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Recent invasion by a non-native cyprinid (common bream *Abramis brama*) is followed by major changes in the ecological quality of a shallow lake in southern Europe

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Running head: Common bream in Lake Montorfano

ABSTRACT

We present an example of how an invasion by a non-native cyprinid (common bream, *Abramis brama* (Pisces: Cyprinidae), hereafter bream) in a natural shallow lake in southern Europe (Lake Montorfano, northern Italy) may have adversely affected the state of the lake's ecosystem. In less than two decades, bream became the most abundant species and characterized by a stunted population with asymptotic length 33.5 cm, an estimated mean length at first maturity of 19.6 cm, a total mortality rate of 0.64 y^{-1} and a diet overwhelmingly dominated by microcrustaceans. Following bream establishment, nutrients and phytoplankton biomass rose, the proportion of Cyanobacteria by numbers increased markedly and water transparency decreased. Total zooplankton abundance increased with a marked increase in small cladocerans and copepods, whereas the abundance of large herbivorous cladocerans did not change. The coverage of submerged macrophytes declined, as did the abundance of native pelagic zooplanktivorous fish. The composition of the fish community shifted towards a higher proportion of zoobenthivorous species, such as bream and pumpkinseed (*Lepomis gibbosus*). Our results indicate that bream affected water quality through bottom-up mechanisms, while top-down effects were comparatively weak. Selective removal of bream and perhaps stocking of native piscivores might improve the ecological status of the lake.

Key words*: invasive alien species IAS, electrofishing, multi-mesh survey gill nets, CPUE, cyprinids, ecosystem functioning*

1. INTRODUCTION

Non-native species, i.e. species outside their natural range which frequently become established and abundant following their introduction (Rejmánek et al. 2002; Cambray 2003), are increasingly recognized as constituting one of the main threats to biodiversity and ecosystem functioning (e.g. Ricciardi and McIsaac 2011) and are often associated with environmental degradation (Biro 1997; Wilcove et al. 1998; Byers 2002). Furthermore, in the case of freshwater fish faunas such biotic homogenization frequently has high ecological and economic costs (Welcomme 1998; Rahel 2000).

Successful non-native species are often characterized by high physiological tolerance and functional characteristics different from those of the members of invaded communities (Moyle and Marchetti 2006; Bollache 2008), enabling them to occupy vacant niches and to spread and increase rapidly. Moreover, successful non-native species have been reported to affect the functional diversity of communities with possible strong impacts on food webs and ecosystem functioning (Hooper et al. 2005; Britton et al. 2010; Simberloff 2011). Additionally, as invasions by non-native species in novel environments are often characterized by boom-bust phenomena (Strayer and Malcom 2006; Salonen et al. 2007; Volta and Jepsen 2008; Liso et al. 2011) with strong recruitment leading to high densities, the adverse effects on ecosystem processes may be further exacerbated.

Southern European fresh waters, including those of Italy and other countries adjacent to the Mediterranean Sea, are isolated from those of the rest of Europe. Mountain ranges have prevented the migration of aquatic and many other organisms from northern and central Europe, thus favouring isolation and allopatric speciation (Bianco 1998; Hewitt 1999; Rayol et al. 2007). However, the anthropogenic introduction of non-native species, a long-lasting and continuing process, has recently led to homogenization of the fish fauna and coexistence of native and non-native species in several southern European basins (Clavero and Garcia-Berthou 2006; Gherardi et al. 2007; Kottelat and Freyhof 2007). In particular, the Italian peninsula has experienced the introduction of several non-native fish species since the Roman and Middle Ages. During the 1800s, stocking of water bodies with new fish species became a widespread practice with the purpose of enhancing the production of commercially valuable fish species and, later, species of angling interest. This has resulted in a local shift from salmonids and coregonids to centrarchids and, more recently, cyprinids (Bianco 1998; Gherardi et al. 2007).

Common bream (*Abramis brama*) (hereafter bream) is native in most European drainages, from parts of the U.K. in the west to the White Sea basin in the east, but it is naturally absent from the Iberian peninsula, the Adriatic basin, Italy, northern and western parts of the British Isles and north of 67°N. However, in recent decades, this cyprinid has been introduced to Spain and Italy (Benejam et al. 2005; Kottelat and Freyhof 2007). Although both adaptable and tolerant to different kinds of water bodies (e.g. Jeppesen et al. 2006; Lapirova and Zabotkina 2010), this potentially large-bodied fish prefers meso-eutrophic shallow lakes with a dense vegetated area or reed belt around the shoreline (Lammens et al. 2004; Mehner et al. 2005; Kottelat and Freyhof 2007). It is a zoobenthivorous species (Lammens and Hoogenboezem 1991; Persson and Brönmark 2002) and is in some cases known to have a significant negative effect on the water quality in shallow lakes (Tatrai et al. 1990; Breukelaar 1994; Vanni 2002). The potential to exert adverse effects on lake food webs and ecosystem functioning operates through at least two mechanisms: i) through a reduction the abundance of large zooplankton followed by increased phytoplankton abundance (top-down mechanism) (Brooks and Dodson 1965; Shapiro et al. 1975; Carpenter et al. 1985; Benndorf et al. 2002) and, ii) through increased nutrient cycling due to an increased excretion rate at the community scale and the disturbance of bottom sediments through 'bioturbation' (Meijer et al. 1990; Vanni 2002, Verant et al. 2007) favouring phytoplankton growth (bottom-up mechanism). Furthermore, bream often has a pronounced migratory behaviour (e.g. Schulz and Berg 1987; Borcherding et al. 2002; Skov et al. 2011) and may consequently move considerable distances to other lakes within a river system. Finally, although often attaining large individual sizes, this species may also develop stunted high density populations becoming locally abundant, with potential negative consequences both within and beyond the local fish community due to competition for food resources (Van de Wolfshaar et al. 2006; Persson et al. 2007) or hybridization (Hayden et al. 2010).

In combination, these features make bream a potentially effective and highly undesirable invader of southern European waters.

The introduction history of bream in Italy began as recently as the 1980s (Delmastro 1983; Marconato et al. 1985). Its distribution is still scattered and in running waters it is currently limited to a few small stretches of slow-flowing rivers and canals in the eastern part of the north-eastern lowlands, and to the main rivers Arno (Tuscany region) and Tevere (Latium region) in central Italy (Mancini et al. 2005). Its presence in lentic waters is known to be confined to only three lakes belonging to different catchments but with similar limnological characteristics: Lake Monticolo Grande (Trentino Alto-Adige Region, Adige river drainage), Lake Fimon (Veneto Region, Tagliamento river Drainage) and Lake Montorfano (Lombardy Region, river Po catchment). These three lakes are shallow (max depth < 9 m), small (area <1 km^2), range from mesotrophic to eutrophic (TP between 20 and 60 $\mu g\ L^{-1}$) and have a dense vegetated area or reed belt around the shoreline.

