Diel Feeding Cycle and Some Effects of Light on Feeding Intensity of the Mississippi Silverside, *Menidia audens*, in Clear Lake, California

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ABSTRACT

A study of the diel feeding cycle of 940 Mississippi silversides, *Menidia audens* Hay, in two 24-hour sampling periods in Clear Lake, California, showed a predominance of crustacean zooplankton in the diet. *Ceriodaphnia* sp., *Daphnia pulex,* and emerging dipterans were the most important food items. A pronounced morning feeding peak indicated visual feeding. Evidence of visual feeding is further given by statistically significant ingestion of larger food items at night and decreased feeding during the one moonless night. Occurrence of emerging midges in the diet during the second period indicates possible selective predation.

Mississippi silversides, *Menidia audens* Hay, were introduced into Clear Lake, Lake County, California in 1967 to help control the Clear Lake gnat (*Chaoborus astictopus*), to reduce algal blooms, and to provide forage for game fishes (Cook and Moore 1970). Since their introduction they have become the most abundant fish in the lake and have spread to a number of reservoirs and streams in the Sacramento-San Joaquin River system, with unknown effects on other fishes (Moyle, Fisher, and Li 1974). This rapid spread following an introduction is taking place in Oklahoma as well (Sisk and Stephens 1964; Gomez and Lindsay 1972). It has thus become important to learn as much as possible about their biology in order to assess their impact on the waters they invade.

The feeding habits of the Mississippi silverside are known only from studies with small sample sizes. Rice (1942) found that silversides from Reelfoot Lake, Tennessee, were feeding predominately on diatoms. Saunders (1959) found both phytoplankton and zooplankton in the stomachs of silversides from Lake Texoma, Oklahoma. The latter study indicated that Mississippi silversides have a diminished feeding rate at night.

STUDY AREA

Clear Lake is the largest natural freshwater lake entirely within California's borders, with a surface area of 17,670 hectares. It is shallow (average depth, 8 m), eutrophic, and lies at a low elevation (440 m) in the Coast Range. Summer temperatures average 20–25 C and the lake is polymictic. The study area was located on the south shore of the upper arm about 500 m east of the mouth of Cole Creek. It is a shallow sandy bottomed area, with a sparse growth of rooted aquatic plants and a border of tule beds (*Scirpus* spp.).

METHODS

The protocol for this diel feeding study was modified from that of Darnell and Meierotto (1962). Collection intervals were established by starving a sample of 100 fish in a closed tank of filtered (80μ mesh size) Clear Lake water, maintained at lake temperature (24–28 C). When dissection of a subsample revealed that the guts were empty, zooplankters collected from the lake with a plankton net were introduced. After introduction of food six fish guts were examined every 15 minutes until each stomach was determined to be filled. The time period from food introduction

