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THE EFFECT OF GREBE PREDATION ON A BRINE SHRIMP POPULATION

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SUMMARY

(1) Investigations were performed at Mono Lake, California, U.S.A., to determine if the marked autumnal decline in the brine shrimp (*Artemia monica* Verrill) population was related to the annual arrival of hundreds of thousands of eared grebes (*Podiceps nigricollis* Brehm). Grebes and brine shrimp were censused through late summer and autumn of 1980 and 1981, and grebes were collected for stomach analyses. Passage times of *Artemia* through grebe stomachs were estimated by feeding dyed *Artemia* to marked grebes and collecting these grebes at intervals after they had been fed.

(2) The mean number of *Artemia* eaten per grebe per day ranged from *c.* 8000 to 70 000. The mean proportion of the *Artemia* population eaten per day tended to increase throughout the autumn, ranging from 0·5% in August to 22% in late October 1980 and from 0·02% in August to 6·6% in late November 1981.

(3) Grebe predation could account for 55–83% of the decline in *Artemia* density in 1980 and 8–27% of the decline in *Artemia* density in 1981. In both years, grebe predation could account for substantial amounts, but not all, of the observed declines in *Artemia* levels, and most *Artemia* mortality was due to other causes in 1981.

INTRODUCTION

Predation has been considered to be one of the most important factors controlling the dynamics of many animal populations (Murdoch & Oaten 1975; Varley, Gradwell & Hassell 1974; Fitzgerald 1977; Kowalski 1977; Hassell 1978; Connell 1970). Assessing the importance of predation to prey population dynamics has often proved difficult because such an assessment requires a detailed knowledge of changes in predator and prey densities through time as well as a determination of predation rates (King 1980; Lewis 1979). As a result, many analyses rely for their conclusions on indirect evidence utilizing prey life table information, potential energy intake for predators, or correlations between predator density and prey mortality rates (e.g. Varley & Gradwell 1968; Kowalski 1977; Lewis 1979; King 1980). In addition, very few studies have attempted to assign statistical confidence bounds to estimates of predation's impact on prey populations. These analyses become especially difficult when dealing with natural multi-species systems.

One approach that circumvents some of these problems is to study natural systems which contain few species and few trophic links; for example, the saline lakes of the world (Williams 1981; Vareschi 1978). We chose to study Mono Lake, a hypersaline lake located in eastern California, which has a simple trophic structure. Although little is known

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of the lake's bacteria and protozoan populations, the principal energy flow appears to begin with coccoid green algae which are eaten by brine shrimp (*Artemia monica* Verrill), which in turn are eaten by aquatic birds (Mason 1967; Winkler 1977). The brine shrimp population in Mono Lake declines precipitously every autumn, shortly after the arrival of hundreds of thousands of eared grebes (*Podiceps nigricollis* Brehm). In the following analyses, we attempt to determine if grebe predation can account for these autumnal declines in Mono Lake's brine shrimp population.

STUDY SITE

Mono Lake is a large (150 km^2), deep ($\bar{Z} = 19$ m) lake located in the Great Basin desert on the eastern slope of the Sierra Nevada in California (lat. 38°N, long. 119°W; Melack 1983). It occupies a closed tectonic basin and, prior to 1940, received most of its inflow from five streams at its western end. Since 1941, the lake's levels have been dropping as much as 60 cm year^{-1}, due to the diversion of four of these streams by the City of Los Angeles, causing the lake's salinity to increase 1·5–2% per year (Loeffler 1977). Currently, the lake's waters are almost three times as saline as the ocean, and the lake is highly alkaline (pH $\simeq$ 10) with high carbonate and sulphate levels. Surface temperatures range from nearly 0 °C in the winter to 25 °C in the summer.

The main primary producer in Mono Lake is a small coccoid green alga (*Coccomyxa*?), and small numbers of other algae are present. During the summer and autumn the principal primary consumer in open-water areas is the brine shrimp (*Artemia monica*), whose only predators are aquatic birds. The larvae of the brine fly (*Ephydra hians* Say, subgenus *Hydropyrus* Cresson) are abundant on hard substances in shallow areas around the lake's edge. In the summer, Mono Lake stratifies thermally, separating into an upper region $\leq$15 m deep with sparse phytoplankton and abundant *Artemia*, and a deep, cold region with very low light, no oxygen, few, if any, *Artemia*, and a dense suspension of viable phytoplankton. In September, the phytoplankton proliferate in the surface waters as stratification weakens, vertical mixing increases, and *Artemia* begin to decline in abundance. During the winter and early spring, phytoplankton densities are high and few *Artemia* are present in the water column.