Most studies on the biology and ecology of bream have been undertaken in temperate-cold regions of Europe (Slooff and De Zwart 1982; Kangur 1996; Specziar et al. 1997; Persson and Hansson 1999; Lammens et al. 2004), while the knowledge of bream populations in southern European and Mediterranean countries is very scarce (Treer et al. 2003; Benejam et al. 2005). This is particularly true for Italian lakes. Hence, an understanding of the life-history features of non-native bream combined with knowledge of the environmental state before and after introduction is essential to the assessment of its possible effects on the ecosystem functioning of lacustrine environments. Such knowledge may also help lake managers to decide on appropriate strategies to be implemented to improve the health of fish communities and the water quality (Mehner et al. 2004, Ribeiro et al. 2008).

In this study we describe the population biology and life-history traits of a bream population introduced to Lake Montorfano in northern Italy and we examine the effects of this invasion on the lake ecosystem using a dataset comprising abiotic and biotic information from before and after the introduction. Finally, we propose measures to control this invasive species and improve the ecological status of Lake Montorfano.

2. MATERIAL AND METHODS

2.1 Study site

Lake Montorfano (45°47′N, 9°08′E) is a small (0.51 km^2) shallow (maximum depth 6.8 m, mean depth 4.15 m) and wind-protected lake located in northern Italy (Lombardy region, Como district) at an altitude of 397 m a.s.l. It is naturally oligo-mesotrophic and fed by underground waters and its outlet is partly regulated by a very small weir immediately adjacent to the lake. There are no significant point sources of pollution as sewage was diverted in the 1980s and is now collected and brought to a treatment plant discharging into its outlet.

The native fish assemblage was described by Monti (1864) as including eight species: bleak (*Alburnus arborella*), common carp (*Cyprinus carpio*), Padanian goby (*Padogobius martensi*), Italian roach “triotto” (*Rutilus aula*), pike (*Esox lucius*), perch (*Perca fluviatilis*), rudd (*Scardinius erythrophthalmus*) and tench (*Tinca tinca*). Largemouth bass (*Micropterus salmoides*) and pumpkinseed (*Lepomis gibbosus*) were stocked during the 1930s (de Bernardi et al. 1985).

2.2 Fish sampling

Fish sampling was carried out from 18 to 20 October 2010 using benthic multi-mesh survey gill nets (Appelberg et al. 1995) and electrofishing. Each net was 30 m long and 1.5 m high and composed of twelve panels with mesh sizes ranging from 5.5 mm to 55 mm and each 2.5 m long). In addition, further panels with mesh sizes of 70, 90, 110 and 135 mm (same length as the other panels) were added to three of the nets in order to catch potentially larger fish. In total 16 gill nets were distributed randomly within three different depth strata (0 to 3 m, 3 to 6 m, 6 m to bottom) on two consecutive days of sampling. On the first day additional larger mesh sizes were added to one net for each depth stratum. Nets were set at dusk between 18:00 and 19:00 and retrieved the following morning between 07:00 and 08:00. The fish collected were all individually measured (total length, L_T), weighed (total body mass, W_T) and scales were taken for age determination. The distribution of fish in the littoral area was further evaluated by electrofishing from a boat. The electrofishing device was a built-in-frame EL64GII (Scubla Acquaculture, 7000 W, 600 V, DC current) set up with a copper cathode (width 2.5 cm, length 300 cm) and with a steel ring anode (thickness 0.8 cm, diameter 50 cm). The Point Abundance Sampling Electrofishing (PASE) method (Copp and Garner 1995) was used, in which the anode is dipped for 20 seconds at each sampling point. A total of 99 points was sampled. The stunned fish were measured (total length L_T); rarer species were also weighed (W_T), and scales were taken for age determination.

The ages of the fish were determined by scale analysis on a subsample of *ca.* 150 specimens of each species randomly selected among the entire catch, with 1 June being selected as the nominal birth date for the bream. Age was expressed in months. Sexual maturity was determined by gonadal inspection on a subsample of 100 specimens. Additionally, digestive tracts of 50 bream, randomly selected and ranging in length between 8 cm to 28 cm, were removed and stored separately in 5% formaldehyde for subsequent diet examination and analysis as described below.

2.3 Fish data analysis

Catch per unit effort (CPUE) for nets was assessed with respect to net area and calculated as biomass per unit effort (BPUE, g m^{-2}) and number per unit effort

(NPUE, individuals m^{-2}). CPUE for electrofishing was calculated as NPUE (individuals dip^{-1}).

The body mass-length relationship was calculated using the equation:

$$W = a \times L^b$$

logarithmically transformed into the equation:

$$Log(W) = Log(a) + Log(L_T) \times b$$

where W is body mass (g) and L_T total length, *a* and *b* are the intercept and the slope of the regression.

Length-at-age data were used to estimate the parameters of the Von Bertalanffy (1938) growth function (VBGF) according to the equation:

$$L_T = L_\infty (1 - e^{-k(t-t_0)})$$

where L_T is total length of the fish at time *t*, L_∞ is the theoretical maximum length an average fish could achieve, *k* is the growth constant which determines how fast the fish approaches L_∞, and t_0 is the hypothetical age at $L_T = 0$.

The Φ' Phi'-prime index (Pauly and Munro 1984) was used to compare the growth performance of bream with those of other populations described in the literature according to the equation:

$$\Phi' = Log(k) + 2Log(L_\infty)$$

where k and L_∞ are parameters of the VBGF.

Mean length at maturity L_m for pooled sexes was estimated from L_∞ according to the equation (Froese and Binholan 2000):

$$L_m = 10^{(0.898 Log(L_\infty) - 0.0781)}$$

where L_m is the theoretical average length at which the fish could have its first reproduction and L_∞ is the asymptotic length calculated by the VBGF.

Additionally, a logistic regression was used to fit sigmoid curves to the proportion of mature fish vs. length.

Total instantaneous mortality (Z) was estimated from the linearized catch curve (Sparre and Venema 1988) using fish captured with multi-mesh survey gill nets using the following equation:

$$Log\left(\frac{N}{\Delta t}\right) = a + bt$$

where N is the number of fish of age *t*, *a* and *b* are estimated through linear regression analysis; *b*, with sign changed, is an estimate of total instantaneous mortality Z.

The natural mortality rate M was estimated using the empirical equation of Pauly (1980), which provides an estimate of M on the basis of L_∞ and *k* of the VBGF and the annual mean water temperature (see below for local data source) according to the equation:

$$Log(M) = -0.0066 - 0.279Log(L_\infty) + 0.6543Log(k) + 0.4634Log(T)$$

where L_∞ is the ultimate length an average fish could achieve, *k* is the growth constant of the VBGF, and *T* is the mean annual water temperature.

2.4 Fish diet analyses

Digestive tracts were opened and their contents dried for 15 minutes on blotting paper. The food items were identified under a stereomicroscope as close as possible to the genus or species level. Benthos and zooplankton were identified according to Campaioli *et al*. (1994) and Margaritora (1983), respectively.

