

## Consequences of elevated temperatures on life-history traits of an introduced fish, pumpkinseed *Lepomis gibbosus*

S. DEMBSKI\*†, G. MASSON\*, D. MONNIER‡, P. WAGNER\*  
AND J. C. PIHAN\*

\*Laboratoire Biodiversité et Fonctionnement des Ecosystèmes, UFR Sci. F.A., Université de Metz, Rue du Général Delestraint, 57070 Metz, France and ‡Conseil Supérieur de la Pêche, Délégation régionale Champagne Ardennes, Lorraine, Alsace, 23 rue des Garennes, 57155 Marly, France

(Received 3 May 2005, Accepted 23 January 2006)

Life-history reactions of a pumpkinseed *Lepomis gibbosus* population in north-eastern France exposed to heated waters were studied. The study was conducted from 2001 to 2003 in an artificial reservoir, adjacent to a nuclear power plant, in which water temperatures are cool in winter (8.2–12.4° C) and rise early in spring (April: 14.7° C) nearly 5° C and 3° C over the temperature of its tributary, respectively. Fast growth among young-of-the-year, precocious maturity and short life span were observed, in contrast to related studies. The short life span appeared to be the price paid for early maturity in breeding fish, which suffered high mortality rates just after their first reproduction.

© 2006 The Fisheries Society of the British Isles

Key words: global warming; *Lepomis gibbosus*; longevity; reproductive strategy; sexual maturation.

### INTRODUCTION

Life-history variations in organisms of the same species can be produced either by genetic differences or by environmentally induced differences among individuals with a given genotype. In fishes, inter-population variability in life-history traits has been attributed to environmental factors such as thermal regime, length of growing season, productivity and food availability, inter- and intra-species interactions and degrees of environmental fluctuation (Alm, 1959; Deacon & Keast, 1987; Reznick *et al.*, 1990; Fox & Keast, 1991; Tomasini *et al.*, 1996).

Temperature, considered as an ecological resource, is one of the most important factors affecting fishes' physiological processes or behaviour. Gonad growth, spawning time and reproductive behaviour all depend on temperature and its

†Author to whom correspondence should be addressed. Tel.: +33 387378421; fax: +33 387378423; email: dembski@univ-metz.fr

related variables (e.g. day length). A widely reported hypothesis concerning the effect of temperature on ectotherms is that of von Bertalanffy (1960), who suggested that growth becomes constrained at high temperatures because the anabolic rate is fundamentally unable to keep up with that of catabolism. Recent studies indicate that an increase in environmental temperature, while increasing growth rates and differentiation, affects the latter more than the former, and thus body size at a given stage of development is reduced (van der Have & de Jong, 1996). As a consequence, most ectotherms mature early, at small body size, in heated waters (Packa-Tchissambou *et al.*, 1981; Atkinson, 1994). Fish species differ in their preference for optimal temperatures at which physiological function is optimized and growth and activity scope is maximized (Jobling, 1996). In addition, the introduction of a species to a new environment may induce changes in its life-history traits due to subsequent increases in energy cost (e.g. expended for physiological regulation, survival, escaping new predators and foraging; Rosecchi *et al.*, 2001).

Known consequences of global warming are generally described as shifts in community structure towards thermophilic and southern taxa (Pörtner *et al.*, 2001; Soto, 2001; Daufresne *et al.*, 2003; Fang *et al.*, 2004; Jansen & Hesslein, 2004) that imply migration and thus a modification in a given species' biogeographic distribution. But in water bodies where migration is not feasible (*i.e.* isolated lakes and reservoirs), there is a need to understand the reaction of both native and introduced species to warmer conditions. Few studies have considered the long-term ecological consequences of multigenerational exposure to elevated thermal regimes (van der Kraak & Pankhurst, 1996). In addition, most studies on the effects of global warming on fishes have focused on summer temperatures, whereas temperature increases at higher, mid-latitudes are projected to be greatest during the winter months (Coutant, 1990). The aim of this study was to analyse the life-history responses of the pumpkinseed *Lepomis gibbosus* (L.), particularly those linked to reproductive cycle and growth, when exposed to heated lacustrine water conditions (e.g. mean annual temperature 3.7° C warmer in the reservoir during nuclear power station functioning). Despite widespread distribution on this continent, few life-history data are available about northern European populations of this introduced species (Copp *et al.*, 2004). Pumpkinseed, noted since 1991 in the Mirgenbach Reservoir (Flesch *et al.*, 1994), were chosen for this study because of their abundance in the reservoir and their occupation of a littoral zone, which could be easily sampled. The higher winter temperatures in the Mirgenbach Reservoir, compared to the local pattern, provided a rare opportunity to evaluate thermal effects on fish performance.

## MATERIALS AND METHODS

### STUDY AREA

The Mirgenbach Reservoir (Fig. 1) fulfils a safety function and acts as a thermic buffer area for the nuclear power plant in Cattenom (Moselle, north-eastern France). This lake has a surface area of 95 ha, a capacity of  $7.3 \times 10^6$  m<sup>3</sup> and a maximum depth of 20 m. In 1985, the reservoir was created in the watershed of the Mirgenbach River,

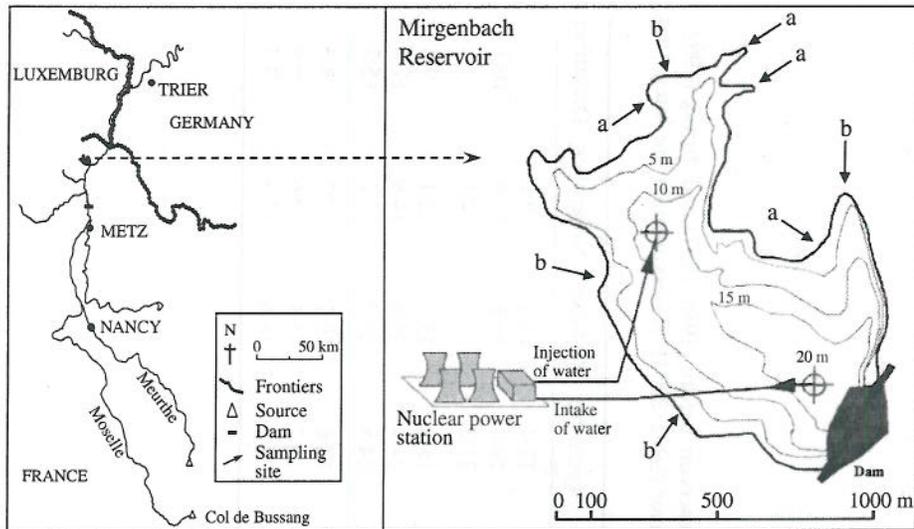


FIG. 1. Location of study site and sampling stations (a and b).