Artemia overwinter as resting eggs which hatch in early spring (Lenz 1980, 1982). This first generation of *Artemia* produces a second generation which reaches maturity in July–August. Mature females produce mostly resting eggs from early July onward.

Up to 50 000 California gulls (*Larus californicus* Lawrence) breed at Mono Lake in late spring and early summer, but have largely vacated the lake by August. The other major bird species, including the Northern and Wilson's phalaropes (*Phalaropus lobatus* Linnaeus, *P. tricolor* Vieillot), and the eared grebe (*Podiceps nigricollis*), use Mono Lake as a migratory staging area (Winkler 1977). Migrating phalaropes reach peak abundances (over 100 000) in July and August, whereas migrating grebes reach population maxima in September, remain at high levels throughout the autumn, and leave in November or December. Because grebes reach extemely high densities (500 000–1000 000 lakewide) and can probably forage at all depths at which *Artemia* occur, we hypothesized that predation by grebes could account for autumnal declines in *Artemia* density. Our analysis of the effects of predation on this prey population was considerably simplified by two characteristics of this system: (i) recruitment to the *Artemia* population was negligible during the study period; (ii) grebes were the only abundant predators in Mono Lake during the study period.

More detailed descriptions of the ecology of Mono Lake can be found in Mason (1967); Winkler (1977); Lenz (1982); Melack (1983); and Melack, Lenz & Cooper (1984).

METHODS

We censused grebes at an index station and brine shrimp at a number of stations located throughout the lake at monthly (or less) intervals in 1981–82. All grebes within a reference area were counted from a vantage point 27 m above the lake atop a wood and plaster volcano on Krakatoa Island (Fig. 1). *Artemia* densities were estimated by taking vertical

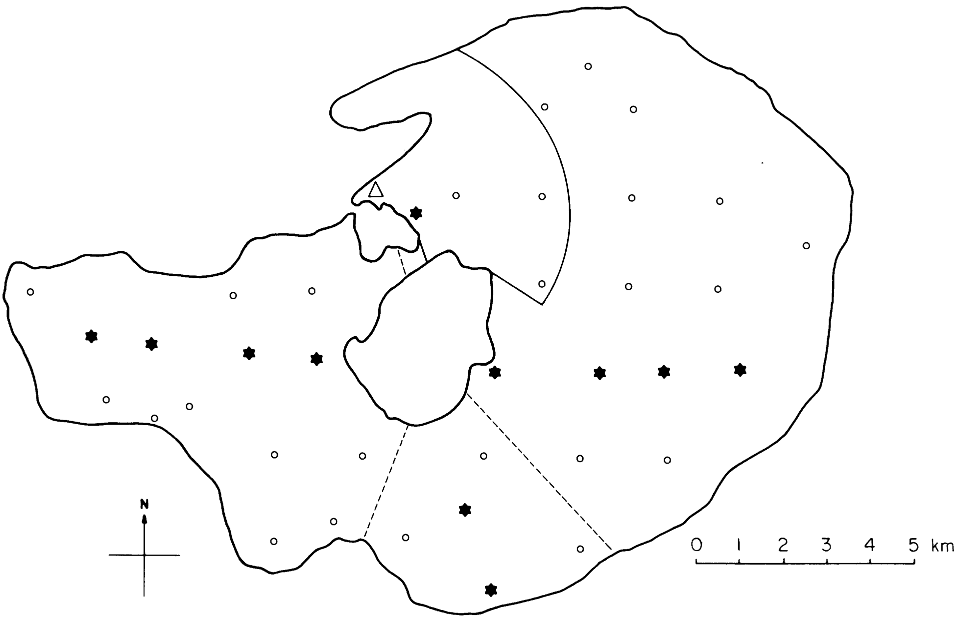

FIG. 1. Mono Lake, California, U.S.A. Stars and small circles indicate stations sampled in 1980; only starred stations were sampled in 1981. Paoha Island is the large island in the centre of the lake, Negit Peninsula is just north of Paoha Island, and Krakotoa Island is near the star just east of Negit Peninsula. The fine line in the north central part of the lake (north of Paoha Is., east of Negit Pen.) encloses the index area censused for grebes in 1981–1982. △ denotes the cove in which gut passage time studies were conducted. The dashed lines delineate the western, southern, and eastern sections of the lake.