Diet analysis was accomplished using Costello's method (Costello, 1990) which is based on a two dimensional representation of the diet, where every point represents, for each prey, the occurrence (the percentage ratio between the number of stomachs where the prey is found and the total number of stomachs) and the abundance (the ratio between the number of organisms into the stomach and the total number of prey). With this method it is possible to assess the importance of the prey in the diet (dominant or rare) and the type of diet (specialized or generalized).

2.5 Sampling and analyses of chemical, physical and biological elements

The limnological characteristics of Lake Montorfano have been determined monthly in a number of years during the last two decades (1991 to 1992, 1998 to 1999, and 2004 to 2007) as a part of a monitoring programme carried out by the University of Milan. Sampling was performed at a central location at the lake site with maximum depth. Water samples for chemical analysis were taken monthly using Van Dorn bottles at the following depths: 0 m, 1 m, 2 m, 4 m, and 6 m. The samples were transferred to the laboratory for immediate analysis. Secchi disk depth, temperature and dissolved oxygen were measured *in situ*. Temperature and oxygen concentrations were determined with an automatic oxygen sensor coupled with a thermistor probe (Microprocessor Oximeter WTW OXI 320).

The following parameters were measured in the laboratory: pH (pH meter Radiometer PHM 83), conductivity (conductimeter Radiometer CDM 83), total phosphorus (Valderrama 1981), nitrate nitrogen (Rodier 1984), silica (APHA 1985) and Chlorophyll *a* (Lorenzen 1967).

Phytoplankton were sampled monthly at six depths in the 0 to 6 m layer and pooled, from which a subsample was fixed in acetic Lugol's solution and later counted under an inverted microscope (see Leoni et al. 2007). The guidelines of Bourrelly (1968, 1970, 1972) and Huber-Pestalozzi (1983) were used to identify the algae, mostly to species level. At least 200 individuals of the most abundant species were counted, with a counting error of about 15% (Lund et al. 1958). The cell volume for each species was estimated according to Rott (1981).

Zooplankton were sampled using a net of 25 cm diameter and 200 µm mesh size. Sampling was performed along a vertical gradient to a depth of 6 m; three samples were taken at each point along the gradient after which the filtered material was mixed and preserved in 4% formalin. The taxa present in the lake were identified using Dussart (1969), Margaritora (1983), Amoroso (1984), and Reddy (1994) and counted with an optical microscope.

2.6 Statistics

Differences in the series of limnological features of Lake Montorfano were tested using one-way ANOVA. If data were not normally distributed, the non-parametric Kruskal-Wallis test was used. If significant differences were detected within a series, appropriate multiple comparison procedures (Holm-Sidak method following ANOVA and Dunn's method following Kruskall-Wallis test, with significance at p level = 0.05) were used to detect differences among groups. The Mann Whitney test was used if only two groups were initially present. Variability of the data was expressed as standard deviations. Statistical analyses were all performed using Sigma Plot statistical package (version 11, Systat software).

3. RESULTS

3.1 Fish

Results of the fish sampling are presented in Table 1. In all 3,867 individuals belonging to nine fish species were caught. By numbers, bream comprised 62% , followed by pumpkinseed (19%), perch (12%) and rudd (5%). Captures of pike, largemouth bass, tench and Italian roach were very infrequent (2% overall).

BPUE of the gill nets ranged from 2.7 g m^{-2} to 99.3 g m^{-2} (mean = 55.9 ±27.1 g m^{-2}) and NPUE from 0.02 to 6.15 ind. m^{-2} (mean = 3.1 ±1.9 g m^{-2}). No fish were captured in the additional larger mesh sizes. NPUE of electrofishing ranged from 1 to 290 ind. dip^{-1} (mean= 17.6 ±34.0 ind. dip^{-1}).

Bream dominated the gillnet catches by both biomass and numbers (Tab. 1) at all depths (Fig. 1a,b) whilst the pumpkinseed was the most abundant species in the in the electrofishing catches of the littoral zone (Tab. 1).

Bream population characteristics

BPUE of bream in the gill nets ranged from 2.7 to 73.2 g m^{-2} (mean=41.3 ±20.4 g m^{-2}) and NPUE from 0.02 to 3.95 ind m^{-2} (mean=2.1 ±1.1 ind m^{-2}). Total length of the bream caught with gill nets (Fig. 2a) ranged from 5.2 to 31.5 cm (mean 11.0 ±4.0 cm) and total body mass was on average 20.2 g (±32.8 g). Average size increased significantly with water depth (ANOVA F= 4.215, d.f.= 2, p=0.033), and the largest fish was thus captured in the deepest lake stratum (Fig. 2b).

In the littoral zone, bream was very scarce with an average NPUE of 0.17 ±1.41 ind dip^{-1}. Mean body length of the bream caught by electrofishing was 8.9 cm (±0.7 cm).

A total of six age classes was identified, i.e. 0 to 5 years. Calculated asymptotic length L_{∞} was 33.5 cm (±0.93 cm $C.I._{95\%}$), and the growth curve parameter *k* was 0.037 (±0.003 $C.I_{95\%}$). Length-at-age is shown in Fig. 2c.

The body mass-length relationship for both sexes pooled and log-log transformed was described by the following equation:

$Log(W_T) = 2.984Log(L_T) - 1.984$ (n = 1287, R^2 = 0.982, p <0.001).

The calculated mean length at maturity L_m was 19.6 cm (C.I.$_{95\%}$. = 18.1 - 21.2 cm), higher than the L_m (14.30 ±0.92 cm, C.I.$_{95\%}$) calculated using the logistic regression fitted to our data (Fig. 1d). As different proportions of male and females occurred in the two samples differences in length are also likely to occur, but both samples strongly indicate early maturity. Estimates of natural mortality M and total mortality Z were similar (0.61 y^{-1} and 0.64 y^{-1}, respectively), suggesting a negligible fishing pressure.

3.1 Bream diet

The contents of digestive tracts consisted entirely of microcrustaceans and rotifers (Fig. 3). The diet of the bream was strongly specialized, chydorids being the most frequent and abundant food item occurring in all the digestive tracts and accounting for an average of *ca.* 62% in terms of numbers. *Bosmina* sp. was also important although not evenly found in the stomachs. Sediment was present in most of the digestive tracts but was not quantitatively measured.