a small tributary of the Moselle River. It was filled with water pumped from the Moselle River, a major tributary of the Rhine River. Since then, the water pumped from the river ( $8 \text{ m}^3 \text{ s}^{-1}$ ) has been heated, the salts concentrated by evaporation ( $3 \text{ m}^3 \text{ s}^{-1}$ ) in the cooling towers and then the water let out through the reservoir ( $5 \text{ m}^3 \text{ s}^{-1}$ ) with a transit time of 12 days before discharge into the Moselle River.

The reservoir presents unique physicochemical and hydrobiological characteristics (Vein *et al.*, 1990). Soon after being filled, the reservoir evolved from its original, oligo-mesotrophic state to a clearly eutrophic state. Constant, thorough mixing resulted from the injection of water from the cooling towers, which explains the absence of stratification (neither thermocline nor oxycline exists). The water level is constant except when the dam is checked for maintenance purposes.

The major impact on the Mirgenbach's water temperature occurs during the winter (Table I). Temperature regimes with prolonged autumns, warm winters and early springs are characteristic of cooling water areas (*e.g.* at thermal power plants; Luksiene & Sandström, 1994). Currently, water temperature throughout the year exceeds  $8^\circ \text{C}$ ; the warming up of the water mass is seasonally early in spite of the regional climate, with temperatures often surpassing  $14^\circ \text{C}$  by the beginning of April. Although the reservoir is always warmer than the Moselle River, it has similar patterns of water temperature fluctuation. Compared to other systems (Table II), the reservoir has summer temperatures closer to those of French Mediterranean water bodies, whereas the Moselle River is closer in value to lakes in the northern part of the pumpkinseed's native range.

## BIOLOGICAL MATERIAL AND SAMPLING

Pumpkinseed are native to North America but have colonized almost the entire French hydrographic network since their introduction in 1880 (Carrel *et al.*, 2001). They are classified as a 'species likely to cause biological imbalances' (Pascal *et al.*, 2003). The fish assemblage in the Mirgenbach (littoral area) is composed of 16 freshwater species, of which *L. gibbosus* is the most abundant.

Although Garcia-Berthou & Moreno-Amich (2000) report pumpkinseed that inhabited deep zones (10–15 m), these fish were predominantly littoral. In the Mirgenbach Reservoir, from 2001 to 2003, vertical gillnets (2.5 m in width) were set for 24 h periods, twice a year (July and October) at various depths (1, 3, 5 and >10 m). At each

TABLE I. Mean, minimum and maximum monthly temperatures ( $^{\circ}$  C) in the Mirgenbach Reservoir before (1986–1987) and during (1992–2003) the functioning of the nuclear power station and compared to those in the Moselle River (1992–2003). Reservoir data are integrated over the whole water column

	January	February	March	April	May	June	July	August	September	October	November	December
Mirgenbach (1986–1987)	6.1	6.1	6.7	9.0 10.7 12.4	15.8 15.9 16.0	18.1 18.4 18.8	22.1 22.1 22.2	20.6 21.0 21.4	17.4 19.4 21.3	14.4 14.8 15.2	9.9 11.0 12.1	10.1
Mirgenbach (1992–2003)	8.2 10.7 12.4	9.8 11.2 13.0	10.7 12.4 13.8	12.9 14.7 16.8	16.3 18.6 23.5	19.2 22.2 25.7	21.5 23.9 26.9	22.9 25.3 27.8	18.8 21.8 24.8	15.7 18.8 21.7	12.1 14.9 17.2	9.0 11.9 15.2
Moselle (1992–2003)	2.1 5.6 8.4	2.4 5.7 8.4	6.8 8.5 10.2	8.1 11.6 14.7	13.0 16.8 20.8	16.7 21.2 26.0	17.3 22.3 25.1	20.8 23.4 27.4	14.6 18.7 22.1	10.7 15.4 18.0	7.7 9.6 12.3	4.3 6.9 9.7

TABLE II. Comparison of main life-history characteristics of pumpkinseed populations from a native area (Ontario lakes: Fox, 1994) and from various water bodies where they have been introduced (Rhône River: Fox & Crivelli, 2001; Cottesmore Pond: Copp *et al.*, 2002)

	Ontario lakes, Canada (44°18' N)	Cottesmore Pond, England (51°09' N)	Rhône River delta canals, France (43°30' N)	Mirgenbach Reservoir, Moselle, France (49°25' N)
Summer 1994 mean temperature (° C) (study period summer)	22.9	20.7	28.1	27.3 (26.3)
Longevity (years)	9	5	3–7	3
Female mean age at maturity (years)	3.4	3.9	1.8	1.0
Female mean $I_G$	5.6	6.1	6.3	7.8
Female mean $L_T$ at maturity (mm)	100	78.5*	70.7	76.6
Mean $L_T$ at age 1 (mm)	46*	33.8*	39.4*	58.6
Maximum $L_T$ (mm)	210	124*	150	168

\*, data computed according to the authors;  $I_G$ , gonado-somatic index;  $L_T$ , total length.

station (two stations for each depth), gillnets of two squared mesh-sizes were used (10 and 20 mm). While pumpkinseed were caught at the stations at 1 m in depth during each attempt, none were caught at >1 m (unpubl. data).

In summer 2002, inshore enclosures were fished to determine adult pumpkinseed traits (*e.g.* total length,  $L_T$ , and age at maturity) during the reproductive period. Additional sampling was carried out to investigate the seasonal variations in individual growth and gonadal development. The pumpkinseed born in 2002 were fished until autumn 2003 to study seasonal growth patterns. Data collected from spring 2001 to autumn 2003 were used to characterize ovary or testis development. The number of degree-days (DD), calculated beginning on 1 January, was used to define four successive periods: late March to late April ('early spring': from 1000 to 1550 DD), mid-May to mid-June ('late spring': from 1800 to 2750 DD), mid-July to mid-August ('summer': from 3050 to 3700 DD), September to November ('autumn': >4200 DD). Year-to-year DD differences did not exceed 10% during each period defined.

