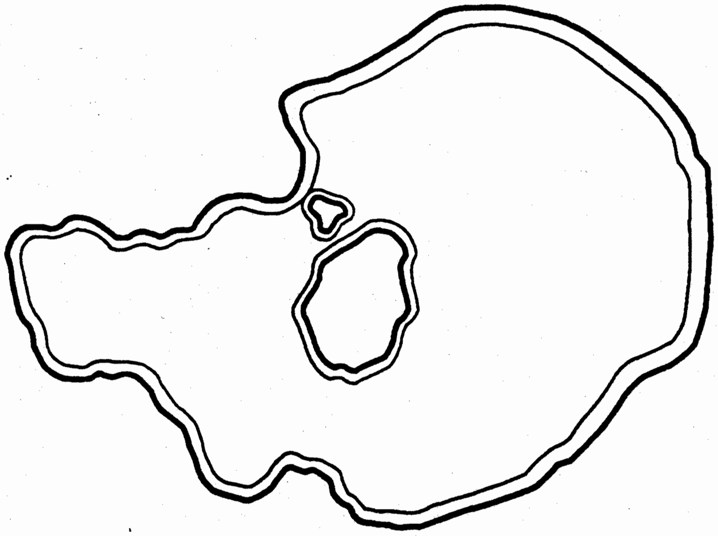
An Auxiliary Report
Prepared for the

MONO BASIN WATER RIGHTS EIR

Feeding Limitations and Ecology of Red-Necked Phalaropes at Mono lake, with Incidental Observations on Other Species



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Mono Basin EIR Auxiliary Report No. 11

An Auxiliary Report Prepared for the Mono Basin Water Rights EIR Project

This auxiliary report was prepared to support the environmental impact report (EIR) on the amendment of appropriative water rights for water diversions by the City of Los Angeles Department of Water and Power (LADWP) in the Mono Lake Basin. Jones & Stokes Associates is preparing the EIR under the technical direction of the California State Water Resources Control Board (SWRCB). EIR preparation is funded by LADWP.

SWRCB is considering revisions to LADWP's appropriative water rights on four streams tributary to Mono Lake, Lee Vining Creek, Rush Creek, Parker Creek, and Walker Creek. LADWP has diverted water from these creeks since 1941 for power generation and municipal water supply. Since the diversions began, the water level in Mono Lake has fallen by 40 feet.

The Mono Basin water rights EIR examines the environmental effects of maintaining Mono Lake at various elevations and the effects of possible reduced diversions of water from Mono Basin to Owens Valley and the City of Los Angeles. Flows in the four tributary creeks to Mono Lake and water levels in Mono Lake are interrelated. SWRCB's decision on amendments to LADWP's water rights will consider both minimum streamflows to maintain fish populations in good condition and minimum lake levels to protect public trust values.

This report is one of a series of auxiliary reports for the EIR prepared by subcontractors to Jones & Stokes Associates, the EIR consultant, and contractors to LADWP. Information and data presented in these auxiliary reports are used by Jones & Stokes Associates and SWRCB, the EIR lead agency, in describing environmental conditions and conducting the impact analyses for the EIR. Information from these reports used in the EIR is subject to interpretation and integration with other information by Jones & Stokes Associates and SWRCB in preparing the EIR.

The information and conclusions presented in this auxiliary report are solely the responsibility of the author.

Copies of this auxiliary report may be obtained at the cost of reproduction by writing to Jim Canaday, Environmental Specialist, State Water Resources Control Board, Division of Water Rights, P.O. Box 2000, Sacramento, CA 95810.

FEEDING LIMITATIONS AND ECOLOGY OF RED-NECKED PHALAROPES AT MONO LAKE, WITH INCIDENTAL OBSERVATIONS ON OTHER SPECIES

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EXECUTIVE SUMMARY/ABSTRACT

The flocks of migratory birds attracted to Mono Lake have long been considered an important biological and aesthetic resource. Despite this fact, recent reviews of the ecology of Mono Lake (e.g., National Academy of Sciences, 1987) note that previous data on prey preferences and feeding rates are inadequate for properly evaluating the effects of decreasing lake level on birds at Mono Lake through salinity effects on prey species. Data on critical prey densities has been lacking altogether. This report details the results of studies specifically designed to address this lack of quantitative data on the effects of declines in prey density and availability on feeding of Red-necked phalaropes, one of the species cited in the NAS Report as likely to be affected first by declines in lake level.

Speculation that brine shrimp are an adequate alternate prey for Red-necked phalaropes in the event of salinity-related declines in brine fly densities at Mono Lake, was shown by laboratory feeding experiments to be false. Red-necked phalaropes rejected brine shrimp as a food source, unless they were within 5 grams of their starvation weight. Phalaropes maintained on a diet of brine shrimp alone lost weight steadily until removed from the diet or until death ensued. In contrast, birds fed diets consisting of adult brine flies maintained their body weight.

Since birds in the laboratory were fed *ad libidum* on densities far exceeding those which are available in Mono Lake, and where energetic costs are minimal these values probably represent an underestimate of potential weight losses of a free-living phalarope at Mono Lake attempting to subsist on a diet of brine shrimp alone. However, Red-necked phalaropes unable to meet their minimal metabolic requirements on brine flies would almost certainly desert Mono Lake before switching to a diet consisting largely of brine shrimp.

Diet data from phalaropes collected in the field, while feeding, corroborate lab-based preference studies, as well as extending Winkler (1977) and Jehl's (1986) assessments of this specie's diet; brine fly larvae constitute a mean 75% by volume of gut contents of collected animals, and occur in 100% of the samples, with brine fly pupae second in predominance, and brine fly adults third. Brine shrimp appeared in quantities too small to measure in the gut contents of only 2 of 38 birds. If different life stages of the brine fly are considered different prey types, then Red-necked phalaropes at Mono Lake might be considered to be pursuing a mixed diet, but it remains clear that lake levels which maximize brine fly production are likely to benefit these birds.

Systematic censuses and observations of feeding birds conducted at Mono Lake demonstrated that phalaropes curently feed in the northeastern sector of the lake. Red-necked phalaropes are feeding just above, or just offshore of, submerged tufa blocks. Prey sampling conducted by Rubega and Obst (unpub.), and Herbst (1992) demonstrated that densities of water-carried larvae were higher in this area than in tufa-free areas of the lake. Prey sampling and feeding rate measures indicate that submerged tufa blocks may be an important source of emergent adult brine flies for juvenile California gulls as well as for phalaropes.

Comparison of these data *with* Jehl's (1988) data indicates that there has been a shift of bird use from the western end of Mono Lake to the eastern end. This shift is apparently coincident with the uncovering of tufa shoals at the Old Marina, and between Black Point and County Park, and implies that the location of feeding activities may be controlled by the availability of submerged tufa blocks as prey

habitat and hence sources of preferred or perhaps critical prey densities. While tufa shoals found in the northeastern end of the lake may provide sufficient prey to sustain some use of Mono Lake by Red-necked phalaropes, it is notable that much of the aesthetic value of the birds is lost to the general public, since this area of the lake is accessible only by boat or by four-wheel drive vehicle. Inundating tufa shoals at the western end of the lake may restore the formerly highly-visible flocks of birds to that area.

Laboratory based feeding experiments designed to examine the effects of changes in prey density on feeding efficiency and feeding rates demonstrated that prey density and bird sex interact to significantly affect feeding. Female Red-necked phalaropes experience a decrease in feeding efficiency at a prey density of 5 larvae/liter of water. This prey density is 100 times that which is, on average, available at Mono Lake presently (Herbst, pers. comm.). Also, females reach an upper limit on feeding rate at a prey density which is 5000 times that which is, on average, currently available at Mono Lake.

In order to validate the results of these laboratory tests, data were gathered in the field on the feeding performance of free-living Red-necked phalaropes. The data indicate that mean feeding efficiencies of birds feeding in the lab on brine fly larvae at our lowest test density (50%) are one and a half times greater than those in the field (33%). This result implies that either i) laboratory experiments accurately predict decreasing feeding efficiency with decreasing prey density or ii)that values for feeding performance across changing prey densities from an artificial laboratory situation are <u>oversetimates</u> of how "well" phalaropes can do at a given prey density, and therefore laboratory experiments are very likely to <u>underestimate</u> the negative effects of decreasing prey density in a field situation, or both.

These important results indicate that, despite what has been referred to as "superabundance" of prey at Mono Lake, under current conditions Red-necked phalaropes are limited in their ability to maximize their feeding rate, an ability that may be important to any migrating shorebird using Mono Lake as a fueling stop. **Lake level impacts should not be assessed on the assumption that current brine fly densities at Mono Lake are non-limiting to Red-necked phalaropes.**

In order to examine the possibility that the numbers of birds at Mono Lake have changed we compare counts of phalaropes, grebes, and waterfowl to Jehl's (1986, 1988) census data. Our limited data suggests that numbers of Red-necked phalaropes using Mono Lake has not changed, but we have no good estimate of the turnover rate of Red-necked phalaropes (and hence the total number of birds visiting Mono Lake) and no way of knowing whether turnover rate has changed over the years diversions have been taking place..

In contrast, our data suggest that there may have been substantial declines in the number of Wilson's phalaropes and Eared grebes at Mono Lake, or large shifts in the timing of their use of Mono Lake. We have no data appropriate for determining the cause of this apparent change in numbers.

Numbers of waterfowl at Mono Lake are very low; if historical and anecdoctal accounts of waterfowl abundance in the early 1900s are true, there has been a massive decline of these birds.

INTRODUCTION TO THE REPORT

Breeding birds at Mono Lake may experience impacts of water diversions through such varied and interacting factors as availability of suitable nesting habitat, predation, and prey availability [e.g., California gulls; see NAS (1987) and CORI (1988) reports for a review.] In contrast, birds using Mono Lake as a migratory stop-over (e.g., phalaropes) will be primarily influenced by effects on their prey. Since food is what they come to Mono Lake for, the limits of their ability to compensate for changes in the prey base will determine the nature, and onset, of diversion effects.

Previous research and Background for these studies

To date, little attention has been given to determining where these limits lie, although attempts have been made to link available data to the potential responses of birds to changing prey composition at Mono Lake. For instance, the report of the National Academy of Sciences panel (1987) makes the assumption that Red-necked phalaropes will take brine shrimp if the more salinity-vulnerable (Dana and Lenz 1986, Herbst 1986) brine flies become unavailable. This attempt to predict responses to changing prey availability was based on an inference made by Jehl (1986; p.192) as part of a discussion of the overwhelming predominance of brine flies in Red-necked phalarope diets. The dietary preference of Red-necked phalaropes for flies is well established at Mono Lake (Winkler et al. 1977, Jehl 1986, also this report, see Section 4, Table 4.1) and elsewhere (Wetmore 1925, Boula 1984). Brine shrimp have been found in Red-necked phalarope guts only in limited instances (Jehl 1986) and only in small amounts (Winkler 1977). The idea that a large-scale switch to an obviously less-preferred prey type was a tactic functionally available to phalaropes was never tested.

The NAS Report also notes a complete lack of information about what constitute "critical prey densities" for Red-necked phalaropes and other birds at Mono Lake. The report fails altogether to address an important question raised by Hurlbert (1991): what defines a "critical prey density" and how do we know whether or not the birds have already felt the effects of water diversions? Most previous authors have noted the apparent high prey densities at Mono Lake; in fact, it has become common to refer to the prey base at Mono Lake as "superabundant" (e.g., CORI Report 1988). The difficulty with the apparent abundance of prey at Mono Lake is that field observations of animals feeding on what we <u>assume</u> to be a non-limiting food supply will give us no information on the densities at which they become limited.

This report therefore addresses these and other linked issues through data collected in both laboratory and field situations to address dietary limitations, and functional and behavioral responses to changing prey densities and availability.

2. PREY SWITCHING: EXPERIMENTAL EVIDENCE OF DIETARY LIMITATIONS

2a. Brine shrimp diet

During experiments initially designed to address the effects of changing prey density on feeding behavior and efficiency (see Section 3) it became apparent that Red-necked phalaropes were very reluctant to eat brine shrimp. Figure 2.1 shows that there was a significant decline in attempt rate with increasing weight of the bird, even at very high prey densities. There was a notable increase in attempt rate at weights below about 31 g; highest attempt rates occurred at weights below 26 g, that is, when birds were within 5 to 6 g of death by starvation. We therefore examined weight changes in birds kept on 2 different experimental diets.

Examination of the daily weight changes of birds kept on a maintenance diet consisting exclusively of brine shrimp (see Methods: Section A1) revealed that Red-necked phalaropes cannot even maintain weight on this diet, much less accomplish the energetic gain we can reasonably expect a migratory bird to be using Mono Lake for. Red-necked phalaropes on *ad libidum* diets of brine shrimp lost weight steadily until they reached weights of 18 to 20 g, at which point death ensued; after this outcome for 12 individuals, birds were removed from the diet when their weights reached 20 g. The mean weight of birds fed brine shrimp showed a significant decline over the period they were kept on the diet (Figure 2.2). Mean weight losses over the initial 3 days of the trial were most severe, at 2.3 g/day. This is consistent with the birds' reluctance to eat in the previously described experiment. Indeed, mean weight at day 3 was 25.9 g, aproximately the same weight at which attempt rates began to increase. Thereafter mean weight loss was

1.8 g/day. These losses were observed even in birds which consumed up to 3 times their initial body weight in brine shrimp over a 12 hour period (Obst, Inouye and Rubega, unpub.). Consequently, weight loss over this period cannot be attributed to self-starvation, but rather to the lack of nutritional sufficiency of the prey.

