Studies of <u>Notonecta</u> <u>undulata</u> Say,

(Hemiptera:Notonectidae)

as a Predator of Mosquito Larvae


by

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# ABSTRACT

In a field survey of 15 southwestern British Columbia fresh-water habitats, Notonecta undulata Say was found to live and reproduce under a wide variety of biotic and physical conditions. Backswimmer abundance appears to be correlated with the presence and abundance of competitors and predators. Water hardness and pH may affect this insect's habitat preferences indirectly by determining the flora and associated fauna present in a habitat.

In the laboratory, the backswimmer stages tested preferred a water temperature of 26.2 ± 2.9°C. Adults tolerated water at 34°C for up to 9 hours. Beyond 34°C, mortality increased with temperature.

A rearing method was devised by which 4 generations of backswimmers per year can be reared in comparison to the 2 generations per year occurring naturally.

In the evaluation of N. undulata as a mosquito larval predator, Aedes aegypti L. larvae were supplied as prey. The effects of predator stage, prey age and prey density on predation rate were examined. Second, third, fourth and fifth instar N. undulata were observed to consume more larvae than either first instars or adults. Although all mosquito larval instars were attacked, second age group larvae were killed most often. The mean number of larvae killed per hour increased with increasing

prey density. Water temperature, over the ranges tested, did not have a significant effect on the predation rate of adult N. undulata.

Starved adult N. undulata required approximately 3 hours of active feeding (equivalent to about 30 fourth instar larvae) before they became satiated. Because all the predation studies involved starved predators the resultant predation rates are probably slightly higher than would occur in nature.

Adult backswimmers consistently selected mosquito larvae and pupae over 6 other aquatic prey types. The backswimmer's predatory behavior, elucidated by video-tape recordings and micro-scope observations, suggests it is well suited to capturing mosquito larvae and pupae.

The response of N. undulata to environmental factors and its resultant habitat preferences are very similar to many species of North American mosquitoes. Its predatory behavior, preference for mosquito larvae and pupae and ability to kill all aquatic stages of mosquitoes at some time in its life history suggest that N. undulata is well adapted as a mosquito predator and that it warrants further consideration as a mosquito control agent.

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INTRODUCTION

In considering possible means of mosquito control, there is a need for detailed studies of the natural predator complex. Many aquatic predator species have been qualitatively evaluated for their possible use in mosquito control programs (Hinman 1934; Graham 1939; Sailor and Lienk 1954; Baldwin, James and Welch 1955; James 1957, 1961; and James and Smith 1958). None of these workers, however, has studied the effectiveness of these predators at different predator-prey stages and densities or water conditions.

Mosquito larvae and pupae are preyed on by numerous predators. Hinman (1934) reviewed a number of short laboratory experiments with various insect predators as well as field observations by early biological control workers. The importance of fish as larval predators was the subject of earlier reviews (Anonymous 1924, Covell 1931). Immature newts are also reported to feed on mosquito larvae (Stebbins (1951).

Hinman (1934) has reported that the following insects are mosquito larval and pupal predators: ephemerid larvae, neuropteran larvae, various odonatid nymphs, notonectids, corixids, nepids, belostomatids, naucorids, veliids, hydrometrids, dytiscids, gyrinids, hydrophilids, cicindelids, web-building caddisfly larvae, predaceous mosquito and midge larvae and a few dipteran adults. Only the aquatic families of Hemiptera and Coleoptera -- especially notonectids and dytiscids -- seem to deserve serious

consideration as larval predators, excluding fish (Hinman 1934, Bates 1965). Christophers (1960) noted that Notonecta spp. and Corixa spp. actively destroy larvae. Various notonectid and dytiscid species are considered effective in controlling the mosquito populations of small water holes, rice-fields and artificial containers (Hamlyn-Harris 1929, Laird 1947).

The majority of Hinman's (1934) references consist of casual observations, made either in the field or in the laboratory, together with a few experiments on one or more species. He points out the need for extensive laboratory experiments where an abundance of other satisfactory food is available to the predators, in addition to the mosquito larvae and pupae. Unless the predator species shows a definite preference for mosquitoes, he believes its value as a biological control agent should be treated with suspicion.

In one laboratory study, Enithares bergrothi Montandon, a notonectid found on several islands in the Pacific and Australia, destroyed large numbers of both culicines and anophelines (Laird 1947). Twice as many of the former were killed. Laird's explanation was that anophelines, lying parallel to the water surface, are not as readily seen by the backswimmers as culicine larvae which hang downwards from the surface. Few pupae were destroyed by this species. The New Zealand backswimmer, Anisops assimilis White, also destroys mosquito larvae readily but only

attacks pupae in the absence of larvae, and then only slowly and in small numbers (Graham 1939). Dempwolff (1904), working in what was then German New Guinea, observed that waters containing Notonecta spp. had no mosquito larvae. By introducing Notonecta spp. into water tanks, he brought about the complete destruction of all mosquito larvae within one week. Bare (1926), claimed that all stages of Notonecta undulata Say feed on either mosquito larvae or pupae in the southern United States but he gave no details.

N. undulata, one of the most common species of Notonecta in North America, is a predaceous water bug found in many freshwater habitats throughout Canada and the United States (Bueno 1905, Brooks and Kelton 1967). It is one of the species considered by Hinman (1934) to be an important mosquito predator. Various aspects of its life history, ecology and behavior are well known (Essenberg 1915; Hungerford 1917, 1919; Clark and Hersh 1939; Ellis and Borden 1969a). Little is known, however, about its predatory habits. Adults may be collected throughout the year, though with difficulty during the winter months. Alternatively, they may be colonized in the laboratory (Ellis and Borden 1969b).

In recent years, many investigations into predator-prey complexes have been undertaken. Several workers have examined the effects of varying predator and prey densities on predatory

efficiency (e.g. Steinmetz 1961; Morris 1963; Turnbull 1962, 1965; Chant and Turnbull 1966; Holling 1966; and Mukerji and LeRoux 1969). Of these, however, only Morris (1963), Holling (1966) and Mukerji and LeRoux (1969) consider insect predators and prey in this regard and serve as models for future predation studies.

The six main objectives of my study of N. undulata were as follows:

1) to expand the general biological knowledge of this species by conducting a survey of its habitats in S.W. British Columbia;
2) to supplement this with laboratory observations to determine its preferred habitat; 3) to develop a rearing method that will enable research to be carried out year round on all instars and adults; 4) to determine the preferred prey of N. undulata;
5) to determine the effects of predator stage, prey age, prey density and temperature on the predation rate; and 6) to observe predation to elucidate the possible behavioral sequences involved.

## GENERAL METHODS

### Backswimmer Rearing

Because of the difficulty in identifying field-caught backswimmer nymphs to species and instar, a laboratory colony of N. undulata was initiated in April, 1967, and maintained for approximately 26 months (Ellis and Borden 1969b). Two 15-gallon aquaria, filled with aerated tap water, were each equipped with a filter-aerator, a standard aquarium heater, sand and several pieces of green rubber-mesh sink matting (Fig. 1). Water temperature was maintained at $25 \pm 1°C$. The pH was 6.5 - 7.0. The aquaria were covered with canopies to prevent the escape of adults and provided with two 25 watt bulbs to facilitate periodic inspection. One of the two aquaria was used as an oviposition tank and held up to 15 adults at a time without significant cannibalism if a surplus of fresh food was provided daily. Almost any small- to medium-sized insect dropped onto the surface film would be readily attacked. If it was impossible to provide food daily, a surplus of live prey was kept in the same aquarium (e.g. damselfly, mosquito or midge larvae).

The rubber-mesh sink matting provided suitable sites for backswimmer oviposition (Fig. 2), cover and anchorage (Fig. 3). Plants, such as Anacharis canadensis Michx. (McPherson 1966; Ellis and Borden 1969b), or even sodden leaves (Clark and Hersh 1939) can be used with some success but, due to water temperature and

Fig. 1  Oviposition aquarium of $\underline{N}$. $\underline{undulata}$ showing pieces of
        rubber-mesh sink matting used for oviposition, cover
        and anchorage.

Fig. 2  Newly-laid egg of $\underline{N}$. $\underline{undulata}$ on rubber-mesh sink matting.

