

Effects on Fisheries and Waterbirds of Raising Water Levels at Kerkini Reservoir, a Ramsar Site in Northern Greece

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ABSTRACT / A new, higher dam was installed at Kerkini Reservoir in 1982, causing habitat and landscape disruption. A decrease in the area of grassland and shallow water areas, the rapid disappearance of reedbeds, the appearance of beds of *Nymphaea*, and the disappearance of half the forest area were all observed between 1982 and 1991. With the new hydrological regime, a lacustrine system was created, with an extensive, rather deep (4–8 m), pelagic zone favorable for the development of coarse fish species throughout the year. After 1982, an increase in fishing effort and a change in the relative abundance of fish species in the catch, including the disappearance of eels and wels, were observed. The impact of the rise in the water level of breeding aquatic birds led to a general decline in species typical of marshy habitats in favor of species preferring deeper open water habitats. A decrease was recorded in bird species that feed largely on invertebrates and to a

lesser extent fish (e.g., glossy ibis) and that require extensive shallow feeding areas. There was a decline in geese, whose nests were regularly flooded, and a major increase in piscivorous birds, particularly diving birds (e.g., cormorants), which prefer deeper open water and benefitted directly from the large increase in coarse fish biomass. The disappearance of birds breeding in flooded meadows (e.g., black-winged stilts) and of those restricted to reedbeds (e.g., marsh harrier) occurred from 1983. Over the same period, the changes in populations of wintering birds at Kerkini were different from those occurring in other wetlands in northern Greece. The changes recorded in the populations of wintering birds at Kerkini did not therefore result from overall regional trends but from the major habitat modifications that occurred to this wetland. As for breeding birds, strictly piscivorous species increased greatly as a result of the increased availability of fish, but also due to the appearance of many suitable night roosting sites (flooded trees) and to the great increase in the area of open water greater than 2 m deep. Today, Kerkini has become the most important breeding site in Greece for a majority of colonial waterbirds. In contrast, wintering shorebirds practically disappeared. The many changes recorded in the status of breeding and wintering birds at Kerkini can mostly be explained by the changes that occurred in the functioning of the ecosystem and in the habitat structure following the inauguration of the new hydrological regime. These changes did not all occur at the same time: some were immediate and others required a delay before they could be detected.

The loss and degradation of natural wetlands is continuing throughout the Mediterranean region, despite the efforts of many conservation organizations (Britton and Crivelli 1992, Psilovikos 1992). Meanwhile, because of the acute problem of water shortage in the Mediterranean region, many artificial wetlands

are being created, particularly irrigation reservoirs. Those tend to be shallower and have less drastic draw-down than hydroelectric reservoirs and, therefore, constitute a new form of habitat that is increasingly used by wildlife, throughout the year (Erwin and others 1986, Heitmeyer 1986, Esler 1990, Chalabi 1992). Unfortunately, there are few studies, either on natural wetlands or on man-made ones, that have established direct relationships between major habitat modification and changes in vertebrate populations (Weller 1981, Kushlan 1986). This is mainly due to the lack of long-term simultaneous studies on verte-

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brates and their habitat at the same site. It is also due to the fact that it is always difficult to separate the effects of local factors from those of a regional or continental nature, responsible for the fluctuations in abundance recorded among vertebrate populations. This is particularly true for migratory species (e.g., birds, fish, and mammals) whose population size depends on survival and reproduction in different geographical areas, sometimes very far apart.

Since a new flooding regime was installed by raising the dam height on the Kerkini reservoir, northern Greece, in 1982, the landscape and habitats have changed radically (Crivelli and others 1995). These changes have involved not only the physiognomy of the area, but also the entire functioning of this ecosystem. Permanent areas of deep open water have been formed, whereas the area that is flooded to a shallow depth in spring has declined, reedbeds have entirely disappeared, the area of flooded forest has been greatly reduced, and a very large stand of *Nymphaea* has appeared. It is highly likely that other compartments of the ecosystem have been greatly affected by these changes. Unfortunately, it is impossible to assess the effects of the new flooding regime on most groups of organisms (e.g., invertebrates, reptiles, amphibians, and mammals), since there are no data for both before and after 1982. Such a situation is not unique to Kerkini, but is generally true for all wetlands in the Mediterranean region (Britton and Crivelli 1992).

Chasen (1921) stated that the Strymon plain was a "terra incognita" in ornithological terms. Since the 1960s, sufficient observations have been made to enable an assessment of the effects on birds of the changes that have occurred to Lake Kerkini. Ornithologists have visited this site both in winter (Hoffmann and others 1964, Visser and Koning 1968, Hafner and Walmsley 1971, Johnson and Carp 1973, Richoux and Lebreton 1976, Hallmann 1982, 1983, 1985, Hallmann and Handrinos 1984, HOS 1986, 1987, 1988, 1989) and in the breeding season (Kraus and others 1969, Biber and Crivelli 1978, Hallmann 1981, Jerrentrup 1990, Tsachalidis 1990, this study). Finally, fishing is an important economic activity on the Kerkini reservoir and information therefore exists on the fish population and the fishery in this reservoir from the start of the century to the present day (Athanasopoulos 1923, Klossas 1975, Kilikidis and others 1987, Economidis 1991, this study).

The aims of this paper are (1) to report changes in bird and fish populations since 1982 and (2) to estimate the role of habitat modifications caused by the new hydrological regime in causing the observed changes.