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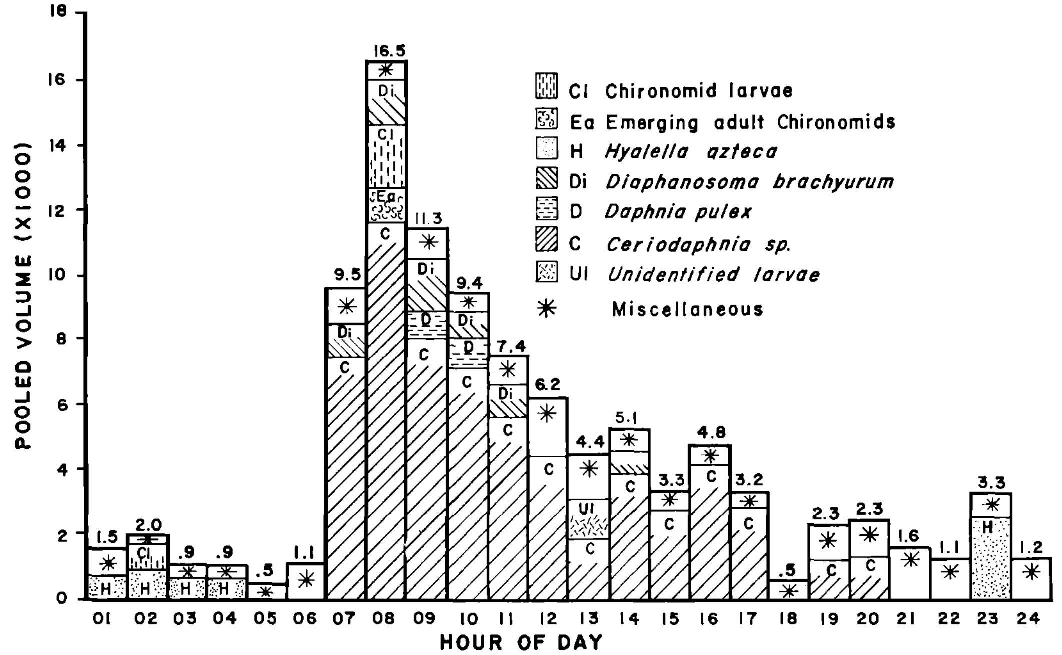

FIGURE 1.—*Diel feeding cycle of the Mississippi silverside, August 19–20, 1973. The bar for each hour represents pooled volume of 20 stomach contents. Numbers over bars refer to percent each hour contributes to total 24-hour volume. Miscellaneous category includes all organisms occurring too infrequently to be graphically represented.*

until the stomachs were entirely filled represents the minimum average time elapsed between the entry of a food item into the fish and movement of that food item out of the stomach. This measure of minimum time of movement of food items through the stomach was then used as the sampling interval necessary for complete assessment of the feeding cycle.

Fish were observed to consume food items immediately after introduction of food into the tank. Dissections performed at 15, 30, and 45 minutes showed only partially filled stomachs. All fish examined at the one-hour interval showed food packed through the entire stomach. Accordingly, a one-hour interval was chosen to allow analysis of all food items which entered the stomachs.

Actual sampling consisted of collecting 20 fish (average standard length 58 mm) each hour for 24 hours on two separate days with a 10 m × 1.2 m, 0.6-cm-mesh seine. Two sampling periods, one beginning at 1900 h on August 19, 1973 (Period I) and the other beginning at 1400 h on August 23, 1973 (Period II) were selected so that during the first a near full moon was visible during most of the dark hours and that during the second no moon was visible during the dark hours. Immediately after capture the spinal column of the fishes was severed and they were placed in 10 percent formalin solution.

Stomach contents of the 940 fish were later removed and individually examined on a microscope slide at 40 ×. Food items were identified and counted, and their volumes estimated using a points system similar to that described by Hynes (1950). This is a relatively rapid volumetric estimation in which the average-sized individual of the smallest food species is assigned one point and larger organisms are assigned a proportionately greater number of points. The food species assigned the one point volume was retained as a reference so that allotment of points was consistent throughout the study. Pooled vol-