The sites were located at depths  $\leq 1$  m. They were chosen using indicators of habitat quality such as shoreline morphology and depth gradient, composition and heterogeneity of the substratum, macrophyte diversity and cover. Sampling sites provided various habitats ranging from the poorest to the richest ones. Poor habitats had a homogeneous substratum with bedrock, pebbles or marl outcrop and no macrophyte beds, whereas complex (or rich) habitats provided a heterogeneous substratum with leaf litter, silt, branches and roots and continuous or discontinuous macrophyte beds (*e.g.* *Typha latifolia*, *Myriophyllum* sp. and *Potamogeton pectinatus*).

Inshore enclosures located at sites providing complex habitats were repeatedly electro-fished to depletion. Parts of the reservoir which were suitable were isolated (mean  $\pm$  s.d. area  $527 \pm 169$  m<sup>2</sup>), at four stations (1 m in depth, stations a, Fig. 1) with nets. Additional fish sampling was done every 2 or 3 weeks according to a standard protocol, using a trawl, beach seine, fyke-nets or electrofishing. All the nets had the same squared mesh-size (2 mm in length) and were used at the same stations (stations b, Fig. 1) where the principal littoral zone habitats were sampled to ensure that there was no size, age or maturity bias due to differential habitat selection.

## DATA ANALYSIS

The pumpkinseed collected were preserved in 4% formalin for further analysis. Specimens were later measured ( $L_T$ , nearest mm) and weighed (nearest 0.1 g). Gonads were inspected to determine sex and maturity state, and maturing and mature individuals were removed and weighed. After removal of the gonads, specimens were eviscerated and reweighed. Temporal patterns in both male and female gonad development were described using the gonado-somatic index ( $I_G$ , gonad mass as per cent of eviscerated body mass; Wootton, 1991). Deacon & Keast (1987) and Fox (1994) indicate 3.0 or 3.5% of total body mass for females collected in the early spring prior to the start of reproduction as a criterion to assess maturity. In the present study, females whose  $I_G$  was  $>4$  of eviscerated body mass were considered newly maturing or breeding individuals.

The  $I_G$  is often incorrectly assumed to be independent of length and isometric growth between the two variables involved (Garcia-Berthou & Moreno-Amich, 1993). To properly appreciate the seasonal variation in gonadal mass, a multivariate analysis of covariance (MANCOVA) was applied to the  $\log_{10}$ -transformed eviscerated and gonadal masses, whose relationship with the reproductive cycle was considered a dependent variable. The  $\log_{10}$ -transformed  $L_T$  was used as the covariate. The factors taken into consideration were season (sample date), cohort (equivalent to age of the individual) and sex (male or female). For cases with significant factor effects, variation was described using the predicted means for each cell, adjusted for the effect of the covariate. The data were divided into three sets: young males and females of the year (cohort 0+), 1 year-old males (cohort 1+) and 1 year-old females (cohort 1+). Older adults, being rare, were excluded from the analysis.

Age at capture was determined by reading scales with a microfilm reader, with annuli identified using the criteria outlined in Regier (1962) and Bagliniere & Le Louarn (1987).

Mean age and  $L_T$  at maturity of females were computed using the formula given by Fox & Crivelli (2001), according to the data collected after enclosure electrofishing in July 2002. Data given in standard length ( $L_S$ ) were converted to  $L_T$ , using conversion factors from Carlander (1977):  $L_S = 0.8 L_T$ .

## RESULTS

### ANNUAL REPRODUCTIVE CYCLE

#### *Females*

Adjusted gonad masses from MANCOVA of adult females (Fig. 2) indicated the different phases of the reproductive cycle. In early spring, there was strong, rapid growth in gonadal mass that indicated the maturation phase. The spawning period began shortly before the first capture of young-of-the-year (YOY) in mid-June ( $L_T < 10$  mm) and continued through summer as indicated by consistently high mean gonadal masses (Fig. 2). Maintaining high gonadal mass while spawning was possible because ovarian growth from a presumably previtellogenic condition to a presumably preovulatory condition occurred in summer. In late spring two groups were distinguished, with significant differences in  $L_T$  (Mann-Whitney  $U$ -test,  $n = 58$ ,  $P < 0.05$ ), in which changes in gonad size could be related to individual size [Fig. 3(c)]. One group, essentially large individuals (mean  $L_T = 92.3$  mm), had high  $I_G$  values (between 3.86 and 17.06). No females were mature under a minimum  $L_T$  of 68 mm. The other group consisted of individuals in which  $I_G$  was  $<2$ , *i.e.* not yet having entered the maturational phase [Fig. 3(c)]. These were among the smallest fish (mean  $L_T = 66.5$  mm). During the summer, fish had grown to maturity since individuals  $>82$  mm had an  $I_G >4$  [Fig. 3(d)]. The two smallest females did not reach this

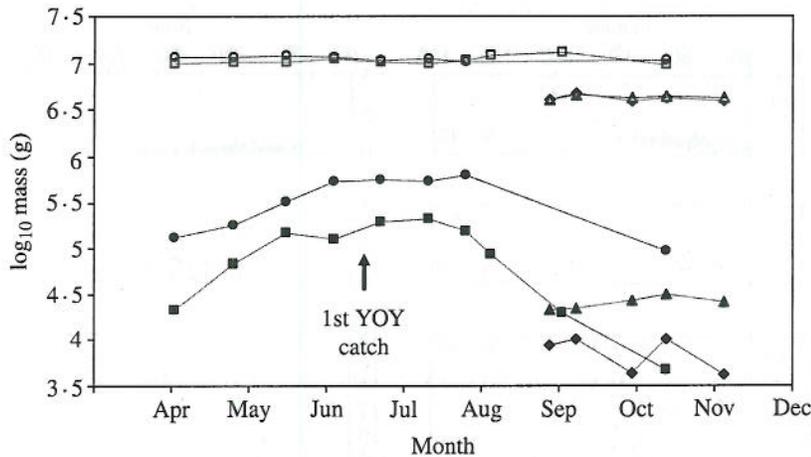


FIG. 2. Predicted seasonal means for pumpkinseed (adjusted for sample covariate effect) of  $\log_{10}$ -transformed masses for adult males (■, gonad mass; □, eviscerated mass) and females (●, gonad mass; ○, eviscerated mass) and young-of-the-year (YOY) males (◆, gonad mass; ◇, eviscerated mass) and females (▲, gonad mass; △, eviscerated mass).