Study Area and Methods

The floodplain at Kerkini (northern Greece) was transformed into an irrigation reservoir by the construction of a dam in 1932. Following major siltation and an increase in the area being irrigated, a new, higher dam was installed in 1982, causing habitat and landscape disruption at this Ramsar site (Matthews 1993). The flooded area increased at all periods of the year. The maximum lake area is now 7321 ha, when the water reaches 35 m asl or more. Land lying above 33 m altitude, which was never flooded under the old water regime, is subjected to flooding for more than six months of the year under the new regime. Landsat and SPOT satellite images taken from 1980 to 1990 show a decrease in the area of grassland and shallow water areas, the very rapid disappearance of reedbeds, the appearance of beds of *Nymphaea*, and the disappearance of half the forest area. The forest is considered as a very important component in the functioning of the wetland. The major features of the hydrological regime and a classification of the habitats of the Kerkini reservoir are described in a previous paper (Crivelli and others 1995).

Fish Populations and the Fishery

Reasonably reliable and detailed information is available on the fish species present, and the number of fishermen and their organization at Kerkini before 1982 (Athanasopoulos 1923, Klossas 1975) and after 1982 (Kilikidis and others 1987, Economidis 1991, Crivelli 1990, this study). The yield (kilograms per hectare per year) from Lake Kerkini has been calculated from the area equivalent to the mean annual level of the lake $[(\text{maximum} - \text{minimum})/2]$ (Babajimopoulos and Antonopoulos 1990). The yield data are based on the official fishery statistics given species by species (Serres Prefecture, Department of Fisheries; E. Tatarakis, personal communication).

Breeding Birds

Before 1982, three censuses of breeding aquatic birds at Kerkini are available: 1967 (Kraus and others 1969), 1978 (Biber and Crivelli 1978), and 1980 (Hallmann 1981). For the period after 1982, the situation is better, as there have been annual counts between 1985 and 1991. The counts carried out in 1985 and 1986 were part of a national census of Ardeidae in Greece (Crivelli and others 1988); those from 1987 to 1991 formed part of an international research program on pelicans (Crivelli and others 1991a,b) and part of a thesis on the ecology of cormorants breeding



Figure 1. Location of Kerkini (4) and other wetlands in northern Greece used in the analysis: 1, Axios–Loudias–Aliakmon Delta; 2, Lake Koronia; 3, Lake Volvi; 5, Nestos Delta; 6, Lafri–Lafrouda; 7, Porto–Lagos; 8, Xirolimni; 9, Karatza; 10, Messi; 11, Ptelea; 12, Mitrikou; and 13, the Evros Delta.

at Kerkini (T. Nazirides in preparation). Population size during the breeding season was estimated from monthly nest counts in April–June using a boat.

Wintering Birds

For the period before 1982, six IWRB (International Waterfowl and Wetlands Research Bureau) mid-January waterfowl counts (= Christmas counts in North America, see Rose and Taylor 1993) were made in northern Greece, including Kerkini, between 1964 and 1981–1982 (1964: Hoffmann and others 1964, 1968: Visser and Koning 1968, 1971: Hafner and Walmsley 1971, 1973: Johnson and Carp 1973, 1976: Richoux and Lebreton 1976, 1982: Hallmann 1982). After 1982, wintering birds were counted regularly from 1983 to 1989 (Hallmann 1983, 1985, Hallmann and Handrinos 1984, HOS 1986, 1987, 1988, 1989). There are no reliable counts available for 1990. To compare the abundance of birds wintering at Kerkini before and after 1982, a nonparametric means comparison test (Mann-Whitney U test) has been used, comparisons being repeated for each year from 1984 to 1989. Only four of the six counts available before 1982 were actually used because for the other two the site coverage in northern Greece was incomplete. The number of observers in a given year, the time spent counting the birds, and the meteorological conditions during the counts are the main limitations of these IWRB mid-January counts. In order to test whether the changes in the observed numbers of birds

wintering at Kerkini were really the result of the habitat modifications recorded on this wetland, it is essential to study the changes in the numbers of the same species over the same period using the same test, but in a wider geographical context. We therefore compared the numbers of waterfowl in 12 wetlands in northern Greece censused in 1971, 1973, 1976, and 1982, with results obtained for the years 1983–1989. The wetlands were the following (Figure 1): Axios–Loudias–Aliakmon Delta (1), Lake Koronia (2), Lake Volvi (3), Nestos Delta (5), Lafri–Lafrouda (6), Porto–Lagos (7), Xirolimni (8), Karatza (9), Messi (10), Ptelea (11), Mitrikou (12), and the Evros Delta (13). We consider that this region constitutes a coherent climatic and biogeographical entity for wintering birds occurring in this region of the Mediterranean.