Fig. 3  Adult backswimmer using matting for anchorage.
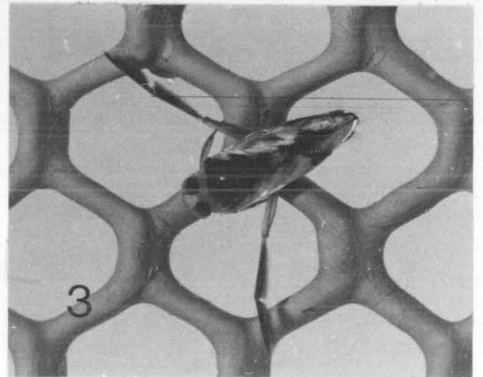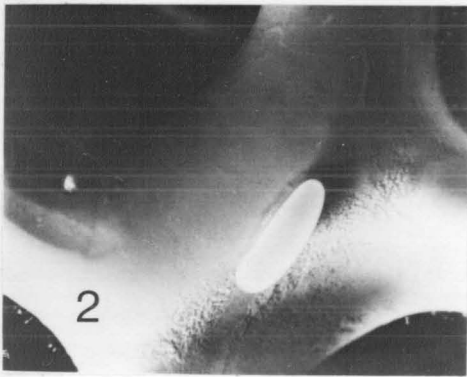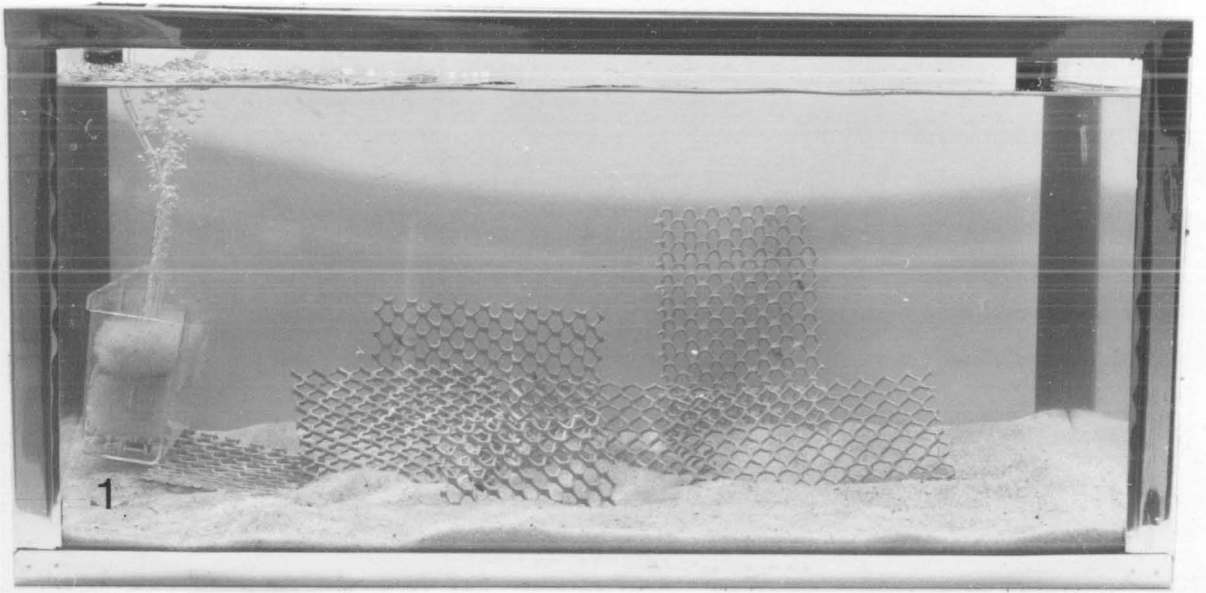
necessary handling, soon deteriorate. Often this occurs before all the eggs hatch. The sink matting, however, keeps its shape and lasts indefinitely. After the eggs were laid, the matting was transferred to the second, or incubation aquarium. Most of the eggs hatched within 1 - 2 weeks. The matting was washed free of empty egg capsules and algae; it was sterilized before being returned to the oviposition aquarium.

First instars were separated within a day of emergence to minimize cannibalism. The nymphs are particularly vulnerable during ecdysis. Hence, each nymph was reared individually in a covered, water-filled 100 ml glass beaker kept at room temperature (21 ± 1°C). The nymphs were provided with food daily (e.g. small mosquito larvae, crustaceans or even flour beetles, Tribolium spp.). After the final moult, the backswimmers were transferred to the oviposition aquarium. Under the above rearing conditions, 4 generations per year could be reared instead of the normal 2 generations per year occurring in southwestern British Columbia.

## Mosquito Rearing

Aedes aegypti L. (obtained from the Canada Department of Agriculture Research Station, Belleville) was chosen as the prey species. Although not a species naturally occurring in this area it has the advantage of having no diapause. Standard procedures were followed in the laboratory rearing of this species (Fay 1964).

Because the exact rearing conditions of the larvae affect the size, an important variable in the experiments, a note on these conditions follows. Eggs were hatched in demineralized water to which a yeast suspension had been added. After emergence, the first instar larvae were maintained in white-enamelled pans (41.5 x 25.5 x 6.5 cm) containing 3000 ml demineralized water kept at room temperature, 21 ± 1°C. The water was changed at the first sign of fouling. Larval rearing density was approximately 1 larva per 10 ml water. Larvae were given a surplus of finely ground tropical fish food daily. Under these conditions larval development was complete in 14 - 15 days. Larvae used in predation studies were divided into 4 larval age groups rather than 4 larval instars: i.e., age group I, 1 - 3 days old (mostly first instars); age group II, 4 - 6 days old (mostly second instars); age group III, 7 - 9 days old (mostly third instars); and age group IV, 10 - 12 days old (mostly fourth instars).

## Predation Studies

All predation trials were made at room temperature (21 ± 1°C) in small, white-enamelled pans (28 x 18 x 5 cm) containing 1000 ml demineralized water (Fig. 4), unless stated otherwise. All backswimmers were starved for at least 24 hours prior to each trial, except those used in the satiation study which were starved for 48 hours. Periodic controls were set up with pans containing only prey; less than 1% larval mortality was due to handling damage.

Fig. 4  Predation study apparatus used to test 2 predator

stage: prey age : prey density combinations.  Inset

shows an adult backswimmer in a 1000 ml pan with 50

mosquito larvae.
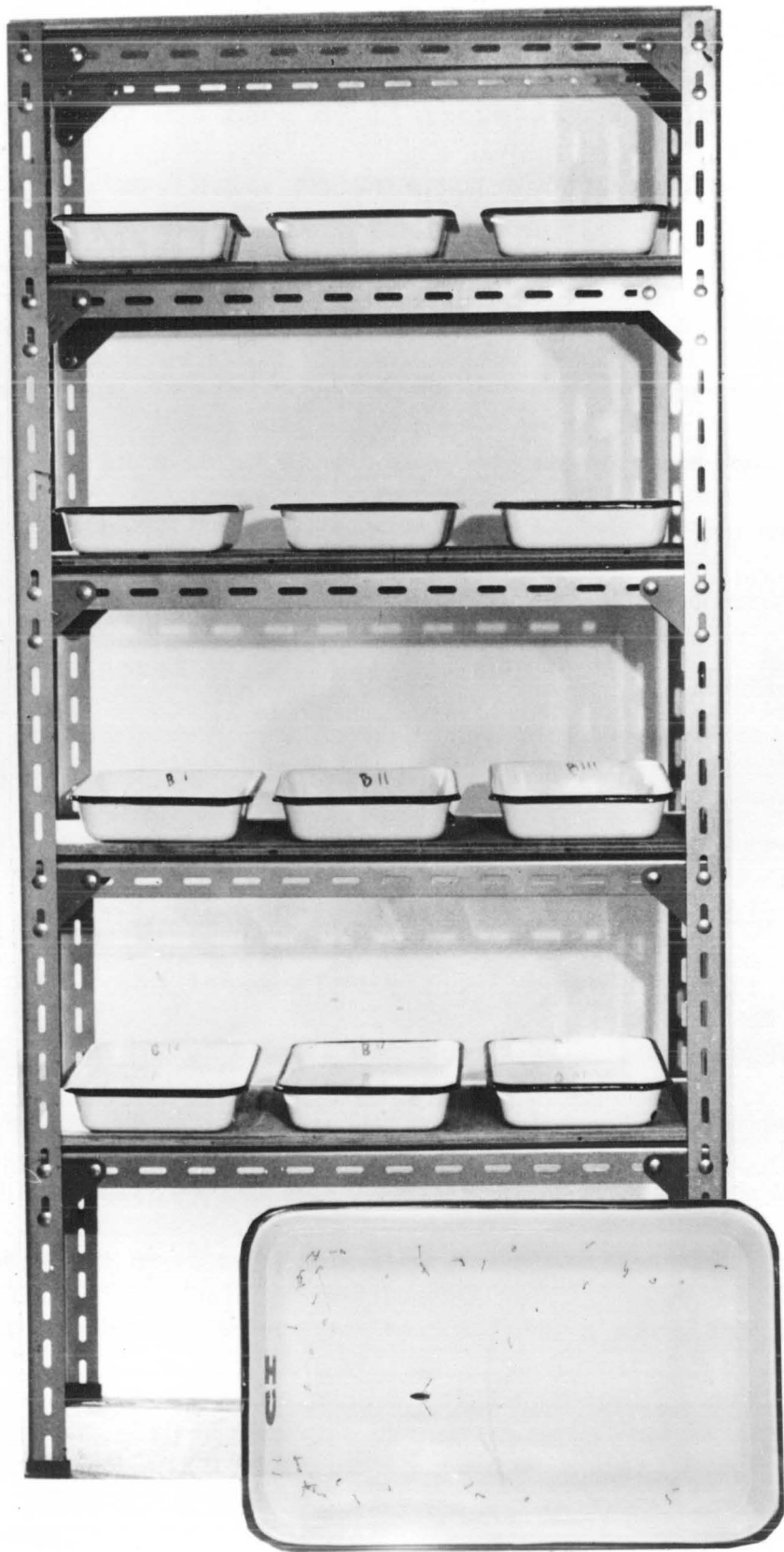
## HABITAT SURVEY

### Methods

A survey was made of 15 fresh-water habitats in the Lower Fraser Valley, B.C., to determine where and under what conditions N. undulata was most abundant. Determinations of the physical characteristics of the backswimmer habitat were made in the field. Each value obtained for temperature, water hardness and pH is a mean of 10 samples taken from the immediate area of the habitat. The latter two characteristics were determined with colorimetric indicators. Conspicuous macroflora and macrofauna were noted.