According to Winkler's (1977; p. 101-104) flight range model, all the birds used in this experiment would have reached their fat-free weight at approximately 25 g. If his model of flight range capabilities is accurate, free-living birds in this condition would not even have been able to meet the energetic demands of the flight to the Great Salt Lake, or to San Francisco Bay, the two closest alternate staging areas.

Interestingly, final mean weight for the brine shrimp-fed group is 6 grams less than the lowest weight Jehl (1986) recorded for wild-caught birds. Final mean weight for the brine fly-fed group (see below), on the other hand, is well within the range for his samples.

2b. Brine fly diet

Weights of birds maintained on a diet consisting only of adult brine flies were strikingly different from birds kept on brine shrimp diets. Brine fly-fed birds neither gained nor lost weight over the 9 day experimental period (Figure 2.3). While Figure 2.3 shows a slight decline in mean weight between days 1 and 6 (mean weight change per day = -0.8 ± 1.1 g) by day 9 mean weight is equivalent to that of day 1 (35.689 ± 5.7 vs. 36.4 ± 4.6 g, n=9) (2-tailed paired t-test; $t = 0.034$, $P > 0.10$; not significant). It should be noted that on day 6 mean weight of these birds exceeded that of birds fed brine shrimp by 9 g. In addition, over an extended trial lasting 27 days this group showed very slow weight gain, until on day 27 mean weight was 4 g greater than at the start (Rubega unpub.).

Further experiments designed to examine the birds' prey preferences (Obst and Inouye unpub.) showed that Red-necked phalaropes prefer the larval life-stage of the brine fly to all other prey available at Mono Lake. Previous diet studies (Winkler 1977, Jehl 1986) did not report the percent occurrence of each life stage of the brine fly found in Red-necked phalarope guts, but it might be guessed that brine fly larvae would be least accessible to phalaropes, since they are found either on submerged tufa or in the top few mm of lake bottom sediment. In order to understand the significance of preferences measured in the lab we examined the gut contents of field-collected birds (see Section 4: Diets of Free-living Red-necked phalaropes) and based experiments to examine the effects of changes in prey density on brine fly larvae as a prey type (see Section 3: Prey Density Effects...)

2c. Applicability of diet experiments to lake management concerns

The most important conclusion to be drawn from these data with respect to lake management concerns is that restriction to a diet consisting of some life stage of the brine fly should at least allow for simple energetic maintenance of these birds at Mono Lake, while similiar restriction to a diet made up wholly or even largely of brine shrimp manifestly would not.

These data confirm that field-collected diet data accurately reflect the reliance of Red-necked phalaropes on brine flies as a prey base at Mono Lake; they also demonstrate that this reliance is obligatory and not purely preferential in nature, and that a switch to brine shrimp as a primary prey source is not functionally possible for these birds.

Both Winkler (1977) and Jehl (1986) report the occurrence of brine shrimp in the guts of field-collected phalaropes. Neither author comments on the body condition of the birds in question. Free-living phalaropes may be taking brine shrimp, which are hypotonic, as a source of fresh water, but the laboratory experiments summarized here demonstrate that brine shrimp cannot be considered a viable alternate food source.

Laboratory measures of weight loss were made on birds feeding *ad libitum* in the absence of energetic expenditures related to searching for food, thermoregulation, predator avoidance, etc. Consequently it is probable that weight loss in a free-living bird attempting to subsist on brine shrimp would proceed more rapidly than in a lab-kept bird. However, Red-necked phalaropes unable to meet minimal metabolic requirements with brine flies would almost certainly desert Mono Lake before switching to a diet consisting largely of brine shrimp.

3. PREY DENSITY EFFECTS: EXPERIMENTAL EXAMINATION OF THE LIMITS OF FEEDING EFFICIENCY

This series of experiments was based on a two-way Analysis of Variance (ANOVA) design. Because Jehl (1988) notes sex-based differences in diet for Wilson's phalaropes, these experiments were designed (see Methods: Section 3) to determine, in a statistically rigorous way, whether or not measures of feeding effort and success were affected by changes in prey density, by sex of the bird, or by the interaction of the two. Birds were fed during 5 min trials at one of 4 experimental prey densities, which were designed to span those available in Mono Lake. Variables measured during feeding trials were total number of prey capture attempts, and total number of successful captures accomplished in a five minute trial period. From these were calculated feeding efficiency (a measure of successful captures per unit effort), attempt rate (number of attempts/min) and feeding rate (number of successful captures/min). These experiments were also designed to allow the comparison of potential effects on Red-necked phalarope feeding on two different prey types; ultimately only very limited direct comparison was possible, because of the overwhelming reluctance of the birds to feed on brine shrimp.

3a. Prey density effects on birds eating brine shrimp

Initially Red-necked phalaropes offered brine shrimp as prey under this experimental set-up appeared unpredictable in their willingness to feed. Some birds would feed at very high rates, while others would not feed at all, even at very high densities. Some individuals would feed one day, and then refuse to feed at the same or higher prey densities the very next day. The reason for this behavior is clear in Figure 2.1, which plots the number of feeding attempts versus the individual's weight, and shows that only birds which had very low weights attempted to feed on brine shrimp. In fact, birds displaying highest attempt rates are all within 5 g of starving to death.

To ensure that differing prey densities were not somehow confounding our understanding of this situation, the data were subjected to a 2-way ANOVA of the effects of prey density and bird weight on feeding attempts. Table 3.1 contains the results of that analysis. Weight has a highly significant effect, and density of prey has a smaller, but still significant effect. There is also a significant interaction effect.

The results of this analysis, and of experimental diet manipulations (see Section 2) made it plain that the planned analysis of this data for the effects of density and sex on feeding would be both statistically improper (since birds weighing more than 30 g could not be assumed to have equivilant feeding motivation, and removal of data associated with these birds unacceptably reduced the sample sizes) and biologically meaningless.

3b. Prey density effects on birds eating brine fly larvae

The experimental procedure was repeated using brine fly larvae as prey. The results of a 2-way ANOVA on the effects of density and sex on feeding are given in Table 3.2. Neither bird sex or prey density, alone, have significant effects on attempt rate, feeding (success) rate or efficiency. However, there is a highly significant effect of the interaction of sex and density on attempt rate, and a significant effect on feeding rate and efficiency. Plots of the data (Figures 3.1a-c) show the high degree of inter-individual variation that (along with small sample size) probably explains this failure to find significant effects of either sex or density, despite significant interaction effects.

Trends in the data indicate that female Red-necked phalaropes are more affected by changes in prey density than are males. Differences between males and females showed up at the extremes of the range of prey densities used in the laboratory. At the middle two densities, there were no differences between males and females in the number of attempts made, the number of successes, or the efficiency of prey capture. However, at the lowest test density, while males did not make more attempts than females they were more efficient, i.e., they succeeded more often. At the highest test density males differed from females not in efficiency, but in the rate at which they were attempting to catch prey; since they tried more often, they caught more prey. Females, unlike males (which maintained increasing attempt rates throughout the range of test densities) have the same mean attempt rate at a density of 5 fly larvae/l as they do of 25 fly larvae/l . What that means is that females reach their maximum feeding rate at prey densities that are 5000 times what is presently available, on average, (Herbst 1992) in Mono Lake. Perhaps more importantly, their mean efficiency at capturing prey declines at a density 100 times what is, on average, presently available in Mono Lake (See Methods: Section 3 for the relation of test densities to densities of brine fly larvae available in Mono Lake.) Red-necked phalaropes therefore are, in some sense, already limited by prey density at Mono Lake.

3c. Applicability of the prey density experiments to lake management concerns

Current lake levels are obviously sufficient to support the minimal food requirements of Red-necked phalaropes. However, these data strongly suggest that feeding rates of Red-necked phalaropes at Mono Lake cannot be maximized at current prey densities. Furthermore, these experiments indicate that free-living birds are currently feeding at sub-optimal efficiencies while at Mono Lake, a finding supported by field data (See Section 5).

4. DIETS OF FREE-LIVING RED-NECKED PHALAROPES

While both Winkler (1977) and Jehl (1986) showed that the bulk of Red-necked phalarope diets at Mono Lake consists of brine flies, neither reports which life stage, if any, of the brine fly predominates. Laboratory preference experiments demonstrated that brine fly larvae are most preferred (see Section 2b). We might expect that larvae are the least accessible of all available prey types to these birds; adult flies are found on the water surface, or along the shoreline, detached pupae are occasionally found in dense "drift lines" on the surface or at the water's edge, while larvae are, for the most part, confined to either submerged tufa or the top 2-3 mm of sediment on the lake bottom. Red-necked phalaropes, on the other hand, are surface feeders. This means that any prey they take must be found on or in the water column, where brine fly larvae densities are quite low relative to substrate densities (Rubega and Obst unpub., Herbst 1992).

We report here data on the composition of the gut contents from a series of 5 collections of actively feeding Red-necked phalaropes in 1990. We examined the gut contents of collected phalaropes (see Methods: Section 4) in order to determine if prey preferences demonstrated in the lab were a reaction to a nutritional, but rarely accessible, food type or a reflection of the real importance of each prey type in the diet of Red-necked phalaropes at Mono Lake.

4a. Diet data from field-collected birds

The data in Table 4.1 show that brine fly larvae are a major portion of the diet of free-living Red-necked phalaropes at Mono Lake. Over the course of 4 collection dates about a week apart in August brine fly larvae occur in the diets of 100% of collected birds, and account for 75% of the total volume of the gut contents (Figure 4.1). Collections were made only once more, on 12 September, the day after a major wind storm, and on that single date brine fly pupae predominate in the gut contents of collected birds. Even when all data is pooled, including that from this apparently unusual day in September, brine fly larvae still appear in the diets of more than half the collected birds, and account for almost half the total volume of gut contents. Brine shrimp parts occurred in only 2 individuals of the total 38 bird sample: the amount of gut content volume accounted for by those parts was too small for measurement with our methods.

4b. Applicability of field diet data to lake management concerns

These data do not represent a new finding in that they merely confirm what Winkler (1977) and Jehl's (1986) data already shows: that in order to maintain a population of Red-necked phalaropes at Mono Lake water must be maintained at a level which ensures a healthy fly population. The new point these data make is that the birds are relying more heavily on brine fly larvae than observations about that prey type's accessibility to them would lead us to expect. The best first-order measure of whether there is a sufficient abundance of brine flies to maintain the Red-necked phalarope population at Mono Lake may be the density of brine fly larvae in the water column. The data reported here are quite limited in terms of temporal scope; the sharp increase in pupal material in the diets of the birds on the last collection date makes it very likely that there is high temporal variability in the bird's feeding strategies, which our sample sizes are insufficient to address statistically. Observations made while collecting feeding rate data in 1991 make it clear that the birds at sometimes of the day or season are capitalizing on adult flies emerging over tufa blocks (Rubega and Elphick, unpub.) Nonetheless, the data presented here demonstrates that the birds are actively seeking out what appears, functionally, to be the least densely-occurring prey type at Mono Lake. This behavior strongly suggests a potentially disproportionate importance of that particular prey type.

5. FEEDING EFFICIENCY OF FREE-LIVING RED-NECKED PHALAROPES AND THE INTERPRETATION OF LABORATORY DATA

Data and conclusions drawn from laboratory experimentation are frequently, and rightfully, subject to the criticism that the laboratory setting does not accurately represent conditions in the wild. Mindful of this difficulty we collected data on the feeding performance of Red-necked phalaropes in the wild at Mono Lake. Our goal was to compare measures of feeding performance in wild birds to those for experimental birds in an effort to determine the validity of our density-effect experiments (see Section 3) as predictors of the effect of changing prey density on Red-necked phalaropes at Mono Lake.

We collected data on actively feeding phalaropes at Mono Lake in much the same way it was collected for birds in the laboratory (see Methods: A3 and A5). We scored videotaped one-minute "trials" for the number of prey capture attempts, successful captures, and calculated from these a measure of feeding efficiency (the number of captures divided by the number of attempts).

There are several unavoidable factors in the nature of the field-collected data that greatly limit the comparisons which can be made to laboratory data. Firstly, we could neither control prey density in the field, nor control the movements of the individuals the data were collected from. Birds in the laboratory were restricted to feeding over a known volume of water; because of that restriction of movement, as birds fed they depleted the available prey. This effect is a constant for all laboratory feeding trials, and therefore does not impinge on intra-experiment comparisons. However, wild birds swim constantly while feeding, and so both inspect larger volumes of water per unit time and also avoid prey depletion in their immediate vicinity by continually moving away from depleted water. For these reasons, direct comparisons of attempt and success rates between lab and field would be questionable, as well as difficult to interpret.