Results

Fish Population and the Fishery

Since 1933 the lake has been rented by the state to one or more individuals or fishing cooperatives, who retain 10% of the total value of the catch. There are currently four fishing cooperatives. The closed season lasts for 40 days in the spring (April–May). The carp, *Cyprinus carpio*, is the most sought after fish as it has the highest market value. In the fishing regulations there is a minimum catch size for carp of 31 cm. In the last 20 years fishermen have used outboard motors and monofilament nylon gill and trammel nets (mesh

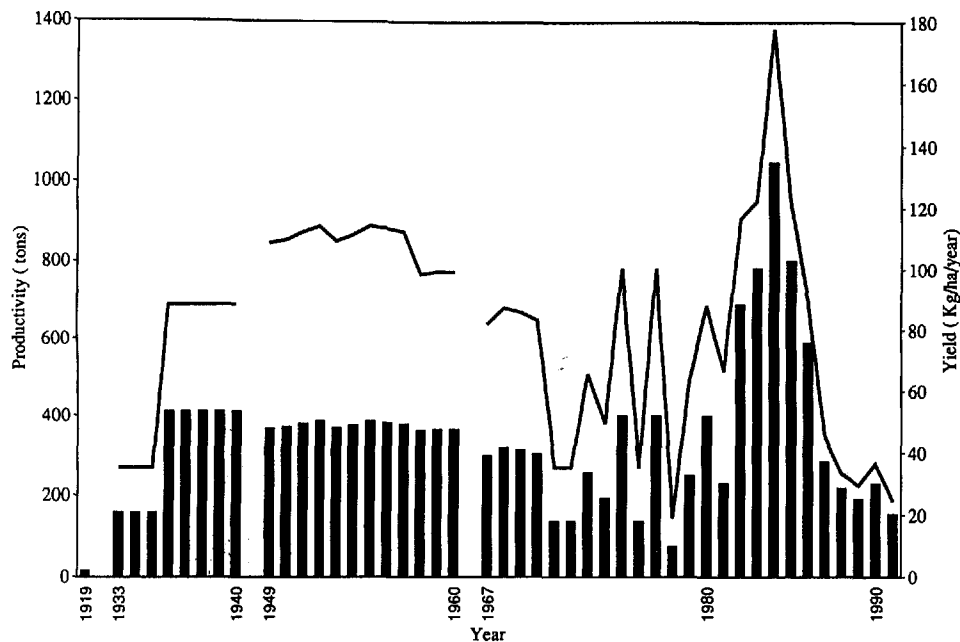


Figure 2. Productivity in tons (broken line) and yield (bars) of the Lake Kerkin fishery based on official fishery statistics.

size 10–80 mm). Fish traps, long-lines, and fyke nets are also used, depending on the season. The use of seine nets has been prohibited since 1982. Before 1982, there were about 70 professional fishermen with 25 to 30 boats (Klossas 1975). After 1982 there were 300–500 fishermen with 140 boats (Kilikidis and others 1987, this study). The density of fishermen has therefore increased from 1.8–2.0/km² before 1982 to 4.5–4.7/km² and thus there has been an intensification of fishing pressure since 1982.

There is patchy information on the yield (kilograms per hectare per year) and the productivity (fishery statistics) from Lake Kerkin between 1919 and 1991 (Figure 2). No data are available for the periods 1923–1932, 1941–1948, and 1961–1966. An increase in catch was noted starting in 1982, with a peak in 1984 of 177.7 kg/ha/yr, followed by an abrupt fall and then a return to a stable level of about 25–35 kg/ha/yr in subsequent years.

The species composition of catches between 1933 and 1991 has shown major changes (Figure 3). In the 1940s, the pike, *Esox lucius*, disappeared entirely and from 1983 eel, *Anguilla anguilla*, and wels, *Silurus glanis*, also disappeared completely from catches. The latter two species were only recorded downstream of the dam after this. Similarly, a strong decrease in the proportion of carp, *Cyprinus carpio*, in the catches and an increase in the proportion of fish of low market value (Cyprinidae such as *Rutilus rutilus*, *Alburnus al-*

burnus, and *Aspius aspius*) in the catches, and an increase and explosive development of the population of goldfish, *Carassius auratus*, were recorded after the installation of the new dam. The latter species was probably introduced from Italy about ten years ago. Other species (*Stizostedion lucioperca*, *Pseudorasbora parva*, *Lepomis gibbosus*) have also been introduced since 1982. They were introduced into Bulgaria and thence colonized the lake via the Strymon River. Only *Carassius auratus* and *Lepomis gibbosus* have, to our knowledge, become abundant up to now.

Breeding Birds

Despite the paucity of data available for before 1982, the changes that have occurred to the bird fauna are fairly clear (Table 1). Five categories of birds can be distinguished. The first is composed of species that did not breed before 1982 and which only started to breed in the period 1982–1991. These are: (1) *Phalacrocorax carbo*, which nested for the first time at Kerkin in 1986 and has continued to increase in numbers since; (2) *Larus ridibundus* and *L. cachinans*, which nested for the first time at Kerkin in 1987 (Jerrentrup 1988) but which have not bred in subsequent years; and (c) *Egretta alba*, which was suspected of breeding in 1978 and reliably recorded as nesting for the first time in 1987. In subsequent years it has continued to breed, but there has been no increase in numbers.

