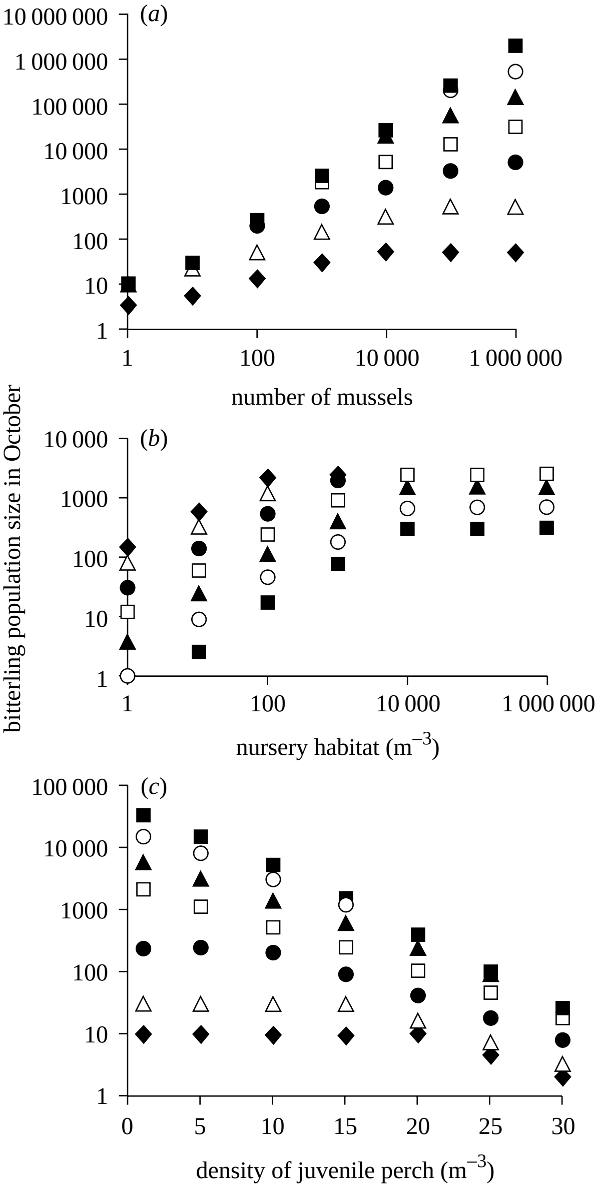

Figure 4. Simulated bitterling population sizes in October. (*a*) Population size as a function of mussel availability over seven nursery sizes, 1 m^3 (filled diamonds), 10 m^3 (open triangles), 100 m^3 (filled circles), 1000 m^3 (open squares), 10 000 m^3 (filled triangles), 100 000 m^3 (open circles) and 1 000 000 m^3 (filled squares), with the perch density held at 10 m^{-3}. (*b*) Population size as a function of nursery size over seven perch densities, 1 m^{-3} (filled diamonds), 5 m^{-3} (open triangles), 10 m^{-3} (filled circles), 15 m^{-3} (open squares), 20 m^{-3} (filled triangles), 25 m^{-3} (open circles) and 30 m^{-3} (filled squares), with the mussel population size held at 1000 mussels (250 each of the four species). (*c*) Population size as a function of perch (*P. fluviatilis*) density over seven mussel population sizes (in each case 25% of mussels were of each of the four species), 1 (filled diamonds), 10 (open triangles), 100 (filled circles), 1000 (open squares), 10 000 (filled triangles), 100 000 (open circles) and 1 000 000 (filled squares), with the availability of nursery held at 100 m^3.

The model from which discrimination by adult bitterling among mussel species was removed showed that this behaviour had a small impact on the model predictions (table 4). The weak effect of species discrimination stems from the fact that the differences between mussels in the density-dependent survival of embryos are less than the

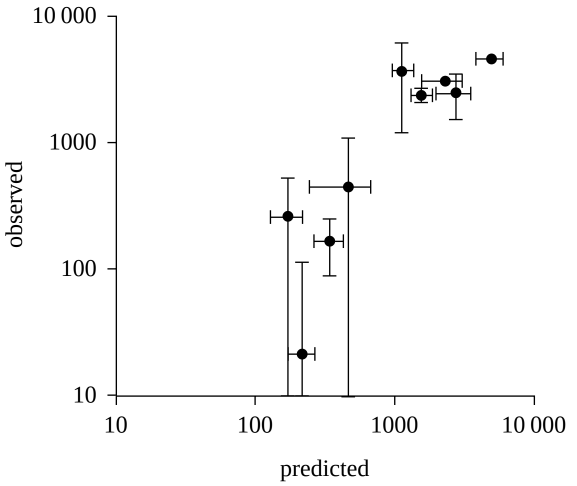

Figure 5. Observed population size based on the population censuses versus the predicted population estimates based on the model predictions for October 1995. Each point represents a different population; estimates ± 1 s.e.

strength of the density dependence within mussels (Smith *et al.* 2000). The negligible effect of the removal of anchorworm on the predictions of population size reflects the relatively minor prevalence of these parasites in the wild (figure 3*b*). The removal of nurseries and perch caused the most marked changes in the predictions of the model (table 4). The removal of nursery areas, which serve as refuges for juvenile bitterling, led to significant underestimates of the population size, whereas the removal of perch resulted in significant overestimates of the population size. The same strong interaction of refuges and predators on survival has been shown in empirical studies of other fish (Killgore *et al.* 1989; Hayes *et al.* 1994; Wootton 1998) and has implications for habitat management intended for fish conservation. Thus, although the behavioural decisions we investigated play a role in the population dynamics of bitterling, other variables are potentially of much greater significance, though behaviour may also play a role in other aspects of bitterling life history, for example in predator avoidance.

