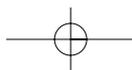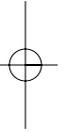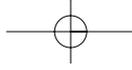# Section II
Bird, fish, habitat interactions

Chapter 10
Interaction between fish and colonial wading birds within reed beds of Lake Neusiedl, Austria

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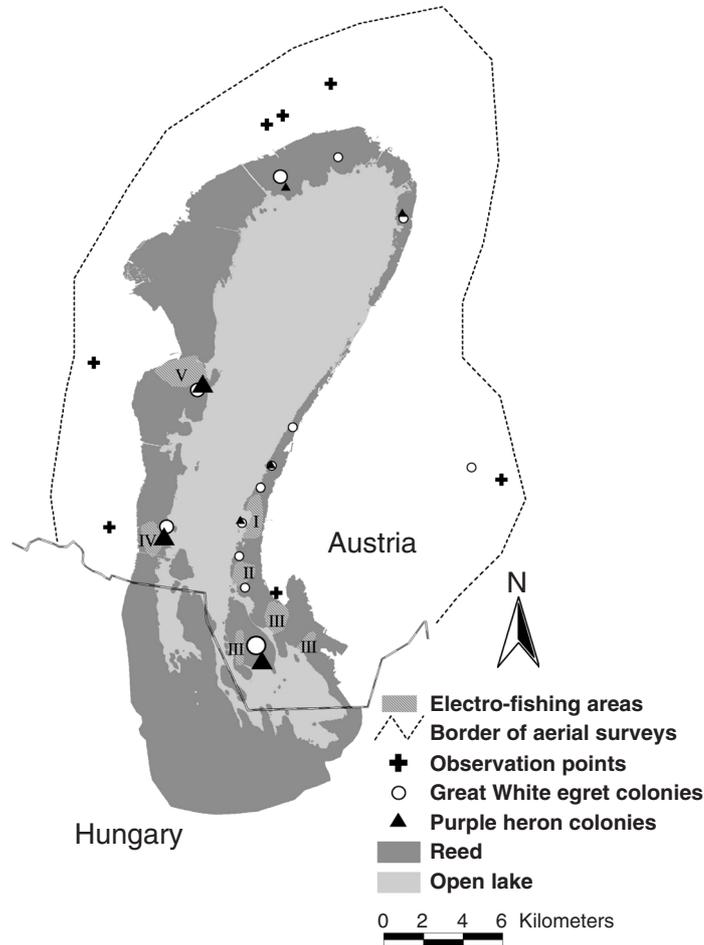*Biologische Station Illmitz, Illmitz, Austria*

Abstract

Data from two projects carried out within the extensive (180 km^2) reed belt of Lake Neusiedl, Austria – one about the fish community and the other about the colonial breeding piscivorous birds, great white egret, *Casmerodius albus* L., purple heron, *Ardea purpurea* L., grey heron, *Ardea cinerea* L., and spoonbill, *Platalea leucorodia* L. – were used to assess the impact of fish-eating birds on the fish population. Piscivorous birds ate about 12% of total fish standing stock within the reed belt. Their food intake was estimated to account for 21% of fish production within a size range of 3–25 cm total length (potential prey size). Competition between fish-eating birds and commercial fisheries was considered to be negligible.

Keywords: fish biomass, heron, piscivorous bird, predation rate, predator-prey.

10.1   Introduction

The extensive reed beds (180 km^2) of Lake Neusiedl on the eastern border of Austria is an internationally important site for bird species (Grimmet & Jones 1989). Of the fish-eating species, the largest population of great white egret, *Casmerodius albus* L., in western and central Europe, and internationally important populations of purple heron, *Ardea purpurea* L., and spoonbill, *Platalea leucorodia* L., are found there. Nearly all the heronries are located in the reed beds which form a belt up to 6.5 km wide around the open lake (Fig. 10.1).

While the importance of reed beds as secure nesting habitat is evident, less is known about the importance of these areas as foraging habitat (Grüll & Ranner 1998).

