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Growth, catches and reproductive biology of ruffe *Gymnocephalus cernuus* in Lake Piediluco (Umbria, Italy)

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Abstract. The ruffe *Gymnocephalus cernuus* L. is an introduced species in Italy. In order to assess the impact of exotic species on native fish communities, the ecology and biology of intruders need to be thoroughly investigated. The aim of this study was to analyse the growth and reproductive biology of the ruffe population in Lake Piediluco. From June 1999 to March 2002, and between July 2004 and May 2005, 1 330 specimens belonging to seven age-classes were captured. Sex was determined in 385 individuals: 327 females and 58 males. The SL-TL relationship for the whole sample was TL = 0.923 + 1.075SL. The SL-W relationship was $W = 0.0154\ SL^{3.102}$ for females and $W = 0.0157\ SL^{3.106}$ for males. The parameters of the von Bertalanffy growth curve for length using back-calculated SL were $L_\infty = 218.29$ mm, $k = 0.27\ y^{-1}$, $t_0 = -0.61$ for females and $L_\infty = 161.54$ mm, $k = 0.32\ y^{-1}$, $t_0 = -0.70$ for males. The results showed that in Lake Piediluco ruffe grow as fast as in their original environments. Seasonal growth and back-calculation showed the possible existence of differential mortality prejudicial to small specimens. Moreover, growth analysis revealed marked sexual dimorphism in growth in the Lake Piediluco population. Sexual maturation occurred in both sexes at the end of the first year of life. Reproduction occurred mostly in May and June. The mean diameter of eggs was 1.12 mm. The mean number of eggs produced by each female was 11 961, and increased with the size of the specimens; with regard to relative fecundity, an average value of 239 eggs g^{-1} was observed. This analysis reveals some important biological characteristics of the ruffe that were not previously well known with regard to the Italian population of the species.

Key words: reproduction, fecundity, back calculation, Lee's phenomenon, condition

Introduction

The fish populations of Italy's inland waters have steadily declined over the years on account of the general deterioration of aquatic ecosystems, mainly as a result of human activities (Lorenzoni et al. 2006). The principal factors involved are the pollution and eutrophication of waterways, variations in fluvial morphology and hydrological regimes, and the creation of barriers to the migration of fish. A further element is the introduction of exotic species, which has been defined as one of the most important and least studied factors in the deterioration of aquatic ecosystems (Lodge et al. 2000, Mack et al. 2000). When exotic species are introduced, biodiversity generally declines. The result is that a few species able to adapt to a broad range of habitats proliferate, often at the expense of indigenous or less adaptable ones (McKinney & Lockwood 1999).

In Lake Piediluco the composition of fish populations has undergone significant changes in recent years, mainly as a result of environmental deterioration due to the eutrophication of its waters (Cioffi & Gallerano 2000) and the introduction of some exotic species

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(Lorenzoni et al. 2007). These modifications have led to a decrease in the quantity of commercially interesting species. One of these is the European perch *Perca fluviatilis* Linnaeus, 1758, which is one of the main resources for the lake's professional fishermen. The ruffe *Gymnocephalus cernuus* (Linnaeus, 1758) is one of the latest species to be introduced into Lake Piediluco (Carosi et al. 1998).

The ruffe displays one of the widest distributions of percids in Europe. It is native to northern, central and eastern Europe, including north-eastern France, England and the rivers entering the Baltic and White seas (Brown et al. 1998). In Asia, the ruffe is native to Siberia only as far as the Kolyma River and the Caspian and Aral Sea basins, but excluding the Amur River and Transcaucasia (Ogle 1998); it is not native to Ireland, Scotland, part of Norway, the Iberian and Balkan Peninsulas, Italy or the Crimea (Lelek 1987). However, this species has been accidentally introduced into several European areas and the North American Great Lakes (Brown et al. 1998, Ogle 1998). Wherever ruffe have become established as an exotic species, changes in the structure of the fish community have been observed (Mills et al. 1993, Adams & Maitland 1998), probably as a result of competitive interactions (Dieterich et al. 2004) or predation on the eggs and larval stages of other species (Kangur et al. 1999). Ruffe and perch have similar feeding and habitat preferences (Dieterich et al. 2004). It can thus be hypothesized that in Lake Piediluco, too, proliferation of the ruffe will further jeopardise the European perch (Lorenzoni et al. 2007).

Managing species that have been introduced is often crucial to maintaining biodiversity and ensuring the functions of aquatic ecosystems (Byers et al. 2002). In order to be successful, however, any management strategy requires a wide range of knowledge of the diffusion, ecology and biology of the species introduced, and of the effects that they exert on the original communities. Our knowledge of the characteristics of Italian ruffe populations is very scant (Chiara 1986, Carosi et al. 1998, Lorenzoni et al. 2007); the information yielded by this study will provide further insight into the biology of this exotic species.

Study Area

The investigation was carried out in Lake Piediluco (longitude: 0° 17' 21" – 0° 19' 17" E; latitude: 42° 30' 54"– 42° 32' 28" N), situated about 20 km SE of Terni in Central Italy, at 368 m above sea level (Fig. 1). With a surface area of 1.67 km^2, this lake (mean depth = 10.90 m; max. depth = 21.48 m) (Mearelli 1988) is the second-largest natural lake in the Umbria Region. Lake Piediluco is a regulated lake, and is used as a daily water storage basin for the Galleto hydroelectric plant. It is a hydraulic complex constituted by two waterways: the Velino River and the Medio-Nera channel, which is derived from the Nera River. From the trophic point of view, Lake Piediluco has undergone a rapid evolution, chiefly as a result of the increase in the input of nutrients from its tributaries (Cioffi & Gallerano 2000). Indeed, on the basis of concentrations of total phosphorus, the lake was considered to be mesotrophic in 1980 (40 μg l^{-1}) (Mearelli 1988), while at the present time it can be classified as hypertrophic, owing to the concentration of chlorophyll α and total phosphorus (maximum chlorophyll values: 80–250 μg l^{-1}; lowest dissolved oxygen concentration: <2 mg l^{-1} at the bottom; highest orthophosphate concentration values: 10–25 mg l^{-1}) (Cioffi & Gallerano 2000).

