



## Changes in reproductive strategy in the ruffe during a period of establishment in a new habitat

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The pattern of maturation, body size and fecundity was examined in a population of ruffe (*Gymnocephalus cernuus* L.) three times during a period of rapid growth, and eventual stabilization, following its introduction to a new habitat. When the ruffe were less common, maturing ruffe were relatively large and immature ruffe relatively small, compared with when the ruffe were abundant. Intermediate ruffe population size showed a maturation pattern intermediate between these two extremes. It is suggested that this pattern of maturation is a response of the ruffe population to changing growth opportunity induced by changing intraspecific competition. This fluctuating maturation pattern is interpreted in terms of a threshold-dependent maturation trigger, operating on the rate of accumulation of energy and a trade-off between somatic growth and gonad development. When the ruffe population was large, high intraspecific competition resulted in low opportunity for growth; only fish with the highest rate of food acquisition were able to mature in a given year—the investment in gonadal tissue reducing somatic growth. When the ruffe population was low, the high rate of energy acquisition in the population resulted in the triggering of maturation, even at small size, only the very smallest fish remaining immature. High growth opportunity allowed maturing fish to develop gonad and maintain somatic growth. The pattern of size related fecundity also changed over the three periods. When growth opportunity was low, size related fecundity was greater than when opportunity for growth was high. This suggests that maturing females faced with poor growth conditions compensated by increasing egg number for a given body size either by decreasing egg size or by increasing total investment in ovarian tissue.

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Key words: *Gymnocephalus cernuus*; ruffe; reproductive strategy; fecundity.

### INTRODUCTION

It is a basic tenet of life-history strategy theory that individual animals can and do alter their reproductive strategy depending upon the environment to which they are exposed (Stearns, 1976). Amongst the teleosts, size and age at first maturation, frequency of subsequent spawning events, total gonadal investment, fecundity, egg size and production of non-maturing gonads have all been shown to alter with the environmental conditions to which a fish is exposed (Wootton, 1979; Policansky, 1983; Randall *et al.*, 1986; Adams & Thorpe, 1989; Rowe & Thorpe, 1990a; Adams & Huntingford, 1997).

Rowe & Thorpe (1990a) and Thorpe (1994a), drawing on an extensive literature for the Atlantic salmon, *Salmo salar* L., have shown that it is some aspect of energy acquisition rate that is the proximate criterion that triggers the

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onset of the gonadal development process. As reproduction is energetically costly and, in salmon, future survival is dependent upon maintaining minimum energy reserves (Metcalf *et al.*, 1988; Rowe & Thorpe, 1990a) it is thought that maturation, at least in this species, but probably also in others, is a trade-off between reproduction and future survival (Wootton, 1979; Roff, 1983; Thorpe *et al.*, 1984; Randall *et al.*, 1986; Thorpe, 1994a).

Although the proximate cues that determine the onset of sexual maturation may be some aspect of energy acquisition rate, clearly this in turn can be affected by a wide range of environmental factors. Laboratory studies on salmon have shown that food availability (Metcalf *et al.*, 1988; Rowe & Thorpe, 1990a, b), food quality (Simpson, 1991, 1993), water temperature (Adams & Thorpe, 1989; Rowe & Thorpe, 1990b) and the competitive environment (Metcalf *et al.*, 1988, 1990) may all affect the rate of energy acquisition. Although pathways can be observed most clearly at the level of the individual, if the environment to which a population is exposed changes significantly, then changes in life history strategy for the whole population may show detectable change (Adams & Thorpe, 1989).

An opportunity to examine the effect of a changing competitive environment on reproductive strategy in a wild population was presented following the invasion and subsequent establishment of a new species into a habitat from which it was previously unknown. The ruffe *Gymnocephalus cernuus* (L.), previously absent from Scotland, was discovered in Loch Lomond in 1982 (Maitland *et al.*, 1983). Following its first discovery, the population grew rapidly until it became highly abundant (Adams & Maitland, 1998). Here, the hypothesis is tested that the changing social and presumptive competitive environment to which the ruffe population was exposed during the period of population growth and establishment, influenced ruffe reproductive strategy.