Figure 10.1   Study area Lake Neusiedl on the border of Austria to Hungary. Roman numerals signify electric fishing areas (see text)

Information about the function of reed areas for the fish community of Lake Neusiedl is scarce. Most have concentrated on the fish fauna of the open lake (e.g. Hacker 1979), while the fisheries of the large reed belt were not examined until the mid-1990s (Wolfram-Wais *et al.* 1999; Wolfram *et al.* 2002).

Data from two projects carried out within the extensive (180 km^2) reed belt of Lake Neusiedl, Austria – one about the fish community and the other about the colonial-breeding piscivorous birds – were used to assess the impact of fish-eating birds on the fish population. The main objectives were to determine the interactions between fish and birds using data on fish availability within the reed beds and the utilisation of these areas by piscivorous birds as foraging habitat, and to discuss the possible implications for commercial fisheries.

10.2   Material and methods

10.2.1   *Study site*

Lake Neusiedl is a shallow alkaline lake (7.5–14.6 mval litre^{-1}, conductivity C_{25} = 1300–3200 µS) with an area of 320 km^2 and an average water depth of 1.1 m. More than half of the lake (180 km^2) is covered by reed beds which form a belt around the lake shore, with one big reed island (6.5 km^2) in the south (Fig. 10.1). The reed area consists of a mosaic of pure stands of *Phragmites australis* (Cavanilles) Trinius *ex* Steudel, channels and open water areas. Water depth in the reed beds depends on the water level of the lake and ranges from 0 to 1.7 m. While the water of the open lake is characterised by a high inorganic turbidity, water within the reed beds is clear and has a reddish-brown colour owing to a high amount of humic substances. In summer, oxygen deficiencies (<1 mg litre^{-1}) frequently occur within the dense *Phragmites* stands. In spring 1994 the southern part of Lake Neusiedl (about 80 km^2) was declared a national park by the Austrian and Hungarian governments.

10.2.2   *Fish data*

The majority of fish were sampled by electric fishing. Gill net fishing was carried out occasionally but produced unsatisfactory results due to the density of the *Phragmites* stands and the shallowness of the water (often <50 cm). Electric fishing (direct current, 8 kW, 200–300 V, one hand-held electrode) was conducted from August 1994 to November 1997 on 27 occasions lasting between 1 and 3 days (in total 68 days). Fishing concentrated on five areas of the reed belt: (i) Illmitz – Biological Station; (ii) Illmitz – south of the public baths; (iii) the southern part of the lake (National Park); (iv) near Mörbischand; and (v) near Oggau (Fig. 10.1). Sampling was undertaken along transects from the reed fringe landward. Thus the sampling site consisted of: the littoral zone of the open lake – *Phragmites* fringe; channels (old structures used by local fishermen and people harvesting the reed); pools within the *Phragmites*; and dense vegetation stands.

At all sampling sites within a transect, a single fishing along a defined stretch of 30 m (=standard catch) was conducted. The total number of standard catches was 599. Fishing was done by boat or at selected shallow water (<50 cm deep) sites by foot. Catchability varied according to turbidity, water depth, structure and density of the reed stands but was estimated to be about 50% in terms of biomass (based on observations of fish occasionally escaping during the fishing). CPUE is always given as the original values; values for standing stock (kg ha^{-1}), however, were calculated with respect to catchability. The fish caught were identified, measured (mm TL) and returned to the water. Biomass was calculated by applying species-specific length–weight regressions defined for Lake Neusiedl during earlier studies (Herzig *et al*. 1994). On several sampling occasions, additional weights were taken for false harlequin, *Pseudorasbora parva* Temminck & Schlegel, and pumpkinseed, *Lepomis gibbosus* (L.), as well as for those fish sampled for subsequent gut analyses (see Wolfram-Wais *et al*. 1999). To calculate

eel biomass, four length groups (<15 cm, 15–30 cm, 30–55 cm and >55 cm) were distinguished with respect to the length–frequency distribution derived during former studies from Lake Neusiedl (Herzig *et al*. 1994). The total biomass for all individuals in each length group was calculated from length–weight regression for eel from the lake.