We detected no conspicuous differences in bitterling appearance or behaviour between populations in relation to predator abundance and refuge availability. Geographical differences in life-history traits have been demonstrated to parallel predator abundance in guppy (*Poecilia reticulata*) populations in Trinidad (Houde 1997) and such changes may evolve rapidly (Reznick *et al.* 1997). In the present study, predators were found at all localities and the predator abundance varied between years.

This study illustrates the importance of behaviour in predicting population size, an important goal in attempts to unify ecology with behaviour (Hassell & May 1985; Parker 1985; Sutherland 1996). Our approach also highlights the importance of detailed demographic analyses combined with behaviour in generating testable models of population ecology; the models described here could be used to predict the consequences of environmental change on bitterling population dynamics. Despite bitterling clearly having an unusual means of reproduction, the approach used here could be tailored to any species where the abundance and quality of reproductive sites can be quantified.

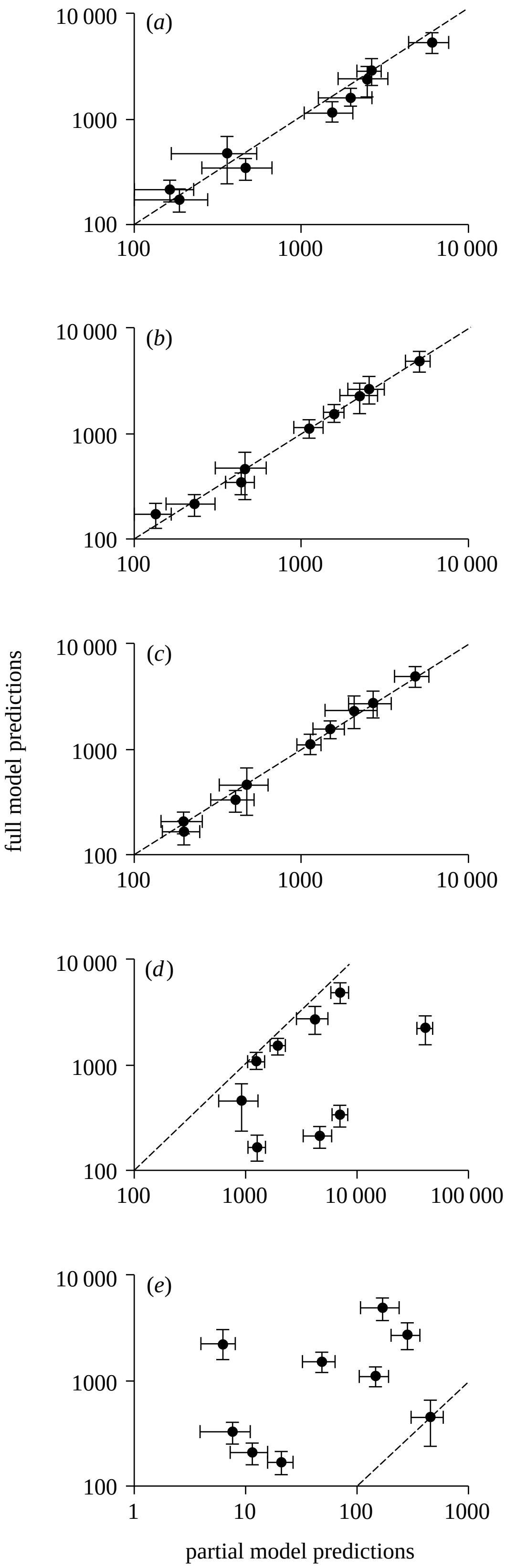

Figure 6. Test of the importance of behaviour and ecology in predicting the bitterling population size. Predictions from the following partial models were compared with those of the full model: (*a*) model with avoidance of superparasitism removed, (*b*) discrimination for mussel species removed, (*c*) parasite *L. cyprinacea* removed, (*d*) perch removed and (*e*) nursery habitat removed. Each point represents a different population for October 1995; estimates ± 1 s.e. Dashed lines represent the 1:1 ratio.

Table 4. *Importance of model components to the correlation between the full and partial models for predicted bitterling population sizes*

(r is the correlation coefficient for the $\log_{10}$ October 1995 population size of the partial model versus the full model. Percentage deviation from the full model is the percentage increase or decrease in population size that results from removal of a model component from the full model. This was obtained as the per cent change from a slope of 1 of the gradient from a linear regression of the fitted population size of the partial model as a funchon of the full model. The intercept has been forced through the origin.)

model component removed	r	% deviation from full model	paired t_{26} value	p
discrimination against superparasitism	0.99	+6	2.40	0.024
discrimination among mussel species	1.00	+1	0.30	0.770
anchorworm infection	1.00	+2	0.73	0.470
nursery	0.68	−48	9.94	< 0.001
perch	0.73	+23	5.23	< 0.001

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