TABLE 1. Number of stations sampled for shrimp, number of transect segments censused for grebes, and number of grebes collected for stomach analyses in 1980 and 1981

	Artemia samples	Grebe transects	Grebe stomachs
1980			
28, 29 August	29	28	5
20, 22 September	28	31	0
5 October	23	24	0
25–27 October	19	17	24
1981			
23, 24 August	11	13	9
22, 23 September	11	12	11
20–23 October	12	15	12
25 November	11	12	0

hauls with a 0·3 m diameter, 150 μm mesh, nylon plankton net from 15 or 20 m. During the stratified period (April–October) these tows sampled the entire oxygenated epilimnion. Detailed descriptions of shrimp sampling and analysis methods can be found in Lenz (1980, 1982).

In 1980 and 1981, we concentrated our attention on late summer and autumnal changes in the densities of grebes and shrimp. On four occasions in 1980 we collected shrimp samples (as above) from nineteen to twenty-nine stations located throughout the lake, and in 1981 we collected shrimp from eleven or twelve stations on each of four occasions (Table 1, Fig. 1). Shrimp samples were preserved in *c.* 5% formalin, and shrimp numbers were determined by direct counts or by volume displacement (Lenz 1980). Other analyses indicate that shrimp densities estimated from vertical tows are approximately 70% of shrimp densities estimated from a Schindler–Patalas trap (Lenz 1982). Consequently, shrimp densities determined with vertical hauls were divided by 0·7 to correct for net filtration efficiency (Lewis 1979). Grebes within 25 m of each side of the boat were counted on transects connecting the shrimp sampling stations. At the boat speeds used (*c.* 22 km h^{-1}), grebes did not have time to swim out of the transect swath before being counted. We attempted to compensate for diving grebes by counting grebes as they dived and surfaced, and by counting rings of ripples left by diving grebes. Densities obtained by this method agree well with densities obtained by other methods (discussed below).

Grebes were collected at shrimp sampling stations in late October 1980 and in August, September, and October 1981 (Table 1). In addition, grebes were collected in the western portion of the lake in August 1980. After a grebe was shot, the digestive tract was immediately removed, injected with formalin, and placed in a jar of 5–10% formalin. Examination of entire digestive tracts revealed that all food items were concentrated in the muscular stomach. Since grebe guts contained prey items in various stages of decomposition, we defined an *Artemia* individual as three or more thoracic segments and associated phyllopods. Initially, stomach contents were placed in a series of Petri dishes and all food items were counted and identified at 6–12X under a dissecting scope. This process was exceedingly time-consuming, however, because grebes eat large quantities of their own feathers. Therefore, to facilitate counting brine shrimp in the stomachs, we boiled stomach contents in 10% potassium hydroxide, stained remaining items with an iodine solution (1·6 g I_2, 10 g KI, 14 ml water), and counted prey items in a concentrated brine at 6–12X under a dissecting microscope. This procedure effectively hydrolyses all protein, converts the chitin in arthropod integument to chitosan, and stains the chitosan brown (Richards 1951). Comparison of counts obtained from both procedures reveal almost identical results.

Gut passage times were determined for one grebe in September 1981, and for four grebes in October 1981. Grebes were captured in the early morning hours just prior to daybreak. Captured grebes were colour-marked with vital stains (Rhodamine B, malachite green, methylene blue), force fed *c.* 200–300 shrimp dyed with vital stains (as above) and released, after daybreak, into a small cove containing hundreds of grebes (Fig. 1). These marked grebes were subsequently shot at intervals, and their stomachs were immediately examined for the presence of dyed shrimp. (In laboratory studies we found that *Artemia* stained with methylene blue would remain stained for at least several hours in concentrated hydrochloric acid.) Stomach contents of these grebes were then preserved in 5% formalin for subsequent analyses. Because grebes do not feed at night, we were able to compare gut passage times determined with this method to gut passage times estimated from diel variations in prey numbers in grebe stomachs.

These methods indicate the amount of time for complete disintegration of all ingested *Artemia*. The literature indicates that, after an initial time period when all ingested prey items are recognizable, the number of recognizable prey items in bird stomachs usually declines exponentially (Custer & Pitelka 1975; Swanson & Bartonek 1970; Coleman 1974). The proportion of total prey ingested which are found in the stomach was calculated by the method of Mook & Marshall (1965) using data presented in Coleman (1974). The product of this proportion (calculated from literature data) and the amount of time for disintegration of all ingested prey (obtained from our gut passage studies) provided us with an estimate of the average amount of time that brine shrimp persist in grebe stomachs. In addition, the four grebes used in gut passage time estimates (see preceding paragraph) did not feed during the experimental period as evidenced by declining numbers of brine shrimp in their stomachs. Consequently, we were able to calculate independently the mean persistence time of brine shrimp in grebe stomachs from this curve (Elliott & Persson 1978).

