ABSTRACT  Experimental exclusion of the Andean flamingo (Phoenicoparrus andinus) from shallow water areas of a salt lake in the Bolivian Andes caused large increases in the biomass of microorganisms inhabiting the surface sediments, especially a large diatom (Surirella wetszelii), amebas, ciliates, and nematodes. This is a conservative demonstration of the influences that water birds in general exert on the structure of aquatic ecosystems.

Of the ≈8,900 species of birds in the world roughly 9% feed entirely or predominantly on aquatic organisms. Their diets range over the entire spectrum of available foods, from fish to invertebrates, from vascular plants to microscopic algae. The more abundant of these birds may strongly affect the dynamics of their prey populations and, indirectly, the dynamics of entire aquatic ecosystems.

However, few experimental studies of these interactions have been attempted (1-4), and we scarcely have an inkling of how the structure and functioning of any aquatic ecosystem would be altered by the disappearance of one or more of the bird species feeding in it.

In this report we document the strong influence exerted by the Andean flamingo (Phoenicoparrus andinus) on lacustrine microbenthos, the assemblage of microscopic organisms inhabiting the surface sediments of a lake bottom. P. andinus is a common inhabitant of numerous shallow, mostly saline lakes of the altiplano region of the central Andes of South America (5-7). Two other flamingos, James' (Phoenicoparrus jami) and the Chilean (Phoenicopterus chilensis), also occur abundantly on many of these same lakes. Other flamingo species are dominant components of salt lake and coastal lagoon ecosystems in Africa and Eurasia, and the fossil record indicates that, in the past, still other flamingos occupied similar environments in North America and Australia (8-10). The role that flamingos play in the functioning of these lake ecosystems is thus of general interest. We suspect that this role is great in consequence of flamingos' high feeding rates and the large size of their feeding flocks.

STUDY AREA AND METHODS

To test this suspicion we conducted an exclosure experiment during January and February 1979 in Laguna Puripica Chico, a small (1.0 km²), shallow (maximal depth, ca. 50 cm), slightly saline (8.2 g/liter), high-altitude (4,393 m) lake in the desertic altiplano of the southwesternmost tip (22°31' S, 67°30' W) of Bolivia: this is one of several lakes scattered around the margin of a salt-encrusted basin called Salar de Chalvirí (Fig. 1). On visits in late December 1978 and early January 1979 we found flamingos to be abundant on this lake and P. andinus to be much more numerous than the other two species; this pattern was maintained throughout our study (Table 1). On earlier visits we had found even larger numbers of flamingos here. Approximately 3,000 (66% P. jami, 29% P. andinus, and 5% P. chilensis) were observed on the lake in December 1973 (6) and about 5,700 (65% P. jami, 33% P. andinus, and 2% P. chilensis) in November 1977 (7). By way of comparison, the lesser flamingo (Phoeniconaias minor) occurs on some African lakes at 10 times these densities (11).

On January 2 we selected a mudflat that was being used as a feeding ground by P. andinus but not by the other species.

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Abbreviations: F, flamingo(s); NF, no flamingo(s).
This was located about 70 m off the eastern shore, had a thin film of water over it, and consisted of 10–15 cm of soft sediments overlying a firm sandy bottom. In a row along this flat and spaced at about 15-m intervals from each other, we fenced off four 4 x 3 m experimental (NF) areas, thereby excluding flamingos from them. Each fence consisted of four stakes projecting about 1.2 m above the water, with two strands of nylon twine connecting them. A total of 10 control (F) areas, two between each pair of NF areas and two at both ends of the row, were delimited by imaginary lines (Fig. 1).