Sixteen species of fish are currently found in the lake, only six of which are autochthonous (eel *Anguilla anguilla* L., pike *Esox lucius* L., tench *Tinca tinca* L., rudd *Scardinius erythrophthalmus* L., chub *Leuciscus cephalus* L., brown trout *Salmo trutta* L.). The European perch population of Lake Piediluco has undergone a rapid decline in numbers; the worsening of environmental conditions caused by eutrophication of the lake and the introduction of exotic fish species that are potential competitors of the European perch are probably the most important determinants of this situation (Lorenzoni et al. 2007). Simultaneously with the decline of the biomass of perch in the lake, an increase has been seen in the abundance of some cyprinids and the ruffe. The ruffe's presence in the lake was first documented in 1996 (Carosi et al. 1998); in the following years, the species acclimatized successfully and became increasingly abundant.

Material and Methods

Ruffe were collected by means of a variety of equipment, including fyke-nets and gill-nets of different mesh size. Sampling was conducted between June 1999 and March 2002, with monthly frequency, and between July 2004 and May 2005, with seasonal frequency. In the periods 1999–2000 and 2004–2005, seasonal sampling campaigns were conducted by means of gill-nets, fyke-nets and long-lines for eels, in order to investigate the overall composition of the fish community living in Lake Piediluco (Fig. 1). Gill-nets were composed of four panels of 20, 28, 30, 45 mm mesh size each (total net area about 762.5 m^2). The panels were arranged in series, according to increasing mesh size, inside the nets. The use of "multi-selective" gill-nets enables efficient and representative sampling to be carried out by allowing specimens of different sizes to be caught (Craig et al. 1986, Degerman et al. 1988). The nets were positioned parallel to the shoreline at 6 p.m. and left in place until 6 a.m. the following morning (a total of 12 hours). The fyke-nets, which were positioned close to the shore and anchored to the lake-bottom, had the following dimensions: mouth-diameter 1.5 m and mesh size 15 mm; wings 4 m in height and 8 m in length, with a mesh size of 20 mm. They were left in place from 6 p.m. to 6 a.m. of the third following morning (total time 60 hours). The long-lines deployed were of the type traditionally used by professional fishermen for catching eels, and consisted of single lines, each bearing 40 hooks baited with earthworms. This tackle was again set close to the shore from 6 p.m. to 6 a.m. the following morning.

From an ecological point of view, three types of environment can be distinguished in Lake Piediluco: lotic, pelagic and paludal. The first corresponds to the area between the mouths of the lake's two artificial inlets, the second to the central area of the lake and the third to the most easterly end of the lake (Fig. 1). The water in the lotic zone has a very rapid turnover rate, owing to the presence of the inlets, a lower mean summer temperature and better oxygenation conditions. The greatest depths are to be found in the pelagic zone, where the banks are also steeper. The paludal zone is shallow, has a low turnover of water and more abundant vegetation, and displays anoxic conditions at the bottom for long periods in the summer (Cioffi & Gallerano 2000). On every sampling date, a series of two gill–nets, one fyke-net and one long-line for eels was set in each zone, at the points indicated in Fig. 1. In addition, sampling was also carried out along two pre-established transects parallel to the lake-shore by means of a 4 kW electric stunner mounted on a boat. The exact location and the length of the stretches sampled were monitored by means of a GPS system. The pattern of sampling was identical in both sampling periods (1999–2000 and 2004–2005), which enabled the results to be compared immediately.

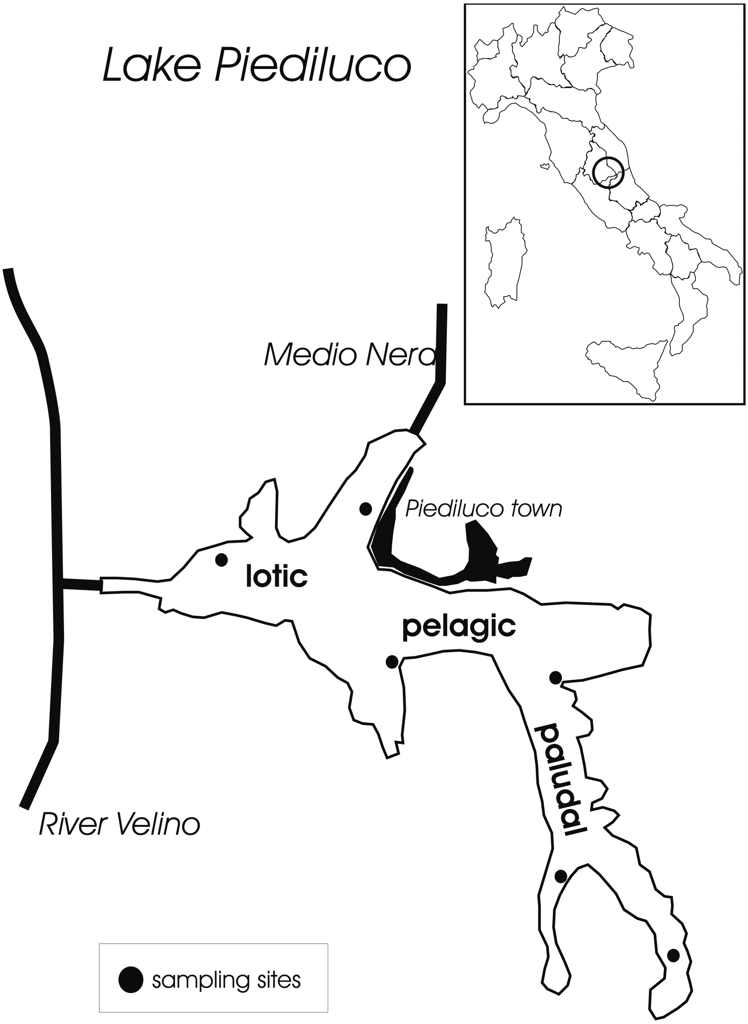

Fig. 1. Study area and sampling sites.