Our calculations of efficiency, however, should be relatively immune to these problems. Since this measure represents only the amount of effort required per prey capture, we might guess, *a priori* , that this measure would be the most likely to be density-independant. In fact, laboratory experiments suggest that mean efficiency (especially for female phalaropes) declines as prey density declines past 2.5 larvae/liter (see Section 3). If our laboratory results somehow underestimate the capacity of the birds to compensate for reduced prey density then phalaropes feeding in the wild, where prey densities are known to be far lower than our lowest test density, should have feeding efficiencies equal to or greater than those of captive birds. Alternatively, field feeding efficiencies significantly lower than laboratory efficiencies would be consistent with the conclusion that laboratory data reflect a real prey density effect.

We report here data on the feeding efficiencies of free-living Red-necked phalaropes feeding on brine fly larvae only (see Methods: A5), and the results of a comparison of these birds with birds in the laboratory feeding at our lowest test density. Since wild birds in winter plumage could not be reliably sexed, comparison is made to the pooled laboratory data for both sexes.

5a. Feeding efficiencies of wild birds

Feeding efficiencies of wild Red-necked phalaropes feeding on brine fly larvae at Mono Lake range from a minimum of 0 successes/attempt (total failure to capture pursued prey) to 0.75 (a value of 1.0 would represent one prey caught for every attempt made). Mean feeding efficiency is 0.33 ± 0.18, which is substantially lower than the mean feeding efficiency of 0.50 ± 0.27 measured in birds feeding in the lab (Figure 5.1) at a prey density of 0.5 larvae/liter (a density 100 times that available, on average, to birds in the field, and 5 - 10 times higher than Herbst's maximum field density). This difference in feeding efficiency means is highly significant (independant two-tailed t-test, $t = 3.060$, $p < 0.01$, $df = 40.7$). Practically speaking, it means that birds feeding in the wild are making about 1.5 times as many attempts to catch a single prey item as birds in the lab.

5b. Implications for lake management concerns

The difference in feeding efficiencies between free-living phalaropes at Mono Lake and captive birds in the laboratory can be explained in one of two ways, or possibly both. First, laboratory birds are feeding at much higher densities than birds in the field, and the 20% drop in feeding efficiency from lab to field may demonstrate the biological reality of a pattern of declining feeding efficiency with declining prey density. If this is so, then declining prey densities would represent not only a decrease in absolute prey abundance for Red-necked phalaropes, but an increase in the number of attempts required, and hence increased costs, in time and/or energy, per prey capture.

Second, differences in feeding efficiencies may simply be due to the fact that birds in the lab are feeding in a bounded volume of water where brightly lit prey are floating over a white (contrasting) background, while birds in the field are feeding in functionally unenclosed volumes of water on dark prey floating over a (usually) dark background. In other words, laboratory conditions may present an unnaturally advantageous prey capture situation. [This line of reasoning, however, fails to explain the decrease in feeding efficiency with decreasing prey density observed in the lab (see Section 3).] If this is the case, then data from laboratory experiments will overestimate how successfully Red-necked phalaropes are liable to feed at any given prey density, and possibly overestimate their ability to compensate for decreases in prey density.

Until reliable measures of the energetic costs of Red-necked phalaropes at Mono Lake are available it will not be possible to predict whether decreases in feeding efficiency will present energetic demands of a limiting nature. It is clear, in any case, that Red-necked phalaropes operating under current conditions at Mono Lake are feeding at suboptimal efficiencies. In view of the wide gap between laboratory and field feeding performance it would seem unwise to base lake management plans on the assumption that current lake conditions and prey densities are energetically or mechanically non-limiting.

6. CENSUS DATA: NUMBERS OF BIRDS AT MONO LAKE, AND LAKE USE.

Much has been made of the question "How many birds use Mono Lake?" Until we have the answer to that question it will not be possible to estimate the wider impact of ecosystem changes at Mono Lake on the species of birds that make use of it.

Researchers estimating numbers of breeding birds (e.g., California gulls) have a period of time in which they may reasonably assume that immigration and emigration from the lake is minimal.

Researchers censusing migratory birds (e.g., phalaropes and grebes) however, have no such assurance that counts over days or weeks either are, or are not, additive. The evidence is good (Jehl, 1988) that grebes most likely arrive at Mono Lake and stay for weeks or months, not least because they become flightless shortly after arriving, and because the data show a steady building of grebe numbers until they quit the lake en masse in late fall or early winter.

It is far more difficult to judge the value of census data for phalaropes. Jehl (1988) very convincingly argues that individual Wilson's phalaropes stay at Mono Lake for a month or more on the basis of increasing mean body mass in Wilson's phalaropes caught over 3 months; conversely he infers (1986; p. 188) that Red-necked phalaropes do not stay at Mono Lake over lengthy time periods because the population shows no such weight gain.

However, reference to the data presented in Section 1 makes clear that the failure of Red-necked phalaropes to exhibit increased body mass over the course of the summer season at Mono Lake may be due to less-than-ideal diet composition, rapid turnover rates of the birds, or both. Even if rapid turnover is the sole explanation for essentially unchanging weights of Red-necked phalaropes at Mono Lake we do not know <u>what</u> the turnover rate is (a critical factor in translating counts into accurate estimates of the total number of Red-necked phalaropes making use of Mono Lake) <u>or if turnover rate has changed over the time period since diversions began</u> in response to changing feeding conditions or other factors. Similiarly, we have no information about what percentage of all Eared grebes (which may not enter molt until weight gain occurs; Gaunt, cited in Jehl 1988) and Wilson's phalaropes leave Mono Lake before beginning molt and weight gain. Until an effort has been made to measure turnover rate directly attempts to estimate the total number of individuals of these species using Mono Lake are likely to be uninformative.

Despite these problems, census data <u>are</u> likely to be useful as an index to changes in the use of Mono Lake by these species. Since feeding is the primary activity of migratory birds at Mono Lake changes over time in where birds choose to feed are clues to the nature and extent of changes in the prey base. Because of our interest in where Red-necked phalaropes were feeding, and the availability of prey in those places, we conducted detailed censuses in 1990 and 1991. Reported herein are our counts for Red-necked and Wilson's phalaropes, and Eared Grebes, as well as observations on the birds' use of different areas of the lake, and incidental observations on waterfowl numbers and juvenile California gulls.

It should be noted that these data are subject to all the problems outlined above, as well as the usual problem of counting animals as mobile as birds. We have tried to overcome the latter by using simultaneous counts in different parts of the lake, by covering as much of the lake as possible, and by conducting counts in a standardized way at approximately the same time of day. Nonetheless, these data should only be used as **minimum estimates of the total number of birds present at Mono Lake on a given day**, or in comparisons of peak number counts (as indexes to population changes) and **not** as seasonal population estimates.

Details of our census methods are laid out in Methods (A6), but briefly, we conducted detailed full-lake censuses on seven dates between 7 August and 16 September in 1990 (with counts being made simultaneously by two ground crews and one boat crew) and on four dates between 10 July and 11 August in 1991 (when counts were made only by a boat crew). Figure 6.1a shows a detailed map of our census transects.

Table 6.1 contains all data for these censuses; Table 6.2 contains data for all sightings of waterfowl; because they were so much less numerous they were counted whenever we spotted them, including on all full-lake censuses.

6a.Numbers of phalaropes and grebes

Red-necked phalaropes were the least abundant of the three species considered here. Our peak count in 1990 was 17,536 on 16 September; our peak count in 1991 was 18,000 on 11 August. Jehl's (1986) data for the years 1981 to 1984 is the most complete and detailed information available for comparison. Compared to his peak total counts (rather than his estimated totals, presumably extrapolated from his counts, or his population estimates) our counts of Red-necked phalaropes do not appear to differ meaningfully. His maximum counts for 1981, 1982, 1983 and 1984 are 10,078 (on 11 August), 10,910 (on 2-3 September), 8000 (an estimated total - no counts given; on 10 August) and 12,000 (again, an estimated total; on 13 August), respectively. If we assume that turnover rates have not changed in that time, and that peak counts are therefore a reliable index to population size, then the total number of Red-necked phalaropes using Mono Lake as a migratory stopover probably has changed little since the early 1980's.

Our numbers of Wilson's phalaropes do seem to differ somewhat from Jehl's (1988; Appendix III) data for the years 1980 to 1987. Our peak count of Wilson's phalaropes in 1990 was 9037 on 7 August (a date, it should be noted, that is past the date when the peak numbers of Wilson's phalaropes are normally expected). Jehl's counts for similiar dates in 1980 - 1987 are in the same range except for 26,000 ± 2000 in 1982 (twice our count) and 15,000 (no error given) in 1985. However, our counts in 1991 span the dates when the peak number of Wilson's phalaropes should have been at Mono Lake. Our peak number of Wilson's phalaropes in that year is 35,225 on 18 July. Jehl's maximum peak count for the years of his study is 70,000 ± 10,000, again approximately twice our maximum. His lowest peak count for those years is 18,500 in 1983, but this value is labeled as a minumum and seems not to have to been the product of a complete census. The average of his peak counts for these years is 53,000.

Our counts of grebes in 1990 and 1992 are of limited value since we were not present in either year when grebe numbers should have been greatest, but there is a striking difference in our peak count for 1990 (the higher and later of the two years we have counts for) of 124,790 on 16 September and Jehl's (1988) counts for dates within 10 days of that date in the years 1981 - 1987. They are 427,090 in

1982; 375,000 in 1984; and 527,000 in 1985, all twice our counts. The lowest of these is from a date 10 days earlier than our count in 1990.

6b.Phalarope distributions; changes in use of Mono Lake

Phalarope distribution on the lake seems to have changed rather substantially. Jehl (1986) provides Red-necked phalarope distribution maps for 14 days in 1981 and 1982. On 9 of 14 dates at least half of the birds present could be found in the west bay of the lake. Jehl states that these distributions are similar for all years, and attributes distributional patterns to the presence of shallowly submerged tufa.

In striking contrast, on all dates in both years that we counted birds in a formalized way less than a third of all the Red-necked phalaropes at Mono Lake were found in the west bay of the lake. Our less formal counts in 1989, and observations on days we were working out on the lake in a boat but not censusing birds confirm this pattern. On 16 September 1990, the date of our peak count for that year, 14,700 of 17,536 birds (or 83%) were found in the northeast sector of the lake. On our peak count date in 1991 all the Red-necked phalaropes were in the east bay. In both years most of these birds were found feeding in the area labeled on Figure 6.1b.

Jehl (1988) maps diurnal roosts for Wilson's phalaropes in the years 1980 -1987, rather than feeding areas, but states that birds fed offshore of the roosts. Birds roosted in the west bay of the lake only 3 of 8 years. We found a diurnal roost of Wilson's phalaropes that appeared to contain nearly all of the birds on the lake in both 1990 and 1992; in both years it was in approximately the same area as Jehl's reported 1981 and 1982 roosts (see our Figure 6.1b). In 1989, 1990 and 1991 we found no roost in the west bay of the lake. Further, Wilson's phalaropes showed a pattern of feeding distribution similar to Red-necked phalaropes in that the vast majority fed in the east bay of the lake. On the date of our maximum count of 35,225 Wilson's phalaropes in 1991, all were found in the east bay of the lake.

6c.Incidental observations on other species of birds: duck numbers, and gull feeding.

While carrying out research on the phalaropes at Mono Lake, less detailed information was collected on a range of other water birds. Although the data for waterfowl constitutes little more than species counts we feel that it is worthy of mention, given historical accounts of the importance of Mono Lake for ducks. Counts of ducks in 1990 and 1991 appear in Table 6.2a & b, respectively. Detailed censuses from August to mid-September 1990 documented a minimum of 1600 ducks, however, at least 1215 of these were only seen flying over (Obst and Rubega, unpubl. data). During the months of July through September 1991 we recorded between 250 and 600 individuals (Rubega and Elphick unpub. data), depending on whether one treats three flocks of Northern Shoveler seen late in September as the same birds or not. Although most counts should be treated as minimums, it is unlikely that the degree of error is very great, as numbers of ducks were always small enough to enable counting of individuals, rather than less-exact methods of estimation.

In addition, a related study designed to obtain information on the foraging ecology of immature California Gulls is further suggestive of the importance of submerged tufa shoals as feeding habitat. Preliminary indications from this work (Elphick and Rubega, unpub.) suggest that well over 50% of all feeding attempts were on either emergent brine flies, or floating brine fly pupae. This is notable in light of the general agreement (see NAS Report for summary) that brine shrimp are the primary prey of California Gulls at Mono Lake. Furthermore, success rates on these prey types appear to be extremely high (Elphick and Rubega in prep.), presumably because these prey have little faculty for avoiding capture, and occur at the water surface. Given that a large proportion of immature gulls appear to occur in inshore areas with abundant tufa blocks, similar to the areas where this data was collected, (Elphick and Rubega pers. obs.) it seems likely that these areas may represent an important source of easily caught food to immature gulls at Mono Lake, and that brine fly production may contribute significantly to the survival of post-fledging gulls.