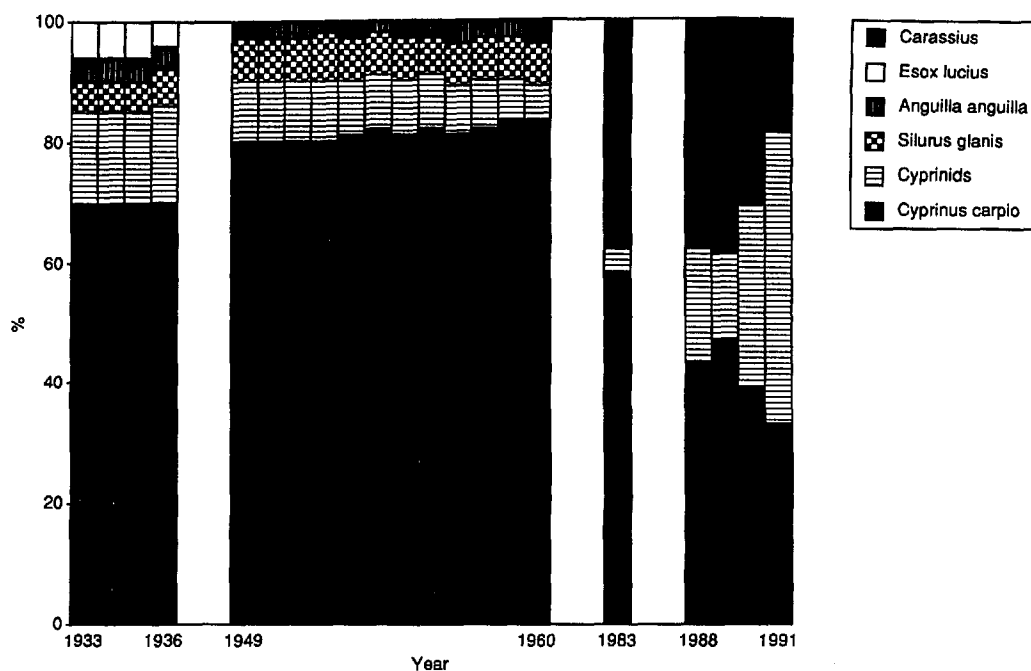


Figure 3. Percentage composition of commercial catches from the Lake Kerkini fishery.

Table 1. Estimates of number of breeding pairs of waterbirds nesting at Lake Kerkini 1969–1991^a

Species	1969	1978	1980	1985	1986	1987	1988	1989	1990	1991
<i>T. ruficollis</i>	–	±6	240	+	+	+	+	+	+	+
<i>P. cristatus</i>	–	+	±120	+	+	+	+	±400	+	+
<i>Ph. carbo</i>	–	0	?	?	40	>100	230	315	500	340
<i>Ph. pygmaeus</i>	7–9	6–10	200	183	46	>100	350	400	570	430
<i>E. garzetta</i>	340	85	700	171	107	>100	310	440	640	445
<i>A. ralloides</i>	550	380	600	85	61	>50	>100	170	200	170
<i>N. nycticorax</i>	220	300	400	98	75	>100	340	510	780	530
<i>A. purpurea</i>	50	2	70	35	15	>5	>10	14	21	14
<i>A. cinerea</i>	–	+	?	155	170	>100	180	220	230	210
<i>E. alba</i>	–	?	?	?	?	+	3	+	3	+
<i>P. leucorodia</i>	100	40	120	24	70	>20	55	58	65	55
<i>P. falcinellus</i>	10	30	150	43	20	+	10	14	15	13
<i>Chl. niger</i>	40	?	50	?	?	+	+	+	+	+
<i>Chl. hybrida</i>	100	±5	90	?	?	+	+	+	+	+
<i>A. anser</i>	+	+	20	10	+	+	+	+	+	+
<i>S. hirundo</i>	–	+	–	5	+	+	+	+	+	+

^a?: breeding suspected; +: breeding but no estimate of the numbers of breeding pairs; –: no breeding.

The second group contains those species that nested before 1982 and that have increased in numbers, sometimes spectacularly, in the period 1982–1991. These are: (1) *Egretta garzetta*, *Nycticorax nycticorax*, and *Ardea cinerea*, all highly piscivorous heron species whose breeding numbers have increased to varying degrees since 1982. *Ardea cinerea* has nested in large numbers since 1985. Half of the breeding population nests away from the lake, although the birds

feed in the lake area. For example there was a breeding colony in a planted *Populus* forest near Limnochori, but the trees were cut down during the breeding season. The birds then re-nested almost immediately in a *Populus alba* forest close to the original colony. (2) *Phalacrocorax pygmaeus* breeding numbers have at least doubled since 1982. (3) *Podiceps cristatus* and *Tachybaptus ruficollis* numbers have increased since 1982 although our data remain fragmentary be-

cause of the problems in counting these two species. (4) The number of nesting pairs of *Chlidonias niger* and *Chlidonias hybrida* has increased to a total of 250. These two species currently nest exclusively on the *Nymphaea* beds.

The third category contains species that nested before 1982 and whose numbers have decreased in the period 1982–1991. These are *Ardeola ralloides*, *Plegadis falcinellus*, *Ardea purpurea*, and *Anser anser*, all of which have declined by a half since 1982.

The fourth category are those breeding species that have not shown any sufficiently clear tendency for them to be placed in any of the above categories. These are *Platalea leucorodia*, *Sterna hirundo*, *Sterna albifrons*, and *Ixobrychus minutus*.

The final category contains those species that ceased nesting at Kerkini immediately after the installation of the new dam, either because they nested exclusively in reedbeds (*Circus aeruginosus*, *Locustella luscinioides*) or because they nested in the wet meadows that are now covered by several meters of water in the spring (*Glareola pratincola* and *Himantopus himantopus*).