threshold value and their minimum size was 75 mm. After that, adult females were absent from captured populations until autumn. Nevertheless, the capture of small YOY ( $L_T < 20$  mm) in September indicated that females continued to spawn through August. Maximum  $I_G$  values reached up to 18 of female eviscerated mass and were observed from mid-May to the end of July. In autumn, YOY  $I_G$  values approached the low adult ones [ $<1.2$ ; Fig. 3(a), (e)].

#### Males

There was a quick maturation before the spawning period that continued until gonadal masses decreased to the lowest level (Fig. 2). In contrast to observations among the females (minimum  $L_T = 68$  mm), there were small males (minimum  $L_T = 33$  mm) among the breeding adults. Small-age 1 year fish did not delay maturity until later in the season, but exhibited gonadal growth [Fig. 3(b)]; development was even exceptional ( $I_G$  from 2 to 16) for the smallest males [ $L_T < 50$  mm; Fig. 3(c)]. Like the females, male mean gonad mass indicated maturity from mid-May to the end of July (Fig. 2), but during the summer, individual males were never  $<60$  mm  $L_T$  nor with  $I_G$  values  $>4.5$  [Fig. 3(d)]. In August, male gonad masses decreased until the lowest values for  $I_G$  were encountered in autumn [ $<0.45$ ; Fig. 3(e)]. The YOY  $I_G$  did not exceed 1 [Fig. 3(a)].

#### BREEDING POPULATION

The samples taken from the enclosure in July 2002 (Table III) showed that, except for YOY, all individuals were mature whatever their sex, age or size (range 43–135 mm  $L_T$ ). There was no significant difference (Mann–Whitney  $U$ -test,  $n = 246$ ,  $P = 0.427$ ) in the median size of either sex. Only non-ovulated and spent females showed significant differences in median  $L_T$  (Mann–Whitney  $U$ -test,  $n = 93$ ,  $P < 0.05$ ) because larger females spawned earlier than smaller

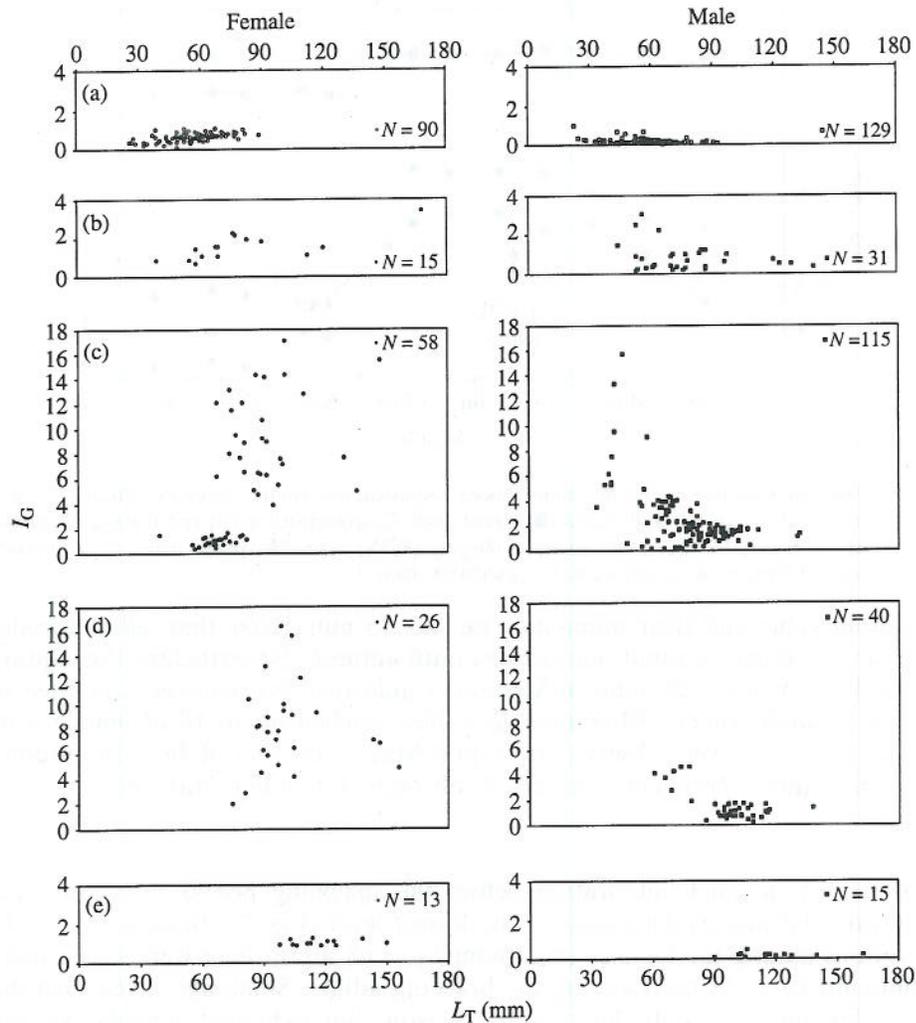


FIG. 3. Individual change in the gonado-somatic index ( $I_G$ ) for (a) young-of-the-year (YOY) pumpkinseed (○, female; □, male) during autumn and for older pumpkinseed (●, female; ■, male) during four periods: (b) early spring, (c) late spring, (d) summer and (e) autumn.

ones. Adult fish >110 mm  $L_T$  represented <5% of the breeding population, whereas adults >1 year were <1%. The sex ratio (M:F = 1.4) indicated that during the breeding period, males were more numerous than females in the reproductive area. Interestingly, the largest YOY had already attained nearly the same size as the smallest 1 year-old males (45 and 43 mm, respectively).