As all fish data were based on linear transects, they were converted to density (kg ha^{-1}) for three sample areas (Figs 10.1) in the east and south of Lake Neusiedl using digitalised aerial near-infrared photographs (1 pixel is approximately 2 m^2). As the results of the calculations were similar for all three sample areas, only data for the sample area near Illmitz (34.9 ha) are presented in detail. Standing stock was estimated in three steps:

(1) The reed area selected was divided into several zones with different reed cover: (a) very dense reed beds with almost no open water areas; (b) very shallow (<50 cm deep), landward areas which dry up in summer; (c) open water pools >0.5 ha; and (d) remaining area characterised by a mosaic of reed stands and pools <0.5 ha.

(2) Mean fish density was determined for each zone. The few, small open water areas of zone (a) were not sampled. It can be assumed, however, that due to the very dense (and often dry) reed stands they are not penetrated from larger pools even by smaller fish. Moreover, low oxygen concentrations (<1 mg litre^{-1}) for long periods makes these small water bodies hostile for fish colonisation (Wolfram *et al*. 2002). Sampling in zone (b) was carried out occasionally at the beginning of the project, but revealed no, or only a few, scattered juvenile fish that inhabited these very shallow areas. Hence, in both zones fish standing stock was assumed to be negligible and considered zero for further calculations. Bigger water areas (zone (c)) were divided further into open water and littoral zone along the reed fringe. The CPUE along the reed fringe (kg per 30 m standard catch) was converted to kg ha^{-1} by assuming a sampling width by electric fishing of 2 m, giving a sampling area of 60 m^2. The fish density estimates calculated in this way were considered reed bed fringe fish densities (RFD). Occasional gill net fishing in the open water areas within the reed belt revealed that most fish concentrate in the fringe area and fish density in the open water areas was 10–20% of the RFD. Zone (d) within the reed belt is a dense mosaic of pools and reed stands (the majority ranging in size from a few to some dozens of square metres). CPUE based on 30 m standard catches from sites within this zone were again converted to RFD values. Taking into account the larger pools of zone (d), the RFD does not correspond, but overestimates the true fish density within this zone. Based on calculations of the proportion of pools and reed stands within zone (d) (using digitalised aerial near-infrared photographs), about 50% of the RFD was estimated to resemble the true fish density within zone (d).

(3) By calculating the proportions of the different zones in the sample area and multiplying these figures by mean fish densities for each zone, the total fish standing stock was determined.

The calculation of fish standing stock within the reed belt must be considered approximate and does not consider seasonal variations or possible differences of fish densities between different years (1994–1997).

10.2.3 *Habitat utilisation by birds and estimation of food intake*

All bird data were collected during the 1998–2000 breeding seasons. Vantage point observations of birds departing from the colonies and aerial counts of foraging birds were used to estimate reed habitat usage. The undulating topography and artificial elevated points allowed observation of birds which departed from their colonies *en route* to their foraging grounds. In good weather conditions birds could be followed by telescope up to a distance of 12 km. Six colonies of great white egrets (87% of the breeding population), two purple heron colonies (49%), one grey heron colony (70%) and one spoonbill colony (100%) were observed. Single colonies were surveyed between late April 2000 and the beginning of July 2000. Observations concentrated on periods of main bird activity and lasted from 30 min to about 4 h per day. In 45 surveys, 1160 departing wading birds were counted (720 great white egrets, 200 purple herons, 86 grey herons and 154 spoonbills). The landing position of the birds was recorded in 72% of all departures. Birds that flew out of view were allocated to feeding grounds within or outside the reed belt according to habitat utilisation data derived from aerial counts.

A combination of vantage point observations (which also comprised the Hungarian feeding habitat) and aerial counts for the great white egrets (which delivered more accurate data for the habitat utilisation on the Austrian side) were used to estimate the proportion of foraging great white egrets within the reed habitat. Aerial counts were made using a Piper PA-18 aircraft over the Austrian part of the study area, which covers about 640 km^2 (Fig. 10.1). During the breeding seasons of 1998–2000, 51 flights were carried out. Each foraging bird (a total of 12 749 observations) was recorded on a map with a precision of about 100–200 m.

On the ground, food intake of foraging great white egrets at selected sites was recorded. One observation lasted up to 20 minutes. Prey sizes were estimated classes in multiples of one-quarter of the average bill size (see Bayer 1985). In 1999, video surveillance of 12 nests allowed partial estimation of prey types.