All the specimens caught during sampling were classified by species and weighed to an accuracy of 0.1 g. To analyse the catches, the data were standardised in terms of Catch Per Unit Effort (CPUE) (Ricker 1975). With regard to the gill-nets, the CPUEs were calculated separately for each mesh size, considering the dwell-time of the nets and the surface area of the panels used. Most ruffe were caught in gill-nets; the pertinent CPUEs were then calculated and the catches were expressed in terms of both number (CPUEs N) and biomass (CPUEs B) by means of the following formulae: CPUEs N = N/tS and CPUEs B = B/tS, where N = number of fish caught; B = biomass of fish caught, expressed in grams; S = surface area of the net in m^2; t = dwell-time of the net used, expressed in hours (Linlokken & Haugen 2006). The CPUEs of the gill-nets were then expressed as ind h^{-1} m^{-2} (CPUEs N) and as g h^{-1} m^{-2} (CPUEs B).

All of the ruffe caught globally in the various samples were measured in terms of both total length (TL) and standard length (SL) (Anderson & Neumann 1996), to an accuracy of 1 mm, and weighed (W) to an accuracy of 0.1 g. Sex was determined by microscopic examination of the gonads, and gonads were weighed (W_g) to an accuracy of 0.01 g. The stage of maturation of the ovaries was determined by means of the Nikolsky (1963) gonad maturation scale. The age of the specimens was determined by means of the microscopic scalimetric method and validated by means of length frequency distribution (Bagenal 1978). The scales were removed from the left side of the fish, below the lateral line and posterior to the pectoral fins (De Vries & Frie 1996) and stored in ethanol (33%) for reuse in back-calculation.

The length-weight relationship $W = a\ SL^b$ was calculated separately for the two sexes, using the least-squares method (Ricker 1975), expressed in cm SL and g W. The relationships between the sexes were compared by analysis of covariance (ANCOVA), and the hypothesis of isometric growth was tested by means of a Student's *t*-test. The relationship between TL and SL was also calculated for the whole sample.

Length and weight by age were evaluated for the 1+, 2+, 3+ and 4+ age-classes only, as the specimens of the other classes obtained were too few to permit statistical analysis. The data were calculated by using the mean SL and W obtained from the age-classes of the captured specimens grouped according to season. The mean values obtained for each age-class in the autumn and winter were compared by means of the *t*-test.

Back-calculated lengths were estimated for 371 specimens, 4 scales from each specimen being examined. The scale radius (R_s), from the centre of ossification to the edge of the scale, and the radius of the age-rings (S_t) were measured for all scales (±0.01 mm) (Bagenal 1978) by means of an image-analysis system (IAS 2000). The relationship between the length of the specimen on capture (SL) and R_s was described by using the regression $SL = a + b\ R_s$. The result was linear and did not pass through the origin. Comparison between the two sexes in terms of the size reached at the various ages was made by means of a *t*-test. To determine whether a Lee phenomenon was operating, the Mann-Whitney U-test was used to compare the back-calculated lengths reached at the various ages of the specimens at age *n* with those of the samples of the older fish ($n + i$) (Lorenzoni et al. 2002).

The theoretical growth in length was analyzed separately for each sex by using the von Bertalanffy (1938) equation: $L_t = L_\infty (1 - \exp^{(-k\ (t\ -\ to))})$, where L_t is the theoretical SL at age t, L_∞ the asymptotic length, k the coefficient of growth (in years^{-1}), and t_o the theoretical age (in years) at length = 0 (Bagenal 1978). This analysis was carried out by using the mean back-calculated lengths at the various ages; only the SL values back-calculated from the last annulus were used in the analysis. Φ' was calculated from the equation: $\Phi' = \log (k) + 2 \log (L_\infty)$ (L_∞ expressed in cm) (Pauly & Munro 1984).

The condition factor (K) was calculated by using the formula of Fulton (Bagenal 1978) $K = 100\ W/TL^3$, with W expressed in g and TL in cm. The somatic condition factor (K_s) was calculated separately for each sex by means of the following formula: $K_s = 100\ (W\text{-}W_g)/TL^3$, with W expressed in g and TL in cm. Calculated in this way, K and K_s represent the individual deviations from the hypothetical ideal fish which displays isometric growth (Weatherley 1972), with and without gonad weight; these indexes enable comparisons to be made between individuals, periods, age-classes and sexes (Ricker 1975). The gonado-somatic index (GSI) represents the percentage ratio between bodyweight (W) and gonad weight (W_g): $GSI = 100\ W_g/W$ (Bagenal 1978). The GSI was calculated separately for each sex in all sexually identified specimens.

In females with gonads at maturation stage V on the Nikolsky scale (1963), the eggs present in the ovaries were counted. This sample was made up of 69 females. The diameter

(δ) of 5 randomly selected eggs from each specimen was also measured (±0.01 mm) by means of an image-analysis system (IAS 2000). The relationship between length of the specimen and the number of eggs was calculated by using the least-squares method (Ricker 1975): n of eggs = a L^b, expressed in mm SL. Relative fecundity (RF) was expressed as the number of eggs produced per unit of bodyweight: RF = n of eggs/W. The relationships RF – L and δ – L were also calculated: RF = a + b L, expressed as n of eggs/g and mm SL; δ = a + b L, expressed in mm δ and mm SL.

Results

Growth

The sample was made up of 1 330 specimens: the mean SL (±1SD) of the sample was 129.74 ±21.94 mm (minimum value = 39.78 mm; maximum value = 194.20 mm), mean TL (±1SD) was 148.90±23.48 mm, mean W (±1SD) was 44.51±21.34 g and mean age (±1SD) was 2.32±0.84 yr. Sex was determined in 385 specimens: 327 females and 58 males. The mean values (±1SD) of the females were higher (SL = 133.54±23.51 mm; W = 52.69±1.49 g; age = 2.85±0.05 yr) than those of the males (SL = 95.60±23.51 mm; W = 18.77±1.22 g; age = 1.86±0.08 yr), the *t*-test revealing highly significant differences for all values (SL: $t = 141.41$; $p = 0.001$) (W: $t = 99.62$; $p = 0.001$) (age: $t = 57.17$; $p = 0.001$). In the overall sample, the 2+ age-class proved to be the most abundant (55.19%), followed by the 3+ (20.00%) and the 1+ (19.77%) classes; few older specimens were caught: 4+ (3.76%), 5+ (0.23%) and 6+ (0.15%). Young of the year (YOY) were also few (0+ = 0.90%), owing to the selective nature of the capture devices used (Cowx 1990). In the overall sample, females (84.93%) far outnumbered males, the ratio being 1 male to 5.63 females. Marked differences were also observed within the various age-classes; female specimens were found in all age-classes (from 0+ to 6+): while 3+ (39.75%) and 2+ (32.72%) specimens were the most numerous, 1+ (17.12%) and 4+ (35.17%) specimens were also plentiful. By contrast, males were present in only 5 age-classes, 5+ and 6+ specimens being absent; moreover, the most numerous male specimens were found in the 1+ (55.17%) and 2+ (9.48%) classes.