#### AGE GROUP AND COHORT STUDY

Maximal longevity was 3 years (Table II). Two age groups were strongly represented among the captured fish: group 1 fish with one winter of life were the majority until June, before the arrival of YOY which remained predominant from then until winter. In late autumn, only YOY were caught.

TABLE III. Nesting site inter-population variability of pumpkinseed variables taken by electrofishing within enclosures during the breeding season (July 2002). Data with the same superscript lower case letters are not significantly different (Mann-Whitney  $U$ -test,  $P > 0.05$ )

	YOY	Adults			
		Female		Male	
Sample size	287	103		143	
$L_T$ interval (mm)	10.5–45.0	71.0–112.0		43.0–135.0	
Mean $L_T$ (mm)	21.2 <sup>a</sup>	94.9 <sup>b</sup>		93.5 <sup>b</sup>	
Per cent at maturity	0	100		100	
Maturity state	Non-ovulated	Ovulated	Spent	Spermiated	Spent
Per cent in maturity stage	59.2	9.7	31.1	88.1	11.9
$L_T$ interval (mm)	71.0–110.0	80.0–105.0	90.0–112.0	43.0–135.0	75.0–114.0
Mean $L_T$ (mm)	92.9 <sup>c</sup>	93.7 <sup>c,d</sup>	99.1 <sup>d</sup>	92.9 <sup>e</sup>	97.9 <sup>e</sup>
Sex ratio (M:F)			1.4		

The size distribution from age 0 to 1 year throughout consecutive stages of life (Fig. 4) showed a highly significant change (median test, d.f. = 1,  $P < 0.001$ ), except during the maturation phase which occurred between early April and mid-June 2003 (median test, d.f. = 1,  $P > 0.100$ ). Pumpkinseed growth was extremely rapid for YOY, especially after the end of breeding in August 2002, whereas it slowed during both the winter and subsequent maturation phase. In autumn, YOY had a high variance for size and this remained the case after the winter as minimum size was 37 mm and larger fish reached 88 mm  $L_T$ . After reproduction in summer 2003, the 1 year-old population showed an increase in median size. By then, the 1 year-old pumpkinseed captured had a low variance for size and their minimum  $L_T$  was 95 mm.

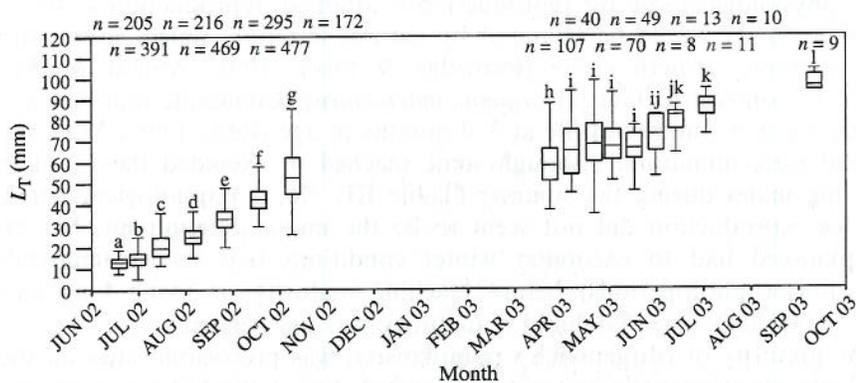


FIG. 4. Changes in the total length distribution of pumpkinseed from the 2002 cohort. —, median; □, first (25%) and third (75%) quartiles; ▭, 95% CI. Data points with the same lower case letters are not significantly different (median test,  $P > 0.05$ ).

## DISCUSSION

This study describes modifications in life-history traits of a species that had colonized a water mass with prolonged autumns, warm winters and early spring conditions, and provides insight into the impact of these adaptations on the dynamics of the population studied. The results were compared with previous research (Table II).

### LINKS BETWEEN TEMPERATURE AND REPRODUCTIVE STRATEGY

Precocious maturity has been the subject of many observations (Crivelli & Mestre, 1988; Luksiene & Sandström, 1994; Sandström *et al.*, 1995; Fox & Crivelli, 2001), though never involving an entire 1 year-old cohort. An increase in temperature affects differentiation more than growth rates and thus body size at a given stage of development is reduced (van der Have & de Jong, 1996). This is in keeping with the present findings in which the average size of females at maturity was lower than that of this species in its native range (Table II). Early maturity can also be explained as a normal reaction to increased food consumption at higher temperatures, leading to faster juvenile growth (Zapata & Granadolencio, 1993; Berrigan & Charnov, 1994). In the Mirgenbach Reservoir, YOY pumpkinseed attained higher average size at age 1 year than in their original environment, in other cold water environments or in warmer waters (Table II), and the average was well above the European mean ( $L_S = 46.9$  and 40 mm in the Mirgenbach and in Europe, respectively; Copp *et al.*, 2004). This acceleration in individual growth probably resulted from an increase in food intake and the available resources under these thermal conditions and to a lengthening of the growth period due to water mass warming. Nevertheless, recent research indicates that the same life-history outcomes for warmer thermal regimes are occurring independently of an increase in growth rate (Dhillon & Fox, 2004). In the present study, this was illustrated by the maturation of smaller as well as larger sized 1 year-old fish. Once a minimum physiological size for reproduction is attained, reproduction at the earliest opportunity would be favoured by natural selection, unless some intrinsic cost of rapid growth exists (Partridge & Sibly, 1991; Arendt & Wilson, 1997). In contrast to bluegill *Lepomis macrochirus* Rafinesque that can mature during the first summer of life at 3–4 months of age (Belk, 1998), YOY pumpkinseed were immature, although some reached or exceeded the  $L_T$  of small breeding males during the summer (Table III). So, a physiological minimum size for reproduction did not seem to be the major determinant, but rather pumpkinseed had to encounter winter conditions (*e.g.* cooler temperatures and shorter photoperiods) before reaching maturity or living long enough (*e.g.* >5000 DD since hatching) if maturity was age related.