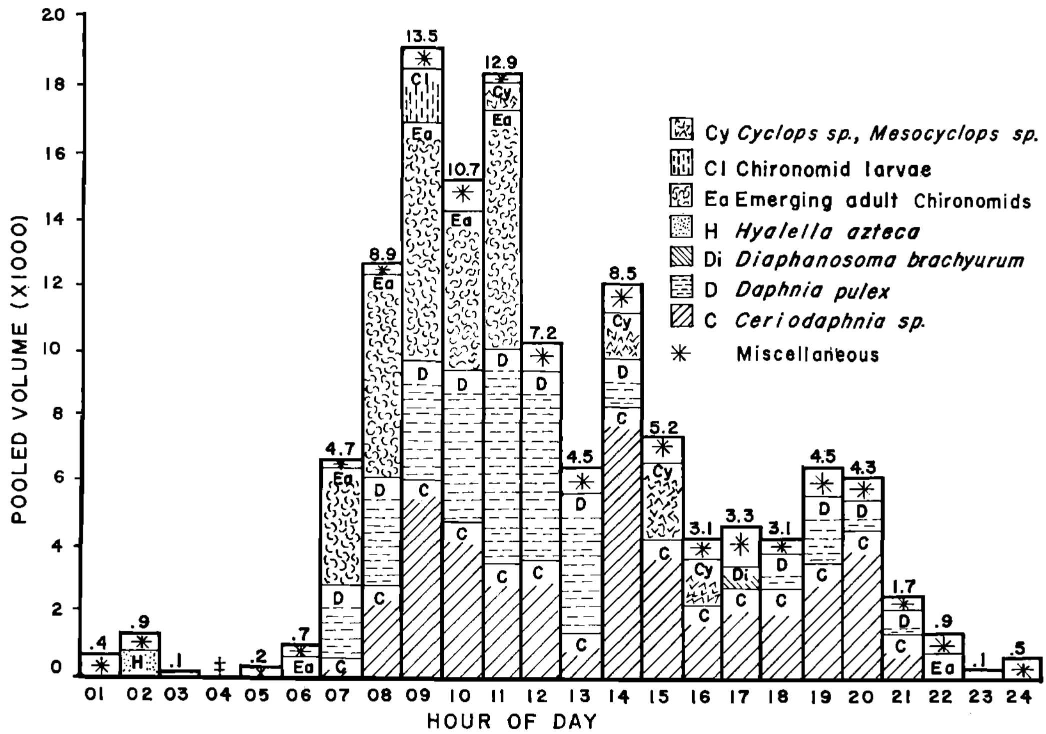

FIGURE 2.—*Diel feeding cycle of the Mississippi silverside, August 23–24, 1973. The bar for each hour represents pooled volume of 20 stomach contents. Numbers over bars refer to percent each hour contributes to total 24-hour volume. Miscellaneous category includes all organisms occurring too infrequently to be graphically represented. Data are missing for 0400 h.*

umes were obtained by summing the points assigned to all organisms of the same species taken by each of the twenty fish of a given hourly sample.

Differences in food intake between moonless and moonlit nights and between food item size for light and dark periods were tested using the *t*-test based on range (Moore 1957). Using this analysis, each hour was treated as an independent sample, thus providing replication within each of the two sample periods. An index of average food item size was obtained by dividing each total hourly volume by the total number of organisms counted for that hour.

RESULTS

The stomach analyses showed that the Mississippi silversides in Clear Lake feed primarily on zooplankton (Table 1) with definite daily peaks in both volume and kind of organisms eaten (Figs. 1 and 2). The most important food organisms were *Ceriodaphnia* sp., *Daphnia pulex*, and emerging dipterans. The information in Figures 1 and 2 is available in detailed tables from the authors.

Most feeding occurred during the period when the sunlight was directly incident on the water surface at and near the sample site (i.e., the hours between the localized sunrise and sunset). Allowing a one-hour digestion lag time after the last hour of direct sun, the samples taken between 0700 h and 2000 h represent fish which were feeding during the hours of direct sunlight. During this time 86 percent of the total daily volume of food was consumed in Period I and 95 percent in Period II.

The feeding peak for both days was rapidly approached after 0700 h, the first hourly sample after which direct sunlight fell on the water (Figs. 1 and 2). The greatest volumes

TABLE 1.—*Percent composition by volume of total daily diet of Mississippi silversides. Each column represents summation of the 24 and 23 hourly pooled volumes for each food item scaled to percentages (Period I–480 fish; Period II–460 fish). The + indicates occurrence of less than one percent.*