### Results and Discussion

N. undulata was observed in a variety of fresh-water habitats: i.e., swimming pool, ditch, excavation pool, creek pools, bog ponds and lakes (Table I). These habitats showed a fairly wide range of physical factors: water temperature, 10.0 to 32.5°C; water hardness, 10 (very soft) to 220 ppm (very hard); and pH, 5.9 to 7.1. Water turbidity could not be properly evaluated because most water bodies were non-turbid. Hatzic Slough water, however, where no backswimmers were found, was very turbid. Water current also could not be properly evaluated. Where backswimmers were present there was usually only a very slight current.

Table I. Survey of backswimmer habitats in the Lower Fraser Valley, B.C., with notes on their physical and biological characteristics.

Backswimmer Habitat

| Characteristics | (1) Excavation Pool | (2) Excavation Ditch | (3) Swimming Pool |
|---|---|---|---|
| Location | Burnaby, B.C. | Burnaby, B.C. | Coquitlam, B.C. |
| Date | 24/7/68 | 24/7/68 | 8/5/67 |
| Water Temp. (°C) | 32.5 | 29.5 | 10.0 |
| Water Hardness (ppm) | 220 | 220 | 30 |
| pH | 7.0 | 7.0 | 6.0 |
| Current | Slight | Slow | None |
| Macroflora | Few emergent grasses. | None | None |
| Macrofauna | Notonectidae ***<br>Gerridae *<br>Dytiscidae *<br>Noteridae *<br>Salietia larvae ** | Notonectidae * | Notonectidae **<br>Gerridae *<br>Dytiscidae * |
| Remarks | N. undulata plentiful; Mating observed; Late instars present; Adults active on surface film and flying from pool. | N. undulata rare in ditch leading from excavation pool. Probably drifted from pool. Mating not observed. | High numbers of N. undulata in spite of high chlorine content (40 ppm); Mating observed 12/5/67; First instars observed 25/5/67; Backswimmers observed feeding on terrestrial insects trapped in surface film. |

Key to symbols: *, present in low numbers; **, present in moderate numbers; ***, present in high numbers; and ****, present in unusually high numbers.

Table I. Survey of backswimmer habitats continued.

Backswimmer Habitat

| Characteristics | (8) Deer Lake | (9) Golf Course Pond | (10) Lost Lake | (11) Gravel Pit Pool |
|---|---|---|---|---|
| Location | Burnaby, B.C. | Burnaby, B.C. | Coquitlam, B.C. | Haney, B.C. |
| Date | 23/5/68 | 15/5/69 | 30/5/68 | 21/5/69 |
| Water Temp. (°C) | 21.0 | 24.5 | 24.0 | 22.5 |
| Water Hardness (ppm) | 35 | 40 | 30 | 10 |
| pH | 7.1 | 6.6 | 6.0 | 6.0 |
| Current | Slight | Slight | Very Slight | Slight |
| Macroflora | Submerged, float-ing and emergent plants plentiful. | Submerged, floating and emergent plants plentiful. | Submerged, floating and emergent plants plentiful. | Few emergent grasses. |
| Macrofauna | Notonectidae *<br>Gerridae *<br>Corixidae ***<br>Dytiscidae **<br>Hydrophilidae *<br>Noteridae *<br>Gyrinidae *<br>Chironomidae *<br>Trichoptera *<br>Odonata *<br>Ephemeroptera *<br>Salmonidae * | Notonectidae ****<br>Gerridae *<br>Corixidae **<br>Dytiscidae *<br>Hydrophilidae *<br>Gyrinidae *<br>Chironomidae **<br>Culicidae *<br>Trichoptera *<br>Odonata ***<br>Ephemeroptera *<br>Salietia * | Notonectidae ****<br>Gerridae *<br>Corixidae **<br>Nepidae *<br>Dytiscidae **<br>Hydrophilidae *<br>Noteridae *<br>Gyrinidae *<br>Chironomidae **<br>Culicidae **<br>Trichoptera *<br>Odonata **<br>Ephemeroptera * | Notonectidae ***<br>Gerridae *<br>Corixidae *<br>Dytiscidae *<br>Noteridae *<br>Hydrophilidae *<br>Trichoptera *<br>Crustacea *<br>Salietia larvae * |
| Remarks | N. undulata re-latively rare; possible related to high number of corixids. Mat-ing not observed. | N. undulata very abundant; Noton-ecta kirbyi low in numbers; Eggs and first instars of N. undulata pre-sent. Mating observed. | N. undulata very plentiful; Buenoa sp. also present; Mating observed; first and second instars present; culicid referred to Chaoborus nyblaei. | N. undulata and N. kirbyi both plentiful. Mating observed; no nymphs. |

Table I.  Survey of backswimmer habitats continued.

Backswimmer Habitat

| Characteristics | (12) Rolley Lake | (13) Jewel Lake | (14) Hatzic Slough | (15) Kanaka Creek |
|---|---|---|---|---|
| Location | Mission, B.C. | Haney, B.C. | Hatzic, B.C. | Mission, B.C. |
| Date | 26/5/69 | 21/5/69 | 27/6/69 | 27/6/69 |
| Water Temp. (°C) | 16.0 | 23.5 | 22.5 | 22.0 |
| Water Hardness (ppm) | 10 | 10 | 30 | 20 |
| pH | 6.1 | 6.0 | 6.2 | 6.0 |
| Current | Very slight | Very slight | Slight | Slight |
| Macroflora | Submerged, floating and emergent plants abundant. | Bog plants abundant, emergent and submerged. | Emergent grasses, plentiful. | Submerged and emergent plants abundant. |
| Macrofauna | Notonectidae * | Notonectidae * | Gerridae * | Gerridae ** |
|  | Gerridae * | Gerridae *** | Corixidae * | Corixidae * |
|  | Corixidae ** | Corixidae ** | Dytiscidae * | Dytiscidae * |
|  | Dytiscidae ** | Dytiscidae * | Noteridae * | Noteridae * |
|  | Hydrophilidae * | Hydrophilidae * | Odonata * | Trichoptera * |
|  | Gyrinidae * | Noteridae * | Cyprinidae ** | Odonata * |
|  | Chironomidae ** | Gyrinidae * |  | Cyprinidae * |
|  | Trichoptera * | Chironomidae ** |  |  |
|  | Odonata *** | Trichoptera ** |  |  |
|  | Salietia *** | Odonata ** |  |  |
|  | Urodela * | Ephemeroptera * |  |  |
|  | Salmonidae * | Salietia * |  |  |
|  | Ictaluridae ** | Urodela * |  |  |
| Remarks | N. undulata scarce. Mating not observed. | N. undulata absent; N. Kirbyi in low numbers. | N. undulata absent; Water was very turbid. | N. undulata absent. |

Macroflora in the habitats examined ranged from a complete absence of plants to a rich and varied array. There does not appear to be any direct correlation between macroflora and backswimmer distribution or abundance.

Macrofauna also varied from the presence of a few species to most aquatic insect families and several vertebrates. Macrofaunal diversity appeared to be directly correlated to the diversity and abundance of aquatic plants. Although the abundance of N. undulata was generally greater when flora and fauna were diverse, the distribution of this backswimmer showed no definite relation to macrofauna. It should be noted, however, that where potential competitors or predators of N. undulata were present in high numbers, backswimmer numbers were relatively low: e.g. Deer L. - Corixidae; Placid L. - Gerridae; Jewel L. - Gerridae, Salamanders; Silver Cr. - Stickleback, Trout; and Gwendoline L. - N. kirbyi.

Mosquito larvae and pupae were absent from most back-swimmer habitats surveyed. Subsequent to the survey, however, an occasional Culex sp. larvae was collected from Lost Lake and the golf course pond.

Active, adult N. undulata are occasionally collected near the surface of ice-covered lakes (4°C); the adults apparently obtain their oxygen from air-pockets between the ice and water (Hungerford 1919). More typically, adults over-winter in bottom

debris (Clark 1928). Thus, N. undulata is able to tolerate a
wide range of water temperatures (4 to 32.5°C). Mating and
oviposition appear restricted, however, to a temperature range
of 10 to 32.5°C. The ability to reproduce over a fairly wide
temperature range and to withstand occasional short periods of
high water temperature (e.g. excavation pool, 32.5°C) would enable
N. undulata to inhabit small, sometimes temporary, water bodies
where the water temperature may rise above the preference level
and fluctuate considerably in a short time.

N. undulata often occurs in the same interior British
Columbia lakes as Notonecta kirbyi Hungerford which lives in
water with a pH of 7.0 to 9.2 (Scudder 1965). N. kirbyi occurred
in habitats with a pH of 6.0 to 6.6 (Table I); thus, its pH range
can be extended to 6.0 to 9.2. If N. undulata occurs throughout
the same pH range as N. kirbyi then it would appear that pH, as
well as water hardness, has little effect on the habitat preference
of N. undulata. These factors may indirectly, however, influence
prey abundance and protective cover by determining the abundance
and species composition of shore plants.

