

A COMPARISON OF THE POPULATION DYNAMICS OF
Unionicola formosa FROM TWO ANODONTINE
BIVALVES IN A NORTH CAROLINA FARM POND

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Abstract: The population dynamics of *Unionicola formosa*, a symbiotic water mite of the freshwater mussels *Anodonta cataracta* and *A. imbecilis*, were monitored for 1 year in a N.C. farm pond. All mussels collected during the study harbored female mites which were significantly overdispersed among their hosts in every month. The density of female mites was significantly greater among *A. imbecilis* when compared with *A. cataracta*. There was no seasonal pattern in the distribution of female mites among *A. cataracta*; however, females in *A. imbecilis* were most numerous during the fall and were least abundant in December. The distribution of male *U. formosa* differed from that of females in that males were significantly underdispersed among their hosts, occurring primarily as one male per mussel. Nymphal *U. formosa* were present in every month among both species of mussel; however, they were most abundant in early summer. Nymphs in *A. cataracta* exhibited a second peak of abundance in mid-winter. In general peaks in the occurrence of nymphs among the mussels preceded periods of maximal density of females by 1-2 months. Mite eggs were present throughout the entire year within both species of mussel. Larval *U. formosa* only emerged from mussels during May-September. Larval mites do not transform to the nymphal stage in the absence of a molluscan host or chironomid dipteran. The significant differences in the population dynamics of this mite as observed in the present study are consistent with the mites from each molluscan species being separate breeding populations which may constitute different species.

Key Words: population dynamics; *Unionicola formosa*; *Anodonta cataracta*; *Anodonta imbecilis*; mussels; mites.

INTRODUCTION

Water mites of the family Unionicolidae are common symbionts of freshwater sponges, gastropods, and mussels (Mitchell, 1957; Davids, 1973; Vidrine, 1980). Their life cycle is complex and includes the egg, prelarva, larva, nymphochrysalis, nymph, teleochrysalis, and adult (Mitchell, 1955, 1965; Böttger, 1977). Some species are free living predators as nymphs and adults, depending upon the host only for sites for oviposition and post larval resting stages, while others are obligate symbionts of their host (Mitchell, 1955; Hevers, 1980). Among those species living with mussels the females deposit eggs in specific tissues of the host (Mitchell, 1955; Vidrine, 1980). Larvae emerge in late spring and summer and are briefly parasitic on chironomid dipterans (Jones, 1965; Booth and Learner, 1978). The larvae eventually reinvade a host, embed in host tissue and enter a quiescent transformational stage, the nymphochrysalis, from which emerges the sexually

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immature nymph. The nymph subsequently transforms through the teleochrysalis to an adult.

The water mite, *Unionicola formosa* (Dana and Whelpley), is an obligate symbiont of several genera of freshwater mussels, especially the genus *Anodonta*. Vidrine (1980) reported *Anodonta cataracta*, *A. imbecilis*, *A. grandis*, *A. hallenbecki*, and *A. peggyae* as hosts of *U. formosa* throughout much of the eastern United States. Field observations (Roberts, 1977; Vidrine, 1980) and behavioral studies (LaRochelle and Dimock, 1981; Downes, 1986) indicate that *A. imbecilis* is the preferred host of this mite in the southeastern United States (Dimock, 1985).

Although patterns of host specificity and zoogeography of *U. formosa* have been described (Dobson, 1966; Vidrine, 1980; LaRochelle and Dimock, 1981; del Portillo and Dimock, 1982; Downes, 1986), studies of the population ecology of this mite have been limited to those of Gordon et al. (1979) and Dimock (1985). Gordon et al. (1979) examined the life history and seasonal dynamics of *U. formosa* from *A. cataracta* in N. B., Canada, while Dimock (1985) monitored the population dynamics of this mite from *A. imbecilis* in N. C. Comparatively, these studies suggest that there are substantial differences in the density and the seasonal distribution of *U. formosa* between these two anodontine hosts, differences which Dimock (1985) suggested could be influenced by factors such as geographic location, host size, and season.