Because of the rapid rise in water level at the start of each spring, *Anser anser* has increasing difficulties in breeding successfully. It is also said that local people collect their eggs to incubate them and raise the chicks for domestic use. Each year, many nests of this and other species are flooded by the abrupt rise in water level. For example in 1988, 50 nests of *Phalacrocorax pygmeus* and 30 nests of *Platalea leucorodia* were flooded (Jerrentrup 1990). In the case of *Egretta garzetta*, Tsachalidis (1990) estimated that 3.5% of eggs laid were lost through flooding. In 1990, 300–320 nests were flooded: 70 of *Nycticorax nycticorax*, 5 of *Phalacrocorax carbo*, 5 of *Plegadis falcinellus*, 15 of *Platalea leucorodia*, 3 of *Ardea cinerea*, 3 of *Ardea purpurea*, 80 of *Egretta garzetta*, and 60 of *Ardeola ralloides*. Most of the birds that lose their clutches or broods attempt to renest higher up in trees.

Wintering Birds

The changes in the abundance of wintering waterfowl following in the modifications that occurred to the flooding regime are also very clear (Table 2). The birds' responses can be grouped into four categories.

The first is composed of bird species that show no significant change before and after 1982. This category includes the largest number of species. They are either species that occur in very low numbers (<100 individuals; e.g., *Tringa totanus*, *Tringa erythropus*, *Philomachus pugnax*, *Gallinago gallinago*, *Numenius arquata*, *Egretta garzetta*, *Platalea leucorodia*, *Podiceps nigricollis*, *Mergus albellus*, *Bucephala clangula*, and *Athya nyroca*)

or abundant species (between 100 and 1000 individuals) that maintained their previous numbers or which showed a slight nonsignificant increase or decrease (e.g., *Phalacrocorax carbo*, *Phalacrocorax pygmeus*, *Pelecanus crispus*, *Egretta alba*, *Ardea cinerea*, *Vanellus vanellus*, *Aythya ferina*, *Aythya fuligula*, *Anas acuta*, *Anas clypeata*, *Anser anser*, and *Larus ridibundus*).

The second category contains two species of dabbling duck (*Anas strepera* and *Anas penelope*), which showed an immediate and strong negative response to the habitat changes that took place, but which returned to their pre-1982 numbers after a few years. These two species were practically absent from Kerkini for three to four years, then gradually returned to their previous numbers and have even tended to increase in the most recent years (1988–1989).

The third group is composed of species that showed a delayed negative or positive response. The great-crested grebe, *Podiceps cristatus*, increased significantly in numbers after five years and maintained this increase until 1989. The white-fronted goose, *Anser albifrons*, showed a significant and constant decrease in numbers after 1988. Such decreases were also recorded for the shelduck, *Tadorna tadorna*, from 1987, for the mallard, *Anas platyrhynchos*, from 1989, and for the teal, *Anas crecca*, from 1988. The latter two dabbling ducks declined spectacularly in numbers from a mean of 20,000 individuals before 1982 to a mean of less than 5000 individuals after 1982. The shelduck decreased from 800 individuals to less than 200 after 1982.

Finally, the fourth category contains the species that showed the most spectacular responses: a significant and immediate positive or negative response that was maintained until 1989. The little grebe, *Tachybaptus ruficollis*, increased significantly from 1984, from a mean of eight individuals before 1982 to more than 240 birds after 1982. The coot, *Fulica atra*, also showed a significant increase from a mean of 500 individuals before 1982 to a mean of more than 4500 after 1982. In contrast, three species showed drastic declines in numbers: the dunlin, *Calidris alpina*, decreased from a mean of 500 individuals to an average of less than 50 birds; the avocet, *Recurvirostra avosetta*, decreased from a mean of 1500 individuals before 1982 to less than 100 after 1982, and the black-tailed godwit, *Limosa limosa*, fell dramatically from a mean of 3000 individuals to an average of 200 individuals after 1982.

The numbers of the same species as those counted at Kerkini, occurring in northern Greece before and after 1982, were also compared (Table 2). The responses were very clear and very different from those

Table 2. Results of comparison of numbers of wintering birds at Kerkini (all species analyzed included in table) and in northern Greece (only those species showing some significant differences are included in table) before and after 1982 (Mann-Whitney U test)^a

	1984	1985	1986	1987	1988	1989
Lake Kerkini						
<i>Podiceps cristatus</i>	NS	NS	NS	+	+	+
<i>Podiceps nigricollis</i>	NS	NS	NS	NS	NS	NS
<i>Tachybaptus ruficollis</i>	++	++	++	++	++	++
<i>Phalacrocorax carbo</i>	NS	NS	NS	NS	NS	NS
<i>Phalacrocorax pygmeus</i>	NS	NS	NS	NS	NS	NS
<i>Pelecanus crispus</i>	NS	NS	NS	NS	NS	NS
<i>Egretta garzetta</i>	NS	NS	NS	NS	NS	NS
<i>Egretta alba</i>	NS	NS	NS	NS	NS	NS
<i>Ardea cinerea</i>	NS	NS	NS	NS	NS	NS
<i>Platalea leucorodia</i>	NS	NS	NS	NS	NS	NS
<i>Anser albifrons</i>	NS	NS	NS	NS	-	-
<i>Anser anser</i>	NS	NS	NS	NS	NS	NS
<i>Tadorna tadorna</i>	NS	NS	NS	-	-	-
<i>Anas platyrhynchos</i>	NS	NS	NS	NS	NS	-
<i>Anas crecca</i>	NS	NS	NS	NS	-	-
<i>Anas strepera</i>	--	--	NS	NS	NS	NS
<i>Anas penelope</i>	--	--	--	-	NS	NS
<i>Anas acuta</i>	NS	NS	NS	NS	NS	NS
<i>Anas clypeata</i>	NS	NS	NS	NS	NS	NS
<i>Aythya ferina</i>	NS	NS	NS	NS	NS	NS
<i>Aythya nyroca</i>	NS	NS	NS	NS	NS	NS
<i>Aythya fuligula</i>	NS	NS	NS	NS	NS	NS
<i>Bucephala clangula</i>	NS	NS	NS	NS	NS	NS
<i>Mergus albellus</i>	NS	NS	NS	NS	NS	NS
<i>Fulica atra</i>	++	++	++	++	++	++
<i>Vanellus vanellus</i>	NS	NS	NS	NS	NS	NS
<i>Calidris alpina</i>	--	--	--	--	--	--
<i>Philomachus pugnax</i>	NS	NS	NS	NS	NS	NS
<i>Tringa erythropus</i>	NS	NS	NS	NS	NS	NS
<i>Tringa totanus</i>	NS	NS	NS	NS	NS	NS
<i>Limosa limosa</i>	--	--	--	--	--	--
<i>Numenius arquata</i>	NS	NS	NS	NS	NS	NS
<i>Gallinago gallinago</i>	NS	NS	NS	NS	NS	NS
<i>Recurvirostra avosetta</i>	--	--	--	--	--	--
<i>Larus ridibundus</i>	NS	NS	NS	NS	NS	NS
Northern Greece						
<i>Podiceps nigricollis</i>	++	NS	NS	NS	NS	+
<i>Egretta garzetta</i>	++	++	++	++	++	++
<i>Ardea cinerea</i>	++	++	NS	NS	NS	NS
<i>Larus ridibundus</i>	++	++	++	++	++	++