Clark (1928) summarized the characteristics of an
optimum habitat for N. undulata in the Winnipeg region: a pool
teeming with aquatic life, vegetation, no current, ample sunlight
and a certain amount of water not covered by algae. Lost Lake
(Coquitlam, B.C.), which fits this description very well, supported

the largest population of N. undulata in the survey, yet the excavation pool had almost as dense a population but with very little vegetation. Also, N. undulata was scarce in Placid Lake (Haney, B.C.), a lake that would be classed, according to Clark's (1928) summary, as optimal. Competition or predation by other aquatic predators may be of more importance than those factors evaluated by Clark (1928).

Mosquito larvae are similar to backswimmers in that they also are able to tolerate a wide range of water conditions (Bates 1965). Happold (1965) states that prevailing temperature, pH and oxygen concentration do not appear to have any limiting effect on mosquito population levels in central Alberta. Neither does there seem to be any correlation between mosquito species and water conditions. Temperature affected his study populations only by determining the times of hatching and the rates of larval development The distribution of mosquito populations depends, rather, on the response of the adult female to vegetation, shade and habitat position (Happold 1965). Significantly, N. undulata is able to occupy many habitats (e.g., bogs, marshes, ponds, lakes) often used by mosquitoes as breeding areas, particularly when these bodies of water have shallow, weedy margins which protect mosquito larvae from wave action (Jenkins 1948, James and Smith 1958, Happold 1965). However, many other mosquito larval habitats (e.g., artificial containers, treeholes, rain and snow pools,

seepage areas) are either too small or too temporary for back-swimmer occupation (Hintz 1951, Bates 1965, Curtis 1967). Introduction of _Notonecta_ sp. into several small larval breeding pools gave no practical results because of their rapid drying (Hinman 1934). It is unlikely that _N_. _undulata_ exerts any influence on the mosquito populations in such habitats. As backswimmers do occur widely in larger semi-permanent and permanent water bodies (Table I), their influence on the mosquito populations of these areas may be significant. However, until the extent to which the habitats of both organisms do actually overlap and until their overall population dynamics, including backswimmer-mosquito interactions, are determined, it is unwise to predict how significant backswimmers could be in practical mosquito control.

## TEMPERATURE PREFERENCE, TOLERANCE AND EFFECT
## OF TEMPERATURE ON PREDATION RATE

### Methods

To determine the temperature preferences of first and
fifth instar and adult N. undulata, a simple temperature gradient
apparatus, similar to that used by Omardeen (1957) for A. aegypti,
was set up (Fig. 5). An aluminum trough filled with wet sand was
placed with one end on a hot-plate, the temperature of which could
be controlled, and the other end in an ice-bath. An aluminum-
based glass trough (15 x 15 x 60 cm) was placed on top of the
sand and filled to 1.5 cm with demineralized water. Water temp-
erature was measured by 9 thermometers suspended at equal intervals
in the glass trough. The temperature ranges for the nine thermometer
positions were as follows: 1) 19.5 to 20.5; 2) 20.5 to 22.0;
3) 22.0 to 23.5; 4) 23.5 to 24.5; 5) 24.5 to 26.5; 6) 26.0 to
28.0; 7) 27.5 to 29.0; 8) 28.5 to 30.0; and 9) 29.5 to 30.5°C.
One insect was introduced singly into the center of the water
gradient and left undisturbed for 5 minutes, after which time its
position in the gradient was recorded. It was them replaced by
another individual and the process was repeated. Fifty different
insects were used for each age group.

The tolerance of adult N. undulata to high water temp-
erature was determined by introducing the insects into large,
covered glass beakers which contained 3000 ml of gently-aerated
water heated by standard aquarium heaters (Fig. 6). Temperatures

Fig. 5   Temperature gradient apparatus used to determine the

mean preferred temperature of <u>N</u>. <u>undulata</u>.
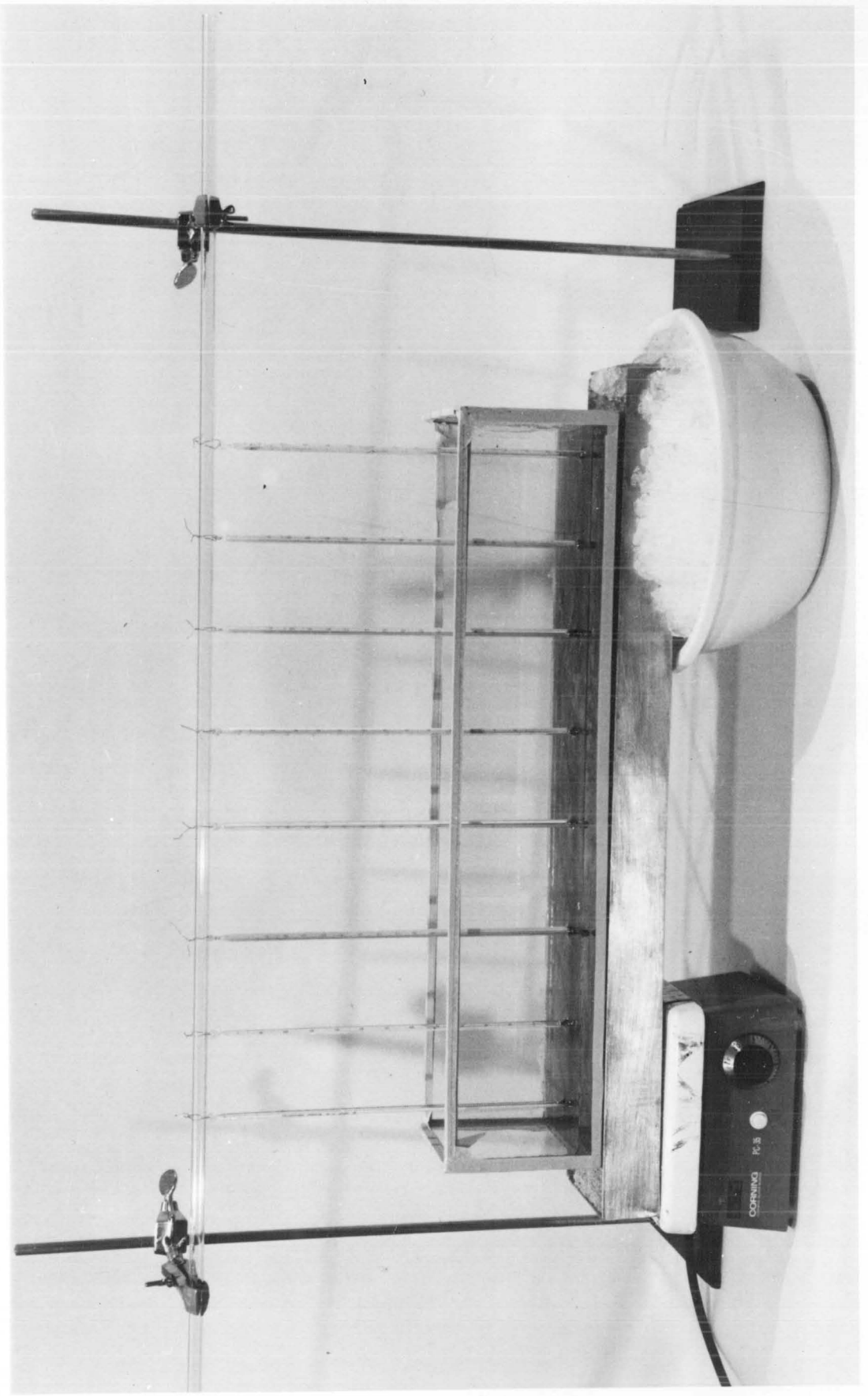
Fig. 6   Lethal temperature apparatus used to determine the