Subsequent observations by our laboratory suggested that significant differences in the population biology of *U. formosa* could occur within the same geographic region. For example, in one piedmont farm pond (Honeycutt's pond) *A. imbecilis* harbored a large population of *U. formosa*, while the sympatric congener, *A. cataracta*, harbored essentially no mites. However, a cursory investigation of a nearby pond (Fisher's pond) indicated that both *A. imbecilis* and *A. cataracta* harbored considerable populations of this mite. Thus, the present study was designed to assess the population dynamics of *U. formosa* from a pond in which there were two species of anodontine hosts. The data reveal significant differences in the population biology of the mites from these two hosts. The differences are consistent with the idea that these populations constitute morphologically indistinguishable sibling species of *Unionicola*.

MATERIALS AND METHODS

Ten *A. cataracta* were collected each month from April 1987 to March 1988 and 10 *A. imbecilis* were collected each month from June 1987 to May 1988 from Fisher's pond, Mt. Pleasant, Cabarrus Co., North Carolina. Mussels were collected by hand or with a clam rake and were placed individually in polyethylene bags to avoid the loss of any mites associated with an individual host. Since the abundance of mites may be correlated with host size (Dimock, 1985), only *A. cataracta* of 80.0–90.0 mm shell length and *A. imbecilis* of 60.0–70.0 mm were sampled. In the laboratory the mussels and the polyethylene bags were thoroughly examined for females, males, and nymphs. The demibranchs were casually examined for the presence of eggs and prelarvae.

While most investigators agree that larval *Unionicola* require a brief parasitic phase with chironomid dipterans (Jones, 1965; Booth and Learner, 1978; Hevers, 1980), Paterson and MacLeod (1979) contend that larval *U. formosa* are capable

of metamorphosis in the absence of an insect host. To test this hypothesis 20 prelarvae were removed from the demibranchs of both *A. cataracta* and *A. imbecilis* and were placed individually in flat bottom well-plates (1.5 cm id) with 3 ml of artificial pond water (APW) (Dietz and Alvarado, 1970). The well-plates were examined daily for the presence of emerging larvae or any transforming to nymphs.

The population data were examined for normality and homogeneity of variance before statistical analyses following the procedures of Gravetter and Wallnau (1985). Comparisons of the data were assessed either by one-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test or by two-factor ANOVA.

RESULTS

All *Anodonta cataracta* and *A. imbecilis* collected harbored female *Unionicola formosa*. There was a mean density of 9.6 females/mussel (SE = 0.75, range = 1–31) among *A. cataracta* and a mean density of 53.4 females/mussel (SE = 1.6, range = 5–97) among *A. imbecilis*. Female *U. formosa* were significantly more abundant in *A. imbecilis* in every month when compared with *A. cataracta* ($p < 0.001$, two-factor ANOVA). The distribution of female mites from *A. cataracta* was significantly overdispersed in every month (overall $S^2/\bar{x} = 5.9$, $\chi^2 > 698$, $df = 119$, $p < 0.05$). With the exception of 2 months (November and February), female mites also were significantly overdispersed among *A. imbecilis* (overall $S^2/\bar{x} = 5.6$, $\chi^2 = 643$, $df = 119$, $p < 0.05$).

There were no significant differences among the monthly mean densities of females among *A. cataracta*. Nonetheless, a seasonal trend in the distribution of female *U. formosa* was apparent with female mites being most abundant in summer (Fig. 1) and least abundant in winter (Fig. 1). In contrast, the occurrence of female *U. formosa* among *A. imbecilis* did vary seasonally. The maximum density of females occurred in the fall (September–October 1987; Fig. 2) and was significantly greater than the winter minimum (December 1987; Fig. 2; $p < 0.05$, ANOVA, Tukey's HSD). No other significant differences occurred among the monthly data for female mites from *A. imbecilis*.