Species-specific food consumption rates were derived from the literature (Marion 2000). Daily food requirements were considered independently for young and adult birds. For grey herons the estimates derived by Feunteun & Marion (1994) were used. In the other cases the daily requirements of the adults were estimated according to the body mass/food consumption relationship derived by Kushlan (1976). For the food intake of young great white egrets, data from Mock (personal communication) was used.

All spatial data on habitat utilisation were processed with Arcview 3.2. Statistical calculations were conducted with SPSS and Statistica.

10.3 Results

10.3.1 *Species composition and dominance structure of the fish community*

From August 1994 to October 1997 more than 32 000 fish from 18 species, with a total weight of about 886 kg, were caught by electric fishing within the reed belt and along

Table 10.1 Species list, occurrence and relative proportion of different fish species during the whole study period at all sampling stations

Species	Occurrence (%)	Relative proportion (% number)	Relative proportion (% biomass)	
			All length classes	3–25 cm excluding eel
Esox lucius L.	23.3	0.7	9.5	2.1
Anguilla anguilla (L.)	68.6	7.9	35.1	–
Abramis brama (L.)	16.0	1.0	1.3	1.9
Blicca bjoerkna (L.)	57.9	25.4	6.0	32.1
Alburnus alburnus (L.)	27.4	5.0	0.1	0.5
Carassius auratus gibelio (Bloch)	47.0	2.8	23.4	16.3
Carassius carassius (L.)	7.6	0.3	0.2	0.8
Cyprinus carpio L.	17.2	0.7	14.2	1.0
Pelecus cultratus (L.)	0.2	<0.1	<0.1	<0.1
Pseudorasbora parva T. & Schl.	36.3	8.4	0.4	2.0
Rutilus rutilus (L.)	54.0	20.3	4.2	18.1
Scardinius erythrophthalmus (L.)	64.0	14.1	1.9	9.9
Tinca tinca (L.)	9.9	0.3	0.3	1.3
Silurus glanis L.	1.6	<0.1	<0.1	<0.1
Gymnocephalus cernuus (L.)	17.8	0.9	0.1	0.7
Perca fluviatilis L.	29.0	2.7	0.9	5.3
Stizostedion lucioperca L.	7.5	0.3	1.0	0.3
Lepomis gibbosus (L.)	45.5	9.0	1.5	7.5

the outer edge of the *Phragmites* stands towards the open water zone (Table 10.1). Sixty-six per cent of all fish caught were young-of-the-year (YOY).

The fish species most commonly caught were eel, *Anguilla anguilla* (L.), rudd *Scardinius erythrophthalamus* (L.), silver bream, *Blicca bjoerkna* (L.) and roach, *Rultilus rutilus* (L.). They were present in more than 50% of all samples (Table 10.1). Crucian carp, *Carassius carassius* (L.), pumpkinseed, false harlequin, perch, *Perca fluviatilis* L., bleak, *Alburnus alburnus* (L.) and pike, *Esox lucius* L., were captured less often, but still with occurrence values above 20%. In terms of abundance (including 0+), silver bream, roach and rudd dominated (relative proportion >10%). Pumpkinseed, eel and false harlequin accounted for 5 to 10% of total individuals caught. Eel, crucian carp, common carp and pike prevailed in terms of biomass, whereas smaller but abundant fishes such as silver bream and roach accounted only for 6.0 and 4.2% of total biomass, respectively. Considering only the length classes that are taken by piscivorous waterbirds (3–25 cm, excluding eel), silver bream, roach and crucian carp dominated in terms of biomass; all three species accounted for 67% of biomass in the 3–25 cm length class (Table 10.1).

10.3.2 *Total fish standing stock*

On average (median) about 30 individuals were caught within one 30 m standard catch. The maximum number was 760 individuals. Median CPUE for fish of age classes >0+ was 10 individuals per 30 m, the maximum was 221 individuals per 30 m.