upper temperature tolerance of $\underline{N}$. $\underline{undulata}$.
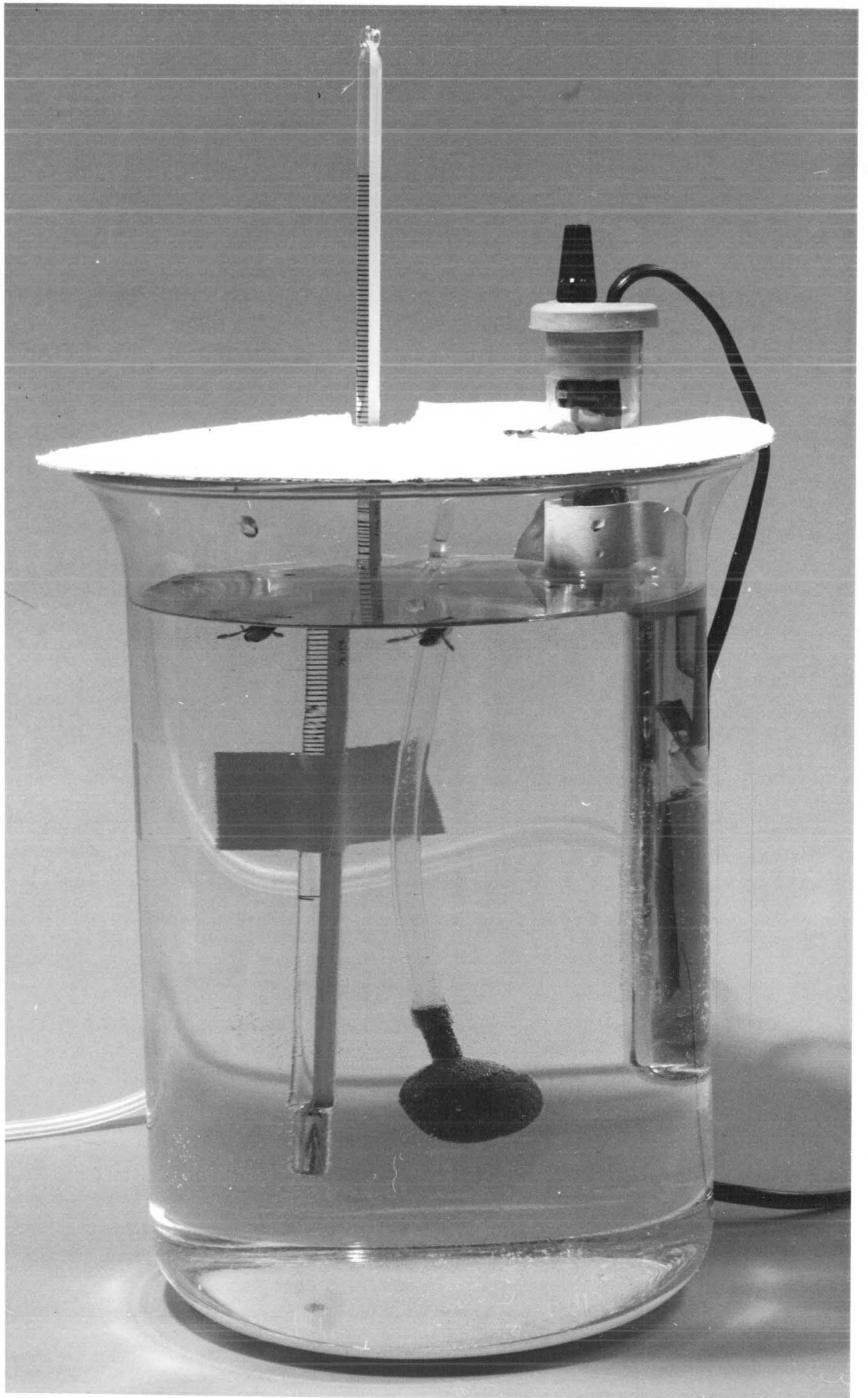
and numbers of adults tested were 34, 35, 36, 37, 38, 39, and
40°C and 6, 22, 13, 21, 17, 20 and 19, respectively. The number
of survivors at each temperature was noted hourly, for nine hours.
Death was verified by returning an insect to 25°C to check for
revival.

To determine the effect of water temperature on the
predation rate of adult backswimmers, a plexiglass trough (120 x
30 x 7 cm) was constructed with a through-flow, tap water system.
Water bath temperature was regulated by adjusting the mixed hot
and cold water flow to the desired level. Six predation study
pans, each containing 1 starved adult and 50 third age group larvae,
could be placed in the bath at once. The 10 temperature ranges and
number of backswimmers tested at each range were 13.0 ± 1, 15.5 ± 1,
18.0 ± 1, 20.5 ± 1, 23.0 ± 1, 25.5 ± 1, 28.0 ± 1, 30.5 ± 1, 33.0 ± 1,
and 35.5 ± 1°C and 81, 27, 36, 41, 26, 25, 28, 25, 26 and 33,
respectively. The number of larvae killed was noted after one hour.

## Results and Discussion

The mean preferred temperatures of first and fifth instars
and adults were 25.7 ± 2.8, 25.9 ± 3.1 and 26.9 ± 2.7°C, respect-
ively (Fig. 7). There was no significant difference (F - test,
P = .05) between the 3 mean temperatures. Thus, the overall mean
preferred temperature for the 3 stages tested was 26.2 ± 2.9 °C.
None of the stages exhibited aberrant swimming behavior in the
temperature gradient. The preferred temperature of N. undulata is

Fig. 7   Mean preferred temperature of first and fifth instar

and adult N. undulata (N=50) in a temperature gradient.
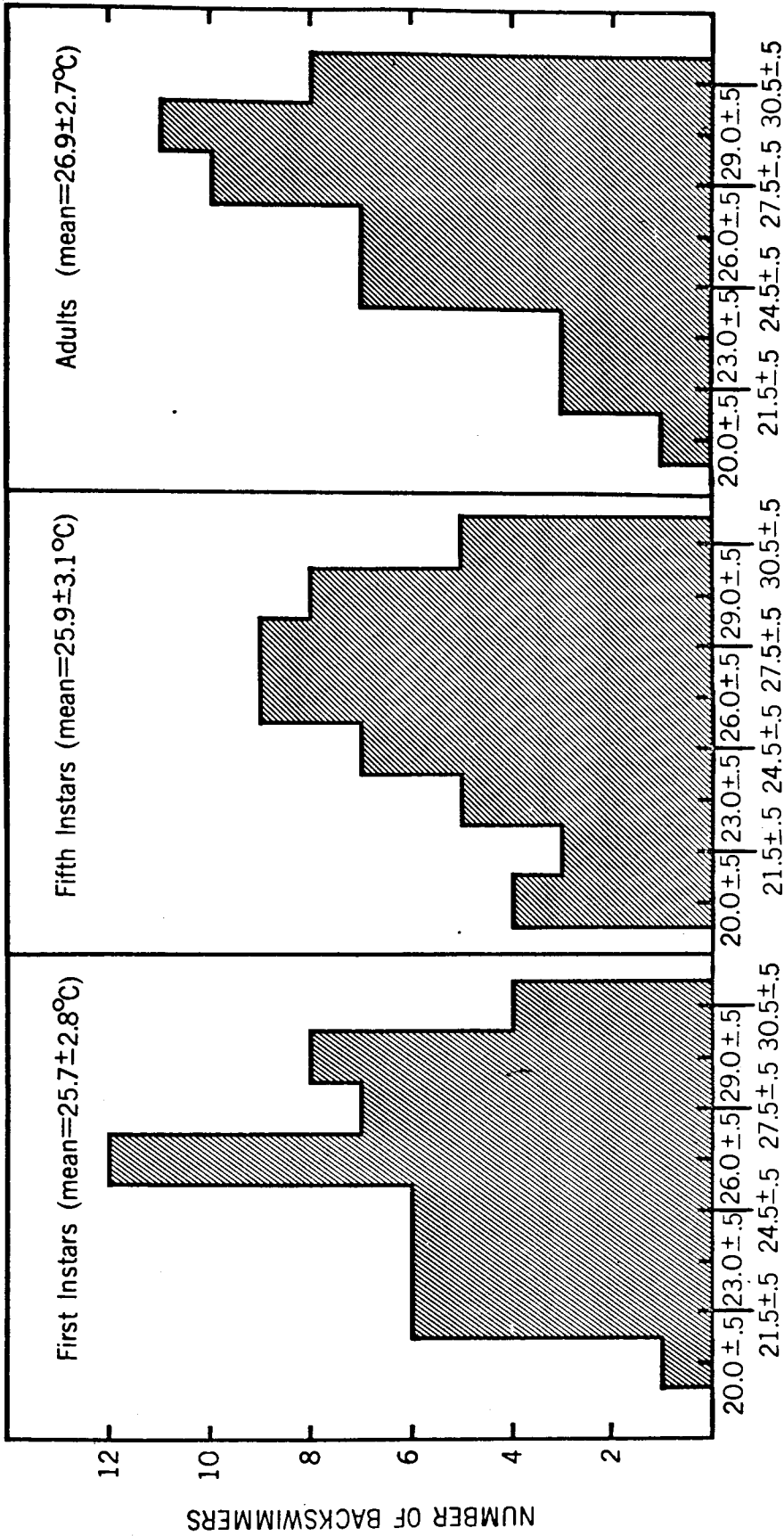
significant in that it is similar to that of many mosquito species
(Omardeen 1957, Bates 1965). No correlation with habitat survey
temperatures (Table I) can be made since these were 'spot' values
which may be subject to frequent and wide variation.

Adults, tested for their tolerance to high water temp-
erature, exhibited no permanent, ill-effects at 34°C, the lowest
temperature tested (Fig. 8). The number of backswimmers surviving
for 9 hours at water temperatures greater than 34°C, slowly
decreased until, at 40°C, there were no survivors. Also, the
interval between backswimmer introduction and initial mortality
diminished with increasing temperature. At 9 hours, percent
mortality varied almost directly with water temperature over 32°C.

At all temperatures tested, the adults exhibited behavior
which is usually preparatory to flight; they swam excitedly below
the surface, swam dorsal-side-up on the surface and climbed out of
the water via the tygon air-line. High temperatures appeared to
interfere with their normal respiratory processes. They spent
much time attempting to remove gas bubbles from their venters.

At temperatures above a critical range of 32 to 34°C
for Notonecta sp. (Beament 1961) and 30 to 35°C for Cenocorixa
expleta Hungerford (Oloffs and Scudder 1966), there is a sharp
increase in water evaporation. This is believed to result from
the disorientation of the cuticular lipid monolayer (Beament 1961)
and, in nature, would result in lethal water uptake or loss.