3.2 Chemical, physical and biotic limnological data

From 1991 to 1999 Secchi depth values were relatively uniform (Dunn's method, $p>0.05$) but they decreased significantly during the 2000s (Dunn's method, $p<0.05$), ranging from 2.1 m to 6.1 m (median= 3.9 ±1.1 m) up to 1999 and from 1.2 to 4.0 m (median=2.1 ±0.7 m) in the two periods, respectively (Fig. 4a). Total phosphorus concentrations in the whole water column increased significantly in the 2000s (Holm-Sidak $p<0.05$), ranging between 8 and 29 μg L^{-1} (median= 12 ±13 μg L^{-1}) up to 1999 and 14 to 34 μg L^{-1} (median= 22 ±7 μg L^{-1}) in the following decade (Fig. 4b). The same trend was observed for total nitrogen (Fig. 4c) and ammonium (Fig. 4d). Total nitrogen never exceeded 800 μg L^{-1} in the 1990s (median=563 ±104 μg L^{-1}) being lower than in the 2000s (Dunn's method $p<0.05$) when they remained higher than 800 μg L^{-1} (median=1151 ±265 μg L^{-1}) and reached values as high as 1600 μg L^{-1}. The ratio between total phosphorus and total nitrogen in the whole water column did not change (Kruskal-Wallis, $p=0.108$ and $p=0.163$ respectively), but in the deeper layer (4 to 6 m) it increased significantly (Dunn's methods $p<0.05$) from 33.9 in the 1990s to 45.5 in the 2000s. Ammonium (Fig. 4d) in the water column was always lower than 400 mg L^{-1} (median= 53 ±128 mg L^{-1}) in the 1990s and increased significantly in the 2000s (Dunn's method, $p<0.05$), when values rose up to 1000 mg L^{-1} (median= 297 ±330 mg L^{-1}). However, in the deeper layers (4 to 6 m), ammonium had already increased in the late 1990s (Dunn's method $p<0.05$). Differences in oxygen concentrations in the whole water column were not significant among the three periods (Kruskal-Wallis, p=0.637), but from 2004 to 2007 anoxic conditions at the bottom of the lake persisted for longer periods in summer (Fig. 4e).

Biotic variables also underwent important changes during the study period. In particular, phytoplankton density increased showing a shift towards more Cyanobacteria (dominated by globular jelly species such as *Gomphosphaeria* spp., *Chroococcus* spp., *Aphanotece* spp., *Aphanocapsa* spp, *Microcystis* spp. and filamentous species such as *Anabaena* sp.) increasing particularly in the late 1990s (Dunn's method p<0.05) (Fig. 4f). Among the Cyanobacteria, *Aphanotece* spp. was most abundant. Additionally, chrysophytese and dinophytes increased significantly in the 2000s (Dunn's method, p<0.05), whilst diatoms, criptophytes and chlorophytes, did not exhibit any significant change (Kruskal-Wallis, p>0.05). Chlorophyll *a* concentrations did not change significantly between the two periods (Kruskal-Wallis, p=0.107) (Fig. 4g).

Overall, zooplankton abundance increased markedly, being higher in the 2000s than in the 1990s (Mann-Whitney, U=6.000, p=0.001, d.f.=1) (Fig. 4h). Among cladocerans, the large-bodied *Daphnia* sp. did not show any significant change (Mann Whitney U=27.0, p=0.267, d.f.=1), but the small-bodied herbivores (*Bosmina longirostris* and *Ceriodaphnia*) (Fig. 4i) increased significantly (Mann-Whitney U=4.0, p<0.001, d.f.=1) as did the proportion of small cladocerans (Mann Whitney Mann Whitney, U=16.0, p=0.007, d.f.=1). Cyclopoids dominated among the copepods and increased notably between the 1990s and 2000s (Mann-

Whitney U=12.0, p=0.005, d.f.=1). Calanoids appeared only at the end of 1990s (Fig. 4j).

4. DISCUSSION

Although zooplanktivorous cyprinid fishes such as rudd, bleak and Italian roach dominate the native fish assemblage of most Italian natural shallow lakes (Volta et al. 2011), substantial changes have been recorded in recent decades. These have included an increase in the number of alien zoobenthivorous species such as bream, roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernuus*) (e.g. Gherardi et al. 2007; Volta and Jepsen 2008; Lorenzoni et al. 2009, Ciutti et al. 2011). Lake Montorfano is no exception to this pattern and its fish community now consists of a mixture of native and non-native species. How bream was introduced to the lake is unknown, although accidental introduction as live bait is a probable explanation as has been concluded for the recent arrivals of this and similar species in lakes of isolated regions of Europe (e.g. Winfield et al. 2011). At the time of the appearance of bream in Lake Montorfano in the late 1990s, fishing regulations concerning the use of live bait and its translocation from different catchments were inadequate and did not take into account the seriousness of threats posed by non-native species. The major limnological characteristics of the lake, such as its meso-eutrophic status, a mean depth of *ca.* 4 m and a dense reed belt, are very favourable for bream existence (Mehner et al. 2005; Kottelat and Freyhof 2007).

Consequently, is not surprising that its introduction has resulted in the establishment of a viable population.

Individuals larger than 35 cm were not captured in our sampling campaign even though the mesh sizes of the nets used could potentially catch such individuals (Psuty and Borowski 1997). According to Živkov et al. (1999), the growth of bream in Lake Montorfano can be classified as 'type b' (25.5cm < L_∞ < 59.0cm), indicating a stunted population. Accordingly, the 'Phi' value is notably lower than for other bream populations (Tab. 2), indicating low growth performance of the individuals in Lake Montorfano. Stunted bream populations have previously been reported in the literature and, in shallow and small lakes, are often associated with very high fish densities (Cazemier 1982; Kottelat and Freyhof 2007). The bream population of Lake Montorfano occurred at all depths, apparently tending to avoid very shallow waters (< 1m) although caution must be taken when comparing catches by gill nets set overnight and daytime electrofishing. However, our results are consistent with those of other studies, indicating that bream inhabits mainly offshore habitats, independently of trophic status (Jeppesen et al. 2006).

The present diet analyses showed specialization of bream on chydorids, which are typically bottom dwelling microcrustaceans, and on small cladocerans, but less on large cladocerans. Also, sediments were found in the digestive tracts, indicating a tendency to feed close to the bottom. An increase in the proportion of small cladocerans among the zooplankton, however, indicates higher predation pressure in the pelagic (Brooks and Dodson 1965; Gliwicz 2003), perhaps as other fish are forced to stay more in the pelagic zone. However, large daphnids were still abundant suggesting that any enhancement of top-down control by fish was relatively weak, as also observed in the shallow eutrophic Lake Balaton (Tatrai et al. 1990). Other studies (e.g. Jeppesen et al. 1997a; Jeppesen et al. 1997b), however, indicate strong top-down control by zoobenthivorous fish in shallow lakes, except for those rich in aquatic vegetation.

Whilst a top-down effect by bream on the food web of Lake Montorfano was apparently relatively weak, a clear bottom-up effect was evident. Despite the fact that the external nutrient loading levels are now low (Buzzi pers. com.), significant increase in nutrient concentrations (both P and N) has occurred in recent years. In addition, enhanced ammonium concentrations were first recorded in the deeper water strata, subsequently followed by an increase through the whole water column. Zoobenthivorous fish constitute an important link between the pelagic and the benthic parts of lake ecosystems, in part because their feeding close to the bottom disturbs sediments and so releases nutrients into the water column (Andersson et al. 1988; Breukelaar et al. 1994). Nutrient release via fish excretion constitutes a further indirect pathway from the benthic to the pelagic zones that can be exacerbated in cases of high fish densities (Vanni et al. 2002; Verant et al. 2007). As nutrient concentrations increased in Lake Montorfano, phytoplankton abundance also increased. In addition, the algae community shifted to Cyanobacteria, dominated by *Aphanotece* spp. and *Anabaena* spp., which are able to fix nitrogen under anoxic conditions. Increase in contribution of cyanobacteria may further have reduced zooplankton grazing on phytoplankton (Gliwicz 2005).