The distribution of male *U. formosa* among *A. cataracta* and *A. imbecilis* was substantially different from that of female mites. Individual *A. cataracta* harbored a mean of 0.90 males/mussel (SE = 0.001, range = 0–2), while *A. imbecilis* had 0.98 males/mussel (SE = 0.001, range = 0–2). Males were significantly underdispersed in every month among both *A. cataracta* (overall $S^2/\bar{x} = 0.12$, $\chi^2 = 14.5$, $df = 119$, $p < 0.05$) and *A. imbecilis* ($S^2/\bar{x} = 0.11$, $\chi^2 = 10.9$, $df = 119$, $p < 0.05$). In fact, 89% of the *A. cataracta* and 91% of the *A. imbecilis* harbored only a single male. There were no significant seasonal differences in the distribution of male mites in either species of mussel ($p > 0.05$, ANOVA, Tukey's HSD).

Nymphal *U. formosa* were present in every month in both *A. cataracta* ($\bar{x} = 1.9 \pm 0.15$ SE, range = 0–10) and *A. imbecilis* ($\bar{x} = 2.9 \pm 0.22$ SE, range = 0–13); however, their abundance was clearly seasonal. A maximum density of nymphs in *A. cataracta* occurred in the summer (June 1987; Fig. 3) and was significantly different from both a spring and autumn minimum (May and October 1987, respectively; Fig. 3; $p < 0.05$, ANOVA, Tukey's HSD). A maximum number of nymphs/mussel among *A. imbecilis* occurred in the summer (July 1987; Fig. 4)

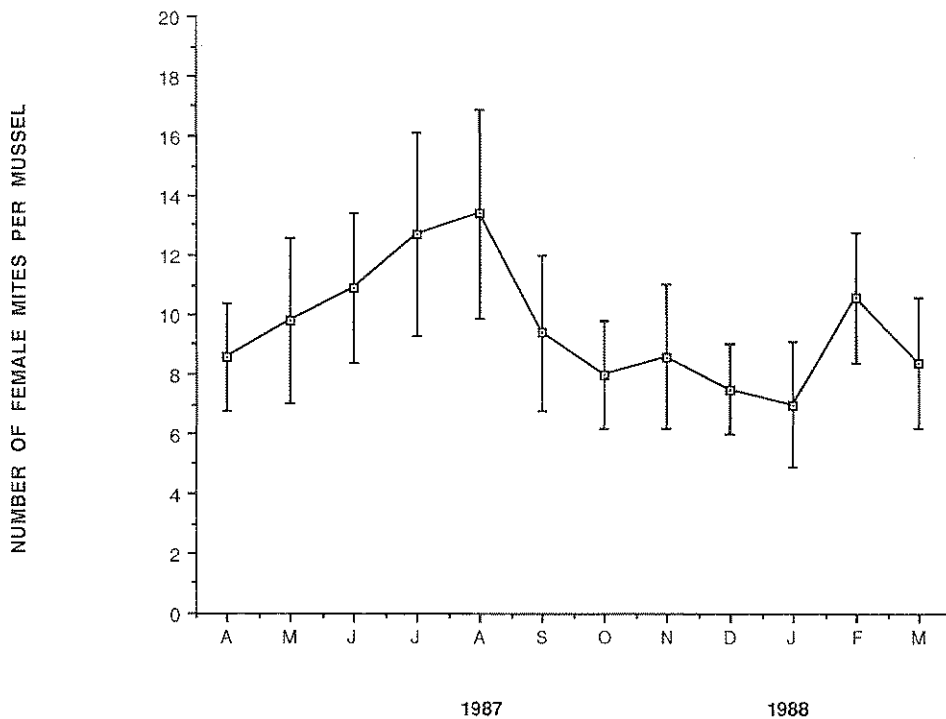


FIG. 1. The distribution of female *Unionicola formosa* among *Anodonta cataracta* over a 1 year period. The boxes are means for 10 mussels/month and the error bars are ± 1 SE.

and was followed by a significantly lower density of nymphs in the fall (October 1987; Fig. 4; $p < 0.05$, ANOVA, Tukey's HSD). The density of nymphs in both June and July was significantly different from all other months, but no other significant differences occurred among the data for nymphs from *A. imbecilis*. Nymphs were randomly distributed among the mussels in 10 of 12 months for *A. cataracta* and in 8 of 12 months for *A. imbecilis*. In the remaining months the nymphs were overdispersed.