Fig. 8  Effect of exposure to high temperature on the survival

of adult $\underline{N}$. $\underline{undulata}$.  Temperatures and number of adults

tested were 34, 35, 36, 37, 38, 39 and 40°C and 6, 22,

13, 21, 17, 20 and 19 respectively.

KEY (°C)
- x 34
- □ 35
- ■ 36
- △ 37
- ▲ 38
- ○ 39
- ● 40

PERCENT MORTALITY

EXPOSURE DURATION (HR.)
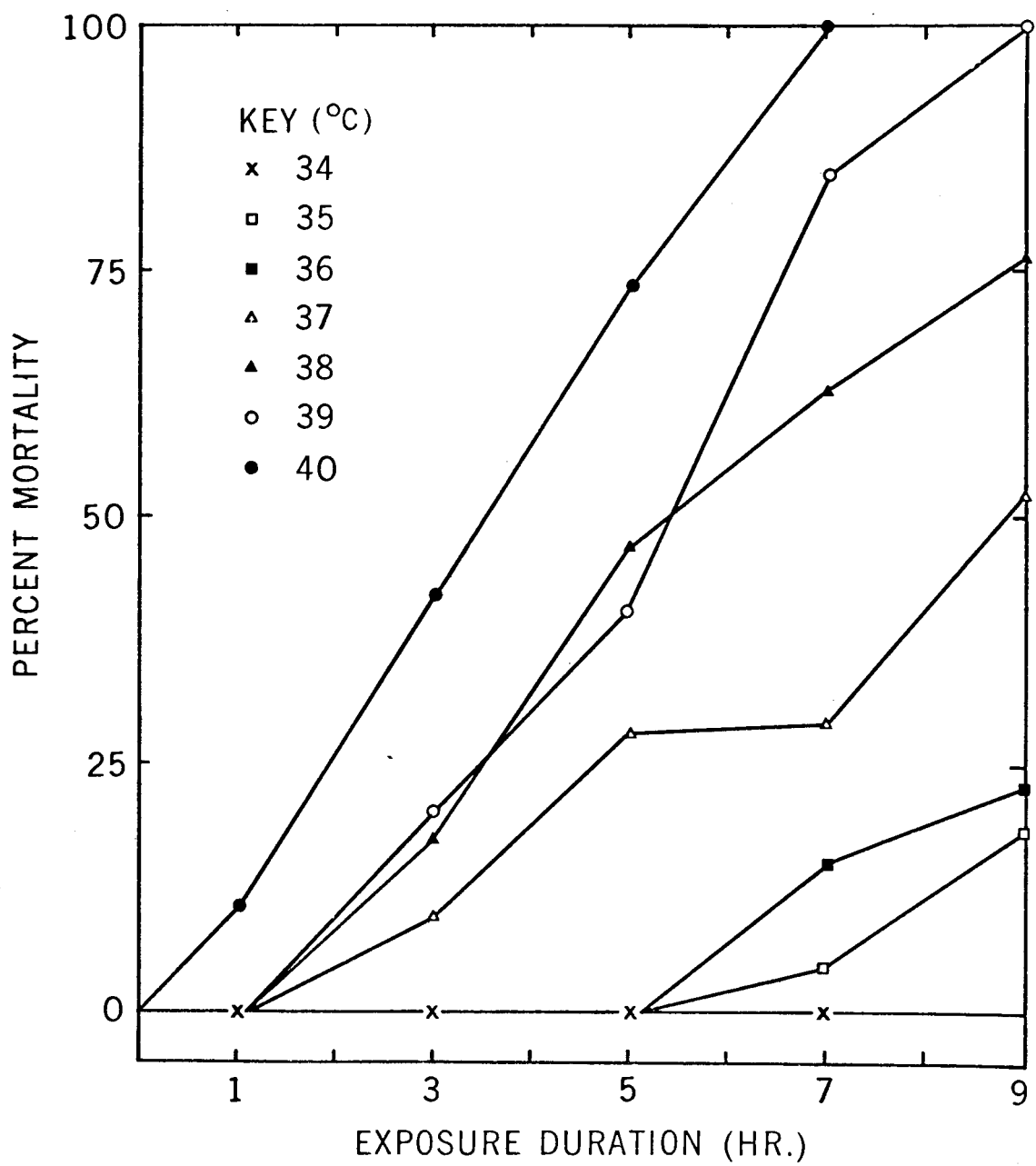
Survival at water temperatures up to 34 C°C suggests that

irreversible breakdown of the water-proofing mechanism of

N. undulata does not occur until water temperature exceeds 34°C.

Unlike adult N. undulata, the flightless nymphs are unable to

emigrate and thus would be more vulnerable to damage.  They can

only move to a cooler area of water.  In the temperature prefer-

ence apparatus (Fig. 5), N. undulata nymphs moved in response to

changes in the temperature gradient, almost invariably remaining

close to their preferred temperature.

Water temperature, over the ranges tested, did not

significantly (P = .05) affect the predation rate of adult

N. undulata ($\bar{x}$ = 2.2 larvae per hour).  Extremes of temperature

did, however, influence both predator and prey behavior.  Although

the mosquito larvae were sluggish and probably more susceptible

to predation at the lowest temperature range, fewer than expected

were killed, probably because the backswimmers were also somewhat

lethargic and spent more time resting at the surface than normally.

At the highest temperature range, the larvae again were sluggish,

staying at the surface and moving only when disturbed.  It appeared

that the death of several larvae may have been due to the effects

of excessive heat rather than the backswimmers.  The predators, at

this temperature range, were quite active and occasionally

attempted to escape from the study pans.

The backswimmer's ability to kill mosquito larvae over

such a wide temperature range may be considered to be further

evidence of its tolerance of a wide range of water conditions.

EFFECT OF PREDATOR STAGE, PREY AGE AND PREY DENSITY
ON BACKSWIMMER PREDATION RATE

## Methods

To determine what effects predator stage, prey age and
prey density have on the rate of predation, 6 predator stages
(5 nymphal instars plus adults) were tested against 4 mosquito
larval age groups at three densities (1 predator vs 5, 10 and
50 prey per 1000 ml water).  The total number of combinations of
predator stage:prey age group:prey density was 72.  Six replicates
of each combination were made.  The number of larvae killed by
the starved backswimmers was noted after 1 hour.  Statistical
analysis (analysis of variance, t - tests) of the resulting data
was done by computer (IBM-360 Series 50).

## Results and Discussion

The mean predation rates of the various combinations
of predator stage, prey age group and prey density (Figs. 9-14),
suggest the following aspects of backswimmer predation: 1) First
instar and adult N. undulata kill fewer larvae than do either
second, third, fourth or fifth instars, whereas fourth and fifth
instars kill more larvae than do second or third instars; 2)
First and second age group mosquito larvae appear to be killed
slightly more often than do third and fourth age group larvae,
at least by the second to fifth instar predators; and 3) More
larvae are killed at the highest prey density than at the lowest.

Figs. 9-14    Effect of predator stage, prey age and prey density

on the predation rate of N. undulata on A. aegypti

larvae.  Each bar represents the mean number of

larvae killed in one hour by 6 backswimmers. Cor-

responding standard deviations are shown.