The number of brine shrimp eaten per grebe per day (K_D) was estimated as

$$K_D = K_G\left(\frac{T_d}{T_p}\right) \qquad (1)$$

where K_G is the number of brine shrimp per grebe stomach, T_d is the number of daylight hours in a day, and T_p is the average amount of time it takes for brine shrimp to disintegrate to fewer than three thoracic segments in a grebe stomach (mean persistence time, in hours).

In these analyses we treat the western, eastern, and southern sections of the lake separately whenever possible, as these sections of the lake tend to support quite different densities of phytoplankton, shrimp and birds (unpublished data). Mean areal lakewide densities of brine shrimp and grebes were calculated by weighting the average densities of brine shrimp and grebes in each section by the proportion of the lake's total area in each section. Approximately 29% of the lake's total area is in the western section, 12% is in the southern section, and 59% is in the eastern section (Fig. 1). Lakewide estimates of grebe consumption rates were computed by weighting the average number of shrimp per grebe gut from each section of the lake by the proportion of the lake's grebe population found in each section.

The proportion of the shrimp population eaten by grebes per day (p_A) was estimated from:

$$p_A = \frac{XK_D}{N} \tag{2}$$

where X is the grebe density (no. m^{-2}), N is the shrimp density (no. m^{-2}), and K_D is as above. Again, whenever possible, p_A was calculated separately for each section of the lake and lakewide estimates of p_A represent weighted averages given the proportion of the lake's *Artemia* population in each section. The proportion of the decline in *Artemia* densities attributable to predation (p_Δ) was estimated from:

$$p_\Delta = \frac{(X_1 K_{D1} + X_2 K_{D2})/2}{(N_1 - N_2)/(t_1 - t_2)} \tag{3}$$

where X_1, K_{D1}, N_1 and X_2, K_{D2}, N_2 represent grebe densities, grebe daily consumption rates, and shrimp densities at times t_1 and t_2, respectively. We used weighted lakewide average values for X, K_D, and N in eqn (3). In eqns (2) and (3), K_D values were not available for late September–early October 1980 and for November 1981. In these cases, we performed the calculations in two ways: (i) By assuming the K_D values for September and early October 1980 were similar to those measured in September–October 1981 and that late November 1981 values were similar to those measured in late October 1980, or (ii) Interpolating or extrapolating K_D values from data obtained in the same year as the missing values. These assumptions and calculations are covered thoroughly in the Results section.

Standard errors for estimates of p_A and p_Δ were calculated by propagating estimates of variation associated with grebe density, shrimp density, and the number of shrimp per grebe stomach through these analyses (Bevington 1969). In most instances we assumed that variables used in eqns (1)–(3) were independent, because the data were inappropriate for analysing covariance between measured variables. When it was possible to calculate the covariance of measured variables, inclusion of covariance terms had little effect on standard error to mean ratios.

RESULTS

Migrating eared grebes, returning from breeding grounds in the northern Great Plains and Great Basin, begin arriving at Mono Lake in July and August and increase to high densities by September and October (Fig. 2). Coincident with the arrival of hundreds of thousands of these migrating grebes, shrimp densities decline precipitously, reaching low levels by October (1980) or November (1981). The decline in grebe numbers at the index station in October–November 1981 was due to grebes moving to other parts of the lake rather than to grebes leaving the lake (Figs 3, 4). Grebes do leave the lake *en masse* in late autumn, reducing population levels by >97%. The timing of grebe departure varied from 1980–81, perhaps related to year-to-year differences in shrimp levels (Fig. 3). In 1980, shrimp densities had declined to low levels by late October and most grebes had departed by mid-November, whereas in 1981 shrimp did not reach low levels until late November, and the grebes did not leave until December. Shrimp and grebe densities remain low throughout the winter (Fig. 2). Adult shrimp densities begin to increase in late May and early June as the first generation of shrimp matures and continue to increase through late

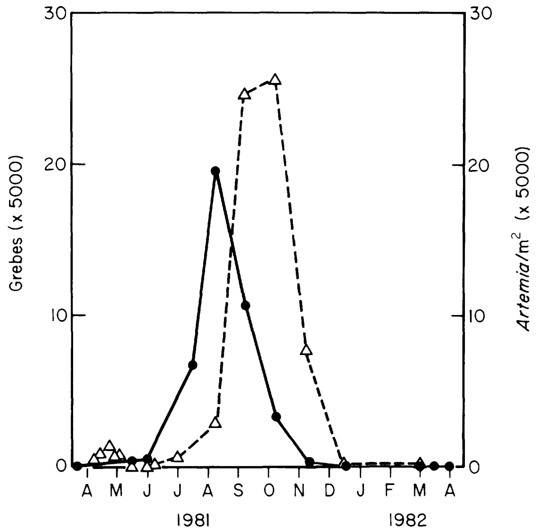

FIG. 2. Numbers of grebes (△) in the index area and mean lakewide densities of *Artenia* (●) in 1981–1982.