The SL – TL relationship for the whole sample was: TL = 0.923 + 1.075 SL ($r = 0.99$; $R^2 = 0.98$; $p = 0.992$). The SL – W relationship was $W = 0.016\ SL^{3.079}$ ($r = 0.98$; $R^2 = 0.97$; $p = 0.000$) for the whole sample, $W = 0.015\ SL^{3.102}$ ($r = 0.98$; $R^2 = 0.96$; $p = 0.000$) for the females and $W = 0.016\ SL^{3.106}$ ($r = 0.97$; $R^2 = 0.94$; $p = 0.000$) for the males. In all cases, allometric growth was observed: indeed, the value of the parameter b was greater than 3, with differences on *t*-testing being highly significant for males, females and the whole sample ($p < 0.01$). Covariance analysis did not reveal significant differences between the sexes ($F = 1.542$; $p = 0.215$).

Length and weight as a function of age (Fig. 2) were calculated for the 1+, 2+, 3+ and 4+ age-classes. The trends were fairly homogeneous in the various age-classes: analysis of the data showed that the average length and weight of the sample increased steadily throughout the whole year, with no time lag in the winter; growth was faster in spring and slower in summer. The annual increase in length and weight tended to diminish in the 4+ age-class. In all age-classes, the mean values of SL and W were noticeably higher in winter than in the previous autumn; however, the differences analysed by means of the *t*-test proved to be highly significant only for the first winter of life, with regard to both length ($t = 10.74$; $p = 0.002$) and weight ($t = 11.88$; $p = 0.001$).

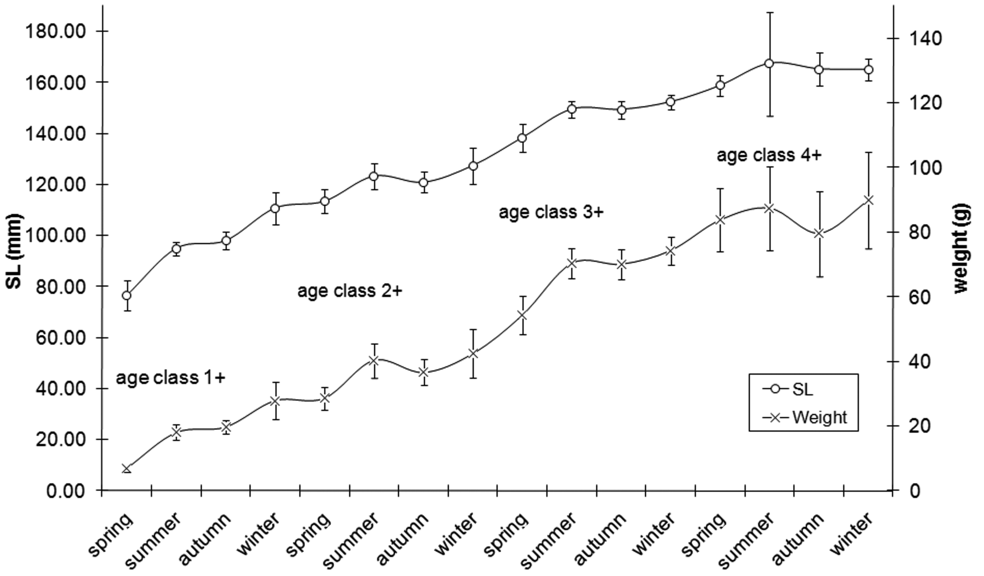

Fig. 2. Seasonal growth with confidence limits (95%).

Data from the scale measurements were used to determine a linear relationship between SL and scale radius (R_s). The following relationship was found: $SL = 37.191 + 31.893\ R_s$ ($r = 0.92$; $R^2 = 0.84$; $p = 0.000$). Back-calculated lengths were greater in females (Table 1) than in males (Table 2), even in the younger age-classes; the difference in length between the sexes being highly significant on the *t*-test ($p<0.01$) for all age-classes. With regard to the Lee phenomenon, the back-calculated lengths reached by females at the various ages showed

Table 1. Back-calculated lengths of females.

Age	n	Lengths at age (mm):				
		I	II	III	IV	V
1	55	76.22				
2	105	77.84	110.76			
3	127	80.49	111.44	135.48		
4	28	80.40	110.39	133.54	153.31	
5	1	79.62	106.41	133.93	157.13	170.57
Mean		78.74	111.02	135.12	153.46	170.57
Confidence limits (95%)		±0.83	±1.40	±1.87	±3.07	

Table 2. Back-calculated lengths of males.

Age	n	Lengths at age (mm):			
		I	II	III	IV
1	30	70.81			
2	22	67.98	91.24		
3	2	62.50	83.19	109.43	
4	1	67.49	87.40	110.66	127.87
Mean		69.42	90.34	109.84	127.87
Confidence limits (95%)		±1.91	±3.61	±7.15	

highly significant differences for age 1 in favour of the older specimens (mean ± 1SD: $SL_1 = 76.22 \pm 5.67$ mm; $SL_{1+i} = 79.36 \pm 7.17$ mm) ($U = 3.52$; p = 0.000). By contrast, no significant differences emerged among males; in this latter case, however, the analysis may have been conditioned by the paucity of the sample. The theoretical growth in length determined by means of back-calculated SL (mm) was $L_t = 218.29\ (1 - \exp^{(-0.268(t + 0.615))})$ ($R^2 = 0.99$) for females and $L_t = 161.54\ (1\text{-}\exp^{(-0.320\ (t + 0.700))})$ ($R^2 = 0.99$) for males. The value of Φ' was 2.106 for females and 1.921 for males.