Table 10.2 Standing stock, production and consumption of fish inhabiting the reed belt of Lake Neusiedl

Standing stock (t)	576
Standing stock (kg ha^{-1})	32
Standing stock size class 3–25 cm (tons)	326
Estimated *P/B* ratio size class 3–25 cm	1.0
Fish production size class 3–25 cm (t yr^{-1})	326
Fate of production size class 3–25 cm):	
consumption by pike and zander (t yr^{-1})	251 (77%)
consumption by birds (t yr^{-1})	68 (21 %)
other mortality including fisheries (t yr^{-1})	7 (2%)

Around Illmitz (Fig. 10.1), CPUE at 9 sites in the larger open water bodies (zone (c)) varied between 0.50 (0.32–0.78) and 1.42 (1.14–1.77) kg per 30 m (geometric mean ± log transformed CL; $n = 6$–23). These figures correspond to RFD (reed fringe fish density) values of 167 (107–261) and 473 (380–589) kg ha^{-1}, respectively. Within moderately dense reed stands (zone (d)), no or negligible fish were caught in about 30% of all samples, mainly as a result of a highly aggregated fish distribution. Mean CPUE of all catches within zone (d) was 0.14 (0.08–0.25) kg per 30 m or 47 (26–85) kg ha^{-1} (RFD), mean CPUE excluding catches with no or negligible fish density was 0.53 (0.39–0.72) kg per 30 m or 177 (130–239) kg ha^{-1} (RFD).

Total standing stock within the sample area was 1.68 t, corresponding to 48 kg ha^{-1}. As the proportion of open water in the sample area near Illmitz was greater than the average of the whole reed belt, fish densities near Illmitz were probably greater than in the remaining study area. Thus the estimate was related to reed structure and was reduced by a factor 0.67, resulting in mean standing stock of 32 kg ha^{-1}. The factor was derived from the amount of open water in the whole reed beds estimated by remote sensing combining satellite data and aerial near-infrared photography (Nemeth *et al.* 2001; unpublished data).

The fish density along the edge of the reed belt towards the open lake is not included in the estimate of 32 kg ha^{-1} and was calculated separately. Mean CPUE along the reed fringe was 1.40 (0.94–2.08) kg per 30 m, which corresponds to a total fish biomass of about 16 t for the whole zone, which has a shore length of 340 km. Summarising, the total standing stock of fish within the reed belt including the edge towards the open lake was about 592 t (Table 10.2).

10.3.3 *Standing stock and production of 3–25 cm size class*

The majority of fish consumed by the great white egrets had a total length of 3–25 cm. Prey size of the other wading birds also probably lies within this range (excluding eel, see Feunteun & Marion 1994). This size class contributed about 55% of the total fish biomass. The fish stock potentially available as food for piscivorous birds was about thus 326 t within the reed belt (exclusive of the edge towards the open water zone). Assuming a production/biomass (*P/B*) ratio of 1 for the size class 3–25 cm, total fish production accounts for 326 t yr^{-1} (Table 10.2).

10.3.4   *Consumption by piscivorous fish*

Among the fish species that inhabit the reed belt only, pike is a major predator of other fish. Standing stock of pike was estimated from its contribution to the relative biomass within the reed belt (Table 10.1) at 56.2 t (3 kg ha^{-1}). Total consumption of pike is about 228 t yr^{-1}, based on estimated daily consumption rates ranging from 0.05% body weight (BW) during winter to 3.5% BW at high temperatures in summer (Diana 1991). Pikeperch, *Stizostedion lucioperca* (L.), inhabits mainly the open water zone and the edge of the reed bed towards the open lake (unpublished data) and is of minor importance as a predator of reed-dwelling fish. Consumption by zander was estimated to about 10% of the consumption by pike (Table 10.2). The fish eaten by pike and zander lie within the same size range as the prey of egrets and herons (Herzig *et al.* 1994).