6d. Applicability to lake management concerns

The counts of birds reported here, and their comparison to previously published data should be interpreted with a good deal of caution, since they are not of a nature that lends itself to robust statistical comparison, and are subject to weaknesses and assumptions already outlined. Nonetheless (if we accept them as indexes of population changes) they may imply a decrease of about half in the number of Wilson's phalaropes and Eared grebes using Mono Lake over the last 10 years, or a shift in the timing of their use of Mono Lake. We have no data appropriate to the task of determining whether these possible changes are an artifact of mortality elsewhere, diversion of birds to other sites during migration, changes in turnover rates, or the effects of water diversions at Mono Lake.

The apparent abandonment of the west bay of Mono Lake as a major feeding ground by phalaropes of both species may be traceable to changes in food availability in that area. Tufa shoals in the west bay, such as those at the Old Marina area, have been largely uncovered since the 1980's by declining water levels. Jehl (1986) notes that Red-necked phalaropes feed mostly over submerged tufa; our observations are in agreement with that assertion. The major phalarope feeding area in the east bay of the lake is over submerged tufa (see Figure 6.1b) and both our prey sampling data, and those of Herbst (pers. comm.) confirm that densities of water-born brine fly larvae are, on average, higher than elsewhere in the lake.

While the lack of change in Red-necked phalarope numbers might imply that this species (the most dietarily restricted of those under consideration) has been largely unaffected by the need to shift feeding locations, it should be remembered that without past and present information on turnover rates we cannot know this for certain. In addition much of the value of the birds as an aesthetic resource is lost to the general public when feeding grounds are restricted to the east bay of the lake, since the east bay is largely inaccessible except by boat or four-wheel drive vehicle. Lake levels that inundate tufa shoals in areas more accessible to the public may restore flocks of phalaropes to the west bay of the lake.

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LITERATURE CITED

Boula, K.M. 1984. Foraging ecology of fall-migrating waterbirds at Lake Abert, Oregon. Unpublished report to the Oregon Dept. of Fish & Wildlife.

Conte, F. P., R. S. Jellison, and G. L. Starrett. 1988. Nearshore and pelagic abundance of Artemia monica in Mono Lake, CA. Hydrobiologia 158:173-181.

CORI report. 1988. The Future of Mono Lake. Water Resources Center, Rept. #68. Univ. of California.

Dana, G.L., and P.H. Lenz. 1986. Effects of increasing salinity on an Artemia population from Mono Lake, California. Oecologia 68:428-436

Herbst, D.B. 1981. Ecological physiology of the larval brine fly, Ephydra hians, an alkaline-salt lake inhabiting Ephydrid. Master's thesis, Oregon State University, Corvallis.

Herbst, D.B. 1992. Mono Lake benthic ecosystem research. Unpublished report to the California State Water Resources Control Board, Jones & Stokes Associates, and the Los Angeles Dept. of Water & Power.

Hurlbert, S.H. 1991. Salinity thresholds, lake size and history: a critique of the NAS and CORI reports on Mono Lake. Bull. So. Cal. Acad. Sci. 90(2):41-57

Jehl, J.R., Jr. 1986. Biology of the Red-necked phalarope (Phalaropus lobatus) at the western edge of the Great Basin in fall migration. Great Basin Nat. 46(2):185-197.

Jehl, J. R., Jr. 1987. Moult and moult migration in a transequatorially migrating shorebird: Wilson's Phalarope. Ornis Scand. 18:173-178.

Jehl, J. R., Jr. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the Nonbreeding Season: a Study of Adaptation to Saline Lakes. Studies in Avian Biology No. 12; the Cooper Ornithological Soc.

Leffler, S. R. 1966. Observations on a captive Northern phalarope. Wilson Bull 78(1):124-125.

Little, P., S. Hurlburt, and T. J. Bradley. 1988. Brine fly spatial distribution in Mono Lake. Unpublished report to the Los Angeles Department of Water and Power.

Mahoney, S. A. and J. R. Jehl, Jr. 1985. Adaptations of migratory shorebirds to highly saline and alkaline lakes: Wilson's Phalarope and American Avocet. Condor 87:520-527.

NAS Report, 1987. The Mono Basin Ecosystem; Effects of Changing Lake Level. National Academy Press, Washington, D.C.

Scheffe, H. 1959. The Analysis of Variance. New York: J. Wiley.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry (second edition). New York: Freeman Press.

Wetmore, A. as cited in: Bent, A. C. 1927. Life histories of North American Shorebirds. Dover, New York.

Winkler, D. W.(ed.). 1977. An ecological study of Mono Lake, California. Institute of Ecology Publ. No. 12. Univ. Calif. Press, Davis, Calif.

Zar, J.H. 1984. Biostatistical Analysis (second edition). New Jersey: Prentice Hall.

APPENDIX: METHODS

A1. General handling of animals

All animals used in experiments outlined below, including prey species, were captured alive at Mono Lake and transported to facilities at the Sierra Nevada Aquatic Research Laboratory of the University of California Reserve System, 30 miles south of Mono Lake, where they were held and experimentation conducted.

Birds were captured in mist nets set over water, and removed from the net immediately. Captured birds were weighed, measured and marked for individual identification. Birds were maintained indoors in 200 gallon fiberglass tanks, fitted with surface-skimming standpipe drains and constantly running clean water from nearby Convict Creek (i.e., non-chlorinated water). Tanks contained groups of five or fewer birds, and were fitted with fixed or floating platforms to allow the birds to get out of the water to preen or rest. Food dishes were located on platforms, and all tanks had at least two food dishes to ensure that birds could not exclude one another from the food supply. Except in the case of birds on experimental diets (see below), birds were maintained on artificial diets consisting of some mixture of hard boiled egg yolk, ground dried cat food or Purina brand Trout Chow, grit and avian vitamin and mineral supplements. This artificial diet was developed to avoid further accidental discoveries of nutritional deficiencies in native Mono Lake prey (see below), and to prevent prey-type habituation which might have influenced experimental work. Initially, birds were weighed every two to three days as a running measure of body condition. However it soon became apparent that body weight was an important variable (see the Report: Section 2a), and thereafter birds were weighed at least daily (more often for some experimental purposes).

Live prey for experimental purposes were collected at Mono Lake and kept in the laboratory in the following manner:

Brine shrimp were collected with dip nets constructed from 0.05 u plankton netting from either the LADWP dock, where there was a dependable plume, or from a boat in deeper areas of the lake. Fresh Mono Lake water was collected at the same time in 50 gallon carboys. Brine shrimp were maintained in Mono Lake water in the lab in 25 gallon aquaria with bubblers to ensure oxygenation.

Brine fly larvae were collected with small dip nets by skimming the top few mm of sediment in shallow lake areas near tufa (predominantly the Old Marina area, because of ease of access). Larvae were transported in buckets of Mono Lake water, and maintained in the lab in 25 gallon aquaria containing Mono Lake water with bubblers.

Brine fly adults were collected with standard insect sweep nets along the shoreline at Mono Lake. Adult flies were maintained in the lab in plastic jars with screen-covered ends; the jars were stored at about 40^{0} F in order to "slow down" the flies, both to prevent rapid death in captivity and to facilitate high feeding rates for the birds in diet manipulation experiments (see below).

A2. Experimental diet manipulations and weight loss

When we began our work with captive Red-necked phalaropes at Mono Lake this series of experiments was not part of the research plan, but, unwittingly, was already underway. Initially, we attempted to maintain all captive birds on a diet of brine shrimp alone because there was essentially no literature (for the sole exception see Leffler 1966) on the long-term captive maintenance of this species and therefore none on an appropriate artificial diet. While previous research (Winkler 1979, Jehl 1986) made it apparent that Red-necked phalaropes preferred brine flies, it also demonstrated that free-living individuals did sometimes eat brine shrimp. Since brine shrimp are much easier to collect than any life-stage of the brine fly, and our research group consisted of only 2 people, caring for 30 birds, we thought it best to feed the birds the most accessible natural prey available while developing an artificial diet. Birds were fed *ad libidum*; food dishes were checked periodically and filled throughout the day as birds emptied them.

Over time it became apparent that birds kept on this diet were losing weight steadily, despite strenuous effort on our part to keep food dishes full. Simultaneously, we found that individuals being used in density-effect experiments (see Methods: Section A3) would only reliably feed during experiments if their weights were 30 g or below. Accordingly, the data for the effects of a brine shrimp diet on bird weight consist of the weight information collected on a daily basis as part of the general care regime outlined above.

The sample of weights for birds on brine shrimp diets is therefore drawn from a cohort of 27 individuals who i) were not all on the diet at the same time and ii) were not on the diet for the same number of days, although none were on the diet for less than 3 days, and most were on the diet for 9 days (no bird survived the diet for longer than 9 days; after the death of twelve birds at weights near 20 g, we began feeding birds raw or hard-boiled egg yolk when they reached 20 g of weight). In this analysis we only include data for birds kept on a pure shrimp diet and which had not yet been subject to the food-deprivation regime outlined below (Methods: Section 3). In contrast to the post-hoc nature of this analysis, experiments to examine the effect of brine fly diets on bird weight were planned and carried out for the express purpose of comparison to the data for birds on brine shrimp diets.

Brine fly diet experiments were conducted with birds kept in groups of 5 or fewer, under the conditions outlined above (see General handling...), and fed only adult brine flies for 27 days. Because of the limitations of the brine shrimp diet data, all comparisons here are made on the basis of a 9 day trial, although longer term results for birds on the fly diet are discussed. Birds were not previously or simultaneously used in other experimental work, and were handled only once daily in order to obtain weights. Food dishes were checked and refilled frequently.

A3. Experimental examination of density and prey type effects

In order to measure the effect of prey type and changing prey density on feeding performance experimental design was based on a nested 2-way Analysis of Variance (ANOVA). Five individuals of each sex were tested 5 times at one of 4 densities, for one of two prey types (brine shrimp or brine fly larvae). This experimental design therefore consisted of 200 experimental trials (5 individuals x 2 sexes x 5 trials x 4 densities) for each prey type. The order in which birds were offered different prey densities was determined arbitrarily.

These experiments involved testing bird feeding performance on a range of densities meant to span those available in Mono Lake. Prey densities that have been reported from field studies in Mono Lake have a very large range. Brine fly densities can be as low as 2 X 10^{-2} larvae/cm^2 for all three larval instars combined on soft substrates or as high as 1 larva/cm^2 on tufa (Little, Bradley and Hurlburt 1989). These higher densities on tufa do not represent available prey, however, because the larvae are hidden in and clinging to the highly folded tufa fragments.

For shrimp, densities are more realistically expressed in prey per liter. In open lake water, the densities of shrimp have been estimated as ranging from 0.03 - 2 shrimp/liter (Lenz, 1980). Certain features in Mono Lake serve to either attract or concentrate shrimp and are therefore associated with increased shrimp densities. Conte et al. (1988) report densities of 10-38 shrimp/l near upwelling freshwater seeps and 5-30 shrimp/l at foam lines.

Our original research plan called for testing birds at densities of 10, 50, 100 and 800 prey per aquarium. The water surface in the tanks used was 1800 cm^2. As each aquarium had 10 cm of water in it (or 18×10^3 cm^3 of volume), prey densities ranged in our experiments from 5.5×10^{-3} to 4.4×10^{-1} prey per cm^2 and from 0.55 to 44 prey per liter. The range of densities we planned to use therefore spanned the realistic range of fly densities available on open flat substrate. Our chosen densities also spanned the expected range of prey densities found in the lake with regard to shrimp. We felt that the low density trials would be particularly instructive in analyzing how phalarope feeding response is affected when prey become scarce. We none the less included both high and low density trials in order to be able to statistically assess the effects of prey density.

This research plan was quickly modified because Red-necked phalaropes made no attempt whatsoever to feed at the two lowest densities when offered brine shrimp. Under the mistaken assumption (see the Report: Section 2) that birds would not feed because these densities were too low we proceeded with testing based on densities of 100, 400, 800, 1600 and 2400 shrimp per aquarium, or 5, 20, 40, 80 and 120 shrimp per liter. These densities do not span the lower range of densities of brine shrimp in open water at Mono Lake, but <u>do</u> realistically span densities of brine shrimp in plumes and foam lines, areas where phalaropes feeding on shrimp might be expected to concentrate their efforts. In any event, our research on dietary limitations demonstrates that even densities of brine shrimp which far exceed those available in Mono Lake are insufficient to nutritionally sustain a Red-necked phalarope.

Planned test densities of brine fly larvae were also modified. The three lowest densities (10, 50 and 100 larvae per aquarium) were retained, but the highest density the birds were offered was 500 larvae per aquarium (or 25 larvae per liter). This change was made because collections and observations in the field (see the Report: Section 4) established that Red-necked phalaropes at Mono Lake were feeding on brine fly larvae floating in the water column, rather than on those on substrate. Preliminary sampling (Rubega and Obst, unpub.) of these prey in the water column indicated that even a density of 25 larvae per liter was far in excess of densities available anywhere in the water column at Mono Lake. More extensive sampling in the following year by Herbst (1992) confirmed this view. Accordingly, the test densities used exceeded the high end of naturally-occurring densities in the lake, but did not span the very lowest naturally-occurring densities. This problem was insoluble, since a test density lower than 0.5 larvae per liter in a closed tank would not have provided us with a feeding bout sufficiently long to be statistically meaningful.