Catches

In the period 1999–2000, a total of 2 069 fish were caught, for a total biomass of 412.37 kg. In the 2004–05 season, 4 297 specimens were caught, weighing 783.10 kg. With regard to species of commercial interest, from 1999–2000 to 2004–2005 a decline was seen in catches of eels (1999–2000 = 28.20% of the biomass; 2004–05 = 14.60%) and brown trout (1999–2000 = 4.80%; 2004–05 = 1.96%). European perch stocks have continued to dwindle in spite of programmes to support the population, a trend which has been underway for many years (Lorenzoni et al. 2007) (1999–2000 = 11.61%; 2004–05 = 5.32%). Among the species of no commercial interest, cyprinids and the ruffe showed the greatest increases; the ruffe caught in 1999–2000 accounted for 1.90% of the total number of specimens and for 0.40% of the biomass, while in 2004–05 these percentages had risen to 20.95% and 4.96%, respectively. The most specimens of this species were trapped by gill-nets (37 specimens in 1999–2000 = 94.87% of the total and 782 specimens in 2004–05 = 85.87%) and fyke nets (1999–2000 = 4.13%; 2004–05 = 0.45%). The long-lines for eels (1999–2000 = 0%; 2004–05

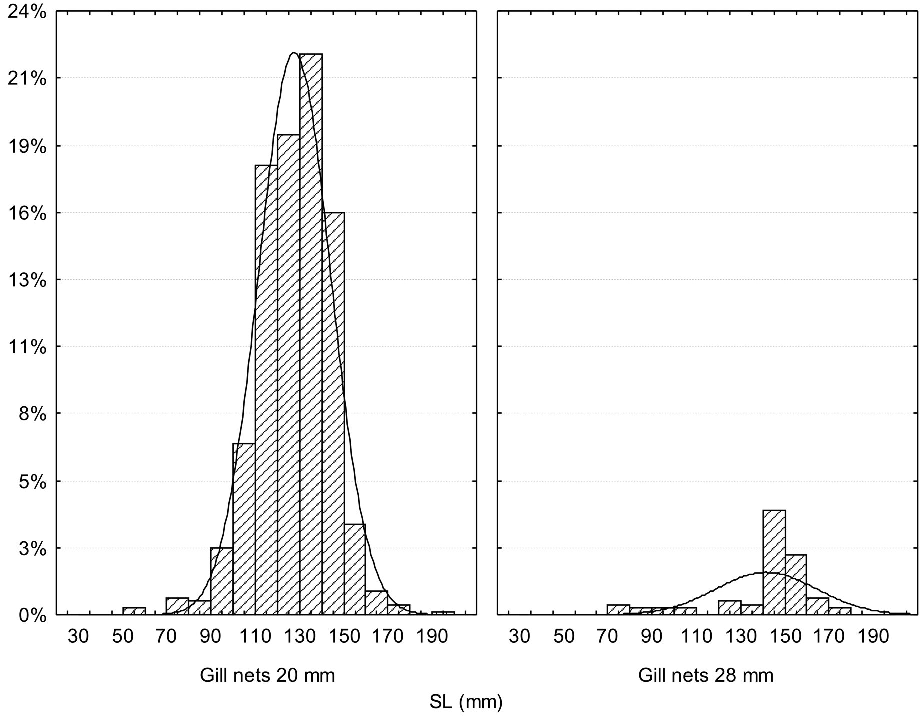

Fig. 3. Breakdown of gill-net catches into SL classes.

= 13.78%) proved to be less effective, and no ruffe was captured by means of the electric stunning device. Subsequent comparisons were based exclusively on the data regarding the gill-nets, as the samples caught by the other devices were too small. The increase in the ruffe population is indicated by the increase in standardised catches (CPUEs): in 1999–2000, the mean (±95% C.I.) CPUEs for the gill-nets were 0.006±0.003 ind h^{-1} m^{-2} and 0.27±0.01 g h^{-1} m^{-2}, while in 2004–2005 these values had risen to 0.051±0.019 ind h^{-1} m^{-2} and 2.07±0.81 g h^{-1} m^{-2}. On the *t*-test, the difference between the sampling years proved to be highly significant with regard to both CPUEs N (*t* = 10.646; p = 0.002) and CPUEs B (*t* = 9.886; p = 0.003).

The ruffe has proved able to colonise all the environments in Lake Piediluco rapidly and successfully; in 2004–2005, the mean (±95% C.I.) CPUEs of the gill-nets were 0.046±0.015 ind h^{-1} m^{-2} and 1.73±1.18 g h^{-1} m^{-2} for those set in the lotic environment, 0.055±0.033 ind h^{-1} m^{-2} and 2.45±1.47 g h^{-1} m^{-2} for those located in the pelagic zone, and 0.046±0.055 ind h^{-1} m^{-2} and 1.67±1.85 g h^{-1} m^{-2} for those positioned in the paludal area. No statistically significant difference emerged from the comparison conducted by means of analysis of variance with regard to either CPUEs N (F = 0.116; p = 0.890) or CPUEs B (F = 0.426; p = 0.657). For what concerns the differences observed in the various sampling seasons, spring proved to be clearly the most propitious season for the use of gill-nets: the mean values (±95% C.I.) of the CPUEs reached in this season were 0.092±0.044 ind h^{-1} m^{-2} and 4.04±1.96 g h^{-1} m^{-2}; subsequently, these values steadily declined to 0.068±0.054 ind h^{-1} m^{-2} and 2.33±1.90 g h^{-1} m^{-2} in summer, 0.020±0.014 ind h^{-1} m^{-2} and 0.88±0.51 g h^{-1} m^{-2} in autumn and 0.013±0.011 ind h^{-1} m^{-2} and 0.52±0.36 g h^{-1} m^{-2} in winter. Analysis of variance revealed highly significant differences among the sampling seasons with regard to both CPUEs N (F = 6.196; p = 0.002) and CPUEs B (F = 6.832; p = 0.001).