Mite eggs were present in every month in the gills of both *A. cataracta* and *A. imbecilis*, and although a quantitative evaluation of their occurrence is not presented, they typically were more abundant in the spring and summer than at other times of the year. Prelarvae were present in the gills of both species of mussel from May–September, during which time larvae were emerging from the gills and could be found swimming in the mussel's mantle cavity.

In the absence of a mussel host, larval *U. formosa* from *A. cataracta* lived an average of 11.2 days (SD = 4.7, range = 7–28) and larvae from *A. imbecilis* lived an average of 14.2 days (SD = 4.8, range = 7–22). None of the larvae transformed to nymphs *in vitro*.

DISCUSSION

The abundance of female unionicolids among unionid hosts is highly variable. For example, Hevers (1980) reported as many as 131 female *Unionicola ypsilon* from *Anodonta cygnea* in Europe, whereas Mitchell (1965) found a maxi-

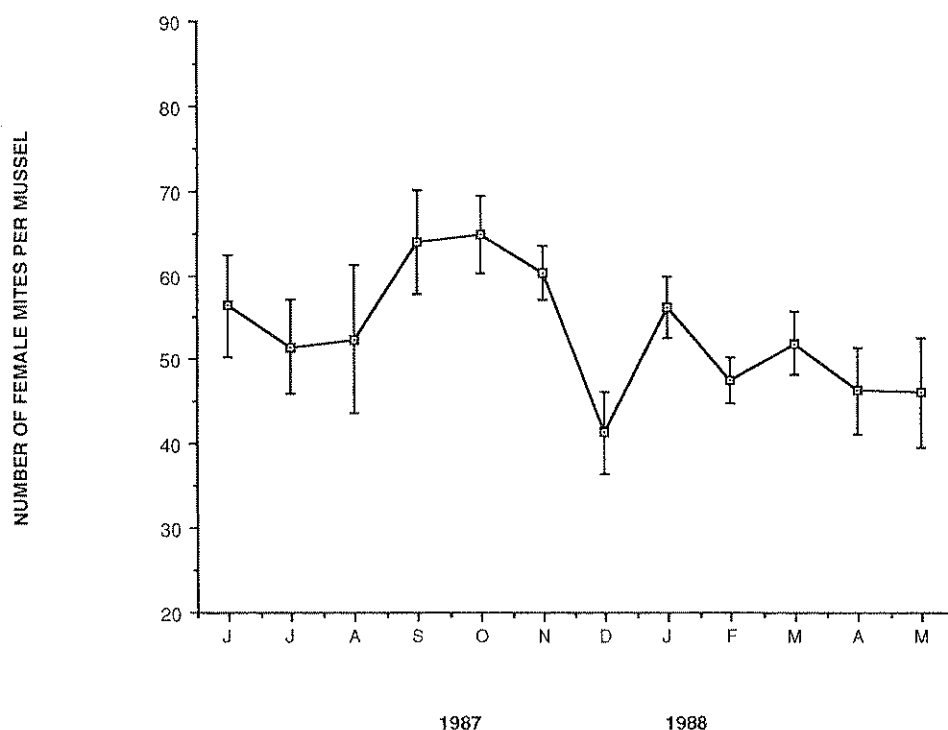


FIG. 2. The distribution of female *Unionicola formosa* among *Anodonta imbecilis* over a 1 year period. The boxes are means for 10 mussels/month and the error bars are ± 1 SE.