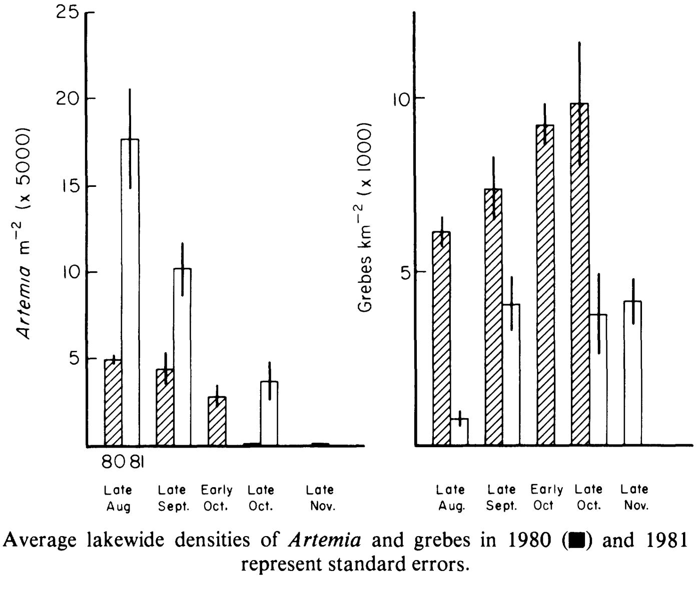

FIG. 3. Average lakewide densities of *Artemia* and grebes in 1980 (■) and 1981 (□). Bars represent standard errors.

summer as the second generation matures. Except for a minor peak of north-bound migrants in late April–early May, grebe densities remain relatively low until July when migrating grebes begin to arrive.

Autumnal shrimp densities were much higher in 1981 than in 1980, and remained at high levels until later dates in 1981 (Fig. 3). Grebe densities, on the other hand, were much higher in 1980 than 1981 (Fig. 3). From our census data we estimated that 598 000 grebes were on the lake on 22 September 1981, which agrees well with an estimate of 513 000

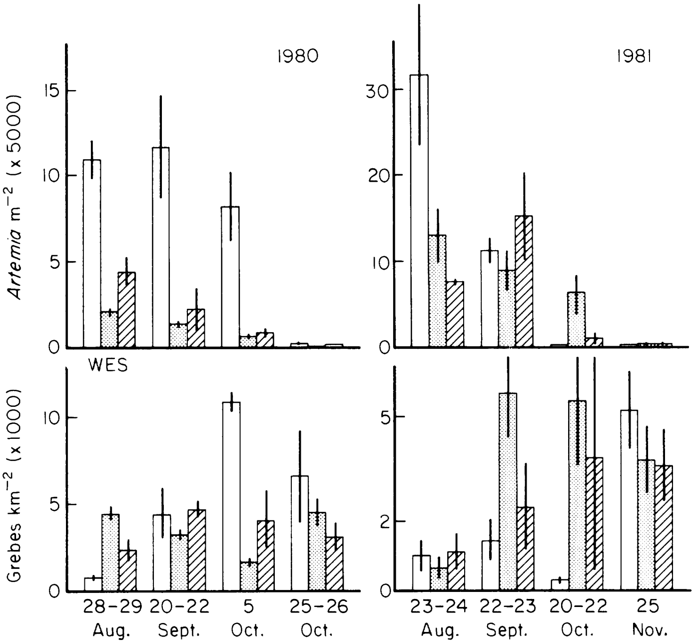

FIG. 4. Densities of *Artemia* and grebes in different sections of the lake in 1980 (left) and 1981 (right): Western (□), eastern (▦) and southern (■) sections. Bars represent S.E.

grebes determined independently from a shore-based census on 18 September 1981 (D. DeSante, personal communication, Point Reyes Bird Observatory). Additional independent surveys conducted from a boat by J. Jehl, Jr (Hubbs-Sea World Research Institute, personal communication) produced population estimates of 410 000–500 000 grebes on 21 September 1981, and 627 000–750 000 grebes on 9 October 1981.