Rather than trying to count out hundreds of brine shrimp or brine fly larvae for 400 five-minute feeding trials, we established that there was a tight linear relationship between the number of prey in a randomly collected mass of prey, and the wet weight of the prey (brine shrimp: $r^2 = 0.9802$, n= 10; 3rd instar brine fly larvae: $r^2 = 0.9838$, n= 16). Test densities were then created by weighing out masses of prey equivalent to the test densities to two decimal places on a Mettler balance.

Birds were introduced to an experimental tank, seeded with the test density of prey, via a closed box at one end of the tank (Figure A3.1). Birds were left in the box for 5 minutes to standardize the effects of handling, then the door leading to the tank itself was opened; the trial began when the bird entered the tank voluntarily. Birds were allowed to feed for 5 minutes, during which time they were videotaped. Videotaping was conducted in color with a Sony Hi8 Handycam on high quality 8mm videotape at 1/4000 s shutter speed. Videos were scored later, at half speed, for the number of capture attempts, and the number of successful captures. Efficiency was calculated by dividing the number of successes by the number of attempts. Attempt and feeding rates were calculated by dividing the total number of attempts and successes, respectively, by 5 min. Birds were deprived of food for the 12 hours prior to trials to ensure comparable motivation. To guard against the effects of satiation, individuals were not tested more than once an hour, and no individual was tested more than 5 times on any given day. The tank was cleared of prey at the end of each trial with a 0.05 u plankton net designed for that purpose, and re-seeded for the next trial.

A4. Diets of free-living phalaropes: field collections

We collected phalaropes at Mono Lake in 1990 in order to compare the dietary preferences of free-living phalaropes to the prey preferences determined experimentally with captive birds. Actively feeding birds were collected with a twelve gauge shotgun from a boat. Immediately after collection, the birds' digestive tracts were filled with 75% ethanol by syringe in order to halt digestive processes that might bias gut composition data. Birds were individually labeled and stored in plastic bags on ice, then transported within 3 hours to the laboratory. Immediately upon return to the laboratory the entire digestive tract was dissected out of the bird, incised open and all the gut contents removed. Gut contents were stored in 75% ethanol in glass vials for later analysis. Birds, if not already sexed by plumage, were sexed by presence/absence of testes or ovaries. Juveniles could not reliably be sexed by either method, and we actively avoided collecting them.

Gut contents were later sorted by prey type (brine shrimp, brine fly adults, brine fly pupae, brine fly larvae, plus grit and other non-food materials). Gut contents were quantified by counting individual prey; since adult brine flies and pupae were rarely whole we counted heads and puparia, respectively. Total volume of the gut contents and of each prey type was measured to the nearest tenth of a ml by displacement of fresh water.

A5. Field feeding rates and efficiency

In order to relate laboratory tests of prey density effects on feeding performance to the feeding performance of birds in the field, we measured the same variables used in the laboratory-based analysis for free-living Red-necked phalaropes feeding at Mono Lake.

Actively feeding birds were videotaped with a Sony 8 mm Camcorder at a shutter speed of 1/4000 of a sec. The camera was equipped with a continuously running (and recording) timer that was accurate to the sec. Birds were videotaped feeding for 1 min "trials". A concious effort was made to sample any single individual only once in a given location, but since we did not have a population of marked individuals it is possible that some of our data consists of repeated measures of some individuals.

Videotapes were later scored at half speed for the number of prey capture attempts, the number of successful prey captures and the type of prey captured. These measures were used to calculate feeding efficiency as outlined in Section A4. We also noted the type of prey captured. As demonstrated by the gut content data outlined in this report, Section 4, Red-necked phalaropes are feeding on more than one life stage of the brine fly. Since our goal was to compare these field data with experimental data it was important that we be able to distinguish capture attempts on brine fly larvae, for which we have extensive experimental data, from capture attempts on other life stages of the fly, for which we do not. Fortunately, we have been able to characterize head and beak kinematics associated with successful capture of different prey types (Rubega and Obst, in review); in addition, adult flies were clearly visible on the videotape.

We report, therefore, efficiencies of birds who only fed on brine fly larvae during the one minute trial. Comparison is made to efficiencies of Red-necked phalaropes feeding on brine fly larvae in the lab at our lowest experimental density (10 larvae per 20 l of water, or 0.5 larvae/l). Laboratory data was gathered over the course of a 5 minute trial; for this comparison the total number of prey capture attempts and successes were divided by 5 to yield attempt rate and success rate, respectively. Laboratory efficiencies used in this comparison were calculated by dividing success rate by attempt rate.

A6. Census data: numbers of birds at Mono Lake, and lake use

During 1990 and 1991 detailed censuses of all birds on Mono Lake were carried out. In 1990 full-lake censuses were carried out on seven dates between 7 August and 16 September; in 1991 full-lake censuses were carried out on four dates between 10 July and 11 August. In 1990 counts were made simultaneously by two shoreline crews of two to three people each, and a boat crew of two to three people. In 1991 counts were made only by a boat crew of two to three people.

Shoreline crews counted birds using binoculars and tripod-mounted telescopes from sites accessible either on foot or by vehicle at the western end of the lake (South Tufa, Lee Vining Tufa, the LADWP boat dock, the Old Marina, the Shrimp plant dock and County Park; see Figure 6.1). The boat crews made counts at standard intervals along transects (Fig. 6.1) designed to cover areas of the lake not visible from shore or easily accessible by vehicle (e.g., Warm and Simon's springs). Shoreline counters were instructed not to count birds more than 50 yards from shore, in order to avoid duplicate counts by the boat crew.

Two counters in any crew counted birds in an area simultaneously, using hand counters and previously discussed landmarks to delineate the group being counted , then compared counts. Counts that differed by more than 10% were repeated. Flocks of fewer than 100 birds were counted, and reported, by the individual; flocks larger than 100 were counted in tens, or in the case of very large flocks, by hundreds, and reported in corresponding round numbers. Censuses began as close to dawn as possible to minimize heat haze present later in the day.

These censuses were meant to provide a picture of phalarope use of Mono Lake during the periods when phalarope populations were at their highest, but we also counted Eared grebes (*Podiceps nigricolis*), California gulls (*Larus californicus*), all the ducks we saw, and all shorebirds. We report here only Red-necked phalarope, Wilson's phalarope and Eared Grebe numbers. We also report numbers of all waterfowl; all waterfowl seen on the lake on 18 days between 5 July and 28 September 1991 (including 4 full-lake censuses) are reported. Most "boat days" that were not spent carrying out full-lake censuses involved travel east from the Shrimp Plant dock, between Negit and Paoha islands, and along much of the north shore, in the area where phalarope and grebe numbers were consistently greatest. Consequently duck sightings are generally from the northern half of the lake. This is the only portion of the lake where large (i.e. >20 individuals) flocks of ducks were seen by us. Observations of waterfowl from land are noted as such, along with information on where they were made, and how large an area was covered at the time of the count.

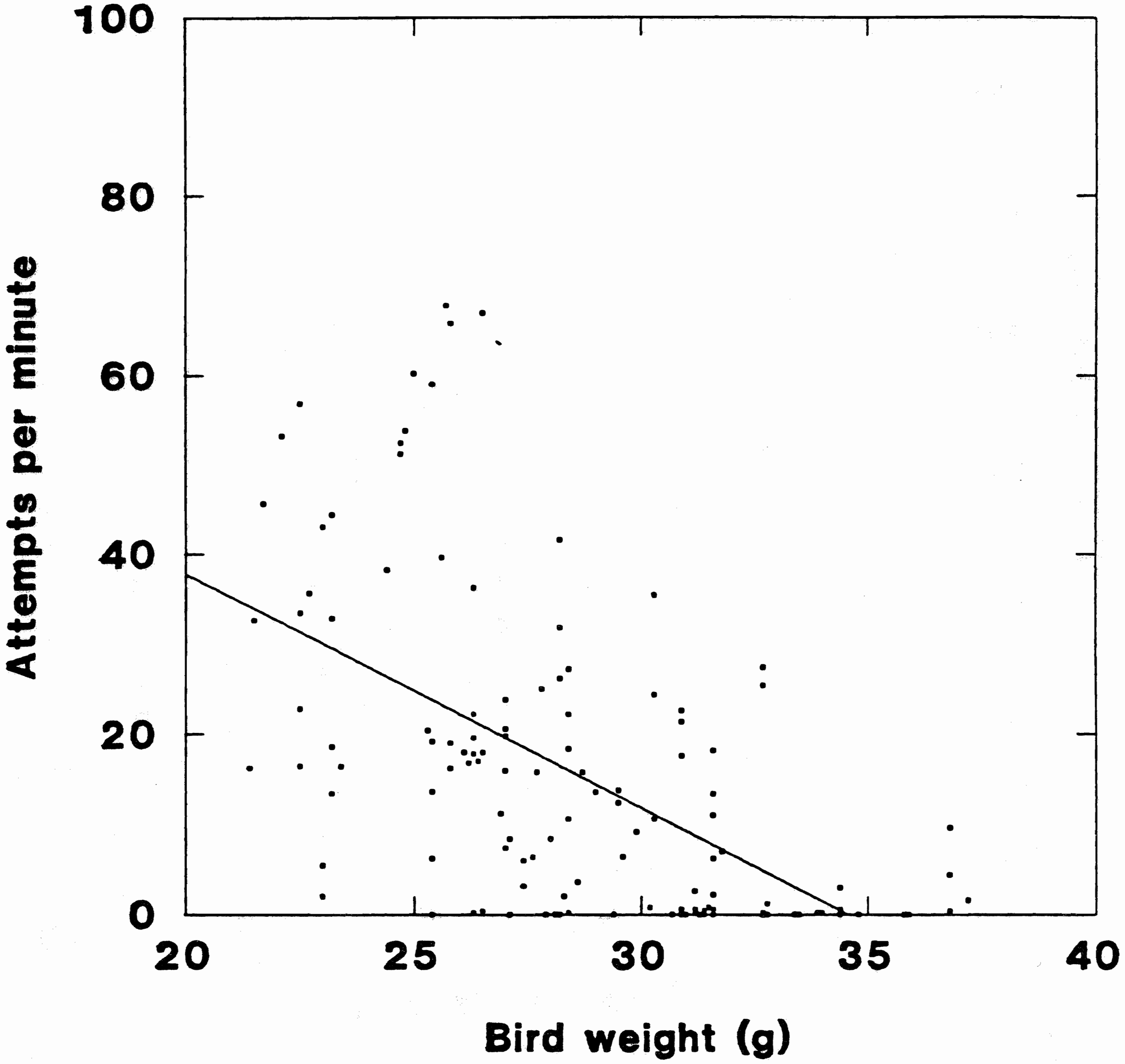

FIGURE 2.1 THE EFFECT OF BODY WEIGHT ON FEEDING ATTEMPT RATE IN RED-NECKED PHALAROPES OFFERED BRINE SHRIMP. Plot of attempt rates vs. body weight for Red-necked phalaropes offered brine shrimp at a wide range of densities. Maximum attempt rates are associated with birds which were within 5-6 g of starvation weight. ($r^2 = 0.329$; $p < 0.001$; $n = 132$.)