## MATERIALS AND METHODS

All fish trapped on the trash screens (8-mm<sup>2</sup> mesh drum screens) at the Ross Priory Pumping Station on the south shore of Loch Lomond, where water is abstracted by pump for domestic supply, have been collected since 1982 (Maitland & East, 1989; Adams & Maitland, 1998). To look for changes in fecundity over time during the period since ruffe were first recorded, a random sample of ruffe was taken from fish removed from the trash screens during the spawning period (April to May) in 1986 (4 years after they were first recorded there), in 1994, and again in 1999. Pumping effort has remained constant between months over all years, therefore catch data were not standardized further for catch per unit effort. Fish were stored initially in 20% formalin and subsequently measured (fork-length), weighed and dissected to assess gonads for maturity status. Both males and females were classified easily as maturing or immature on the basis of gonad size and appearance. Males either had large, well developed milky white testes and were clearly mature or had thread-like, undeveloped testes and were immature. Likewise females had either large ovaries containing obvious, well developed eggs or had greatly reduced ovaries with no evidence of egg development (Nikolsky, 1963). Sex was determined easily in immature fish following dissection by identification of pre-maturing gonadal tissue (Ricker, 1968). For maturing females, the ovary was removed intact and soaked in Gilson's fluid for at least 4 days to loosen eggs, which were then counted under a low power microscope. Unfortunately, because the fish had been stored in formalin, age determination using otoliths was not possible for these fish. In addition, scales showed no clear annuli and were also discarded as an ageing technique in these fish.

ANOVA was used to compare relative ruffe population size, and fish size between years. ANCOVA was used to test for between-group differences in fish size-fecundity relationships. To stabilize variance in regressions of fecundity on weight, fecundity was  $\log_{10}$  transformed.

## RESULTS

### SIZE OF THE RUFFE POPULATION

During the three 2-year periods prior to the season in which maturation and fecundity measurements were made (i.e. 1984–1985, 1992–1993, and 1997–1998), the ruffe population size differed significantly ( $F_{2,3}=13.824$ ,  $P=0.031$ ) [Fig. 1(a)]. *A posteriori* tests showed that population size was significantly larger in 1992–1993 than 1984–1985 ( $F_{1,2}=21.95$ ,  $P<0.05$ ) and marginally larger in 1997–1998 than 1984–1985 ( $F_{1,2}=14.04$ ,  $P=0.06$ ) [Fig. 1(a)]. Differences in population size between 1992–1993 and 1997–1998 were not significant ( $F_{1,21}=6.64$ ,  $P=0.123$ ) [Fig. 1(a)].

### SIZE OF MATURE FISH

Mature female ruffe collected during the spawning period were larger (weight) than immature fish in each of the 3 years in which maturity status was determined 1986 ( $F_{1,39}=32.73$ ,  $P<0.001$ ), 1994 ( $F_{1,36}=14.81$ ,  $P<0.001$ ), and 1999 ( $F_{1,35}=24.23$ ,  $P<0.001$ ) [Fig. 1(b), (c)]. However, immature female ruffe showed a significant difference in mean size between years ( $F_{2,30}=11.67$ ,  $P<0.001$ ). *A posteriori* comparisons showed that immature female ruffe were significantly larger in 1994 than in 1986 (LSD test,  $P=0.001$ ), and in 1994 than in 1999 (LSD test,  $P<0.001$ ), but that there were no significant differences in size between 1986 and 1999 (LSD test,  $P=0.357$ ) [Fig. 1(b)]. Mean weights of mature females collected during the spawning season at Ross Priory were also significantly different between years ( $F_{2,80}=11.90$ ,  $P<0.001$ ). Mature females were significantly smaller in 1994 than in 1986 (LSD test,  $P<0.001$ ) and in 1999 (LSD test,  $P<0.001$ ), but there was no significant difference in mature female weight between years 1986 and 1999 (LSD test,  $P=0.227$ ) [Fig. 1(c)].