PREDATOR–PREY DENSITY

1:5   1:10   1:50

⑨ FIRST INSTAR NYMPHS

⑩ SECOND INSTAR NYMPHS

⑪ THIRD INSTAR NYMPHS
12.8

⑫ FOURTH INSTAR NYMPHS
8.4

⑬ FIFTH INSTAR NYMPHS
25.8   11.7

⑭ ADULTS
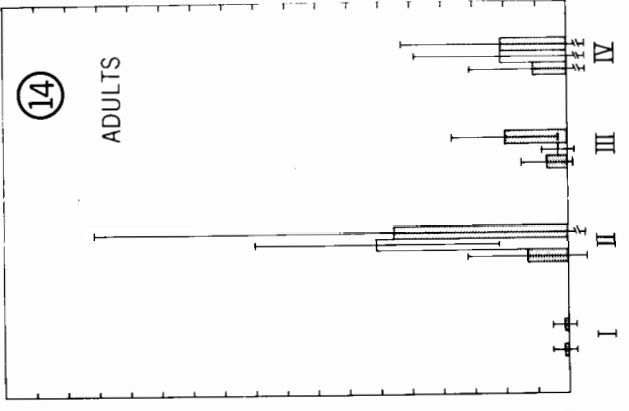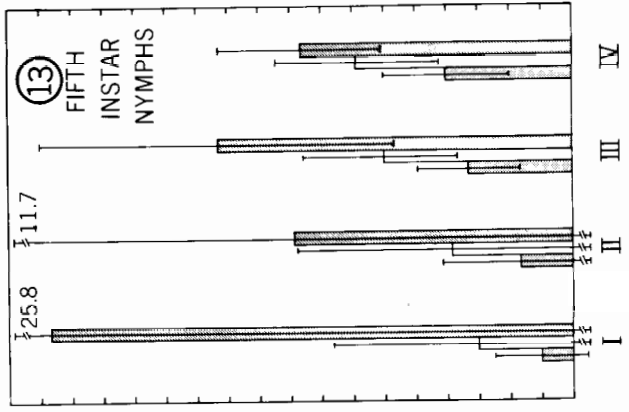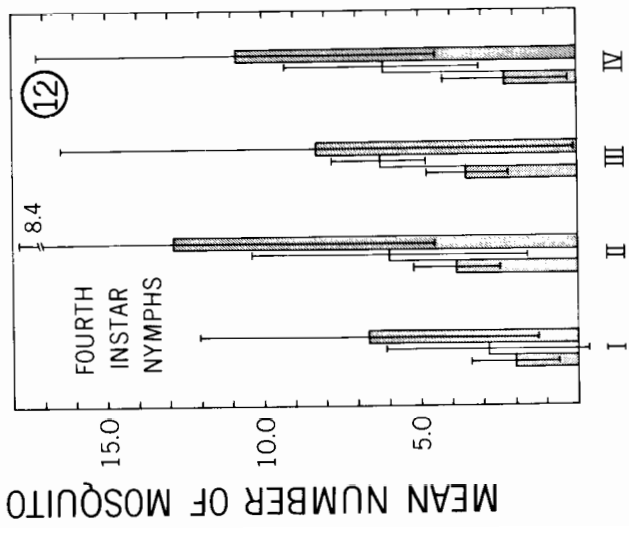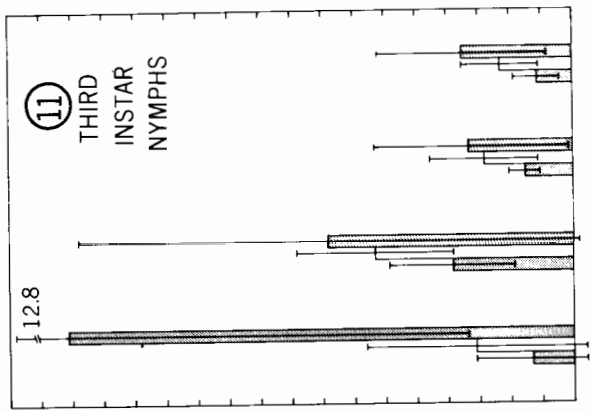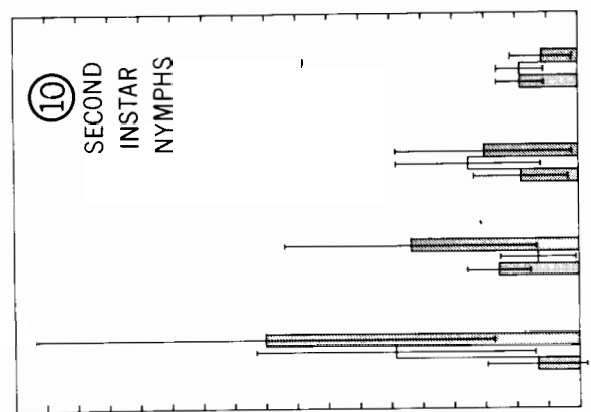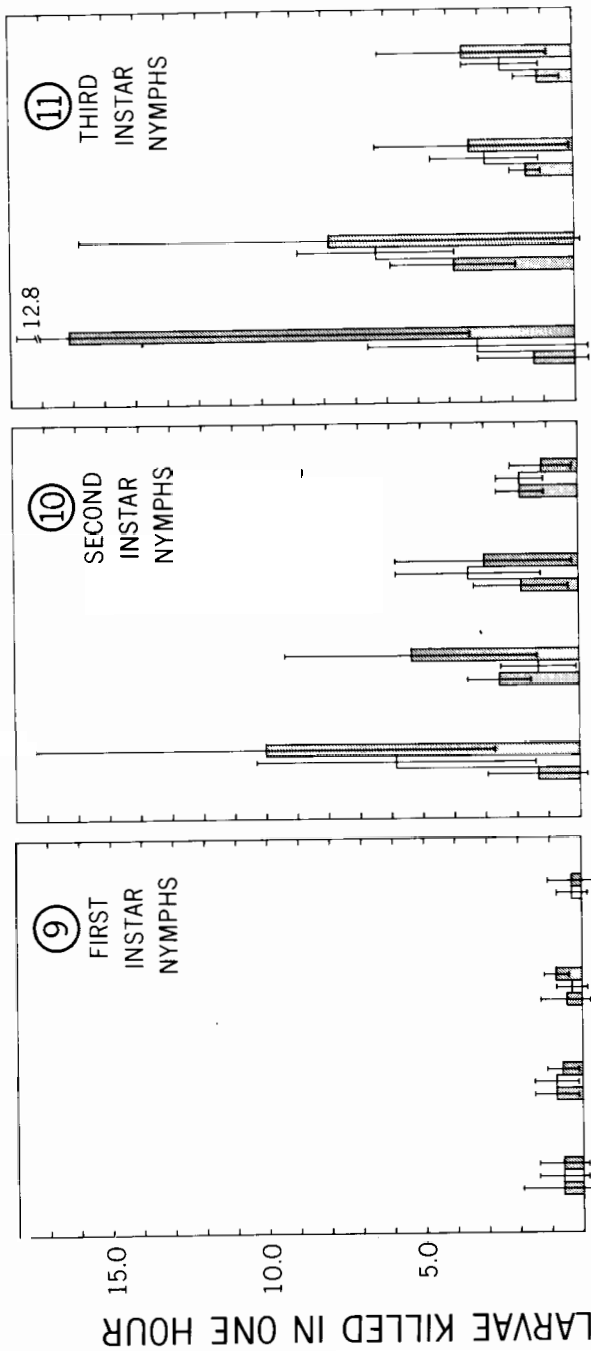
MEAN NUMBER OF MOSQUITO LARVAE KILLED IN ONE HOUR

15.0   10.0   5.0

MOSQUITO LARVAL AGE GROUP

I   II   III   IV

These aspects were examined statistically.

Data processing involved an analysis of variance (S.F.U. Computer Center Program AVAR23) which determined that differences in the predation rate were due to differences in predator stages, in prey age groups and in prey density. There were significant differences ($P = .01$) for each of these 3 variables. In addition, the test revealed differences due to interactions between predator stage and prey age group ($P = .01$), between predator stage and prey density ($P = .05$), and between all 3 independent variables ($P = .05$).

The analysis of variance also generated an overall picture of the 3 factors affecting the predation rate of N. undulata on A. aegypti larvae (Figs. 15-17, line graph inserts). The mean values for each factor were derived by blocking out the interactions of the other 2 factors.

Each line graph insert provides an overall summary of the relationship of each factor to predation rate. The older predators (except adults) kill more larvae than do the younger predators (Fig. 15, insert), while the adult predation rate is comparable to that of the first instars. In regard to the overall effect of prey age group on predation rate (Fig. 16, insert), the mean predation rates on the first, third and fourth prey age groups are fairly similar, whereas slightly more second age group larvae were killed. When prey density levels are compared

Figs. 15-17    Analysis of predation by N. undulata on A. aeqypti

larvae showing the effect of differences in predator

stage (Fig. 15), prey age (Fig. 16) and prey density

(Fig. 17) on predation rate.  For any comparison of

2 factors (shown below each grid, e.g. 'Al:A2') the

significance level is shown by a shaded square (see

'key to significant differences').  Line graph in-

serts in each figure represent the mean predation

rates when the interactions of each of the 2 other

factors are blocked.  Symbols are as follows:  Al

to A6 represent the 5 nymphal instars (Al to A5) and

adults (A6) of N. undulata; Bl to B4 represent the

4 larval age groups of A. aeqypti (1 - 3, 4 - 6, 7 - 9,

and 10 - 12 days old, respectively); and Cl to C3

represent the 3 prey densities (5, 10 and 50 larvae

per 1000 ml, respectively).