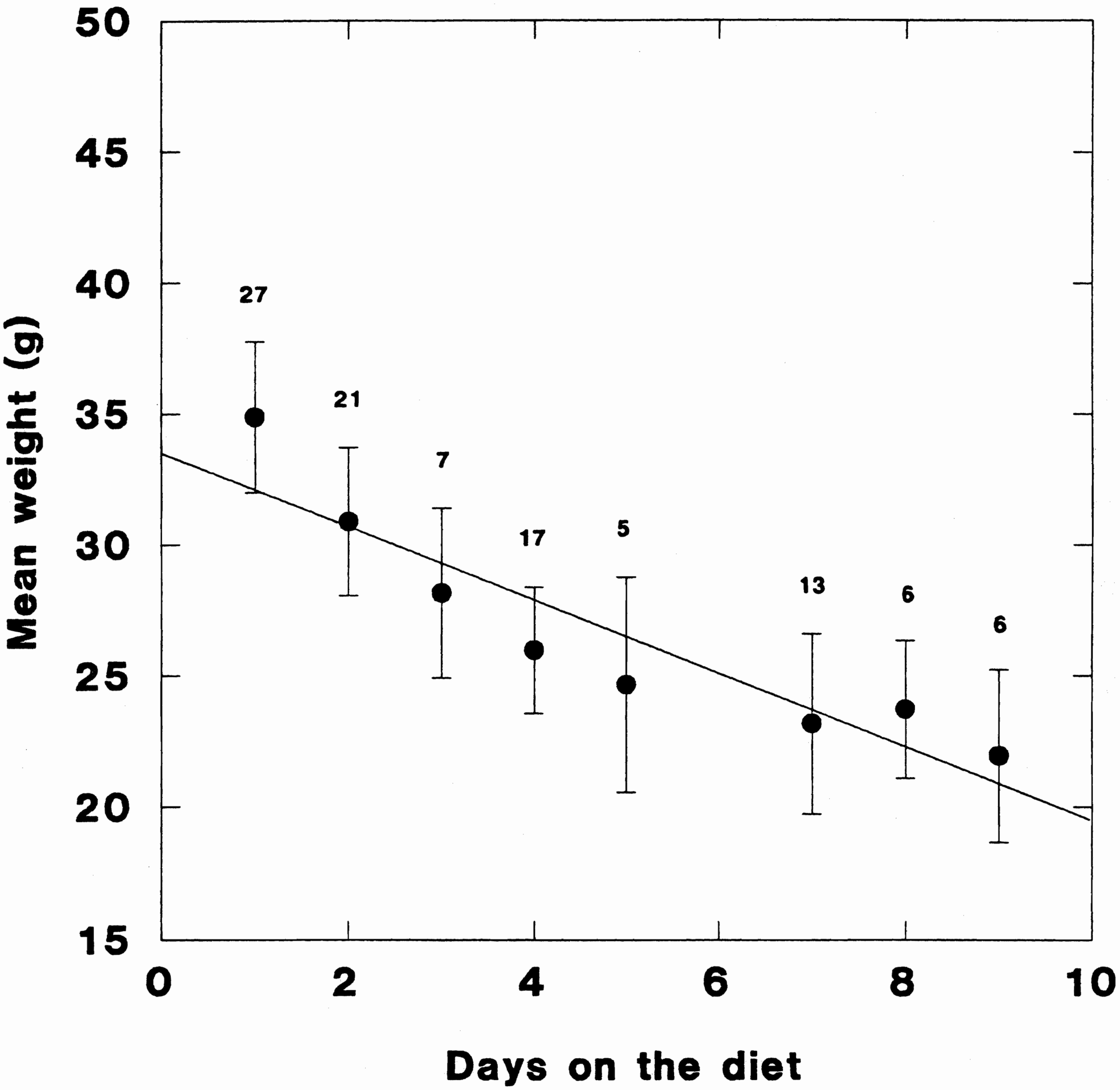

FIGURE 2.2 THE CHANGE IN BODY WEIGHT OF RED-NECKED PHALAROPES FED A BRINE SHRIMP DIET

Mean weights (± standard deviation) pooled by day. ($r^2 = 0.832$, $p = 0.001$; n appears above each mean.) A total of 27 birds contributed to the data. Twelve birds kept on a brine shrimp diet after reaching 20 g weight died; thereafter, all others were removed from the diet upon reaching 20 g.

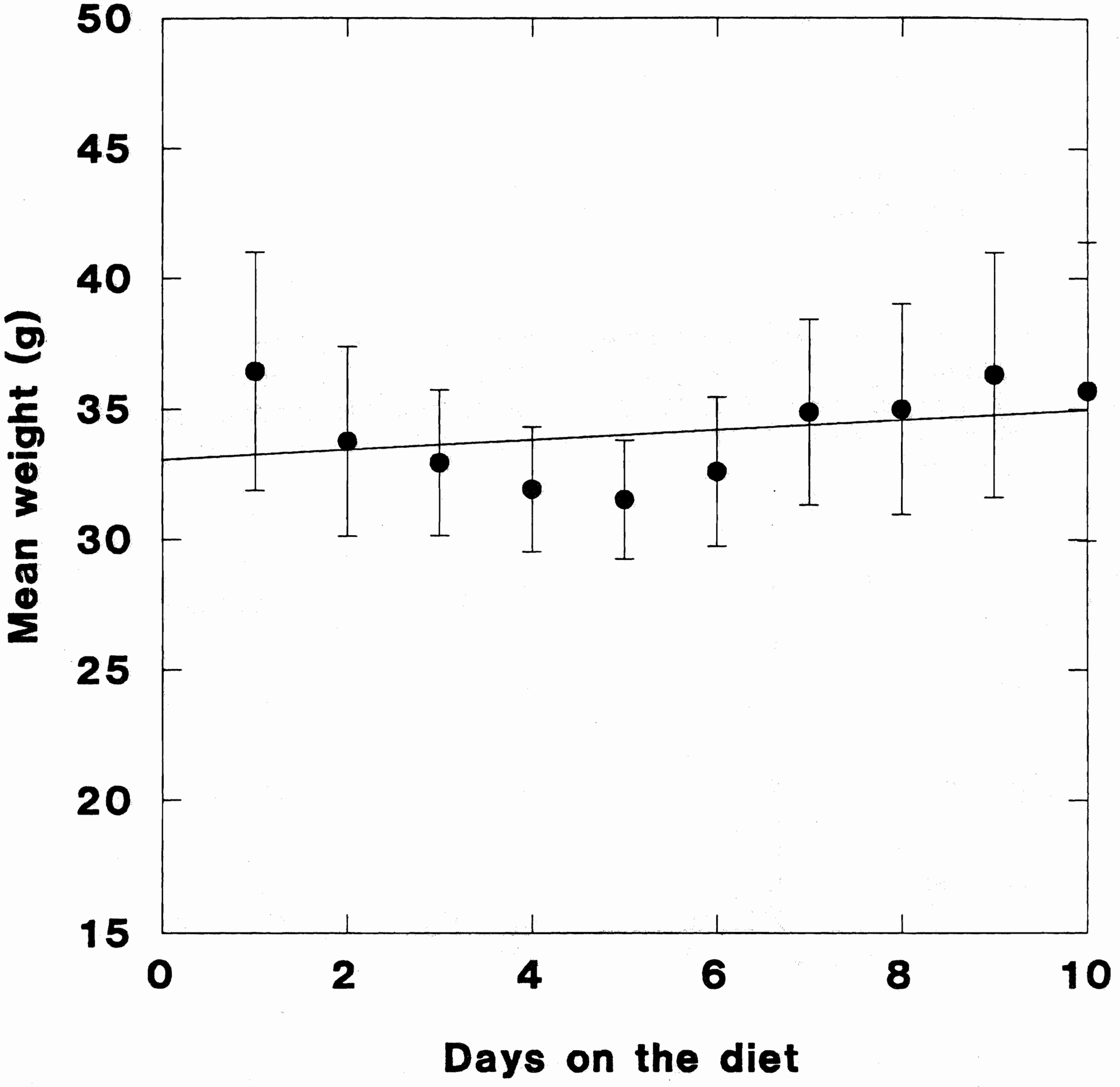

FIGURE 2.3 THE BODY WEIGHT OF RED-NECKED PHALAROPES FED A BRINE FLY DIET

Mean weights (± standard deviation) pooled by day. (No correlation; $r^2 = 0.000$, $p = 0.615$, not significant; $n = 9$.) Birds were fed a diet of adult brine flies only. Mean weight on day 9 is not significantly different from mean weight on day 1 (see text), but over an extended trial of 27 days (data not shown here) mean weight increased 4 g.

	F-statistic	P value
Bird weight (df=2;122)	19.124	< 0.001
Prey Density (df=5;122)	2.758	< 0.05
Weight x Density (Interaction effect) (df=10;122)	2.121	< 0.05

TABLE 3.1 THE EFFECTS OF BIRD WEIGHT AND PREY DENSITY ON FEEDING ATTEMPTS. Two-way Analysis of Variance test for the effects of weight and prey density on the feeding attempt rates of Red-necked phalaropes offered brine shrimp in densities ranging from 5 - 120 brine shrimp/ l of Mono Lake water.

	Attempts	Successes	Efficiency
Sex (df=1; 3)	NS	NS	NS
Prey Density (df=3; 3)	NS	NS	NS
Sex x Density (df=3; 119)	4.336 (P<0.01)	3.911 (P=0.0105)	3.892 (P=0.0108)

TABLE 3.2 THE EFFECT OF BIRD SEX AND PREY DENSITY ON FEEDING IN RED-NECKED PHALAROPES FEEDING ON BRINE FLY LARVAE. Two-way Analysis of Variance test for the effects of bird sex and prey density on 3 measures of feeding performance of Red-necked phalaropes offered brine fly larvae in densities ranging from 0.5 - 25 brine fly larvae/ l of Mono Lake water.

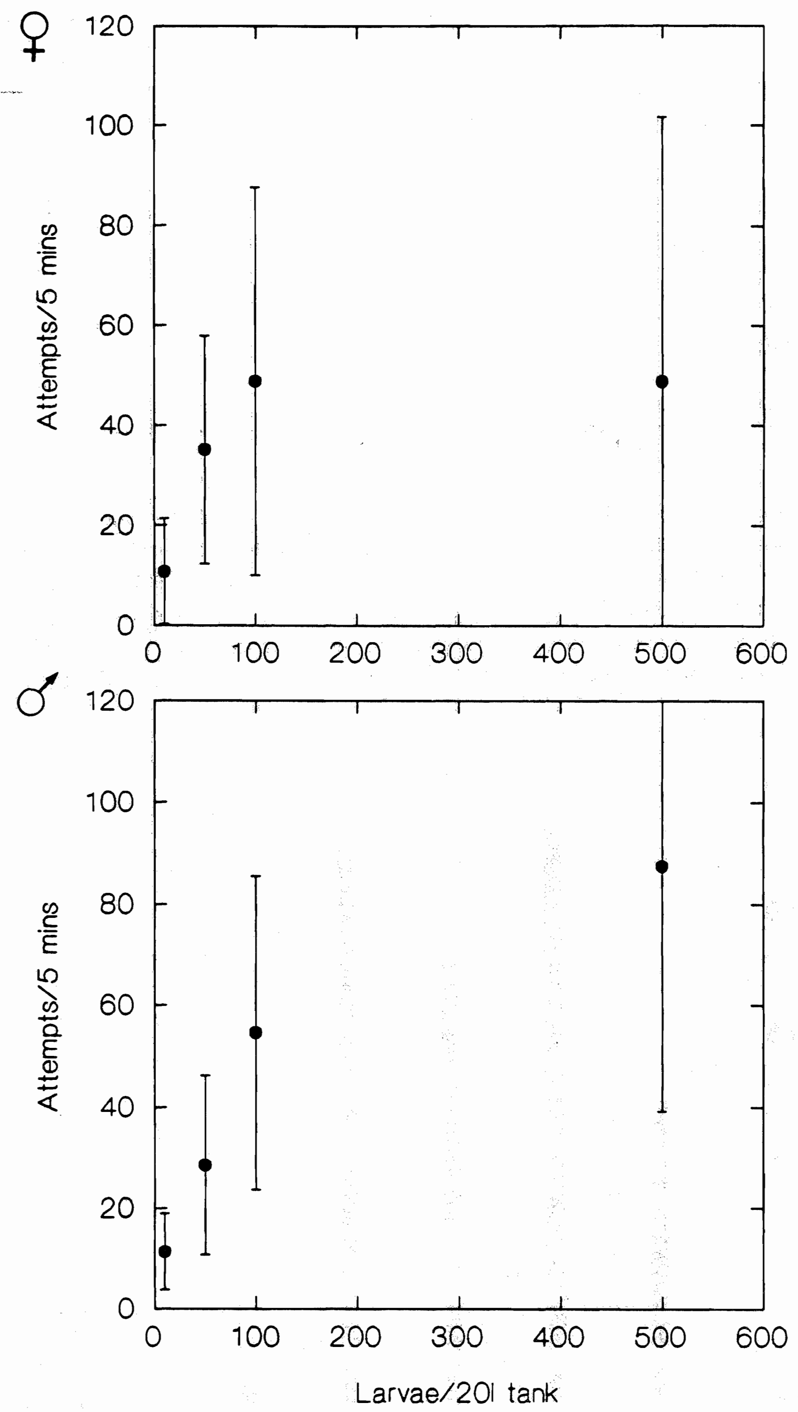

FIGURE 3.1a CHANGES IN TOTAL NUMBER OF PREY CAPTURE ATTEMPTS WITH CHANGING PREY DENSITY FOR BOTH SEXES OF RED-NECKED PHALAROPE FEEDING ON BRINE FLY LARVAE.
Means ± standard deviations. N = 16 - 20.