Males showed a similar size maturation pattern to that of females [Fig. 1(d), (e)]. Mature males were bigger than immature males caught on spawning grounds at Ross Priory in all years: 1986 ( $F_{1,31}=70.26$ ;  $P<0.001$ ); 1994 ( $F_{1,58}=10.84$ ;  $P=0.002$ ), and 1999 ( $F_{1,65}=15.18$ ,  $P<0.001$ ). In addition, immature male ruffe size also varied across years ( $F_{2,32}=4.55$ ;  $P=0.02$ ). Ruffe in 1994 were larger than ruffe in 1986 (LSD test,  $P=0.005$ ), but there was no significant difference in size between 1994 and 1999 (LSD test,  $P=0.1$ ) nor between 1999 and 1986 (LSD test,  $P=0.19$ ) [Fig. 1(d)]. As with the mature females, mature males were significantly different in size between years ( $F_{2,122}=35.31$ ,  $P<0.001$  for both paired comparisons). As with mature females, mature males were

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FIG. 1. Annual mean number of ruffe on the trash screens of the Ross Priory Pumping Station on the south shore of Loch Lomond in the 2 years prior to measurement of maturity and fecundity (a); mean body size of female immature (b) and mature ruffe (c); mean body size of male immature (d) and mature ruffe (e); mean egg number per female fish in each of the years 1986, 1994 and 1999 (f). All error bars are  $\pm$  s.e.