Macrophyte coverage in Lake Montorfano showed a major decrease following the establishment of the bream population. Two surveys carried out in the 1980s (Provincia di Como 1985) and late 1990s (Garibaldi, data unpublished) described an aquatic vegetation characterized by six submerged species (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Najas marina*, *Potamogeton pusillus*, *P. lucens*, *P. perfoliatus*) and two floating-leaved species (*Trapa natans*, *Nynphaea alba*). In contrast, the early 2000s were characterized by an almost complete loss of submerged macrophytes, the aquatic vegetation (from shoreline to the middle of the lake) being composed of *Phragmites australis* and *Typha latifolia, T. natans, N. alba* and rare stands of *Ceratophyllum demersum* (Bianchi et al. 2000; Volta pers. obs.). This development is not surprising as vegetation is quickly lost when a critical turbidity is exceeded (Scheffer et al. 1993).

The changes in the limnological features of Lake Montorfano were moreover accompanied by significant changes in the fish fauna's composition. The fish community had remained stable until the beginning of the 1990s, being dominated by open water zooplanktivorous fish such as rudd, bleak and Italian roach (de Bernardi 1985). A survey undertaken in the early 1990s (Negri 1995) reported the following abundance percentages (based on numbers) for catches in multimesh gillnets: rudd (68%), perch (13%), largemouth bass (11%), tench (3%) and pumpkinseed (3%), other species including small cyprinids (2%). In this early 1990s survey, however, the mesh sizes of the nets were too large to capture small fish (smallest mesh size 18 mm) and a negative bias towards small pelagic cyprinids should therefore be taken into account. Our results indicate a substantial shift in the fish community from dominance of open water zooplanktivorous species to dominance of zoobenthivorous such as bream and pumpkinseed. What triggered the sharp declines in small native cyprinids in Lake Montorfano is unknown, but the deterioration of the ecological status of the lake might have played a major role. Grimaldi (1971) reports severe mortality events in bleak populations of north Italian lakes resulting from eutrophication, and Giussani et al. (1976) suggested that high levels of ammonium predispose the gill apparatus of small cyprinids to fungal and bacteria diseases. Hence, the high level of ammonium occurring in recent years together with longer periods of low oxygen concentrations may have adversely affected the populations of small cyprinids in the lake. As Hayden et al. (2010) reported that bream has a high potential for hybridization with roach (*Rutilus rutilus*) (F bream x M roach), it could be argued that small cyprinids declined due to hybridization with bream.

At present, there is an apparently negligible predation pressure on bream in Lake Montorfano. Non-native largemouth bass and pike are the only significant piscivorous predators in the lake because perch are on average very small (Table 1). In the present study, only adult specimens of largemouth bass were observed and the catch of only a few small specimens indicates weak reproductive success and recruitment. Compared with the survey of Negri (1995) in the early 1990s, the abundance of largemouth bass has declined markedly. This in agreement with studies showing that in shallow lakes or ponds high densities of zoobenthivorous fish (Wolfe et al. 2009) or bluegills (*Lepomis macrochirus*) (Guy and Willis 1990; Brenden and Murphy 2004) can adversely affect largemouth bass populations by predation on eggs or by food competition at juvenile stages. Moreover, pike density in Lake Montorfano is low compared to other small, shallow lakes (Snow 1978; Margenau et al. 1998; Margenau et al. 2008). As bream population control through predation or fishing is weak, the number of bream in the lake is unlikely to decrease significantly in the near future. Biomanipulation by the removal of large amounts of bream from offshore waters (e.g. Søndergaard et al. 2007) can be used as a management tool to improve water quality and promote piscivorous predator recovery (de Roos and Persson 2002; de Roos et al. 2003; Persson et al. 2007). Substantial stocking of young of the year pike from the local stock might be considered in order to enhance predation on small bream (Berg et al. 1997) and promote a return to the clear state with extensive macrophytes (Søndergaard et al. 1997), but in most cases the effects of such manipulations in northern Europe has been poor (Skov et al. 2003, 2007).

In conclusion, Lake Montorfano has recently shifted towards a more turbid state with higher nutrient concentrations despite the fact that the external nutrient loading levels are now stable and low. This environmental deterioration followed the introduction and successful establishment of non-native bream in the late 1990s. Furthermore, this cyprinid has recently become the dominant fish species in the lake. The present study results suggest that bream may have contributed to the observed changes in the ecological status of the ecosystem via bottom-up mechanisms, while top-down effects were less apparent. The size structure of the bream population, characterized by dominance of relatively small specimens, has probably exacerbated the release of nutrients into the water column. Site-specific adaptive management, as suggested by Mehner et al. (2004), including control of the fish community composition and abundance, supplemented perhaps by stocking of piscivorous fish could be used to improve the ecological status of the lake.

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Table 1

Species composition, total number of specimens, NPUE and BPUE, mean total length and age range determined for the fish captured by multi-mesh survey gill nets and by electrofishing in Lake Montorfano. Data from the 2-day sampling event are pooled.

Species name	Common name	N° ind. gillnets	N° ind. electrofishing	NPUE (±SD) (ind m^{-2})	BPUE (±SD) (g m^{-2})	Mean length gillnets (±SD) (cm)	NPUE electrofishing (ind dip^{-1})	Mean length electrofishing (±SD) (cm)	Age range (years)
Abramis brama	Common bream	1481	17	87.1 ±53.2	1747.9 ±996.0	11.0 ±4.0	0.2 ±1.5	8.9 ±0.7	0-5
Carassius carassius	Crucian carp	0	3	-	-	-	0.04 ±0.02	33.4 ±2.2	2
Esox lucius	Pike	2	29	0.1 ±0.3	139.1 ±486.4	52.2 ±18.1	0.3 ±0.6	37.6 ±16.0	1-7
Lepomis gibbosus	Pumpkinseed	458	1270	26.9 ±22.6	61.9 ±43.2	5.0 ±0.7	14.9 ±29.1	4.5 ±1.0	0-5
Micropterus salmoides	Largemouth bass	6	11	0.4 ±0.7	83.2 ±172.5	25.2 ±4.7	0.1 ±0.4	26.2 ±4.5	2-4
Perca fluviatilis	Perch	284	0	16.7 ±15.1	275.5 ±249.6	10.8 ±2.5	-	-	0 -5, 8
Rutilus aula	Italian roach "Triotto"	2	0	0.1 ±0.2	0.5 ±2.2	11.5 ±1.5	-	-	2

Scardinius erythrophthalmus	Rudd	126	166	7.4 ±10.9	206.7 ±313.2	12.0 ±3.6	1.9 ±6.5	9.4 ±2.2	2, 5-6
Tinca tinca	Tench	3	7	0.2 ±0.4	0.5 ±1.2	6.0 ±0.9	0.1 ±0.3	12.2 ±7.1	0, 2-3

Table 2

Comparison of life history parameters between the bream population in Lake Montorfano and other European waters. *If missing, L_m has been calculated from L_∞ using the empirical equation from Froese and Binholan (2000). ** **Z** has been calculated as the average between **Z** for males and females specimens, nd= no data available. [§]maximum length registered. For the Danish lakes the value is a median) of the maximum lengths of the bream captured in the different lakes.