The maturity of Mirgenbach's pumpkinseed was precocious since all the individuals surviving their first winter matured during the following season (*i.e.* late spring or summer). During the summer, some females [ $I_G = 2.0$  and 2.8; Fig. 3(d)] had not yet reached the threshold value for maturity ( $I_G = 4$ ) but they would probably undergo vitellogenesis later in the season. During the

summer, no females had  $I_G < 2$  [Fig. 3(d)]. Females with low  $I_G$  in late spring [ $< 2$ ; Fig. 3(c)] probably had grown before reaching maturity. Pumpkinseed absence at  $\geq 3$  m in depth tended to support this idea. All the individuals did not share the same life history since both maturation and spawning were asynchronous. According to Ridgway *et al.* (1991), the annual schedule of gonadal recrudescence and reproductive activity of centrarchids may be directly affected by size-dependent differences in metabolism and energy stores. The presence in late spring of two groups yielded the protracted breeding season [Fig. 3(c)]. As Danylchuk & Fox (1994) and Vila-Gispert & Moreno-Amich (2000) had previously reported, small previtellogenic females that would undergo vitellogenesis by late summer reproduced later in the season than their larger conspecifics (Table III). The YOY that were born later would probably experience a shorter favourable growth period than earlier born conspecifics. Except when some countergradient variation existed (Arendt & Wilson, 1999), they would attain a smaller size in autumn, tending to produce smaller parents the following year. It is hypothesized that the late spawners would have 'daughters' that were also small, late-spawning parents, but 'sons' that could spawn early even if small. Even given the evolutionary advantage of a longer growth period by producing offspring as early as possible (Danylchuk & Fox, 1996), variation in the timing of reproduction among individuals may provide insurance in the face of unpredictable conditions, ensuring that at least some of the young produced have optimal conditions for growth and survival (Koslowski, 1992; Garvey *et al.*, 2002). Among the males, individuals were mature at the beginning of the breeding season, regardless of their size. They exhibited strong differences in their reproductive gonadal allocation according to their size since the small males ( $L_T < 50$  mm) had higher  $I_G$  than their larger conspecifics [Fig. 3(c)]. The small-sized adults captured ( $L_T \leq 60$  mm) were almost exclusively male. Consequently, the minimum physiological size for reproduction was sex dependant. Small males that mature precociously and develop unusually large gonads are known as 'cuckolders' and reproduce by sneaking fertilization when females are being courted by parental males (Neff *et al.*, 2003). According to Gross (1982), the fastest growing juvenile males become the cuckolders. In the Mirgenbach Reservoir, YOY exhibited strong growth patterns and most of the breeders were 1 year old. The fastest growing juvenile males became the parental males, whereas the slowest growing juveniles became the cuckolders. As reported by field observations during electrofishing in summer 2002, small males were spawning, although this may result in reduced fitness for their offspring and compromise their own overwinter survival (Danylchuk & Fox, 1996). Much of the somatic growth occurs after reproduction (Fox & Keast, 1990), so late-breeding fish, already exhausted by the energy expenditure in reproduction, experienced a shortened growth period that they had to share with fast-growing YOY.

#### COSTS AND BENEFITS OF PUMPKINSEED LIFE-HISTORY STRATEGIES

The survival cost is higher in populations which reproduce early and at a small size (Belk, 1998; Bertschy & Fox, 1999) because fishes allocate energy

to reproductive tissues at the expense of somatic tissues [e.g. gudgeon *Gobio gobio* (L.); Rosecchi *et al.*, 2001]. Although rapid growth may evolve to allow organisms to reach a size which discourages predators, early maturation could in fact counteract this due to a slower increase in size during the maturation phase. In addition, pumpkinseed would be at greater risk from predators because they engage in risky reproductive behaviour; males build and defend nests in relatively open areas, or frequent nesting areas if they act as cuckolders, and females visit nests to spawn (Belk, 1998). High YOY growth levels, together with low individual growth in fish which had invested energy for reproduction, led to the fast-growing progeny catching-up in size to their small, adult parents by the summer (mid-July).

No individual fish exceeded 3 years of age, and 2 or 3 year-old individuals were very rare. There was high mortality of small-sized fish after first-time reproduction since only individuals >95 mm were captured in the autumn. The mortality rate would not, therefore, affect all the parents equally according to size, reproduction date and reproductive allocation. A change in relative mortality rates for different age or size classes can change the optimal age and size at maturity (Michod, 1979). Selective pressure from a low adult to juvenile ratio is strong enough to favour the evolution of increased reproductive efforts in pumpkinseed, even when it results in the decline of an already low adult survival rate (Bertschy & Fox, 1999). Pumpkinseed subjected to non-native conditions (*i.e.* elevated temperatures) adapted by reproducing earlier and investing more heavily in reproduction presumably because the major effect of these conditions was higher adult mortality. Delaying maturity and allocating available energy to growth leads to increased female fecundity and male reproductive success, thus decreasing mortality from gape-limited predators and enhancing offspring survival potential through improved parental care by larger individuals (Belk, 1998). But this delay is also associated with an elevated risk of mortality prior to first reproduction because of the prolonged juvenile period (Bell, 1980; Stearns, 1992). In the Mirgenbach Reservoir, pumpkinseed had not shifted their first maturation to the following season; regardless of sex or size, fish surviving past their first winter opted for maturation. Although some females delayed maturity until later in the season, none of them delayed it until the following year. Thus, the low survival rate of pumpkinseed, especially the smaller ones, beyond their second summer was accompanied by early reproduction, ensuring at least one reproductive attempt. Some species can sacrifice reproduction in favour of growth and reduced risk of mortality, whereas some fishes invest all their energy in reproduction at the expense of survival (Mann *et al.*, 1984). Temperature could thus act as a warning sign of future risks of mortality and alter the optimal time to mature (Atkinson, 1995).

The pumpkinseed population was divided into two strong age classes: the young ones, whose recruits replenished the adult stock, and the 1 year fish which assured the main reproductive effort. The limited number of cohorts weakened the population since its renewal was potentially compromised by the absence or failure of reproduction during just one season. Nevertheless, both the characteristics of the environment and the auto-ecology of the species explained its persistence. The reservoir did not exhibit any physicochemical

conditions likely to prevent a given stage of the reproductive cycle, or the survival of YOY since no fluctuation in water level or summer anoxia occurred and winter temperatures were cool. In addition, the species opted for a strategy in which all recruits participated in the reproductive effort.