^aAreas marked with pluses and minuses indicate significant results. NS, not significant, $P > 0.05$; +, significant increase, $P < 0.05$; ++, significant increase, $P < 0.01$; -, significant decrease, $P < 0.05$; --, significant decrease, $P < 0.01$.

obtained in Kerkini. These responses are classified below according to the same categories as recorded at Kerkini.

The first group involves species that showed no significant increase or decrease (no change in mean numbers before and after 1982). Among these species, the numbers of fish-eating species (grebes, cormorants, and herons) were stable or increased

slightly. Geese declined and shelduck were stable. Most ducks and coots showed a tendency to decline, as did shorebirds.

The second category includes *Podiceps nigricollis*, which showed a slight but significant increase (1984 and 1989), and *Ardea cinerea*, which seemed to increase (1984, 1985) but which did not confirm this trend in subsequent years.

In northern Greece, no species belonged to the third category, which contains species showing a delayed negative or positive response.

Finally, the fourth category included *Egretta garzetta* and *Larus ridibundus*, which are species that are constantly increasing in numbers. The increase of the little egret was low, increasing from a mean of 25 individuals before 1982 to 100 individuals on average after 1982. In contrast, the increase in the black-headed gull was spectacular, since it increased from 2000 individuals to an average of more than 11,000 individuals after 1982.

Discussion

Because they are easy to observe and sensitive to habitat factors, birds can be good indicators of changes occurring to wetlands (Kushlan 1986, Hunter and others 1987, Weller 1988, Fredrickson and Heitmeyer 1988, Crowder and Bristow 1988, Esler 1990, 1992). The results of this study confirm this assertion by showing that the changes occurring in the status of breeding and wintering birds, and to a lesser extent to the fish populations, were not just due to chance, but can be explained by changes occurring to the physiognomy of the habitat and to the ecosystem functioning following the installation of the new water regime. The discussion will start with the fish, because changes in them seem to be an important factor responsible for some of the changes observed in the status of breeding and wintering birds.

Fish Populations and the Fishery

As has been recorded in other reservoirs in which water levels have been raised (Travade and others 1985, Balvay 1985, Kimmel and Groeger 1986, Ploskey 1986), the yield of fish at Kerkini increased greatly in the two to three years immediately after the inauguration of the new hydrological regime. The catches then decreased before stabilizing at a level of 25–35 kg/ha/yr in the last three years, i.e., among the lowest values ever recorded at Kerkini. It should be noted that the yield reflects catches only of marketable fish species (e.g., *Cyprinus*, *Carassius*) and takes little account of the nonmarketable species (*Alburnus*, *Rutilus*, *Aspius*, and *Lepomis*), which are usually thrown back into the lake and which are proliferating. Under the former hydrological regime, and particularly with its low water level in winter, the lake was more like a fluvial system with its floodplain than a lacustrine system. With the new hydrological regime, a lacustrine system was created with an extensive, relatively deep (4–8 m) pelagic zone existing throughout the year, favorable for the development of coarse fish species

such as *Alburnus alburnus*, *Carassius auratus*, *Lepomis gibbosus*, and *Rutilus rutilus*. Such a development was particularly rapid because the water in Lake Kerkini is eutrophic (Kilikidis and others 1987) and temperatures are high in summer. The disappearance of predatory fish (e.g., *Esox lucius*, *Silurus glanis*, *Perca fluviatilis*), caused partly by overfishing, the change in river course, and the exclusion of *Anguilla anguilla* by the new dam, meant that these coarse fish have no predators other than fish-eating birds (Tsachalidis 1990, Nazirides unpublished data), and their populations can proliferate. In addition, the development of extensive stands of macrophytes (e.g., the *Nymphaea* beds on the east side of the lake and the macrophyte beds in the former course of the Strymon) favored the production of invertebrates, which constitute the main food for these fish (Cyr and Downing 1988, Lodge 1985, Miller and others 1989, Talbot and Ward 1987). These macrophyte stands also serve as spawning supports and shelter for young fish of the year. In this respect, the *Nymphaea* bed seems, from our observations, to be a most important nursery for young fish of the year, playing a role comparable to that of mangroves in coastal areas. The decrease in the carp, *Cyprinus carpio*, is due mainly to overfishing of commercially important fish species, which occurs widely in Greece (Crivelli 1990). It is not always easy, however, to distinguish the effect of overfishing from those of changes to the ecosystem. The habitat changes observed since 1982 (e.g., reduced spawning areas) could also be implicated in this decline.