In the gill-net catches of ruffe no specimen was caught by the 30 and 45 mm mesh nets, as these meshes were too large. The ruffe caught by the 20 mm mesh nets displayed a mean (±1SD) value of 127.17±16.27 mm; these specimens varied from 50 to 190 mm in length, the most numerous being of 130 mm SL (22.09%) (Fig. 3). The catches were seen to become significant from the 90 mm SL class (2.65%) upwards, to increase for the 100 mm SL class (6.75%), and to become abundant especially for the classes from 110 to 140 mm SL (72.60% of the total). The gill-nets with a 28 mm mesh caught a very small number of ruffe; the SL interval of these specimens was narrower, varying from 70 to 170 mm, with a mean value (±1SD) of 140.96±22.67 mm; while the modal class proved to be 140 mm SL (4.10%), the catches were significant only for the classes from 140 to 150 mm SL (7.10% of the total). The differences between the mean standard length calculated for the two different mesh sizes proved to be highly significant on the *t*-test (*t* = 42.96; p = 0.000).

Condition

The mean value (±1SD) of the condition factor (K) of the entire population was 1.24±0.17; the mean K was 1.34±0.17 for the females and 1.23±0.15 for the males. Although the *t*-test did show a highly significant difference between the values recorded in males and females (*t* = 21.73; p = 0.000), the subsequent analyses were nevertheless performed without taking into account the differences between the sexes, owing to the small number of specimens. Comparison of the condition factor among the various age-classes revealed an increasing trend during growth; the mean value of K (±1SD) was lowest in the youngest age-class (0+) (1.17±0.17), rose to fairly similar levels in the two subsequent classes (1+ = 1.21±0.18) (2+ = 1.22±0.16), increased more sharply in 3+ specimens (1.32±0.15), and then fell back slightly

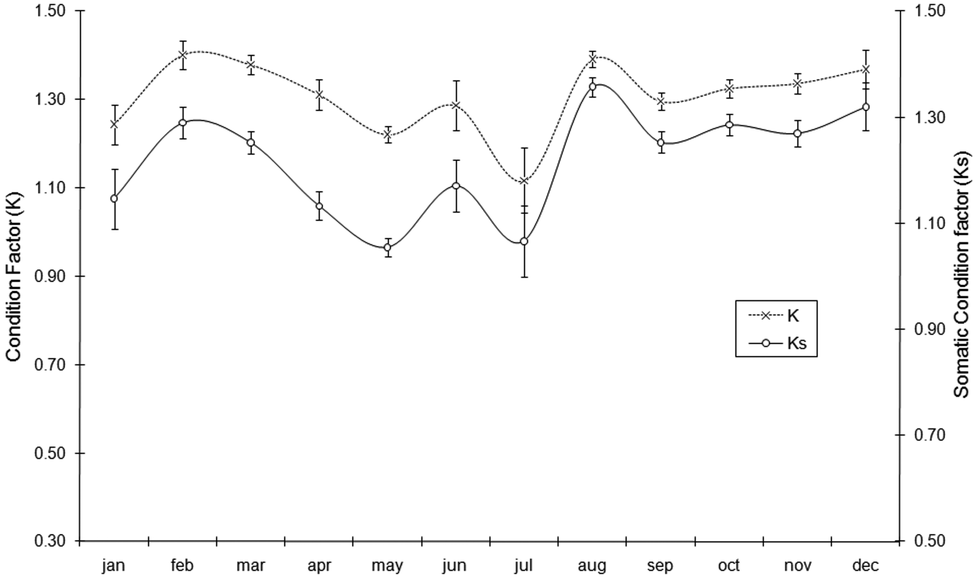

Fig. 4. Annual trend of K and K_s in females with confidence limits (95%).

in the 4+ class (1.31±0.15). Analysis of variance showed the differences between the mean K values in the age-classes to be highly significant (F = 14.50; p = 0.000).

The mean value (±1SD) of the somatic condition factor (K_s) of the entire population was 1.23±0.19; the mean somatic condition proved to be better in females (1.86±0.249) than in males (1.15±0.16), the differences being highly significant on the *t*-test (*t* = 15.43; p = 0.000). The monthly trend in the mean values of K and K_s in the sample of females (Fig. 4) revealed that the somatic condition reached its peak at the end of the summer and remained at a high level throughout the autumn. By contrast, the somatic condition was at its lowest in January, increased in February, but then remained low throughout the spring and for much of the summer, with particularly low values of K_s being recorded in May and July. A very similar trend was seen with regard to K, which reached its highest mean values in February and August and its lowest value in July. Comparison of the trends in K and K_s yielded useful information on the seasonal development of the ovary, as well as the duration of the reproductive period. While the differences between K and K_s began to emerge in September, they increased considerably in February and were particularly marked in May, when ovary development is maximal. The disparity between the two indexes began to shrink in June and continued to do so in July; the mean values of K and K_s were almost identical in August, when the gonads are quiescent.

Reproductive biology

The mean GSI (±1SD) was 6.83±5.27 for the females and 5.09±4.11 for the males, the differences between the sexes being significant on the *t*-test (*t* = 2.53; p = 0.012). The trend in the mean value of the GSI in females over the various months of the year (Fig. 5) substantially confirms the results of the analysis of the condition factor; i.e. the GSI values peaked in April and May, declined in June and July, and fell to their lowest levels in August. This was confirmed by examination of the ovaries; in April, 100% of the ovaries were at stage

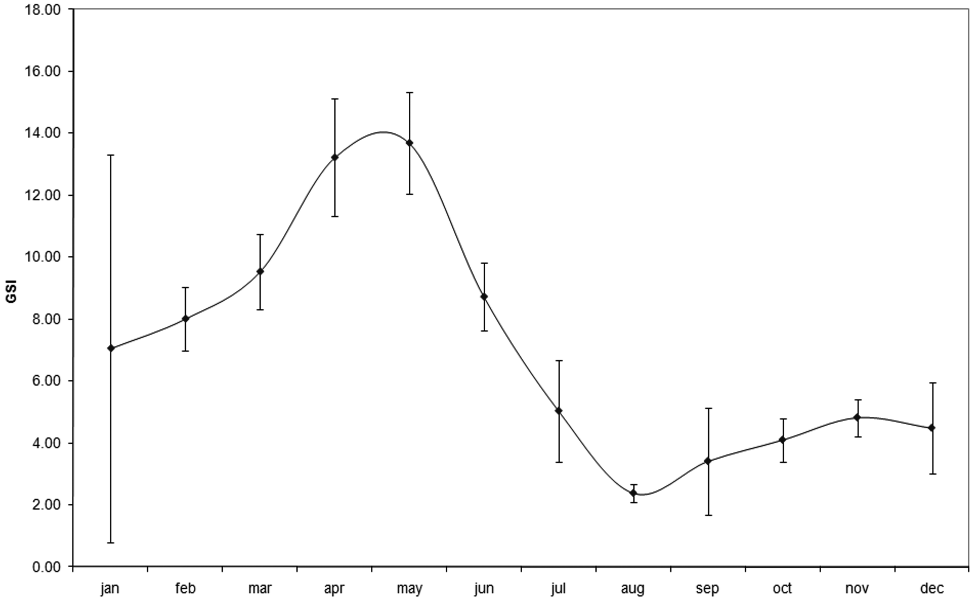

Fig. 5. Trend in monthly mean GSI values in females.