There were also differences in the abundance of both brine shrimp and grebes among different lake sections. In 1980, shrimp were consistently more abundant in the western section of the lake than in the eastern section, while grebes were more abundant in the eastern section in late August but had become more abundant in the western section by early October (Fig. 4). In 1981, shrimp were more abundant in the western than eastern section in August, but the opposite was observed in late October. Grebe densities in the western and eastern sections were comparable in late August and late November, but grebes were considerably more dense in the eastern than western section in late September and late October. Our observations indicate that lakewide patterns of grebe distribution may persist for up to 1 week, but that shifts in their distribution become apparent when censusing at biweekly to monthly intervals (Fig. 4).

From 75 to 80% of the grebes collected in 1980 had diets dominated by shrimp, whereas 90% of the grebes collected in 1981 had diets dominated by shrimp (D. W. Winkler and S. D. Cooper, unpublished). Remaining grebes had diets dominated by brinefly (*Ephydra hians*) larvae, brinefly pupae, or terrestrial arthropods. The numbers of shrimp found in grebe stomachs were very similar in August of both years (Fig. 5). The number of shrimp per grebe stomach increased substantially through September and

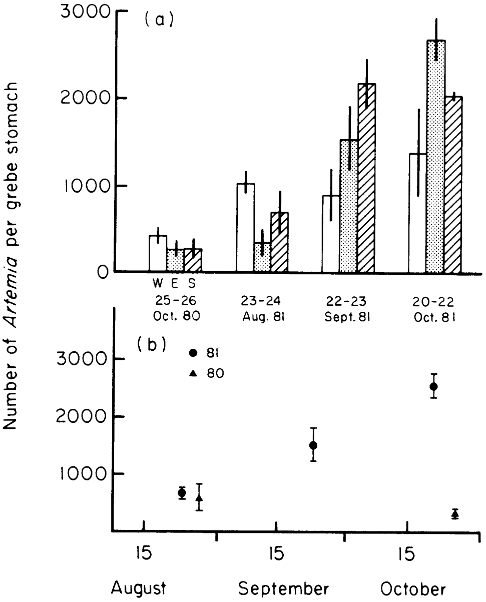

FIG. 5. The number of *Artemia* per grebe stomach ($\bar{X}$ ± S.E.) for each section of the lake (a) or lakewide (b).

October 1981. Data collected in late October 1980 indicate low grebe consumption rates at a time when shrimp levels were low, just prior to grebe departure. At some times there were section-to-section differences in grebe consumption rates (Fig. 5).

On 23 September 1981, a colour-marked grebe collected 4·5 h after it had been fed dyed shrimp contained no dyed shrimp. On 23 October 1981, we found dyed shrimp in grebes collected 20, 35, and 60 min after being force-fed dyed shrimp but not in the grebe collected after 120 min. This suggests that all ingested shrimp disappear within 1–2 h. Analysis of the stomach contents of these four grebes reveals a steady decline in the number of shrimp per grebe stomach, suggesting a prey disappearance time of approximately 2 h. In other investigations we found that grebes collected at night did not contain shrimp, even though nearly all grebes collected during the day contained them, suggesting that grebes do not feed at night (D. W. Winkler & S. D. Cooper, unpublished). Three grebes collected approximately 0·5–1 h after sunset on 26 October 1980 did not contain shrimp. Grebes vary in the times they cease feeding in the evening, but our observations of diel feeding patterns suggest a prey disappearance time on the order of 1 h. The above observations suggest that all brine shrimp disappear from grebe stomachs within 1–2 h.

As a first step in calculating the mean persistence time of brine shrimp in grebe stomachs, we selected four prey types from Coleman (1974, Table 1) which were either soft-bodied (earthworms) or which exhibited similar disintegration rates as brine shrimp in grebe stomachs (weevils, houseflies, spiders). Using prey disintegration curves for these prey and our estimated total disintegration times (see previous paragraph), we calculated a mean persistence time of 19–38 min for brine shrimp in grebe stomachs (see Methods).

Our own data on the persistence of brine shrimp in grebe stomachs was well described by the equation.

$$y = 263\, e^{-0{\cdot}04x} \quad (r^2 = 0{\cdot}91) \qquad (4)$$

where y is the number of shrimp in grebe stomachs and x is the time in minutes. Average shrimp persistence time was calculated to be 1/0·04 or 25 min (Elliott & Persson 1978). Because our limited data on brine shrimp persistence in grebe guts is generally supported by literature data (see above), we used a mean persistence time of 25 min in the following calculations.

We assumed that grebes exhibited similar feeding patterns in 1980 and 1981; consequently, stomach content data from September and late October 1981 were extrapolated to September and early October 1980. We assumed that consumption rates of grebes in late November 1981 were most similar to those observed in October 1980, because brine shrimp densities at these two times were similar and because grebe emigration occurred shortly thereafter.