The proliferation of introduced species, particularly *Carassius auratus*, is a recent phenomenon recorded not only at Kerkini but also in other Greek lakes (e.g., Lake Kastoria and Lake Mikri Prespa; Crivelli unpublished data). The same is true for the disappearance of species such as pike and wels (e.g., from Lake Koronia: Economidis and Voyadjis 1981; Lake Megali Prespa: Crivelli unpublished data).

The negative effects of overfishing of commercial fish species, associated with socioeconomic factors, are threatening the future of the professional fishery on Lake Kerkini (Crivelli 1990). In contrast, there is no reason to believe that the biomass of noncommercial fish is likely to decline in the future. On the contrary, this could still increase due to eutrophication of the water and a probable decline in fishing effort and could thus favor populations of fish-eating birds, provided that they do not depend entirely on species of commercial interest.

Breeding Birds

The impact of the rise in water level on breeding birds has led to a general decrease in species typical of

marsh habitats and an increase in species preferring deeper open water habitats. There has been: (1) a decrease or downward population trend for birds feeding mainly on invertebrates and only to a small extent on fish (*Ardeola ralloides*, *Platalea leucorodia*, *Plegadis falcinellus*) as well as *Anas platyrhynchos*, birds that require extensive shallow feeding grounds. These decreased by 75% in area in spring and summer under the new water regime (Crivelli and others 1995); (2) a decrease in the numbers of greylag geese (*Anser anser*), whose nests were flooded regularly; and (3) a major increase in fish-eating birds, particularly the almost exclusively piscivorous herons (*Egretta garzetta*, *Nycticorax nycticorax*, and *Ardea cinerea*) and even more so of diving fish-eating birds such as grebes and cormorants that prefer deeper open water (the pelagic zone) and that benefitted directly from the great increase in the biomass of coarse fish. The disappearance of birds breeding in the wet meadows (e.g., black-winged stilts and pratincole) and of species restricted to reedbeds (e.g., marsh harrier) completes, in a spectacular fashion, the response of breeding birds to the ecosystem changes that took place in Kerkini.

The period from 1982 to 1988 was sufficiently long for most breeding bird species to adapt to the new lake regime and stabilize their numbers at new levels. From 1989 to 1991, the number of breeding pairs became stable. This timing fits perfectly with a period of transition and then stabilization to the new water regime (Crivelli and others 1995).

In the years before 1982, most of these species (ardeids, spoonbills, ibis, and pygmy cormorants) nested in the large reedbeds and only to a lesser extent in trees (Kraus and others 1969, Biber and Crivelli 1978). Now all these species nest only in trees in one or more colonies, depending on the year. Cormorants, which do not nest in reeds, started to breed in 1986 in trees that died as a result of the new water regime and have increased constantly since that date. As for the marsh terns (*Chlidonias* spp.), they have benefitted from the appearance of an extensive bed of *Nymphaea alba*, which provides an ideal support for their nests. Formerly they nested in other less extensive macrophyte stands (*Nymphoides peltata*, *Potamogeton* sp.), located either along the river courses or in open water areas among the reeds.

Thus, Kerkini has now become the most important breeding site in Greece for *Nycticorax nycticorax* and *Podiceps cristatus*, and together with Lake Mikri Prespa in northwestern Greece, the most important site for two cormorant species (*Phalacrocorax carbo* and *P. pygmeus*), the great white egret (*Egretta alba*), and greylag goose (*Anser anser*). The breeding colonies of marsh terns (*Chlidonias hybrida* and *C. niger*) at Kerkini are

the largest in all of Greece. For other species, such as *Platalea leucorodia* and *Plegadis falcinellus*, which have declined, Lake Kerkini undoubtedly remains a site of prime importance for the populations of these birds in the Balkans.

The comparison between the changes in the number of breeding birds at Kerkini and the changes of the same species over the same period in the rest of Greece (Jerrentrup, Catsadorakis, Naziridis and Crivelli unpublished data) shows that the increase in fish-eating birds such as *Nycticorax nycticorax*, *Phalacrocorax pygmeus*, *Egretta garzetta*, and *Egretta alba* is specific to Kerkini and can be considered a direct consequence of the changes in fish population that have taken place at Kerkini since 1982. In contrast, the trends observed with other species, whether these be negative (*Ardeola ralloides*, *Ardea purpurea*, *Platalea leucorodia*, and *Plegadis falcinellus*) or positive (*Phalacrocorax carbo* and *Ardea cinerea*), are the same as those recorded elsewhere in Greece.

Although some species have decreased or disappeared, the new hydrological regime at Kerkini has had consequences that, on the whole, are favorable for breeding aquatic birds, by providing numerous nesting sites and an abundant food supply, particularly of fish. This conclusion is valid only for the period 1982 to 1992, and it is not certain that this will remain true in the next ten years, because of the slow disappearance of the flooded forest, because of a new project of raising dikes and water level, and because of the instability of this ecosystem.