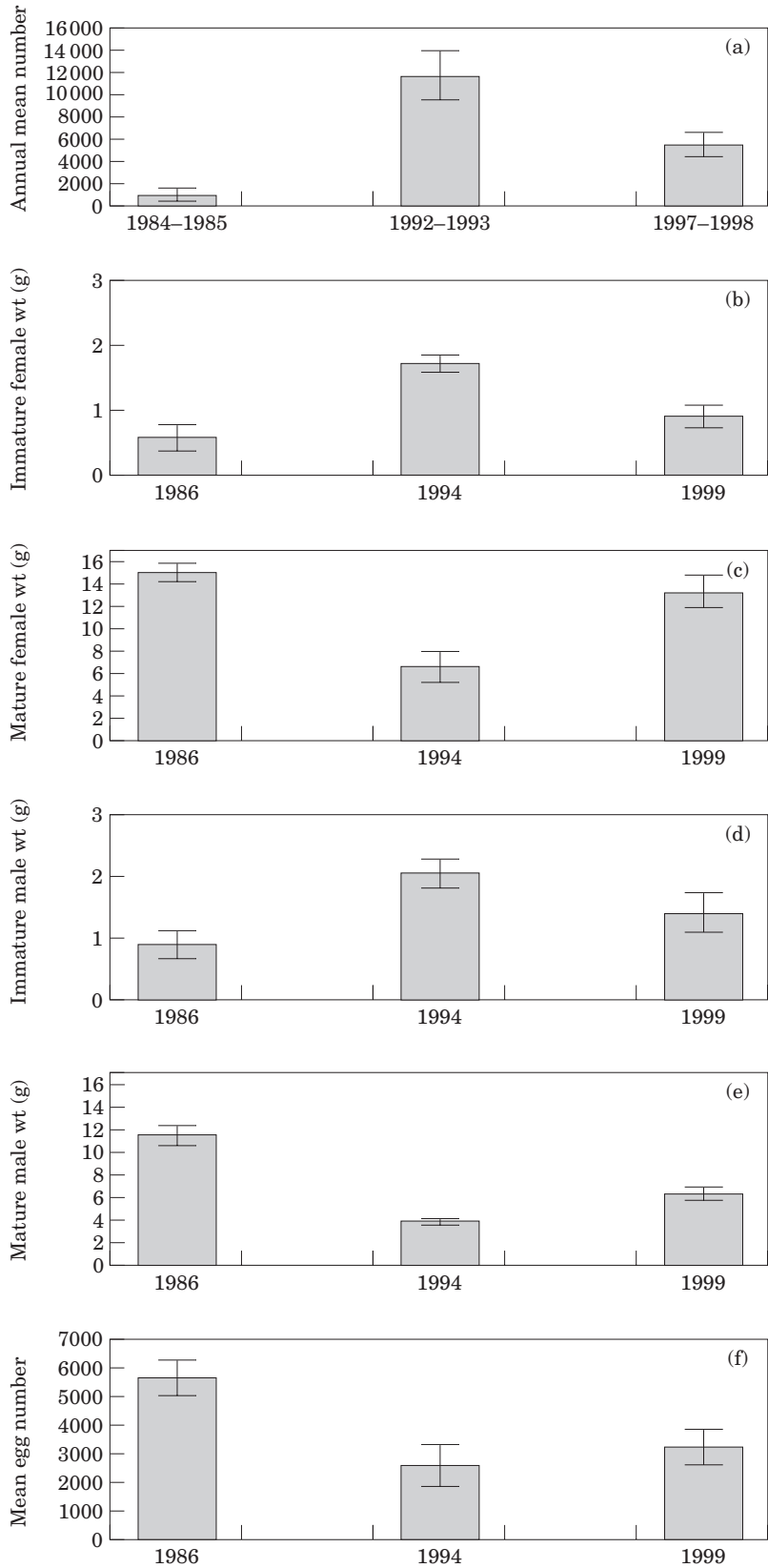


FIG. 1. For legend see facing page.

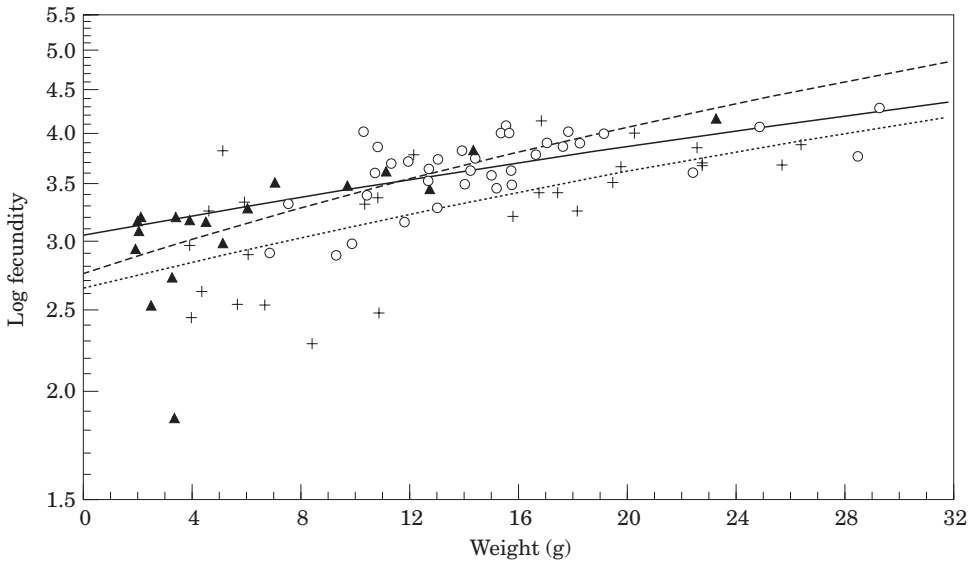


FIG. 2. Female fecundity (egg number) regressed on size for years 1986 (○), 1994 (▲) and 1999 (+). Correlation of all years combined is significant ( $r^2=0.546$ ,  $F_{1,81}=96.33$ ,  $P<0.001$ ). Individual regressions are also significant: 1986 ( $r^2=0.367$ ,  $F_{1,35}=20.28$ ,  $P<0.001$ ); 1994 ( $r^2=0.547$ ,  $F_{1,16}=19.29$ ,  $P<0.001$ ); 1999 ( $r^2=0.652$ ,  $F_{1,26}=46.87$ ,  $P<0.001$ ).

significantly larger in 1986 and 1999 than in 1994 (LSD test,  $P<0.001$ ), and also males maturing in 1986 were larger than those maturing in 1999 (LSD test,  $P<0.001$ ) [Fig. 1(e)].