num of only two female *U. fossulata* in *Lampsilis siliquoidea* from Mich. Dimock (1985) observed a large population of female *U. formosa* in *A. imbecilis* from N.C. (e.g., one individual harbored as many as 78 female mites), but found virtually no females in a sympatric congener, *A. cataracta*. Gordon et al. (1979) never found more than 11 female *U. formosa* in *A. cataracta* from Canada. In spite of these significant differences in abundance among different species, a female biased sex ratio is typical for many of the unionicolids (Mitchell, 1965; Davids, 1973; Gordon et al., 1979; Hevers, 1980; Dimock, 1985; Baker, 1987), and there is evidence to suggest that territoriality and intrasexual aggression exhibited by males are responsible for this distribution (Dimock, 1983; Davids et al., 1988).

The abundance of female *U. formosa* among *A. imbecilis* and *A. cataracta* as observed in the present study is similar to the observations of both Gordon et al. (1979) and Dimock (1985) in that females were significantly more numerous in *A. imbecilis* than among *A. cataracta*. However, both Gordon et al. (1979) and Dimock (1985) reported a lower mean density of females in the respective species than were observed in the present study. For example, *A. cataracta* from Fisher's pond harbored an average of 9.6 females/mussel, but *A. cataracta* in Canada (Gordon et al., 1979) only had an average of 1.6 females/mussel. The mean density of females among *A. imbecilis* in the present study was 53.4 mites/mussel, whereas Dimock (1985) found an average of only 30.8 females/mussel in the same species

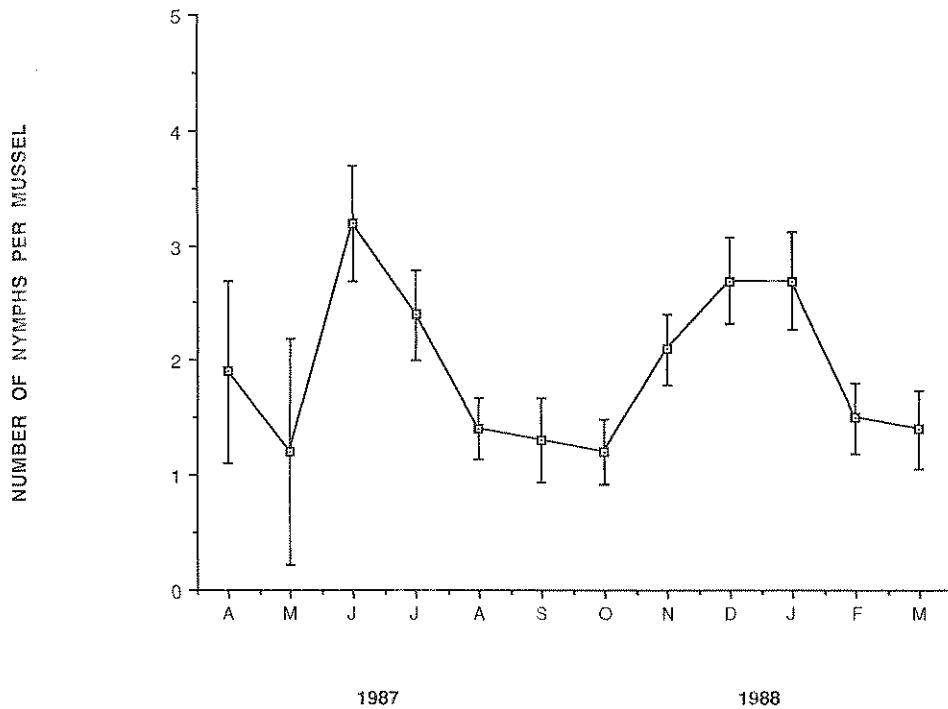


FIG. 3. The distribution of nymphal *Unionicola formosa* among *Anodonta cataracta* over a 1 year period. The boxes are means for 10 mussels/month and the error bars are ± 1 SE.

from a nearby pond. Thus, it is clear that substantial differences in the population dynamics of female *U. formosa* can occur among different populations of mussels.