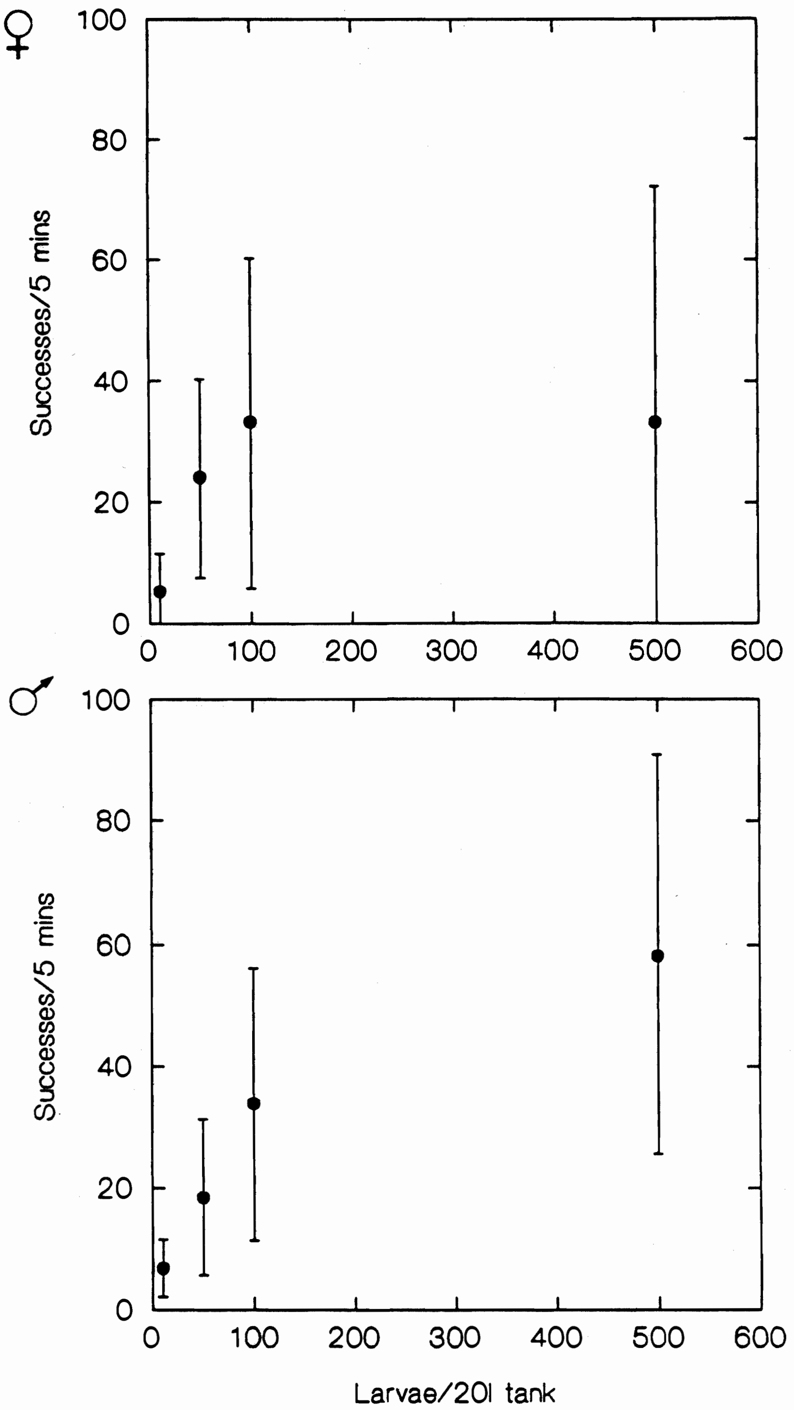

FIGURE 3.1b CHANGES IN TOTAL NUMBER OF SUCCESSFUL PREY CAPTURES WITH CHANGING PREY DENSITY FOR BOTH SEXES OF RED-NECKED PHALAROPE FEEDING ON BRINE FLY LARVAE. Means ± standard deviations. N = 16 - 20.

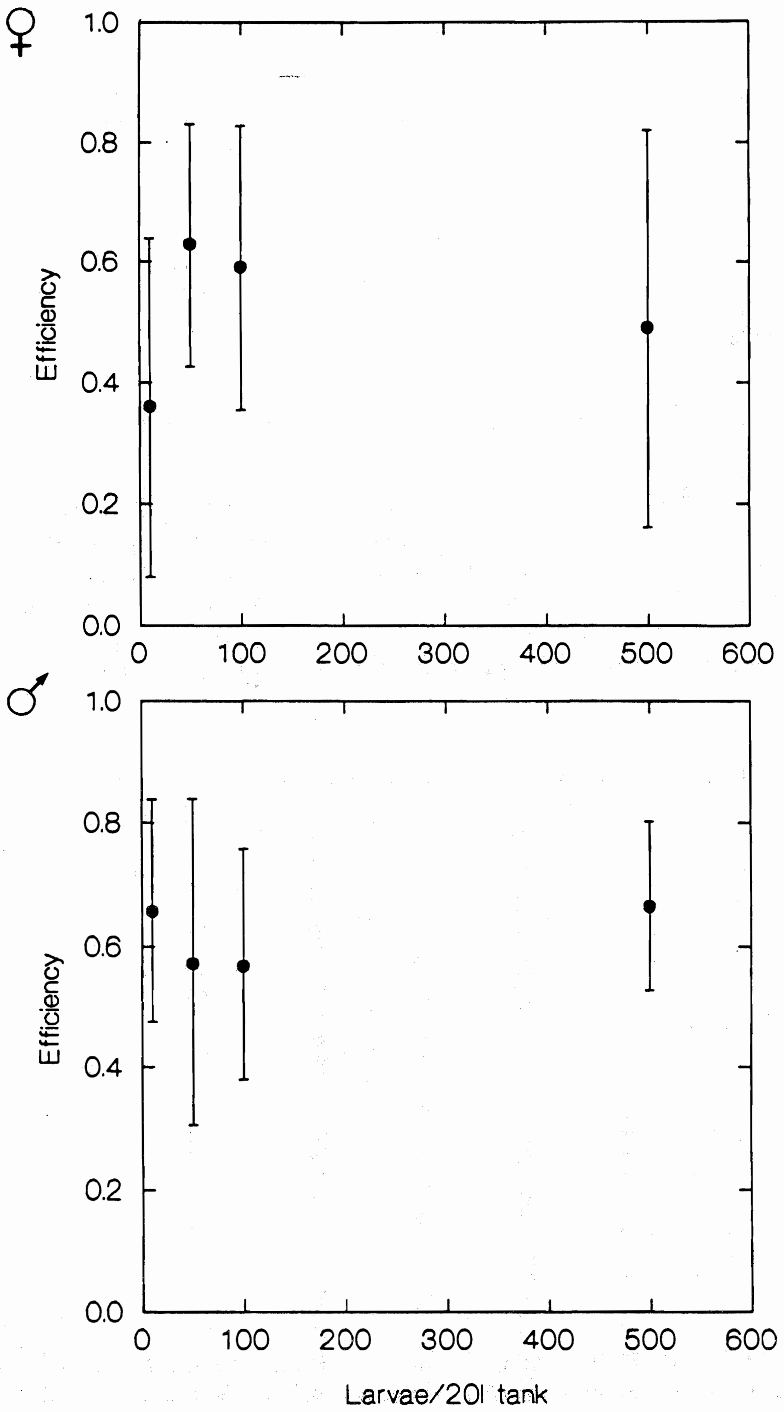

FIGURE 3.1c CHANGES IN FEEDING EFFICIENCY WITH CHANGING PREY DENSITY FOR BOTH SEXES OF RED-NECKED PHALAROPE FEEDING ON BRINE FLY LARVAE.
Means ± standard deviations. N = 16 - 20.

	BRINE FLY: Larvae	Pupae	Adults	BRINE SHRIMP
August 1990 collections (n = 20)	100	75	45	5
August & September 1990 collections (n = 38)	66	87	37	5

TABLE 4.1 DIETS OF FREE-LIVING RED-NECKED PHALAROPES; PERCENTAGE OF DIET BY OCCURRENCE. Data from the gut contents of Red-necked phalaropes collected at Mono Lake while actively feeding. August collections were made on August 7, 17, 21, and 27, 1990; sample sizes are for each of those dates are 7, 7, 3, and 3, respectively. August and September collections represent all August dates pooled with a single collection in September (on 12 September 1990; n=18) in which there was an unusual predominance of pupae both in the water column and in the birds' guts.

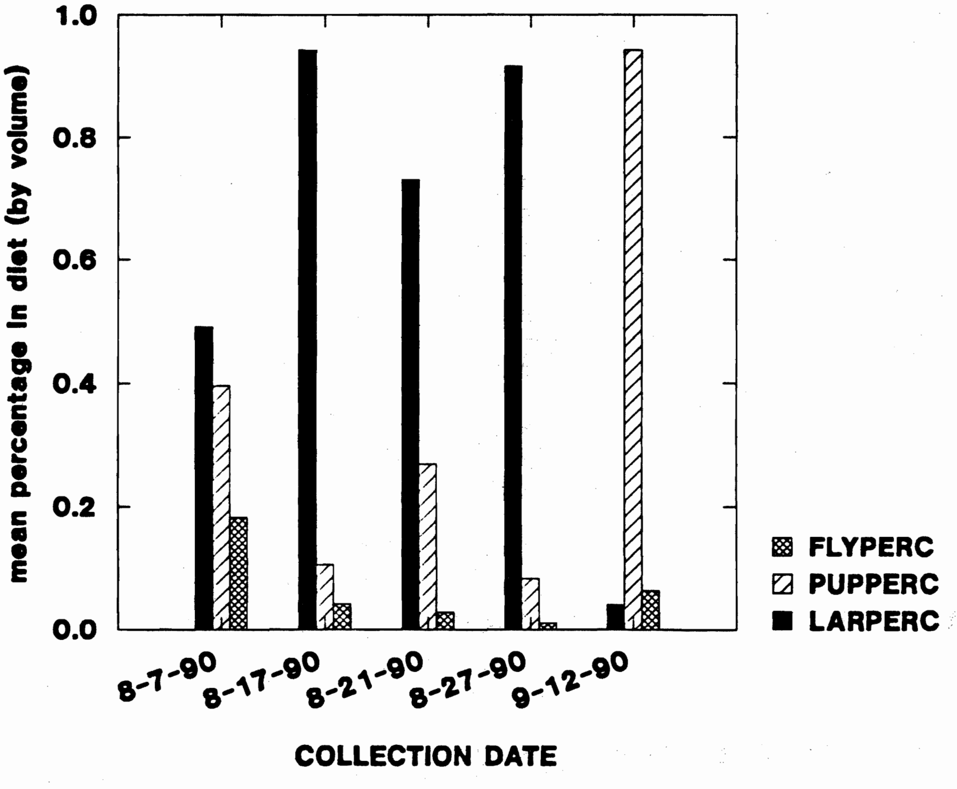

FIGURE 4.1 DIETS OF RED-NECKED PHALAROPES; PERCENTAGE OF DIET BY VOLUME.
Mean percent, by volume, of the gut contents of Red-necked phalaropes collected on four dates in 1990 made up of each life stage of the brine fly. Brine shrimp occurred in only 2 individuals of 38, in volumes too small to measure with our methods. Refer to Table 4.1 for sample sizes. Flyperc = adult (emergent) flies, pupperc = pupae, larperc = larvae. When data for all dates in August are combined, brine fly larvae account for 75% of the total volume of the gut contents , pupae for 22% and adult flies 8%. If all data for all dates, including 12 September, are combined brine fly pupae account for 57% , larvae for 41% and adult flies for 7% of the total volume of the gut contents.

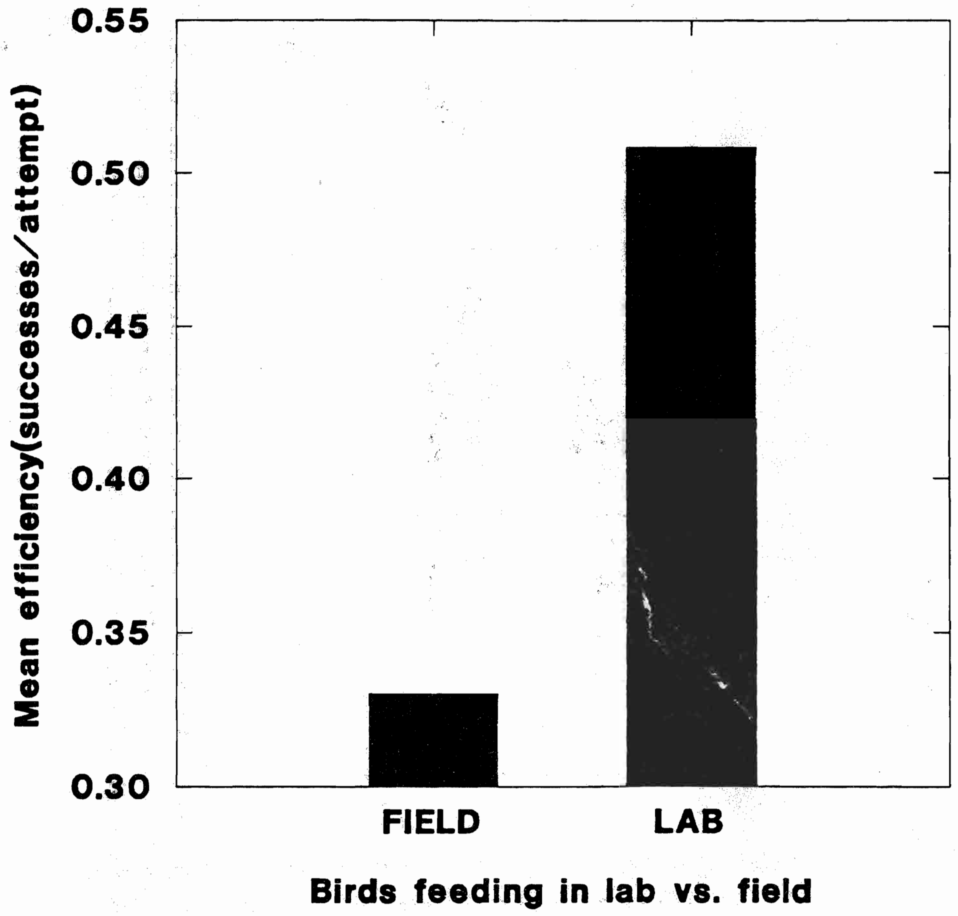

FIGURE 5.1 FEEDING EFFICIENCIES OF RED-NECKED PHALAROPES FEEDING IN THE LABORATORY AND IN THE FIELD. Mean feeding efficiency (calculated from the number of successful captures divided by the number of attempts per minute) in phalaropes on brine fly larvae. Sample sizes for field and lab groups are 53 and 23, respectively. The difference between means is statistically significant (see text for description of test), and practically means that birds feeding in the field are making one and a half times as many attempts per prey caught as birds feeding in the lab.