#### FECUNDITY

Female fecundity (egg number per female) differed across the 3 years ( $F_{2,79}=6.59$ ,  $P=0.003$ ) [Fig. 1(f)]. Average egg number per fish was highest in 1986, and significantly higher than both 1994 (LSD test,  $P=0.002$ ) and 1999 (LSD test,  $P=0.005$ ). Mean egg number did not differ between 1999 and 1994 (LSD test,  $P=0.547$ ). In all years, fecundity (egg number  $\log_{10}$  transformed) was highly correlated with size (Fig. 2). Covariance analysis showed no significant difference in regression slopes between years but a significant difference in elevations between years (comparison of fecundity size regression all years,  $F_{2,78}=7.58$ ,  $P=0.001$ ). Fecundity was higher for a given fish weight in 1986 compared with 1999 [ $F_{1,61}=15.14$ ,  $P<0.001$  (slopes not significantly different,  $P=0.17$ )], and in 1994 compared with 1999 [ $F_{1,42}=7.50$ ,  $P=0.009$  (slopes not significantly different,  $P=0.63$ )]. However, there was no significant difference in fecundity between 1986 and 1994 [ $F_{1,52}=0.238$ ,  $P=0.627$  (slopes not significantly different,  $P=0.12$ )].

## DISCUSSION

#### POPULATION SIZE AND THE COMPETITIVE ENVIRONMENT

Here and elsewhere (Maitland & East, 1989; Adams & Maitland, 1998), it has been shown that the ruffe population size in Loch Lomond changed significantly over the years following its introduction. Relatively small in the 2 years prior to

1986, the ruffe population, estimated by catches using constant effort at one site, increased in size *c.* 11-fold by the 2 years prior to 1994. Following this, the ruffe population stabilized and contracted slightly (Adams & Maitland, 1998) such that by the years 1997–1998, the estimated population size was around five times that of 1984–1985. Similar patterns of rapid population growth and eventual stabilization have been recorded in other newly established ruffe populations. Popova *et al.* (1998), for example, observed a period of rapid growth by ruffe populations in the former U.S.S.R. during the initial period of their life in a new reservoir when populations were small and intraspecific density-dependent competition was low. Subsequent rapid population expansion was followed by a period in which the ruffe population eventually decreased to a more stable level.

The mechanisms regulating ruffe population size in general, and in Loch Lomond in particular, are not known. However, as the ruffe population was growing rapidly in 1984–1985, had peaked around the years 1992–1993, and had then declined by 1997–1998 (data presented here and see Adams & Maitland, 1998), the intraspecific competitive environment to which ruffe growing during these three specific periods were exposed, was likely to be significantly different. With a small but rapidly expanding population in 1984–1985, intraspecific competition must have been low, partly because the population was relatively small and partly because competition was clearly not constraining population size (Elliott, 1994; Adams & Maitland, 1998; Hölker & Thiel, 1998). In 1992–1993, however, the population was around an order of magnitude larger and entering a period of size stabilization. Although it is not known what mechanisms were operating to constrain population size at this time, the competitive environment to which ruffe were exposed was probably very different from that of 1984–1985. Similarly, it can be argued that the competition to which ruffe were exposed in 1997–1998 is likely to be somewhat intermediate between these two other periods.

#### PATTERNS OF MATURATION

In this study, the body size of sexually mature ruffe varied with relative population size and the presumed competitive environment to which they were exposed in the 2 years prior to maturation. Although the age of maturing ruffe could not be determined, both female and male maturing fish were larger when relative population size in the 2 previous years was small and possibly the intraspecific competitive environment was low (1986), smaller when competition and relative population size in the previous 2 years was high (1994), and intermediate when population size and the competitive environment was intermediate (1999). Conversely, both male and female sexually immature fish size were smaller when relative population size and the competitive environment was low, larger when population size was high, and intermediate when relative population size was intermediate.