On January 3 and at 2- to 3-wk intervals over the following 2 months, the microbenthos was sampled with a microcorer in each of the four NF and ten F areas. The microcorer took a triangular plug with a surface area of 6.9 mm² and a depth of 5 mm. Eight plugs were taken haphazardly from the central region of each area and combined to yield a single composite sample for that area. The only locations avoided in our sampling were where the sediment was covered by eelgrass or had a deep depression (fresh flamingo track) in it. The larger more active organisms—e.g., nematodes—may have been under-represented by this sampling method. Samples were preserved in 5% formaldehyde and analyzed on return to San Diego. An amount of sample equivalent to 0.015, 0.094, 0.17, or 3.3 mm² of bottom sediment (depending on the taxon) was examined under a compound microscope; linear dimensions were measured and biomass (strictly speaking, biovolume) was calculated for every organism estimated to have been alive at time of sampling.

During the experiment, P. andinus continued to feed in the F areas but were completely excluded from the NF areas. P.
jamesi and P. chilensis preferred to feed in other parts of the lake and were never observed closer than 50–100 m to our study site. Light but frequent rains in January caused a gradual rise in water level (Table 1), which later dropped when dry weather set in about January 28. As evidenced by their tracks, P. andinus fed in the F areas much less (and possibly not at all) during the high water period (February) than during earlier and later periods. Water temperature probably fluctuated daily from a low of 0–5°C to a high of 12–22°C, averaging cooler in February than in January. These estimates are based on several series of temperature measurements made during this period at another similarly situated shallow lake (Laguna Colorada, 4,278 m) 40 km to the NNW.

**RESULTS AND DISCUSSION**

By 17 days after establishment of the enclosures, a marked difference had developed between F and NF areas in the appearance of the sediment surface. Inside the fences, the sediments were smooth and more or less uniformly tan. Over the rest of the mudflat, including the F areas, the sediment surface showed disturbance by flamingo beaks and feet and ranged in color from tan to black, the latter color due to recently exposed sulfide-rich sediments. Ciliates and amebas had become significantly more abundant in the NF areas, but no clear responses of other organisms were apparent. By the “high-water” sampling date (February 4), there was no strong evidence of a difference between F and NF areas for any taxon. But 3 wk later, after water levels had dropped and P. andinus had recommenced heavy feeding in the F areas, all major taxa (phyla) except the blue-greens became markedly and significantly reduced in abundance in the F areas, as did total microbenthos biomass (Table 1).

The abundance of the large, oval diatom *Surirella wetzeli* (Fig. 2) at Laguna Puripica Chico and its dominance of the microbenthos were notable (Table 1). Because only about 110 S. wetzeli are required to cover completely 1 mm² of sediment surface, that diatom by itself was sufficiently abundant in NF areas at the end of the experiment to form a continuous layer almost 1/2 cells thick, on average, over the sediment surface; and even in the F areas, it covered about half of the sediment surface (Table 1). This abundance perhaps should have been predictable, given the density of *P. andinus* on the lake. The genus *Surirella* is the principal food of *P. andinus* and is a dominant component of the microbenthos in many altiplano lakes (unpublished data). The correlation between their distributions is sufficiently strong that anyone wishing to collect quantities of live *Surirella* in the Central Andes could best locate these diatoms by means of a birding telescope! The commonest *Surirella* species in altiplano lakes appear to be *S. wetzeli*, *S. striatula*, and *S. sella*. Frustules, but no live cells, of *S. sella* and *S. linearis* were found in the sediments of Laguna Puripica Chico, each in numbers 5–10% of those of live *S. wetzeli*.

The size structure and taxonomic composition of the microbenthos was altered in a complex way. On the one hand, organisms very much larger than *Surirella* (nematodes) and very much smaller (amebas) both increased (F vs. NF areas, February 24) proportionately more than did *Surirella* itself. On the other hand, *Surirella* showed a greater response to flamingo exclusion than did any of the smaller diatoms, causing an upward shift in the diatom size (length–frequency) distribution. For example, on February 24 diatoms <100 µm long accounted for 15.5% of total diatom biomass in F areas but only 7.3% of it in NF areas (Mann–Whitney U test, *P* < 0.05), whereas initially (January 3) they accounted for 22.2% and 25.4% (*P* > 0.25), respectively. *Surirella* by itself accounted, at the end of the experiment, for 81.5% of total diatom biomass in F areas but 89.4% of it in NF areas (*P* > 0.05), whereas initially it accounted for 74.1% and 73.3% (*P* > 0.05), respectively.