Taxon	Date and sampling period	
	August 19–20 I	August 23–24 II
Cladocera		
Bosmina longirostris	3	1
Ceriodaphnia sp.	63	38
Daphnia pulex	5	27
Diaphanosoma brachyurum	9	2
Copepoda		
Cyclops sp., *Mesocyclops* sp.	1	6
Unidentified nauplii	+	+
Amphipoda		
Hyalella azteca	6	1
Ostracoda	+	+
Diptera		
Chironomid larvae	6	2
Emerging *Chironomus* and *Procladius*	5	23
Unidentified larvae	2	+
Rotatoria	+	+

of food were obtained from the 0800 h sample in Period I and the 0900 h sample Period II. Feeding occurred at a higher level throughout the sunlit hours of Period II than of Period I. The occurrence of *Ceriodaphnia* sp. closely parallels the total hourly volumes on both days. During Period II, however, the larger size and probable increased availability of *Daphnia pulex* and emerging dipterans apparently depressed the amount of *Ceriodaphnia* sp. consumed, especially before 1400 h. Between 0700 h and 1400 h in Period II), *Daphnia pulex* and emerging adult dipterans accounted for 32 percent and 30 percent, respectively, of the total volume for that period while accounting for only 5 percent and 1 percent between 1500 h and 2000 h.

During the dark hours of Period I, when a nearly full moon was shining, 14 percent of the total daily volume of food was consumed, while only 5 percent of the total daily volume was consumed during the dark moonless hours of Period II. When the 0400 h samples are eliminated from both periods because of the missing data in Period II, this difference between percent of total daily volume consumed during the dark hours of the two sample periods is significant at the 99 percent confidence level.

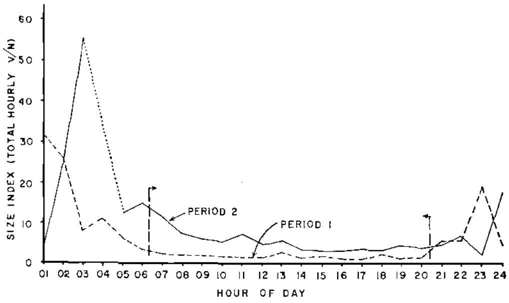

FIGURE 3.—*Diurnal changes in the average volume of food organisms consumed by Mississippi silversides. Each point was calculated by dividing pooled hourly volume (V) by pooled hourly numbers (N) of all food items. Vertical dashed lines bracket hours that stomach contents were consumed during direct sunlight on water. Dotted line connects sample hours enclosing missing sample. Period I—moonlit; Period II—moonless.*

Night time feeding was primarily on larger, and presumably more visible, organisms. For example, in Period I, 97 percent of the relatively larger and nocturnally active *Hyalella azteca* were eaten between 2000 h and 0600 h, while in Period II, 82 percent of the *Hyalella* were eaten during this period. Figure 3 shows the index of average food item volume plotted by hour for the two sample periods. A significant difference ($P < 0.01$) was found in the average volume of individual food items selected between daylight and dark hours for each of the two sample periods.

DISCUSSION

Visual feeding is strongly indicated for the Mississippi silverside in three ways. The first is the dramatic increase in stomach content volume occurring after direct sunlight fell on the water at 0700 h. The second is the statistically significant greater percentage of total daily volume consumed between 2000 h and 0600 h during Period I (moonlit) than during Period II (moonless). Visual feeding is also indicated by the consumption of larger organisms during the dark hours (Fig. 3). Chironomid larvae, and *Hyalella*, are the larger organisms contributing to the stomach contents during the dark hour samples.

The increased incidence of emerging adult chironomids in Period II is probably closely related to emergence times. Mosquito Abatement District personnel have found evidence for morning emergences in Clear Lake (J. Prine, personal communication). This is reflected in the high percentages of midges in the 0700 h to 1100 h stomachs in Period II. Although prey availability studies are required to demonstrate selective predation, a comparison of Figures 1 and 2 indicates that the silverside may be capable of selective predation as a function of prey availability.

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