Because *Artemia* levels were much lower in 1980 than in 1981 and because grebes ate more alternative prey in 1980 than 1981, these extrapolations may have overestimated the effect of grebes on the *Artemia* population in 1980. On the other hand, grebe consumption rates in 1981 greatly increased at the same time that *Artemia* levels were drastically declining. To explore all possibilities, we also performed the analyses using gut content values for late September–early October 1980 interpolated from the gut content data acquired for late August and late October 1980, and we extrapolated gut content data for late October 1981 to late November 1981 (Tables 2, 3).

The mean number of *Artemia* eaten per grebe per day ranged from *c.* 8000 in late October 1980 and late November 1981 to *c.* 70 000 in late October 1981 and early October 1980 (Table 2). The mean proportion of the *Artemia* population eaten per day

TABLE 2. Calculated number of *Artemia* eaten per grebe per day (K_D) and calculated percentage of Mono Lake's *Artemia* population eaten by grebes per day (100 p_A) in 1980 and 1981. Means ± S.E. are shown. Numbers in parentheses are estimates interpolated or extrapolated from gut content data collected in the same year (see text)

	Number of *Artemia* grebe^{-1} day^{-1} (K_D)	% of *Artemia* population eaten/day (100 p_A)
1980		
28, 29 August	18500 ± 8000	0·5 ± 0·2
20, 22 September	43600 ± 8900†	1·4 ± 0·4†
	(13900 ± 5200)	(0·5 ± 0·2)
5 October	70700 ± 6000†	4·6 ± 1·1†
	(11600 ± 3700)	(0·8 ± 0·3)
25–27 October	8000 ± 1700	22 ± 8
1981		
23, 24 August	20900 ± 3300	0·02 ± 0·007
22, 23 September	43600 ± 8900	0·3 ± 0·1
20–23 October	67600 ± 5700	1·3 ± 0·6
25 November	7600 ± 1600*	6·6 ± 2·1*
	(59900 ± 5100)	(52 ± 13)

* Using gut content data from 1980.
† Using gut content data from 1981.

TABLE 3. Mean change in the density of *Artemia* (± S.E.) and percentage of the change in *Artemia* density (100 p_Δ) attributable to grebe predation ($\bar{X}$ ± S.E.) in 1980 and 1981

	Decline in *Artemia* density day^{-1} (no. m^{-2})	% of decline attributable to predation (100 p_Δ)
1980		
28 Aug.–21 Sept.	90 ± 200	(see text)
21 Sept.–5 Oct.	588 ± 391	83 ± 56
5 Oct.–26 Oct.	658 ± 147	55 ± 14
28 Aug.–26 Oct.	410 ± 30	24 ± 7*
1981		
23 Aug.–22 Sept.	1244 ± 568	8 ± 4
22 Sept.–20 Oct.	1172 ± 338	18 ± 7
22 Oct.–25 Nov.	528 ± 169	27 ± 12
22 Oct.–25 Nov.	528 ± 169	47 ± 18†

* Estimate based only on 1980 data.

† Estimate assumes number of *Artemia* per grebe stomach in November 1981 = number of *Artemia* per grebe stomach in late October 1981.

tended to increase throughout the autumn, ranging from 0·005 in August to 0·22 in late October 1980 and from 0·0002 in August to 0·07 in late November 1981 (0·52 if we extrapolate from October's gut content data). This trend was apparent regardless of which estimates were used.

Because the decline in brine shrimp density from 28 August to 21 September 1980 was insignificant, it was impossible to estimate the proportion of this 'decline' which could be attributed to grebe predation. In the remainder of 1980, grebe predation could account for 55–83% of the decline in shrimp density, whereas in 1981 grebe predation could account for 8–27% of the decline in shrimp density (Table 3). If we assume that the distribution of p_Δ is approximately normal, then the limits for the 95% CL for mean p_Δ would encompass 0 and 1 for September–early October 1980 and would be 0·27 and 0·73 for the early to late October interval. In 1981 the upper limits would range from 0·16 to 0·51, the lower from 0 to 0·04. These analyses suggest that grebe predation could account for substantial amounts, but not all, of the decline in shrimp density. In 1981 there was a large proportion of shrimp mortality which could not be accounted for by grebe predation, and grebe predation was not primarily responsible for autumnal shrimp declines.