Alteration of the microbenthic assemblage by *P. andinus* may have resulted not only from the flamingos’ grazing but also from their concomitant defecation (once every few minutes when feeding) and trampling of sediments. The separate influences of these three activities cannot be assessed with our data. One possible effect of sediment oxygenation by trampling is the inhibition of nitrogen fixation by photosynthetic purple sulfur bacteria and nonheterocystous blue-green algae, organisms often extremely abundant just beneath the surface sediments of lakes in this region that are little utilized by flamingos (unpublished data).

Several factors tended to minimize the impacts observed in our experiment. One was its brevity. Another was the unimpeded exchange of water, and microorganisms in suspension, between the F and NF areas; this occurred daily in response to the strong afternoon winds characteristic of the region. A third was the temporary avoidance of the F areas by *P. andinus* when the water level rose (represented by February 4 sampling date). If flamingos had been excluded from the *entire* lake and for a long period of time, much more extensive changes would likely have occurred.

Though the experimental system was somewhat unusual in its details (flamingos on a high-elevation salt lake), we believe our results are representative, in a conservative way, of the impact that water birds have on aquatic ecosystems. Their feeding activities can be intense in a great variety of aquatic environments, especially swamps, marshes, coastal lagoons, marine intertidal and shallow subtidal zones, rivers, and the ponds and shallow lakes of prairies, tundras, deserts, coastal plains, and other landscapes. Any well-designed experiment that excludes either a single abundant species of water bird or all water birds collectively from such a habitat is likely to show the birds to be a dominant influence. Their exclusion will produce changes in the abundance and distribution not only of their prey but also of innumerable other species. Large changes in the taxonomic composition, size structure, and productivity of the aquatic community and even in various physicochemical properties of the system often will occur. Such influences are likely to be comparable in magnitude to those exerted by fish, which have been demonstrated experimentally to be extensive (12–16).

How can water birds do this, given their limited abilities to forage in deep water and the vagility of their flocks? Four factors are important. First, in some habitats the fish community itself is strongly regulated by fish-eating birds (1). Second, birds have high metabolic and feeding rates, much higher, on a gram for gram basis, than those of fish. Third, these rates are greatest in cooler regions or seasons (or both), when their aquatic prey populations are growing and reproducing most slowly and...
therefore least able to recover from predation. Finally, the momentary feeding or predation pressure exerted by a flock of water birds can be very high, much higher than the momentary predation pressure exerted by the fish assemblage in a given water body is ever likely to be, because the momentary abundance of water birds, unlike that of fish, is not limited by the past food conditions of a given water body. Thus, a not inordinately large flock of birds visiting a water body for only a few days or weeks might have impacts on that ecosystem that persist for a year or longer (4).

This last point has a significant consequence for methodology: purely descriptive studies comparing aquatic ecosystems with water birds present (at some given moment) to similar systems without water birds are likely to prove uninformative and misleading as to the influences exerted by the birds. This stands in contrast to the wealth of insight provided by the early descriptive studies comparing lakes with and without fish (17–19). Progress in ornitholimnology will be more dependent on carefully controlled, large-scale, long-term exclosure experiments.

We thank G. Bejarano and Flora y Fauna Silvestre (Ministerio de Agricultura, La Paz) for permission to study the flamingos; A. Barrero and the personnel of Mina Laguna Verde for hospitality and logistical support; J. Keith, C. Mitchell, and T. Saire for field assistance; J. Verfallie, K. English, and C. Nuss for assistance in data reduction; M. Noffsinger and J. Alexander for nematode identification; C. Land for figure preparation; and J. Keith and G. Cox for helpful comments. The work was supported by grants from the National Geographic Society, National Science Foundation (DEB-76-02888), and San Diego State University Foundation.