10.3.5   *Wading birds within reed beds and the amount of eaten fish*

Reed beds were the most important feeding habitat for all wading bird species (Table 10.3). Fish was the food in 96% of feeding events of great white egrets bring food to their young ($n = 165$). Ninety per cent of the food items of foraging great white egrets within reed beds ($n = 65$) was again fish. Other prey items were frogs (4%) and insects. Most of the unidentified prey items were smaller than 3 cm and therefore contributed

Table 10.3   Foraging wading birds and amount of eaten fish from April to September 2000. Presence of wading bird species at the lake was estimated in months: grey heron 6 months, purple heron and great white egret 5 months and spoonbill 4 months. Calculations of daily food requirements of adults and young according to Feunteun & Marion (1994), Kushlan (1976) and Mock *et al.* (1987). An average breeding success of 1.5 young was assumed. Young birds of all three heron species were expected to stay one month after leaving the nest in the foraging area

Species	Great white egret	Purple heron	Grey heron	Spoonbill	Total
Breeding pairs	753	307	85	77	1222
% foraging within reed beds	80	82	56	61	77
% foraging at reed/lake border	2	8	16	0	23
Total consumption (tons)	50.8	18.4	8.3	5.7	83.2
Total fish intake within reed beds (tons)	40.6	15.1	4.7	3.5	63.8
Total fish intake at reed/lake border (tons)	1.0	1.5	1.3	0	3.9
Fish intake kg ha^{-1} within reed area	2.3	0.9	0.3	0.2	3.8
% of total standing stock reed fish	7.0	2.7	1.0	<1	11.7
% of standing stock reed fish 3–25 cm	12.7	5.1	1.8	1.0	21.3

little to the food intake. There remains, however, uncertainty as to how much non-fish prey is eaten. Based on observations of foraging great white egrets, approximately 10% of prey intake in reed beds was not fish (Table 10.3). Average fish total length was 5.1 cm ($\pm$2.1 standard error, $n = 185$), with a range from 3 to 25 cm. Eel was excluded as a major contribution to the diet of the great white egret since it was observed only once as prey at the nests and never observed in foraging birds. The same probably applies for spoonbill (which feeds in areas with low eel density, unpublished data). No direct information was available for the diet of grey heron and purple heron, although eel may contribute to the diet of these species. However, all herons forage in the same area and it seems reasonable that prey of grey heron and purple heron resembles that of great white egret.

10.4   Discussion

The littoral zone of Lake Neusiedl forms a highly structured and complex mosaic of pools and *Phragmites* stands, which are responsible for the patchy distribution of fish. Large areas are characterised by very shallow open water bodies, which may dry up during the warm summer months and thus are scarcely inhabited by fish. More than half of the reed belt is formed by very dense reed stands that are not colonised by fish. Apart from these spatial constraints, low summer oxygen levels in the densely covered parts of the inner reed belt cause problems to the fish fauna (Wolfram *et al.* 2002). Highest fish biomass was found along the fringe zones between the *Phragmites* stands and open water, both in the bigger pools, within the reed belt, and along the edge of the reed towards the open water zone of Lake Neusiedl.

There are very few shallow lakes within Europe with such an extended reed swamp as found at Lake Neusiedl. Lake Grand Lieu in western France is probably the most similar. In the late 1980s, Feunteun & Marion (1994) found a fish standing stock of 270 kg ha^{-1} in open water areas within the marsh, but 30 kg ha^{-1} in the marsh as a whole, findings which lie within the range for Lake Neusiedl.

The production of fish with a total length between 3 and 25 cm within the reed belt of Lake Neusiedl was 326 t yr^{-1}. This value was derived from an estimated turnover (*P/B*) ratio of 1, but the ratio for fish populations is usually below 1. However, this study concentrated on the part of the population below 25 cm, which has a higher turnover ration (Downing & Plante 1993). Also a significant proportion of total fish production is formed by the YOY (Mathews 1971; Mann 1991). Considering only age groups $\geq$1+, Hacker (1974) and Meisriemler (1974) found turnover ratios of 0.82–0.9 for silver bream and 1.01 for ruffe respectively, in the open water zone of Lake Neusiedl during the 1970s. They considered that the *P/B* ratio might have exceeded these values if 0+ fish had been included in their calculations. Woollhead (1994) estimated *P/B* ratios for Lake Esrom distinguishing between non-piscivores (*P/B* = 1.25) and piscivores (*P/B* = 0.625). Turnover ratio of 0.6 to 1.11 were also found in several lowland cyprinid fish populations in Britain (Chapman 1978). Considering these figures, a *P/B* ratio of 1.0 for reed-dwelling fish between 3 and 25 cm for Lake Neusiedl seems appropriate.