Location	*t* (years) oldest age-class determined	L_∞ (cm)	Curvature parameter (*k*)	Overall growth performance (*Φ'*)	Mean length at first maturity L_m (cm)	Natural mortality M (y^{-1})	Total mortality Z (y^{-1})	Source
Szczecin lagoon (Poland)	16	54.14	0.136	2.60	30.1*	0.25	nd	Kompowski (1988)
Lake Dąbie (Poland)	16	44.62	0.175	2.54	25.3*	0.15*	nd	Kompowski (1988)
Lake Braassem (Netherlands)	>12	43.6	0.18	2.53	24.8*	nd	0.42**	Slooff and De Zwart (1982)
Lake Ijssel (Netherlands)	>12	64.6	0.09	2.57	35.3*	nd	0.58**	Slooff and De Zwart (1982)
Rive Rhine (Netherlands)	>12	44.0	0.18	2.54	25.0*	nd	1.15**	Slooff and De Zwart (1982)
Lake Balaton (Hungary)	10	50.1	0.083	2.32	28.1*	nd	nd	Specziar *et al*. (1997)
River Danube (Croatia)	16	57.7	0.087	2.46	31.9*	nd	nd	Treer *et al*. (2003)
Ovcharitsa reservoir (Bulgaria)	10	62.3	0.098	2.58	34.1*	nd	nd	Živkov *et al*. (1999)

Lake Montorfano	**6**	**33.5**	**0.037**	**1.62**	**19.5**	**0.61**	**0.64**	**(this study)**

FIGURE CAPTIONS

Fig. 1

NPUE (a) and BPUE (b) of the nets for the different fish species in the three sampling strata in Lake Montorfano. Data from the 2-day sampling event were pooled. Error bars are standard deviation.

Fig. 2

Characteristics of the Lake Montorfano bream population: (a) length frequency distribution (% by numbers) of the bream caught during the whole sampling period, (b) box plot (median, 5, 25, 75 and 95 percentiles) showing the length of the bream in the three lake depth strata, (c) the length (cm) of bream at different ages (months), and (d) the proportion of mature fish at different lengths (95% confidence bands are indicated).

Fig. 3

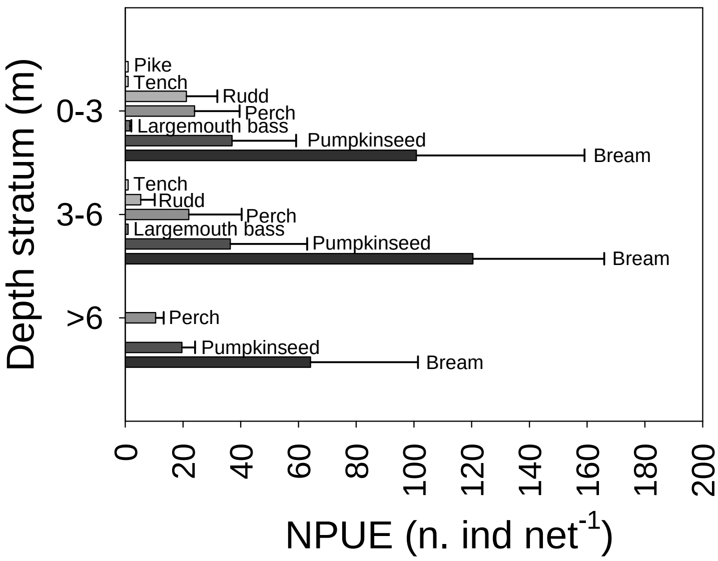
Diet of the Lake Montorfano bream population. Data are presented according to method of Costello (1990).

Fig. 4

Temporal variations in chemical, physical and biological limnological data of Lake Montorfano: (a) transparency (Secchi depth), (b) total phosphorus, (c) total nitrogen, (d) ammonium, (e) dissolved oxygen at 6m depth and (f) chlorophyll a, (g) phytoplankton (Cyanobacteria and all the others taxa); (h) zooplankton (cladocerans and copepods), (i) copepods (calanoids and cyclopoids) and (j) herbivorous cladocerans.

FIGURE 1

(a)


Pike
Tench
Rudd
Perch
Largemouth bass
Pumpkinseed
Bream
Depth stratum (m)
0-3
3-6
>6
0
20
40
60
80
100
120
140
160
180
200
NPUE (n. ind net-1)

(b)

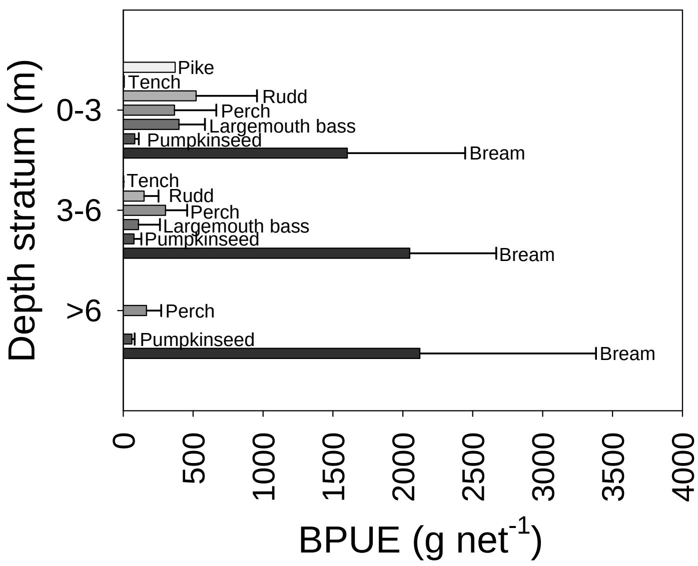

Pike
Tench
Rudd
Perch
Largemouth bass
Pumpkinseed
Bream
Depth stratum (m)
0-3
3-6
>6
0
500
1000
1500
2000
2500
3000
3500
4000
BPUE (g net-1)