Conditions that promote growth (such as water temperature, food availability, and foraging opportunity) in the period prior to the onset of sexual maturation in seasonally spawning fish, modify the probability of maturation (Alm, 1959; Policansky, 1983; Thorpe *et al.*, 1984, 1989; Randall *et al.*, 1986; Adams & Thorpe, 1989; Rowe & Thorpe, 1990*a, b*; Thorpe, 1994*a, b*; Adams &

Huntingford, 1997). Thorpe (1986) developed a model combining the relationship between season and opportunity for growth. This model has now been extensively tested for Atlantic salmon. In a cohort of salmon, it is the fish growing fastest prior to the period during which the maturation pathway commences, that have the greatest probability of becoming sexually mature. The resulting trade-off between the high energetic investment in gonad and somatic growth can mean that somatic growth of non-maturing fish may subsequently overtake that of maturing fish despite the greater growth potential of the former group. Although the exact mechanisms through which growth influences the triggering of the sexual maturation trajectory is not known for ruffe, in Atlantic salmon, the rate of acquisition of lipid is thought to be the proximate cue used to determine energy availability (Thorpe, 1994a). In salmon, the intraspecific competitive environment to which individuals are exposed, influences their rate of growth (Metcalf, 1986, 1991; Metcalf *et al.*, 1988) and the probability of becoming sexually mature in any given year (Simpson, 1991, 1993).

Assuming that changing ruffe population size, possibly acting through intraspecific competition, influences food availability, then the observed changes in maturation pattern in ruffe reported here can be interpreted in terms of changing growth opportunity and a trade-off between gonadal investment and somatic growth. Prior to 1986, ruffe were exposed to a low competitive environment which offered good opportunities for growth. High rates of energy acquisition in the population enabled maturation at small size (and possibly at a young age—although we have no data to support this suggestion) and only the slowest growing of fish remained immature in this year. As a result of the high growth opportunity, ruffe maturing in 1986 were able to invest in gonad yet maintain somatic growth. Ruffe in the years prior to 1994, were faced with significantly lower growth opportunity, resulting from the larger population size. A much reduced opportunity for growth resulted in a larger proportion of the population delaying maturation in this year. Because the accumulation of energy was much more limited in 1994 than 1986, fish that did opt for maturation, unlike ruffe maturing in 1986, were forced to allocate energy resources to gonad production at the expense of somatic growth. Because a higher proportion of fish remained immature in 1994, the immature group included fish with a greater potential for growth than those of the same group in 1986. Thus immature fish in 1994, despite being constrained by poorer opportunity for growth, grew to larger size than those of 1986. Further support for the argument that growth opportunity is influencing the pattern of growth and maturation is given by the data for 1999, when presumptive growth opportunity was intermediate between the other two years and the observed size maturation pattern in this year was intermediate between the two extremes. The fact that immature fish had a larger absolute size in 1994 compared with 1986 strongly supports the hypothesis that, as for salmon (Thorpe, 1994a) it is the rate of accumulation of energy as opposed to absolute size that promotes the onset of the sexual maturation process.

Although we show that the pattern of body size and maturation varies with population size, the pattern of egg production in females also varied with time. Mean fecundity (egg number) was high when the population size was low (in 1986), low when population size was high (in 1994), and intermediate when

population size was intermediate (1999). As fecundity increases with body size in fish (Wootton, 1979; Roff, 1983; Thorpe *et al.*, 1984; Randall *et al.*, 1986; Adams & Huntingford, 1997), this pattern is not surprising. Also, relative fecundity changed between years. The number of eggs produced per unit of body weight (fecundity) was greater in 1994 than in 1986 indicating that despite having a smaller mean body size, maturing female ruffe were tending to increase their fecundity by producing more eggs per unit body weight than ruffe in 1986. To achieve this, ruffe in 1994, despite poorer presumptive growth conditions, must either have been investing more in total ovary size or producing smaller eggs. This finding contrasts with that of Adams & Thorpe (1989) who found that growth opportunity in salmon was positively correlated with increased investment in non-maturing ovarian tissue.

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