IV or V of maturation, in May 91.96% of the ovaries were at stage V, in June the percentage was 46.87%, while in July all the females had reproduced (stage VI). Macroscopic examination of the gonads showed that sexual maturity was reached in the first year in both sexes; indeed, all specimens observed, both male and female, presented stage V gonads from the 1+ age-class onwards.

Table 3. Descriptive statistics for egg diameter (mm) in the sample broken down by age-class.

	n	Mean	Minimum	Maximum	Median	Std deviation
1+	20	0.94	0.89	1.03	0.94	0.07
2+	100	1.20	0.83	1.39	1.21	0.15
3+	155	1.14	0.79	1.48	1.17	0.19
4+	45	0.94	0.81	1.05	1.00	0.11
5+	5	1.15	1.15	1.15	1.15	0.00
all	325	1.12	0.71	1.59	1.12	0.19

Egg diameter varied considerably, ranging from a minimum of 0.71 mm to a maximum of 1.59 mm, and displaying a mean (±1SD) value of 1.12±0.19 mm (Table 3). Analysis of linear regression between egg diameter (in mm) and SL (in mm) of the females led us to conclude that, in the ruffe population in Lake Piediluco, egg diameter is not directly proportional to the size of the female specimens; indeed, the relationship found was: $\delta = 1.298 - 0.0014$ SL ($r = -0.110$; $R^2 = 0.03$; $p = 0.150$).

The number of eggs produced by each female varied from a minimum of 550 to a maximum of 52 160, with a mean (±1SD) of 11 961.40±9 239.99. The relationship between fecundity and length was multiplicative: n of eggs = $0.0004\ SL^{3.458}$ ($r = 0.81$; $R^2 = 0.65$; $p = 0.000$).

Relative fecundity, expressed as n eggs g^{-1} of body weight of the females, displayed a fairly broad interval, from a minimum of 72.37 eggs g^{-1} to a maximum of 513.58 eggs g^{-1}, with a mean (±1SD) of 239.41±111.67 eggs g^{-1}. Relative fecundity did not depend on size, the linear regression between the number of eggs g^{-1} and the SL being: n of eggs $g^{-1} = 200.93 + 0.29$ SL ($r = 0.07$; $R^2 = 0.004$; $p = 0.588$).

Discussion

Recently introduced into Lake Piediluco, the ruffe has adapted very well to the environmental conditions of the lake and has proliferated rapidly to become one of the dominant species in the fish community. Similar patterns of rapid population growth have been recorded in other newly established ruffe populations (Maitland & East 1977, Pratt et al. 1992, Devine et al. 2000). As a result of its broad ecological adaptability and its ability to feed even in conditions of poor visibility, which are typical of eutrophic lakes (Janssen 1997, Schleuter & Eckmann 2006), the ruffe has successfully colonised the entire lake.

The analyses carried out provide further insight into the biological characteristics of the ruffe population in Lake Piediluco, which may prove to be particularly important in drawing up plans for the containment of this population (Busiahn 1996).

The ruffe in Lake Piediluco have a maximum lifespan of over 6 years and a greater maximum size (SL = 191.0 mm; W = 141 g) than that recorded in other Italian populations (Carosi et al. 1998). The lifespan of this species does not generally exceed 6–7 years (Fedorova & Vetkasov 1974, Lind 1977, Holker & Hammer 1994), though exceptionally it may reach 11 years (Ogle 1998); the maximum length attained by the ruffe only rarely exceeds 250 mm TL (Lelek 1987, Ogle 1998), and is normally around 150 mm (Lind 1977). In Lake Piediluco, the ratio between the sexes in the overall sample is markedly skewed in favour of the females (84.93% females, 15.07% males; 1 male for 5.63 females), and appears even more unbalanced in the older age-classes; males are very scarce in the 3+ and 4+ classes and totally absent from the subsequent classes. The sex ratio is also influenced by the time when the fish are caught, though this may be the result of differential mortality between the sexes, to the detriment of the males.

The regression coefficient of the SL – W relationship – 3.08 in the overall sample, 3.10 in females and 3.11 in males – was always significantly greater than 3, a value which indicates isometric growth (Bagenal 1978).

Analysis of the scales utilised for back-calculation showed that in the ruffe only one annulus per year is formed (Jamet & Desmolles 1994), and that its formation occurs around April, in concomitance with the beginning of the reproductive period. Sexual dimorphism in the growth of the ruffe has already been indicated in previous studies (Fedorova & Vetkasov 1974, Kolomin 1977, Holker & Hammer 1994) and in Lake Piediluco comparison between the sexes showed that the females were bigger than the males at all ages. The theoretical growth in length, evaluated on the basis of back-calculated SL (in mm), was $L_t = 218.29\ (1 - \exp^{(-0.268\ (t + 0.615))})$ for females and $L_t = 161.54\ (1 - \exp^{(-0.320\ (t + 0.700))})$ for males. The Φ’ value was 2.106 for females and 1.921 for males.

Our analysis of growth in the various age-classes revealed that growth in length does not take place in a constant manner throughout the year; rather, it mainly occurs in spring and autumn, while in the summer it may still suffer the consequences of the reproductive effort. No growth stasis was observed in the winter period; however, it is possible that the increase in length recorded during the winter may not be due to the real individual growth of the specimens, but rather to an increase in the mean size of the population as a result of differential mortality which penalises the smaller specimens.

In Lake Piediluco, female ruffe generally appeared to be in better condition than males, and displayed higher mean values of both K and K_s. The condition of the specimens tended to improve with age: however, this may be due to the fact that, in the presence of allometric growth, the value of K is influenced by the form variations that occur during a fish's development (Weatherley 1972).