FIGURE 2

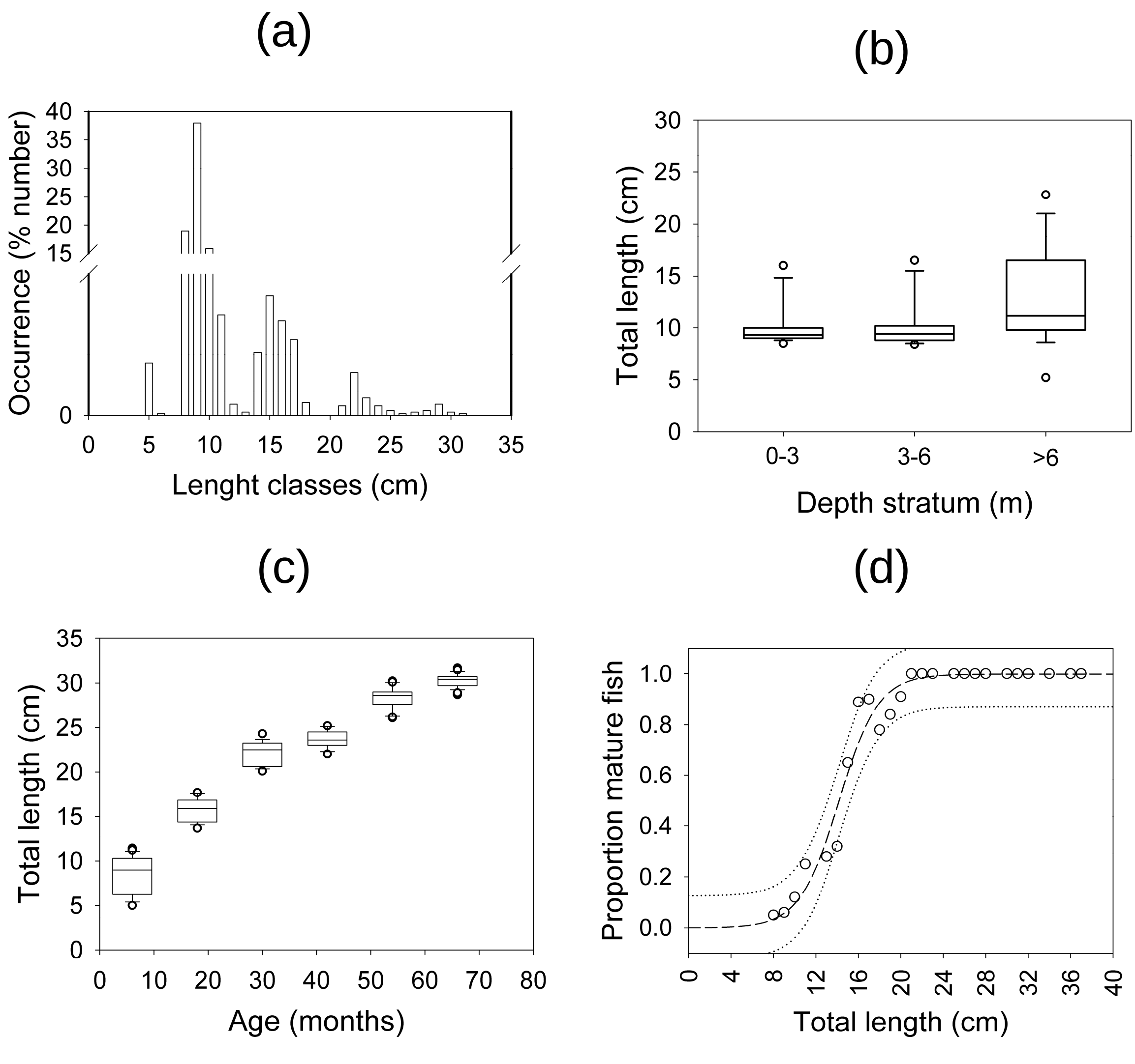

(a)
Occurrence (% number)
40
35
30
25
20
15
0
0
5
10
15
20
25
30
35
Lenght classes (cm)
(b)
Total length (cm)
30
25
20
15
10
5
0
0-3
3-6
>6
Depth stratum (m)
(c)
Total length (cm)
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
Age (months)
(d)
Proportion mature fish
1.0
0.8
0.6
0.4
0.2
0.0
0
4
8
12
16
20
24
28
32
36
40
Total length (cm)