#### GLOBAL WARMING IMPLICATIONS

In the Mirgenbach Reservoir, pumpkinseed have occupied an environment which is warmer than its original habitat area. This illustrates both the 'opportunistic' life-history strategy of the species, which tolerates a wide range of environmental conditions (Vila-Gispert *et al.*, 2002), and the fact that reservoirs generally provide a favourable environment for the establishment of non-native species (Irz *et al.*, 2004). The modification in reproductive dynamics, symbolized by a very short generation time due to the renewal of adult stock from 1 year to the next, might have favoured a quick adaptation of the organisms to their environment. A better understanding of the mechanisms underlying the developmental and evolutionary relationships between temperature and body size may aid in predicting ecological responses to climatic change (Atkinson & Sibly, 1997). A preliminary analysis of the bio-ecological characteristics of all the Mirgenbach ichthyofauna species revealed a strong convergence with the results obtained for pumpkinseed (unpubl. data). Strong growth in YOY coupled with precocious maturity, and thus shorter life span, seemed to be adaptive reactions. This leads to the conclusion that, within a global warming context, age structure of fish populations would change.

This research was supported by the Cattenom nuclear power plant (EDF). The authors would like to thank the CSP DR3 staff for their help with fish sampling. We are also grateful to A. Cartier for correcting the English version, and to S. Devin and to two anonymous referees for providing helpful comments on an earlier version of the manuscript.

#### References

- Alm, G. (1959). Connection between maturity, size and age in fishes. *Reports from the Institute of Freshwater Research, Drottningholm* **40**, 5–145.
- Arendt, J. D. & Wilson, D. S. (1997). Optimistic growth: competition and an ontogenetic niche-shift select for rapid growth in pumpkinseed sunfish (*Lepomis gibbosus*). *Evolution* **51**, 1946–1954.
- Arendt, J. D. & Wilson, D. S. (1999). Countergradient selection for rapid growth in pumpkinseed sunfish: disentangling ecological and evolutionary effects. *Ecology* **80**, 2793–2798.
- Atkinson, D. (1994). Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research* **25**, 1–58.
- Atkinson, D. (1995). Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *Journal of Thermal Biology* **20**, 61–74.
- Atkinson, D. & Sibly, R. M. (1997). Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* **12**, 235–239.
- Bagliniere, J. L. & Le Louarn, H. (1987). Scale characteristics of the main freshwater fish species in France. *Bulletin Français de la Pêche et de la Pisciculture* **306**, 2–39.
- Belk, M. C. (1998). Predator-induced delayed maturity in bluegill sunfish (*Lepomis macrochirus*): variation among populations. *Oecologia* **113**, 203–209.

- Bell, G. (1980). The costs of reproduction and their consequences. *American Naturalist* **116**, 45–76.
- Berrigan, D. & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* **70**, 475–478.
- von Bertalanffy, L. (1960). Principles and theory of growth. In *Fundamental Aspects of Normal and Malignant Growth* (Nowinski, W. N., ed), pp. 137–259. Amsterdam: Elsevier.
- Bertschy, K. A. & Fox, M. G. (1999). The influence of age-specific survivorship on pumpkinseed sunfish life histories. *Ecology* **80**, 2299–2313.
- Carlander, K. D. (1977). *Handbook of Freshwater Biology*. Ames, IA: Iowa State Press.
- Carrel, G., Crivelli, A. J. & Fox, M. G. (2001). La perche soleil *Lepomis gibbosus* (Linné, 1758). In *Atlas des poissons d'eau douce de France* (Keith, P. & Allardi, J., eds), pp. 322–323. Paris: MNHN.
- Copp, G. H., Fox, M. G. & Kovac, V. (2002). Growth, morphology and life history traits of a cool-water European population of pumpkinseed *Lepomis gibbosus*. *Archiv für Hydrobiologie* **155**, 585–614.
- Copp, G. H., Fox, M. G., Przybylski, M., Godinho, F. N. & Vila-Gispert, A. (2004). Life-time growth patterns of pumpkinseed *Lepomis gibbosus* introduced to Europe, relative to native North American populations. *Folia Zoologica* **53**, 237–254.
- Coutant, C. C. (1990). Temperature-oxygen habitat for freshwater and coastal striped bass in a changing climate. *Transactions of the American Fisheries Society* **119**, 240–253.
- Crivelli, A. J. & Mestre, D. (1988). Life history traits of pumpkinseeds, *Lepomis gibbosus*, introduced into the Camargue, a Mediterranean wetland. *Archiv für Hydrobiologie* **111**, 449–466.
- Danylchuk, A. J. & Fox, M. G. (1994). Seasonal reproductive patterns of pumpkinseed (*Lepomis gibbosus*) populations with varying body-size characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 490–500.
- Danylchuk, A. J. & Fox, M. G. (1996). Size and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). *Canadian Journal of Zoology* **74**, 1834–1840.
- Daufresne, M., Roger, M. C., Capra, H. & Lamouroux, N. (2003). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology* **10**, 124–140. doi: 10.1046/j.1529-8817.2003.00720.x
- Deacon, L. I. & Keast, A. J. (1987). Patterns of reproduction in two populations of pumpkinseed sunfish, *Lepomis gibbosus*, with differing food resources. *Environmental Biology of Fishes* **19**, 281–296.
- Dhillon, R. S. & Fox, M. G. (2004). Growth-independent effects of temperature on age and size at maturity in Japanese Medaka (*Oryzias latipes*). *Copeia* **2004**, 37–45.
- Fang, X., Stefan, H. G., Eaton, J. G., McCormick, J. H. & Alam, S. R. (2004). Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios: Part 3. Warm-water fish in the contiguous US. *Ecological Modelling* **172**, 55–68.
- Flesch, A., Masson, G. & Moreteau, J. C. (1994). Comparaison de trois méthodes d'échantillonnage utilisées dans l'étude de la répartition de la perche (*Perca fluviatilis*) dans un lac-réservoir. *Cybium* **18**, 39–56.
- Fox, M. G. (1994). Growth, density, and interspecific influences on pumpkinseed sunfish life-histories. *Ecology* **75**, 1157–1171.
- Fox, M. G. & Crivelli, A. J. (2001). Life history traits of pumpkinseed (*Lepomis gibbosus*) populations introduced into warm thermal environments. *Archiv für Hydrobiologie* **150**, 561–580.
- Fox, M. G. & Keast, A. (1990). Effects of winterkill on population-structure, body size, and prey consumption patterns of pumpkinseed in isolated beaver ponds. *Canadian Journal of Zoology* **68**, 2489–2498.