Few studies have assessed quantitatively the impact of heron predation on fish in natural habitats (Marion 2000). Predation rates range from 6% in permanent flooded marshes in France (Feunteun & Marion 1994) to 72% of fish biomass in seasonally flooded ponds in the Everglades (Kushlan 1976). In Lake Neusiedl, piscivorous birds consume 11.7% of the total fish standing stock. This confirms the similarity between Lake Neusiedl and Lake Grand Lieu, not only in terms of fish biomass (see above), but also as regards the trophic impact of fish-eating birds. In both systems they play a minor role compared to piscivorous fish. However, in Lake Neusiedl, herons and spoonbills consume one-quarter of the total production of fish <25 cm (Table 10.2). Thus they potentially have a considerable impact on the fish community.

Moreover, in restricted reed areas a marked depletion of fish stock by birds seems possible. The reed belt often acts as a trap. Falling water levels during the summer force the fish to withdraw into deeper pools without connection to the open lake. In the morning, fish often have to perform water surface respiration because of oxygen deficiencies as a result of decomposition of organic matter and nocturnal respiration of macrophytes. Such situations are exploited by large aggregations of herons, mainly great white egret. As a consequence, great white egrets were able to increase their fish intake in terms of biomass from 8 g in 10 min for birds fishing alone ($n = 75$) to 121 g in 10 min for birds feeding in groups on fish exhibiting aquatic surface respiration ($n = 32$).

The estimates of fish consumption suggest that a small amount of the production of reed bed fish (size class 3–25 cm) is not consumed by herons or pike. These fish probably die due to parasites, diseases or physiological stress as a result of oxygen deficiencies within the reed belt. Fish mortality due to midsummer oxygen depletion would be higher without bird predation, thus similar to seasonal ponds in the Everglades (Kushlan 1976), heron predation at Lake Neusiedl might substitute for mortality from other sources.

The main commercial fish species at Lake Neusiedl are eel (more than 90%), carp, pike and zander. Total catch of eel exceeded 100 t in the1980s (Herzig *et al.* 1994); there are no reliable data on fish yields in recent years. Direct competition between piscivorous birds and fisheries appears to be negligible because birds are confined to smaller size classes of prey. However, the indirect impact of predation on smaller sized fishes which could potentially grow to larger fish should be considered. In terms of biomass, carp, pike and zander <25 cm account for 3.5% of possible prey for fish-eating birds. Eels might be eaten to some extent by grey heron and purple heron, but their food intake of these species within the reed beds will be well below the commercial yield.

The fish populations of the reed beds are the most important food resource for herons at Lake Neusiedl. This dependence may explain the increase in population size of the great white egret from about 120 breeding pairs at the beginning of the 1980s to more than 700 at the end of the 1990s (Grüll & Ranner 1998). At the same time eutrophication and, hence, an improvement of food resources resulted in a ten-fold increase in biomass of cyprinid fish in the open lake (Herzig 1994; Mikschi *et al.* 1996), which probably corresponds to an increased abundance of fish in the reed zones.

Acknowledgements

References

Aumen N.G. & Gray S. (1995) Research synthesis and management recommendations from a five-year, ecosystem-level study of Lake Okeechobee, Florida (USA). *Archiv für Hydrobiologie, Special Issues of Advanced Limnology* **45**, 343–356.

Chapman D.W. (1978) Production. In T.B. Bagenal (ed.) *Methods for Assessment of Fish Production in Fresh Waters*. IBP Handbook No. 3. Oxford: Blackwell Scientific Publications, pp. 202–217.

Diana J.S. (1991) Energetics. In J.F. Craig (ed.) *Pike. Biology and Exploitation*. London: Chapman & Hall, pp. 103–124.

Downing J.A. & Plante C. (1993) Production of fish populations in lakes. *Canadian Journal of Fisheries and Aquatic Science* **50**, 110–120.

Feunteun E. & Marion L. (1994) Assessment of grey heron predation on fish communities: The case of the largest European colony. *Hydrobiologia* **279/280**, 327–344.