DATE	RED-NECKED PHALAROPE	WILSON'S PHALAROPE	PHALAROPES, SP.	EARED GREBE
7Aug90	15501	9037	120	22730
13Aug90	10444	755		24906
18Aug90	nc	nc		5700
26Aug90	6330	208	1050	37750
30Aug90	12233	<50		50224
5Sept90	10751	<50		56200
16Sept90	17536	0		124790
10jul91	200	30000		15597
18jul91	1950	35225		13864
1Aug91	8790	5010		12519
11Aug91	18000	10000		56855

TABLE 6.1. MONO LAKE CENSUS DATA, 1990 & 1991. Data from full-lake counts of phalaropes and grebes. "Phalaropes, sp." represents phalaropes which could not be positively identified by the observer, not total numbers of phalaropes; nc = not counted.

DATE	DETAILS	TEAL, SP.	GADWALL	SHOVELER	RUDDY	N. PINTAIL	W.W. SCOTER	DUCK TOTALS	AMERICAN COOT
7 Aug	FLC	0	0	0	0	0	0	0	0
13 Aug	FLC	0	0	0	0	0	0	0	1
18 Aug	FLC	0	0	0	0	0	0	0	0
1-28 Aug		100's	30	-	-	2	-	100's	
26 Aug	FLC	1000+ *	0	0	0	15	0	1015	0
30 Aug	FLC	0	0	0	0	0	2	2	0
5 Sept	FLC	0	0	250	0	0	0	250	0
12 Sept		-	-	200 *	-	15 *	-	215 *	
16 Sept	FLC	0	0	0	100's	0	0	100's	0
19 Sept	Co. Park	205+	-	20	-	-	-	225	

Table 6.2a. Mono Lake Minimum Waterfowl Counts , 1990. Data from direct counts of all waterfowl seen in 1990 at Mono Lake. FLC = Full-lake count; Co. Park = data from the County Park area only; * = birds only seen flying over the lake; zeros only given for days on which full-lake counts were carried out.

DATE	DETAILS	MALLARD	TEAL, SP.	GADWALL	SHOVELER	WIGEON	RUDDY	DUCK TOTALS	CANADA GOOSE	WHITE FRONTED GOOSE	AMERICAN COOT
5 July		-	-	-	-	-	-	-	-	-	-
10 July	FLC	2	9	0	0	0	0	11	0	0	0
16 July		-	-	-	-	-	-	-	-	-	-
18 July	FLC	10	0	0	0	0	0	10	0	0	0
22 July		-	-	-	-	-	-	-	-	-	-
23 July		-	-	-	-	-	1	1	-	-	-
24 July		-	-	-	-	-	-	-	-	-	-
29 July		-	-	-	-	-	-	-	-	-	-
1 Aug	FLC	0	0	0	0	0	0	0	0	0	0
4 Aug		-	-	-	-	-	-	-	-	-	-
7 Aug		-	-	-	-	-	-	-	-	-	-
9 Aug		-	-	-	-	-	-	-	-	-	-
11 Aug	FLC	0	0	0	0	0	0	0	5	0	0
22 Aug		-	11	-	-	-	-	-	-	-	-
25 Aug		-	-	-	-	-	-	-	-	-	-
28 Aug		-	-	5	150	-	-	-	-	-	-
29 Aug		-	-	-	-	-	1	1	-	-	-
5 Sept	Co. Park	-	10	-	-	1	-	11	-	-	-
8 Sept		-	-	-	200+	-	4	204	-	-	-
28 Sept	N shore	-	-	-	c200	-	-	200	-	-	-

Table 6.2b. Mono Lake Minimum Waterfowl Counts, 1991. **Data from direct counts of all waterfowl seen in 1991 at Mono Lake. FLC = Full-lake count; Co. Park = data from the County Park area only; N. Shore = data from a walk along six miles of shoreline, from 10 Mile Rd. east; * = birds only seen flying over the lake; zeros only given for days on which full-lake counts were carried out.**

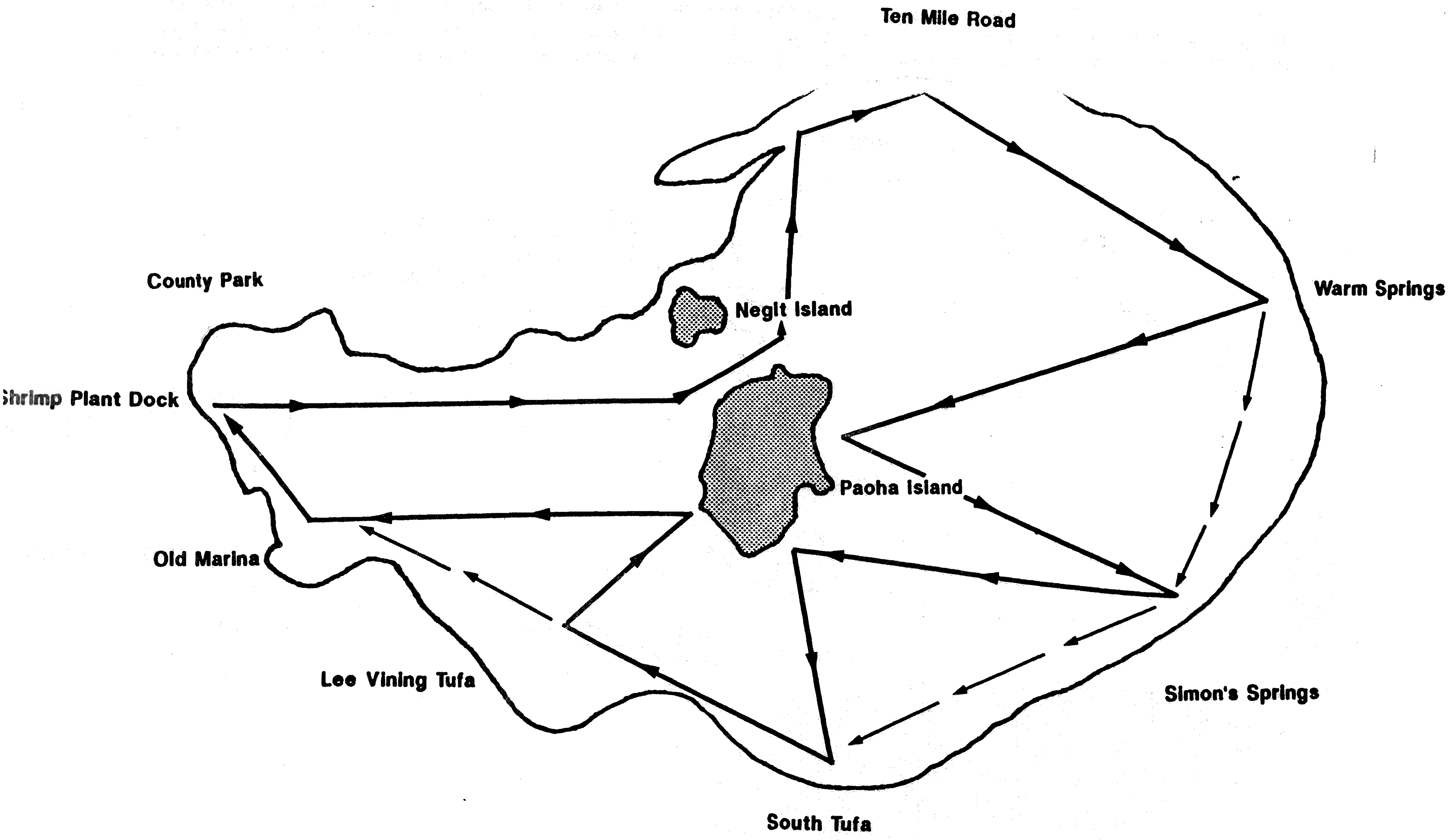

FIGURE 6.1a. MONO LAKE CENSUS SCHEME , 1990 & 1992. Lines represent transects followed by the boat crew while censusing; arrows indicate direction of travel. Broken lines represent (a) alternate route taken on one date in 1990, (b) the route between Simon's Springs and South Tufa regularly used in 1991, and (c) an alternate route taken on one date in 1991. Two separate shoreline crews counted birds at South Tufa, Lee Vining Tufa, and Old Marina/ Shrimp Plant Dock and County Park at the same time that the boat crew was counting.

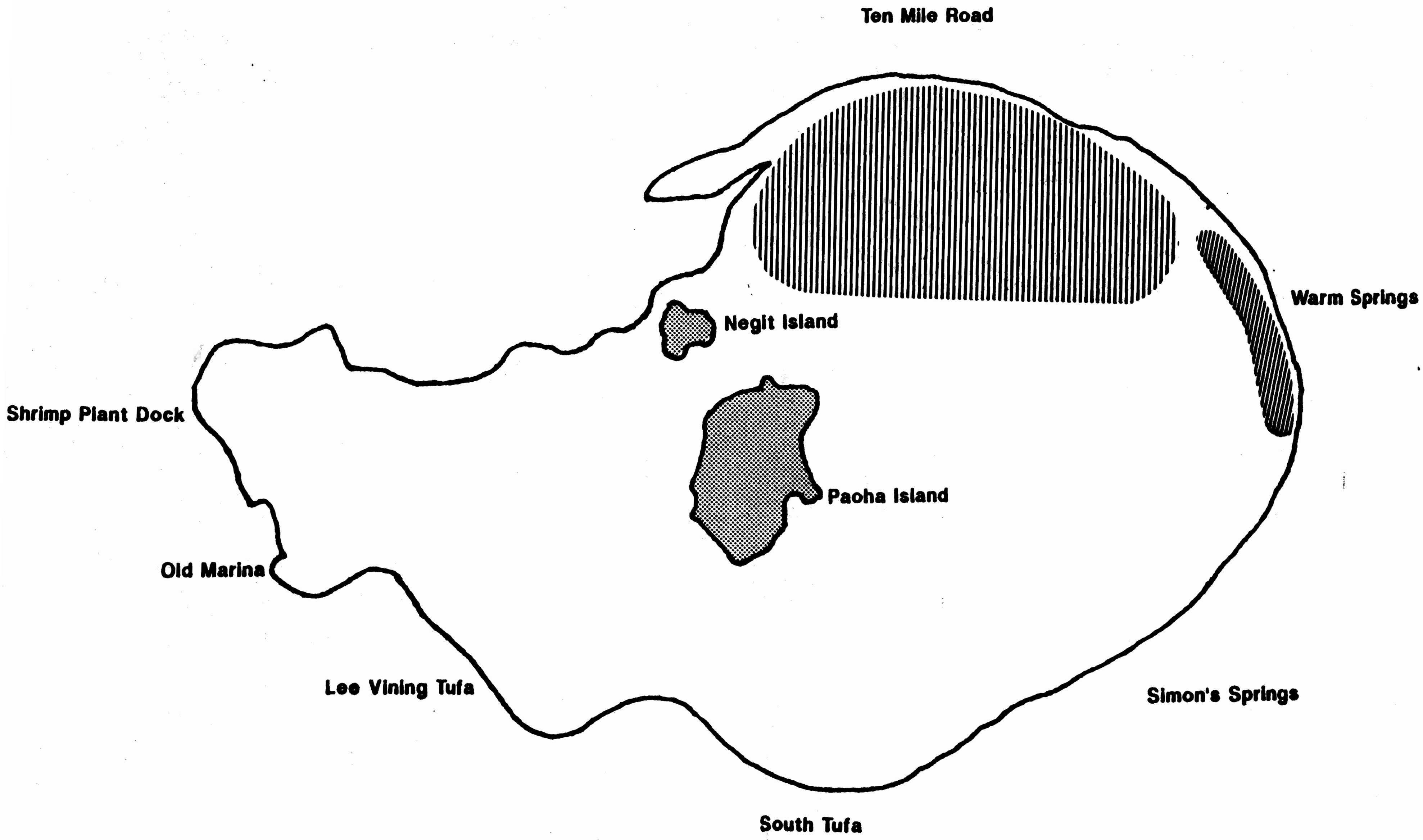

FIGURE 6.1b. DISTRIBUTION DATA: PHALAROPES AT MONO LAKE, 1990 &1991. Vertically hatched area = area of most Red-necked phalarope feeding activity. Vertically hatched area = the diurnal roosting area of Wilson's phalaropes in 1990 &1991. Large numbers of Wilson's phalaropes also fed in the northeast sector of the lake, and both species fed offshore and in nearshore areas around the east end of the lake.