Several hypotheses have been proposed to explain the differences in the abundance of symbionts among their hosts. For example, Dimock (1985) suggested that factors such as geographic location and host size may be influential while Vidrine (1980) proposed that lentic versus lotic conditions might influence the population ecology of symbionts of mussels. The correlation of the size of the host and the abundance of mites (Gordon et al., 1979; Dimock, 1985) could result from larger hosts being able to accommodate more mites or possibly serving as a larger 'target' for colonization by individuals not already present (Downes, 1986). The fact that *A. imbecilis* is considerably smaller than *A. cataracta*, yet harbors more mites, does not lend credence to this hypothesis. Furthermore, the almost twofold difference in the abundance of females in *A. imbecilis* from Fisher's pond (this study) as compared with *A. imbecilis* from Honeycutt's pond (Dimock, 1985) cannot be attributed to differences in the size of mussels since the same size range of hosts was surveyed in the two studies. Baker (1987) suggested that both physical and chemical properties of a body of water may influence the abundance of unionicolids among unionid hosts. Since *A. cataracta* and *A. imbecilis* in the present study occurred sympatrically, the physical and chemical properties of the water surrounding them are likely to have been nearly identical.

Host suitability may be very influential in determining the abundance of mites among different unionids. Since the work of Dogiel et al. (1964), it has been

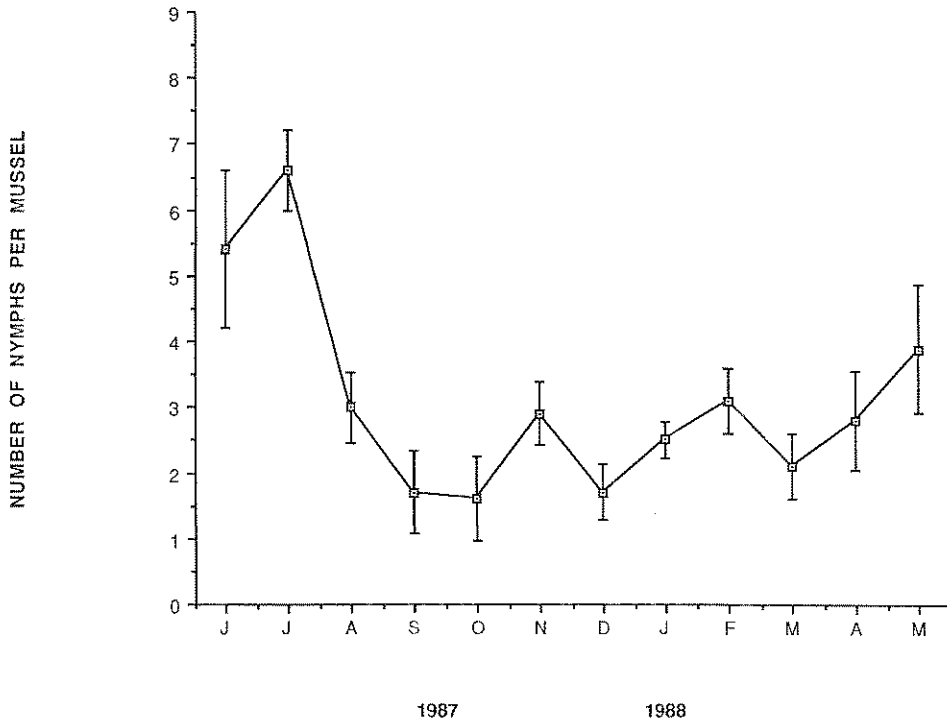


FIG. 4. The distribution of nymphal *Unionicola formosa* among *Anodonta imbecilis* over a 1 year period. The boxes are means for 10 mussels/month and the error bars are ± 1 SE.

recognized that the presence of a parasite in a particular host does not imply that the host is especially suitable. As a rule parasites which are shared by different host species typically occur more frequently and are more abundant in only one of the species (Holmes, 1976). Thus, even though both *A. imbecilis* and *A. cataracta* serve as hosts for *U. formosa*, perhaps *A. imbecilis* is for some reason more suitable.