- Fox, M. G. & Keast, A. (1991). Effect of overwinter mortality on reproductive life-history characteristics of pumpkinseed (*Lepomis gibbosus*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1792–1799.
- Garcia-Berthou, E. & Moreno-Amich, R. (1993). Multivariate analysis of covariance in morphometric studies of the reproductive cycle. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1394–1399.
- Garcia-Berthou, E. & Moreno-Amich, R. (2000). Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology* **57**, 29–40. doi: 10.1006/jfbi.2000.1285
- Garvey, J. E., Herra, T. P. & Leggett, W. C. (2002). Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. *Ecological Applications* **12**, 194–205.
- Gross, M. R. (1982). Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie* **60**, 1–26.
- van der Have, T. M. & de Jong, G. (1996). Adult size in ectotherms: temperature effects on growth and differentiation. *Journal of Theoretical Biology* **183**, 329–340.
- Irz, P., Argillier, C. & Proteau, J. P. (2004). Contribution of native and non-native species to fish communities in French reservoirs. *Fisheries Management and Ecology* **11**, 165–172.
- Jansen, W. & Hesslein, R. H. (2004). Potential effects of climate warming on fish habitats in temperate zone lakes with special reference to lake 239 of the experimental lakes area (ELA), north-western Ontario. *Environmental Biology of Fishes* **70**, 1–22.
- Jobling, M. (1996). Temperature and growth: modulation of growth rate via temperature change. In *Global Warming: Implications for Freshwater and Marine Fish* (Wood, C. M. & McDonald, D. G., eds), pp. 225–253. Cambridge: Cambridge University Press.
- Koslowski, J. (1992). Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology & Evolution* **7**, 15–19.
- Luksiene, D. & Sandström, O. (1994). Reproductive disturbance in a roach (*Rutilus rutilus*) population affected by cooling water discharge. *Journal of Fish Biology* **45**, 613–625.
- Mann, R. H. K., Mills, C. A. & Crisp, D. T. (1984). Geographical variation in the life-history tactics of some species of freshwater fish. In *Fish Reproduction: Strategies and Tactics* (Potts, G. W. & Wootton, R. J., eds), pp. 171–186. London: Academic Press.
- Michod, R. E. (1979). Evolution of life histories in response to age-specific mortality factors. *American Naturalist* **113**, 531–550.
- Neff, B. D., Fu, P. & Gross, M. R. (2003). Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology and Sociobiology* **14**, 634–641.
- Packa-Tchissambou, E., Stryjak, J. F., Leglize, L., Nourisson, M. & Descouturelle, G. (1981). Impact du réchauffement artificiel d'un milieu dulçaquicole sur les cycles biologiques d'un Crustacé Décapode (*Atyaephyra desmarestii desmarestii* Millet) et d'un Mollusque Prosobranchie (*Bithynia tentaculata* L.). *Bulletin de la Société Zoologique de France* **106**, 372.
- Partridge, L. & Sibly, R. (1991). Constraints in the evolution of life histories. *Philosophical Transactions of the Royal Society of London B* **332**, 3–13.
- Pascal, M., Lorvelec, O., Vigne, J. D., Keith, P. & Clergeau, P. (2003). Evolution holocène de la faune de Vertébrés de France : invasions et disparitions. *Rapport au Ministère de l'Ecologie et du Développement Durable (Direction de la Nature et des Paysages)*. Paris: INRA, CNRS, MNHN.
- Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T. & Knust, R. (2001). Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research* **21**, 1975–1997.

- Regier, H. A. (1962). Validation of the scale method for estimating age and growth of bluegills. *Transactions of the American Fisheries Society* **91**, 362–374.
- Reznick, D. A., Bryga, H. & Endler, J. A. (1990). Experimentally-induced life history evolution in a natural population. *Nature* **346**, 357–359.
- Ridgway, M. S., Shuter, B. J. & Post, E. E. (1991). The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Journal of Animal Ecology* **60**, 665–681.
- Rosecchi, E., Thomas, F. & Crivelli, A. J. (2001). Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. *Freshwater Biology* **46**, 845–853.
- Sandström, O., Neuman, E. & Thoresson, G. (1995). Effects of temperature on life history variables in perch. *Journal of Fish Biology* **47**, 652–670.
- Soto, C. G. (2001). The potential impacts of global climate change on marine protected areas. *Reviews in Fish Biology and Fisheries* **11**, 181–195.
- Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Tomasini, J. A., Collart, D. & Quignard, J. P. (1996). Female reproductive biology of the sand smelt in brackish lagoons of southern France. *Journal of Fish Biology* **49**, 594–612.
- Van Der Kraak, G. & Pankhurst, N. W. (1996). Temperature effects on the reproductive performance of fish. In *Global Warming: Implications for Freshwater and Marine Fish* (Wood, C. M. & McDonald, D. G., eds), pp. 159–176. Cambridge: Cambridge University Press.
- Vein, D., Gignoux, M., Flesch, A., Pierre, J. F., Marzou, R. & Pihan, J. C. (1990). Trophic evolution of a reservoir with overheated waters: nuclear power station at Cattenom, Moselle, eastern France. *Annales de Limnologie—International Journal of Limnology* **27**, 87–98.
- Vila-Gispert, A. & Moreno-Amich, R. (2000). Fecundity and spawning mode of three introduced fish species in Lake Banyoles (Catalunya, Spain) in comparison with other localities. *Aquatic Sciences* **61**, 154–166.
- Vila-Gispert, A., Moreno-Amich, R. & Garcia-Berthou, E. (2002). Gradients of life-history variation: an intercontinental comparison of fishes. *Reviews in Fish Biology and Fisheries* **12**, 417–427.
- Wootton, R. J. (1991). *Ecology of Teleost Fishes*. London: Chapman & Hall.
- Zapata, S. C. & Granadolorencio, C. (1993). Age, growth and feeding of the exotic species *Lepomis gibbosus* in a Spanish cooling reservoir. *Archiv für Hydrobiologie* **127**, 561–573.