FIGURE 3

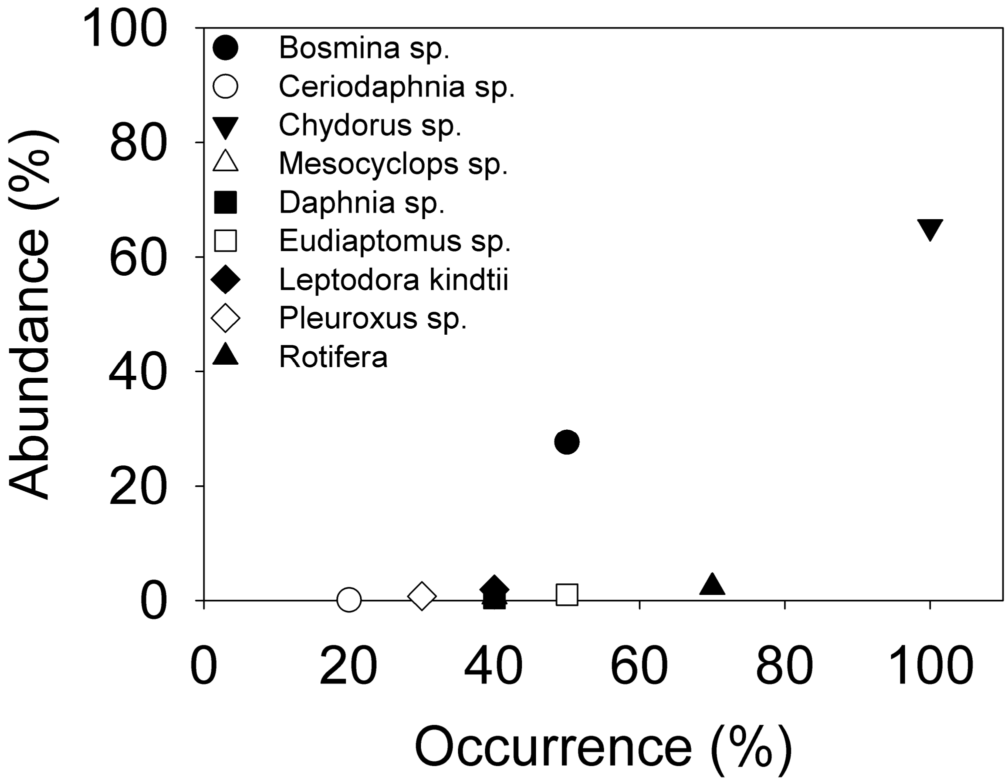
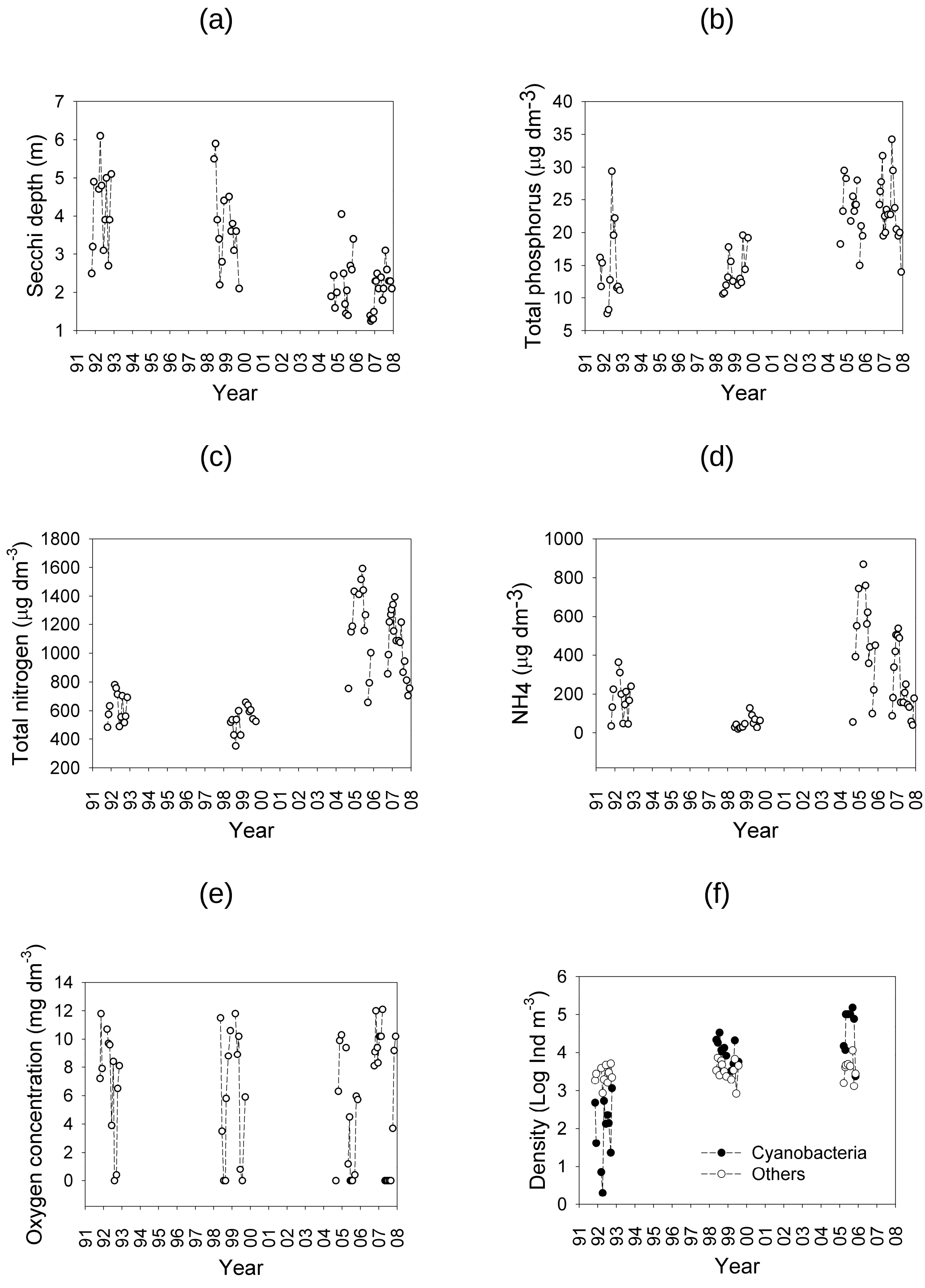
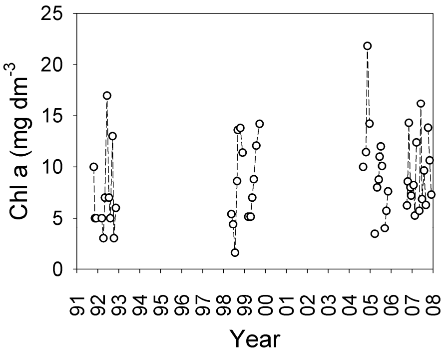

Abundance (%)
Occurrence (%)
0
20
40
60
80
100
0
20
40
60
80
100
Bosmina sp.
Ceriodaphnia sp.
Chydorus sp.
Mesocyclops sp.
Daphnia sp.
Eudiaptomus sp.
Leptodora kindtii
Pleuroxus sp.
Rotifera

FIGURE 4

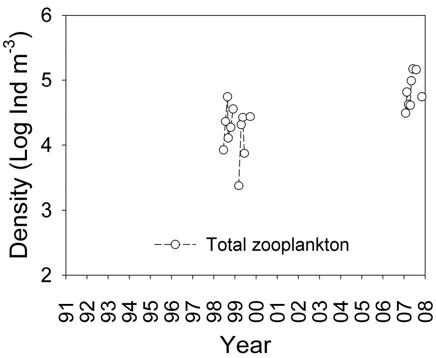


(a)
(b)
Secchi depth (m)
Total phosphorus (μg dm^{-3})
(c)
(d)
Total nitrogen (μg dm^{-3})
NH4 (μg dm^{-3})
(e)
(f)
Oxygen concentration (mg dm^{-3})
Density (Log Ind m^{-3})
Cyanobacteria
Others
Year

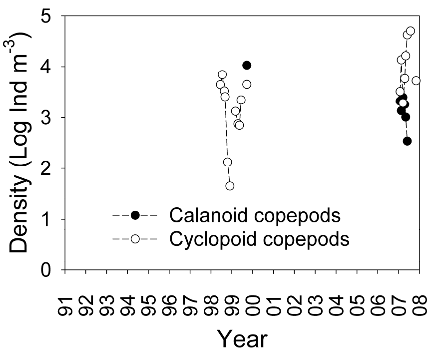
(g)


Chl a (mg dm^{-3})
Year
0
5
10
15
20
25
91 92 93 94 95 96 97 98 99 00 01 02 03 04 05 06 07 08

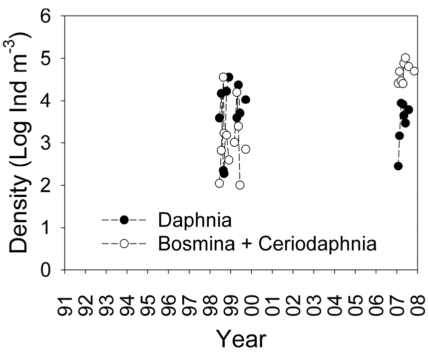
(h)


Density (Log Ind m^{-3})
Year
Total zooplankton
2
3
4
5
6
91 92 93 94 95 96 97 98 99 00 01 02 03 04 05 06 07 08

(i)


Density (Log Ind m^{-3})
Year
Calanoid copepods
Cyclopoid copepods
0
1
2
3
4
5
91 92 93 94 95 96 97 98 99 00 01 02 03 04 05 06 07 08

(j)


Density (Log Ind m^{-3})
Year
Daphnia
Bosmina + Ceriodaphnia
0
1
2
3
4
5
6
91 92 93 94 95 96 97 98 99 00 01 02 03 04 05 06 07 08