The seasonal pattern of the condition factor is probably linked to the biological cycle of the species and to variations in some environmental factors, especially temperature. In the ruffe, the lowest K_s values are observed in spring, i.e. during the period of reproduction; indeed, during the reproductive period many species of fish markedly reduce their food intake and increase their energy expenditure, which impoverishes their physical condition (Weatherley 1972). The condition of the ruffe population in Lake Piediluco is at its best at the end of summer and in autumn, when optimal climatic conditions favour the growth of the specimens. In addition, once reproduction has taken place, the fish's bodyweight is further reduced as a result of the emptying of the gonads. The fact that the lowest mean values of K_s and K are recorded in spring supports the hypothesis that the ruffe's feeding activity is reduced during reproduction.

Analysis of the reproductive biology of the ruffe population in Lake Piediluco revealed that the reproductive period is chiefly concentrated in May and June, when the temperature of the water is about 14°C. The minimum GSI value was recorded in August, when the gonads are quiescent. The ovaries begin to develop in September, at first fairly slowly, and then more rapidly from January onwards; their maximum development is reached in April and May, when reproduction begins.

In Lake Piediluco, sexual maturity is reached early: within the first year in both sexes, and at an SL of about 70 mm in males and 75 mm in females. In general, the ruffe matures at the age of 2 or 3 years, though some populations are reported to reproduce at 1 year (Fedorova & Vetkasov 1974, Willemsen 1977, Neja 1988, Rosch & Schmid 1996, Ogle 1998). Early sexual maturity may be the result of the very rapid growth of the ruffe in Lake Piediluco (Devine et al. 2000), as the first reproduction in many fish species appears to be determined more by size than by age (Alm 1953, Adams & Thorpe 1989) and the factors that promote growth modify the probability of maturation. Nevertheless, the possibility that eutrophication may influence the early attainment of sexual maturity by increasing the rate of development of the specimens (Hartman 1975) cannot be ruled out.

The mean size of the eggs of the population analyzed was in line with that reported in the literature; in the ruffe, egg diameter is normally slightly larger than 1 mm, though it may vary from 0.34 to 1.31 mm (Kovalev 1973, Fedorova & Vetkasov 1974, Kolomin 1977, Jamet & Desmolles 1994, Ogle 1998). In many fish species, older females produce larger eggs than younger specimens. We did not observe this phenomenon. In the Lake Piediluco population, the mean number of eggs produced per female was about 12 000, ranging from a minimum of 550 to a maximum of about 52 000, and fecundity was highly correlated with size. The relative fecundity observed in our sample was almost 240 eggs per g of weight, ranging from a minimum of over 72 eggs g^{-1} to a maximum of 513 eggs g^{-1}, regardless of the size of the specimen.

In dealing with invasive species, eradication is obviously the favoured strategy and several studies have demonstrated its success. However, success has been limited to small, isolated biotopes, on a local scale and in the early stages of invasion (Zavaleta et al. 2001). Fishery experts concur that eradication of the ruffe is not possible (Busiahn

1996), as the species is capable of rapid population increase and range expansion. Reducing the numbers of ruffe by using appropriate technologies has, however, proved to be possible, though this is difficult as the species implements various adaptation strategies to compensate for high mortality rates (Ogle 1998). Reproducing ruffe populations may be vulnerable to physical removal (Neuman & Karas 1988, Busiahn 1996); in lakes, netting probably remains the most common and effective method (Rosch & Schmid 1996), although this requires substantial effort. Indeed, a removal rate of 50% would not effectively reduce the population of a prolific species like the ruffe (Busiahn 1996). Ideally, surveillance and monitoring programmes should make use of a variety of sampling gear (Edwards et al. 1998). The small size of ruffe makes gill-nets with a 20 mm mesh particularly effective, as these are able to capture specimens of all sizes, from first-time reproducers upwards. While spring and summer are the most favourable periods for the use of such nets (Neuman & Karas 1998), in Lake Piediluco they also display some measure of success even in winter. Unfortunately, the other types of fishing tackle did not prove to be so efficacious in catching ruffe. Electro-fishing and fyke-nets would have considerably reduced damage to non-target species (Edwards et al. 1998). However, the bottom-living habits of the ruffe and its reluctance to swim close to the shore, even during the reproductive period, limit the capturing capacity of these devices.

Conclusions

Ruffe populations in Italy have not been studied exhaustively. The present research highlights some of the most important and, as yet, little-known aspects of the biological characteristics of these populations. One of the indications that emerge from the study is that some intra-species or inter-species interactions (inter-species competition and predation) may prove to be of particular importance in the ecology of the population present in Lake Piediluco. Indeed, it would appear that differential mortality occurs, to the detriment of smaller individuals and males, which grow more slowly than the females.

In the ruffe, competition for food resources could cause greater mortality among smaller specimens, especially those of 1 year of age, as shown by the inverse Lee phenomenon. This mortality occurs chiefly in winter, when the conditions are harshest. Size-dependent selective mortality during the first winter of life would also explain the differences recorded in seasonal growth trends. In the light of the above considerations, size-dependent mortality, rather than the lack of growth in certain individuals, would seem to be the best explanation. Winter is a critical period for many fish species, owing to increased mortality, particularly among smaller, undernourished specimens as a result of intra- and inter-species competition (Buijse & Houthuijzen 1992, Eckmann 2004).

This situation increases concern for the state of the population of European perch, a species already waning in Lake Piediluco as a result of environmental deterioration, and which is likely to suffer further, especially if ruffe stocks continue to grow at their present rate. Ruffe have the potential to compete with native fishes and perch (Fullerton et al. 1998, Schleuter & Eckmann 2006), and, indeed, recent research (Lorenzoni et al. 2007) has uncovered a strong negative interaction with the European perch in Lake Piediluco.

In Lake Piediluco, the resumption of professional fishing, of which the European perch is one of the main resources, seems to be conditioned by a set of complex problems that require a whole ecosystem approach. The most important steps to take are to alleviate the effects of eutrophication by reducing the inflow of nutrients into the lake and to control stocks of some of the recently introduced species. The information yielded by the present research will certainly contribute to the realisation of any plans that may be drawn up in order to control the ruffe population.

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