DISCUSSION

Before we discuss the basic conclusions of this study we should consider some of the sources of error associated with our estimates of brine shrimp density, grebe density, and grebe consumption rates used to calculate p_A and p_Δ. We believe our collection and processing methods provided good estimates of brine shrimp densities and grebe stomach contents, but grebe populations were often difficult to census and we have limited data on prey persistence times in grebe stomachs. Our 1981 grebe censuses agree well with censuses conducted independently (see Results), and lakewide population estimates agree well with estimates published previously (Winkler 1977). However, grebes are very mobile, and any census may underestimate grebe densities by failing to consider the proportion of the grebe population underwater. Limited time budget data suggest that, in the worst possible case, we may miss no more than 20–33% of the birds, which would have little effect on our estimates of p_A and p_Δ (D. W. Winkler & S. D. Cooper, unpublished). Data on prey persistence in grebe stomachs are difficult to obtain because grebes are difficult to capture; consequently, our estimates of gut passage times are based on a small sample size. As an independent check on our consumption rate estimates, therefore, we calculated daily energetic requirements for grebes using equations in Kendeigh, Dol'nik & Gavrilov (1977). Our estimates of grebe energetic requirements included energetic costs and/or benefits associated with existence metabolism, moulting, swimming, diving, and fat deposition with adjustments for the efficiency of digestion. These estimates were compared to estimates of grebe energetic intake calculated from our consumption rate estimates and length–weight and weight–energy conversion factors for Anostraca (Mason 1963; Cummins & Wuycheck 1971). Mean estimated dietary requirements for eared grebes in 1981 (125·7 kcal grebe^{-1} day^{-1}) agree closely with independently-determined intake rates (115·2 kcal grebe^{-1} day^{-1}), corroborating our estimates of grebe consumption rates. Grebe consumption rates of 70 000 shrimp grebe^{-1} day^{-1} require grebes to consume two shrimp every daylight second. This feeding rate may seem high, but male shrimp outnumber females in the autumn and as many as four to five male shrimp are amplexed with each female shrimp. Because the shrimp usually swim around in 'packages' of two to six, and because shrimp densities are high, it is quite possible for grebes to capture a number of shrimp simultaneously.

The analyses indicate that migrating grebes had a larger effect on the shrimp population in 1980 than in 1981, owing to the higher grebe densities and lower shrimp densities in 1980. In some respects this resembles other situations where predators eat large proportions of prey populations when prey levels are low, but have little effect when prey are abundant (Pulliam & Parker 1979; DeSteven 1983; Neave 1953; Karban 1982). Despite large standard errors for our estimates of p_A, there was also a distinct pattern of increasing mean p_A values through the autumn as shrimp densities declined. Many studies have reported an increase in the proportion of the prey population eaten with decreasing prey densities, a situation presumed to result in unstable predator–prey linkages (King 1980; Murdoch & Oaten 1975; Holling 1959). In the case of Mono Lake, however, grebes apparently play little role in the regulation of the brine shrimp population. By the time the grebes arrive *en masse*, the brine shrimp females have already spent 1–3 months producing overwintering cysts (resting eggs) and the grebes consume only a small proportion of the shrimp population during most of the time they are present. Consequently, grebes probably have little effect on shrimp recruitment in the following spring. This is corroborated by the extremely high abundance of shrimp eggs in bottom sediments, even in years with low naupliar recruitment (P. H. Lenz & G. Dana, personal communication).

At first sight, the 1981–82 data (Fig. 2) suggest a cause–effect relationship between the arrival of migrating grebes and autumnal declines in shrimp density. This study, however, shows that shrimp levels in 1981 were not declining due to grebe predation. What, then, is responsible for this autumnal decline in shrimp density? Mason (1967) suggested that toxic quantities of botulin may be injected from the hypolimnion into the epilimnion during autumnal mixing; however, subsequent investigations showed no botulin or other toxic substances in hypolimnetic water. Autumnal shrimp declines were not precisely associated with autumn overturn because shrimp levels declined from late August to late November 1981, while autumn overturn did not occur until *c.* 20 October (unpublished data). We did observe, however, large numbers of dead shrimp floating at the surface of the eastern section of the lake directly after overturn. Possibly, the senescence of mature *Artemia* in conjunction with changing physical-chemical conditions account for autumnal *Artemia* declines (P. H. Lenz & J. Melack, personal communication).

In summary, in 1980 grebe predation could account for large proportions of the decline in *Artemia* density (55–83%), whereas in 1981 grebe predation accounted for smaller proportions of the decline in *Artemia* density (8–27%). In both years grebe predation could account for substantial amounts, but not all, of the observed decline in *Artemia* levels, and, in 1981, most *Artemia* mortality was due to other causes. Grebe predation may increase the rate of *Artemia* declines, but probably has little long-term impact on the size of Mono Lake's *Artemia* population.

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