The seasonal variation in the occurrence of female *U. formosa* among *A. imbecilis* in this study in which females were most numerous in summer and fall and least abundant in winter contrasts with that of Dimock (1985) who reported a maximum density of females in the winter and a minimum number of female mites in late spring and summer. These differences are surprising, especially since the mussels with their respective mite populations were from ponds no further than 1 km apart. It is possible that local differences in the physical and chemical characteristics of these ponds may have contributed to the different distributional patterns. Unfortunately, no data are available on the physical and chemical properties of these ponds or of such potentially important parameters as overall productivity. Furthermore, there are no data which suggest that abiotic factors can strongly influence the population dynamics of *Unionicola*. Since chironomid larvae presumably play an important role in the life cycle of unionicolid mites, differences in the population dynamics of these insects could markedly influence the dynamics of a mite population. There currently are no quantitative data available on the chironomid populations from each of the two ponds surveyed. In contrast to the population ecology of *U. formosa* in *A. imbecilis*, there were no

significant seasonal patterns in the density of female mites among *A. cataracta*. These results are similar to those of Gordon et al. (1979) who reported no seasonal differences in the abundance of female mites among *A. cataracta* in Canada.

The seasonal pattern in the distribution of nymphs among *A. cataracta* and *A. imbecilis* was in some respects consistent with the pattern of abundance of adult females. The occurrence of a large number of nymphs in the population was generally followed by an abundance of adult females. Previous studies of other unionicolids have suggested that there is a maximal occurrence of nymphs in the winter which is followed by a summer minimum (Gordon et al., 1979; Baker, 1987). In the present study nymphs were more numerous in the summer and less numerous in the fall. Baker (1987) noted that nymphal *U. ypsilophora* from *A. cygnea* were the dominant stage of the life cycle for 8 months of the year. Nymphs were far less abundant than females in the present study.

Although a quantitative evaluation of oviposition and larval development was not undertaken in this study, certain generalizations can be made. For example, the seasonal occurrence (May–September) of larval mites and the presence of eggs in every month among both species of mussel are similar to those of other members of the family Unionicolidae (Mitchell, 1965; Gordon et al., 1979; Hevers, 1980; Dimock, 1985). Despite a continuous presence of mite eggs, Dimock (1985) detected a seasonal pattern in their occurrence. Maximum oviposition by *U. formosa* occurred in early spring and was positively correlated with the maximum number of eggs found in the gills. During larval development there is a decrease in the number of eggs in the gill which is followed by an increase during the winter.

It is widely accepted that larvae of the genus *Unionicola* require a brief parasitic phase with a chironomid dipteran in order to complete their life cycle. However, Paterson and MacLeod (1979) argued that larval *U. formosa* were capable of metamorphosing to the nymph without an insect host. It is clear from the present results that larval *U. formosa* cannot metamorphose into a nymph *in vitro* in the absence of a chironomid; however, since larval mites were not monitored in the presence of a molluscan host, it is still possible that larval mites can metamorphose to the nymph without involving a chironomid.

Overall, the results of the present study suggest that the population dynamics of *U. formosa* may be markedly influenced by the host species with which they are associated in the field. However, recent behavioral and genetic information (Edwards and Dimock, unpubl.) suggests that the mites from *A. imbecilis* and *A. cataracta* constitute separate breeding populations and hence are morphologically indistinguishable sibling species. Therefore, the observed differences in the population dynamics of mites from *A. imbecilis* and *A. cataracta* may simply result from the fact that the mites from each host mussel are not the same species.

Acknowledgments: We are grateful for the ideas and assistance that Jeff Jack and Travis Knowles provided. We particularly thank John Foil for his invaluable assistance in the field and also Malcolm Vidrine for confirming the identity of the mites.

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Received 22 September 1988