Wintering Birds

The changes that have taken place in the numbers of wintering birds at Kerkini are quite different from those occurring in other wetlands in northern Greece over the same period. The changes at Kerkini do not therefore result from regional trends, but rather from the major habitat modifications that have occurred on this single wetland.

Among the diving fish-eating birds, wintering as well as breeding birds have practically all increased, although some of these increases are not significant. It is quite likely that the two species of cormorant, the black-necked grebe, and the great white egret will show further and significant increases in numbers in the near future. These species have benefitted not only from the increased availability of fish, but also from the appearance of numerous sites suitable for night roosts (flooded trees) and the great increase in the area of open water greater than 2 m deep. In the 1970s there was practically no lake in winter, just the bed of the River Strymon and a few pools (Hafner and Walmsley 1971, Johnson and Carp 1973)—a situation

unfavorable for both fish and for diving fish-eating birds. The increase in the number of breeding birds at Kerkini and a degree of sedentariness among these species could also have contributed to the increase in the wintering populations.

With the exception of the fish-eating species, only one other species, the coot (*Fulica atra*) has increased greatly in the winter. This diving herbivorous species has benefitted from the increase in winter of the area of shallow water (<2 m) rich in macrophytes (Crivelli and others 1995). In contrast, two dabbling ducks, the teal (*Anas crecca*) and mallard (*Anas platyrhynchos*), have greatly decreased in winter at Kerkini. Teal feed on small seeds sieved from moist soil, and the mallard is an omnivore. The optimum foraging depths for mallard and teal are 15–25 cm (Fredrickson and Heitmeyer 1988, Pirot and others 1984). It is evident that such shallow water areas are much less extensive now than before 1982 because of the new hydrological regime. In addition, a decrease in the areas of aquatic grasses (e.g., *Paspalum* sp.) and of nonhelophyte plants has been recorded, which would proportionately reduce the quantity of food available, especially for the teal.

Other species have decreased drastically since 1984 and have practically disappeared from Kerkini as wintering species. These include all the shorebirds, particularly *Limosa limosa*, *Calidris alpina*, and *Recurvirostra avosetta*. Before 1982, Lake Kerkini was the main wintering site for *Limosa limosa* in Greece and the birds that have disappeared from Kerkini have not turned up elsewhere in Greece. All these species feed on invertebrates, especially annelids living in or on mudflats. On the satellite image of 6 February 1982, when the lake level was at 29.5 m asl, 761 ha of mudflats were measured at the mouth of the former course of the Strymon and there were 2191 ha of wet temporarily floodable areas. These latter were the favored feeding sites for these birds. In 1982 these areas were in the littoral zone and only in spring and summer (after the wintering birds had left) were flooded, to a maximum depth of 2 m. With the new hydrological regime, such habitats hardly exist, except for about 150–200 ha of mudflats at the mouth of the new course of the Strymon; also, from samples that we took in February 1990, it would appear that these mudflats are almost devoid of invertebrates. This is probably because they are no longer in the littoral zone, but are flooded to a depth of more than 4 m by turbid, probably anoxic, water in spring and summer (Cooper and Knight 1985, McCrady and others 1986).

Apparently, all the other species of wintering birds

have been virtually unaffected so far by the changes that have occurred to the ecosystem at Kerkini.

In addition to wintering and breeding birds, it should be noted that in spring and summer there has been a great increase in the numbers of nonbreeding fish-eating birds such as dalmatian pelicans, *Pelecanus crispus*, and great white pelicans, *Pelecanus onocrotalus* (Crivelli 1987, Crivelli and others 1991b). For example, in spring 1986 and 1991, particularly wet years, up to 500–600 pelicans were counted feeding on the spawning sites of fish in newly flooded areas. Such concentrations were never seen at this season before 1982 (Kraus and others 1969, Biber and Crivelli 1978). Again, these birds have benefitted from the increased biomass of fish and the new daytime and night roosting sites provided by the flooded forest in spring and summer.

Conclusion

The many changes that have been recorded in the status of breeding and wintering birds at Kerkini can be explained chiefly by the changes that have occurred to the functioning of the ecosystem and in the physiognomy of the habitats, following the installation of the new hydrological regime. These changes did not all occur simultaneously: some were immediate but for others there was a delay before they could be detected. Since the habitats are continuing to evolve, it is likely that further changes in the fish and bird populations will be recorded in the future, but a minimal annual monitoring effort will be required to detect these. For the changes that have taken place among the fish populations and the fishery, it has in fact proved much more difficult to establish such relationships, mainly because the data available are of poorer quality and less complete.

The balance of changes that have taken place in the fish and bird faunas from 1982 to 1991 is positive, if the diversity and abundance of the organisms using the Kerkini ecosystem are compared before and after 1982. Unfortunately, this optimism must be strongly tempered by our conclusions (Crivelli and others 1995) on the future of the flooded forest, in our view a key factor determining Kerkini's biological richness. The forest is in fact continuing to decline, overgrazing is preventing any reestablishment of new reedbeds, the spring and summer water levels are at their highest, and there are only slight possibilities of alternative management of the water regime. If the international importance of Kerkini is to be conserved and its status as a Ramsar site justified, it is urgent to set in place new management measures that would reconcile eco-

conomic interests (irrigation, fishing, grazing) with those of the conservation of the wildlife and flora.

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