Grimmet T.R.F.A. & Jones J.A. (1989) *Important Bird Areas in Europe*. ICBP Technical Publication No. 9. Cambridge: International Council for Bird Preservation, 888 pp.

Grüll A. & Ranner A. (1998) Populations of the Great Egret and purple heron in relation to Ecological Factors in the Reed Belt of the Neusiedler See. *Colonial Waterbirds* **21**, 328–334.

Hacker R. (1974) *Produktionsbiologische und nahrungsökologische Untersuchungen an der Güster* (Blicca björkna L.) *im Neusiedler See*. Doctoral thesis, University of Vienna, 93 pp.

Hacker R. (1979) Fishes and fisheries in Neusiedlersee. In H. Löffler (ed.) *Neusiedlersee: the Limnology of a Shallow Lake in Central Europe*. The Hague: Dr Junk; by publications, *Monographiae Biologicae* **37**, 423–438.

Herzig A. (1994) Predator-prey relationships within the pelagic community of Neusiedler See. *Hydrobiologia* **275/276**, 81–96.

Herzig A. & Wolfram G. (in press) Fish distribution and limiting factors in the littoral of a shallow lake. In R. Field, R.J. Warren, H. Okarma & P.R. Sievert (eds) *Wildlife, Land, and People: Priorities for the 21st Century. Proceedings of the Second International Wildlife Management Congress*. Bethesda: The Wildlife Society.

Herzig A., Mikschi E., Auer B., Hain A., Wais A. & Wolfram G. (1994) Fischbiologische Untersuchung des Neusiedler See. *BFB-Bericht* **82**, 1–125.

Kushlan J.A. (1976) Feeding ecology of wading birds. In A. Sprunt IV, J.C. Odgen & S. Winckler (eds) *Wading Birds*. Research Report of the Audubon Society No. 7, pp. 249–297.

Mann R.H.K. (1991) Growth and production. In I.J. Winfield & J.S. Nelson (eds) *Cyprinid Fishes. Systematics, Biology and Exploitation*. London: Chapman & Hall, pp. 457–482.

Marion L. (2000) Aquaculture. In J.A. Kushlan & H. Hafner (eds) *Heron Conservation*. London: Academic Press, pp. 269–292.

Mathews C.P. (1971) Contribution of young fish to total production of fish in the River Thames near Reading. *Journal of Fish Biology* **3**, 157–180.

Meisriemler P. (1974) *Produktionsbiologische und nahrungsökologische Untersuchungen am Kaulbarsch* (Acerina cernua (*L.*)) *im Neusiedlersee*. Doctoral thesis, University of Vienna, 110 pp.

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Mikschi E., Wolfram G. & Wais A. (1996) Long-term changes in the fish community of Neusiedler See (Burgenland, Austria). In A. Kirchhofer & D. Hefti (eds) *Conservation of Endangered Freshwater Fish in Europe*. Basel: Birkhauser Verlag, pp. 111–120.

Mock D.W., Lamey T.C. & Ploger B.J. (1987) Proximate and ultimate roles of food amounts in regulating egret sibling aggression. *Ecology* **68**, 1760–1772.

Nemeth E., Dvorak M., Busse K. & Rössler M. (in press) Estimating distribution and density of reedbirds by aerial infrared photography. In R. Field, R.J. Warren, H. Okarma & P.R. Sievert (eds) *Wildlife, Land, and People*: *Priorities for the 21st Century. Proceedings of the Second International Wildlife Management Congress*. Bethesda: The Wildlife Society.

Wolfram G., Mikschi E. & Wolfram-Wais A. (2002) Fischökologische Untersuchung des Schilfgürtels des Neusiedler Sees. *BFB-Bericht*. (in press).

Wolfram-Wais A., Wolfram G., Auer B., Mikschi E. & Hain A. (1999) Feeding habits of two introduced fish species (*Lepomis gibbosus*, *Pseudorasbora parva*) in Neusiedler See (Austria), with special reference to chironomid larvae (Diptera: Chironomidae). *Hydrobiologia* **408/409**, 123–129.

Woollhead J. (1994) Birds in the trophic web of Lake Esrom, Denmark. *Hydrobiologia* **279/280**, 29–38.