KEY TO SIGNIFICANT DIFFERENCES  P>.10 ☐   P=.10 ☐   P=.05 ▦   P=.10 ▨   P=.05 ▨   P=.01 ▨
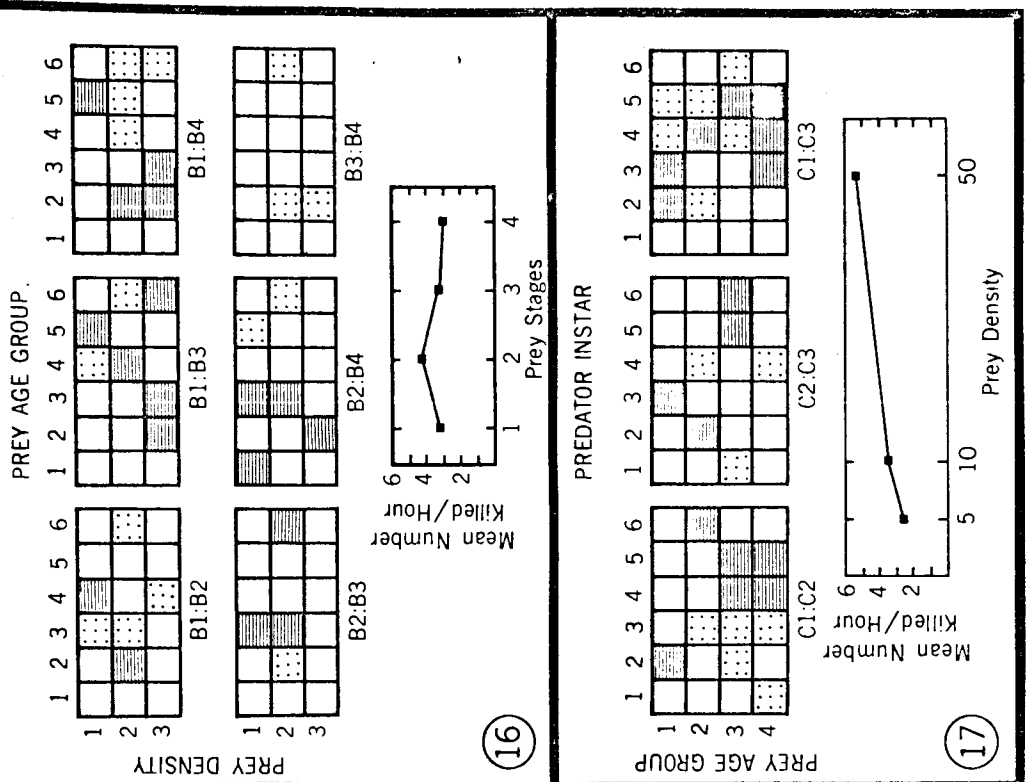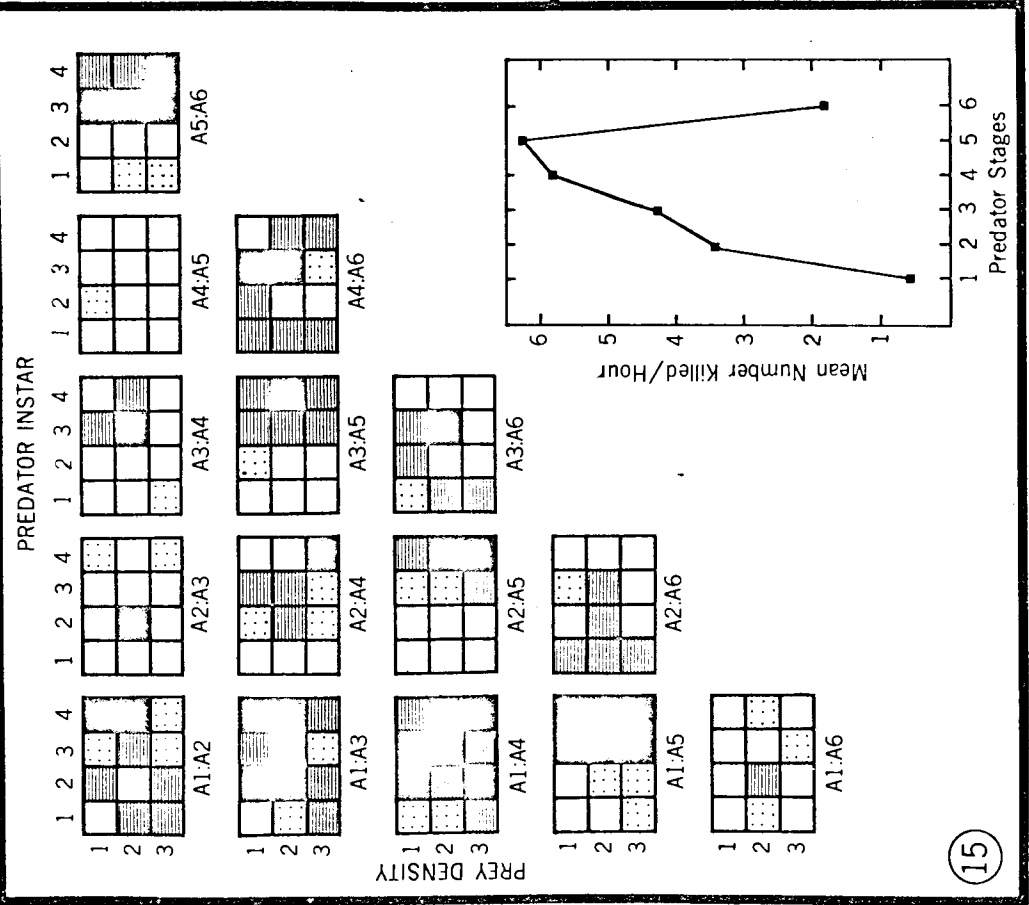
(Fig. 17, insert), the greater the density the higher is the

predation rate. The predation rate, however, is not directly

proportional to prey density: i.e., the effect on the predation

rate diminishes with increasing prey density.

A t - matrix (S.F.U. Computer Center Program ( TSTAT )

was generated to determine which predator stage:prey age:prey density

combinations specifically differed from each other. The results

are shown graphically (Figs. 15-17, grids). Detailed discussion

of this statistical analysis follows.

A. Effect of Predator Stage on Predation Rate.

(1) Predator Stage 1 vs. Predator Stages 2 to 6

Comparing the predation rates of first and second instar

N. undulata (Fig. 15; A1:A2), strong differences are observed

with most prey age groups and at most densities. Since the

predation rates of the second instars are consistently higher than

those of the first instars (Figs. 9, 10), the comparisons suggest

that the second instars are better adapted for catching and kill-

ing the various mosquito larval age groups at all 3 larval densities.

The analysis also suggests that the second instars may show a

stronger preference for mosquito larvae than the first instars.

Another alternative is that fewer prey are required to satiate

first instars.

A comparison of first and third instar predation rates

(Fig. 15; A1:A3), reveals that differences are greater between

these 2 instars than between first and second (Fig. 15; A1:A2).
Third instars fed at a significantly higher rate than first
instars on all prey age groups and at all but 1 density level
(Figs. 9, 11).

A comparison of first and fourth instar predation rates
(Fig. 15; A1:A4), reveals that the fourth instars fed at a sign-
ificantly higher rate than did first instars on all prey age
groups and at all prey densities (Figs. 9, 12).

A comparison of the predation rates of first and fifth
instars (Fig. 15; A1:A5), reveals that they also differ sign-
ificantly in the majority of combinations.  On older prey age
groups and at higher prey densities, the number of significant
differences increases.  In all cases, the predation rates of the
first instars are lower than those of the fifth instars (Figs.
9, 13).  It appears that first and fifth instars differentiate
strongly between only the 2 older larval age groups.  They may
exhibit a lack of differentiation with the younger prey for
different reasons: e.g., first instar backswimmers may be too small
to kill sufficient larvae to have a definite effect whereas fifth
instars may not be able to manipulate the small prey, thus lower-
ing their predation rates on these prey groups.

A comparison of first instar and adult N. undulata
(Fig. 15; A1:A5), reveals that they are similar in their feeding
rates on all age groups, differing only slightly at the second
prey density.

(2) Predator Stage 2 <u>vs</u>. Predator Stages 3 to 6

Considering these predator stage comparisons, it is evident there is little difference between the second and third instars (Fig. 15; A2:A3), some differences between the second and fourth instars (Fig. 15; A2:A4), on the middle 2 prey age groups (B2, B3), some differences between the second and fifth instars (Fig. 15; A2:A5) on older prey (B3, B4), and some differences between the second instars and adults (Fig. 15; A2:A6) on the younger prey (B1, B3) at lower densities. As expected, the younger predator killed more younger prey than the older predator (Figs. 9, 14).

(3) Predator Stage 3 <u>vs</u>. Predator Stages 4 to 6

The predation rates of third and fourth instars are similar except with older prey (B3, B4) at low densities (Fig. 15; A3:A4). This may be related to the ability of the respective instars to kill older larvae; i.e., fourth instars killed more older prey than did third instars (Figs. 11, 12).

As expected, there were greater differences between the third and fifth instars and between the third instars and the adults (Fig. 15; A3:A5, A3:A6) than between the third and fourth instars. Fifth instars killed more older prey (Bs, B4) at all densities than did third instars (Figs. 11, 13), whereas third instars killed more prey of all age groups at lower densities than did the adults (Figs. 11, 14). Also as expected, the adults killed very few first age group larvae in comparison to the third instars which, because of their ability to handle small prey, had the predatory advantage.

(4) Predator Stage 4 vs. Predator Stages 5 and 6

There was essentially no difference between the predation rates of fourth and fifth instars (Fig. 15; A4:A5); where there was a slight difference (P = .10), fifth instars killed more larvae than did fourth instars (Figs. 12, 13).

Comparing the fourth instars and adults (Fig. 15; A4:A5), one observes that their predation rates were different on all prey stages except the second (B2). The fourth instars killed more larvae of the first, third and fourth prey age groups than did the adults (Figs. 12, 14).

(5) Predator Stage 5 vs. Predator Stage 6

The analysis of fifth instars versus adults (Fig. 15; A5:A6) was comparable to that of fourth instars versus adults. One might have expected the adults to have at least preyed on the older prey at a higher rate than the first instars (Figs. 9, 14). The discrepancy may be due to one or more of several factors. For example, the predators may be too large for the prey. The prey preference study (below), however, showed that the adults prefer older mosquito larvae over larger prey types offered (Fig. 19) Another factor is that adult behavior other than feeding was dominant during the experiments. Some adults, when confined in the predation study pans, frequently attempted to escape; nymphs never attempted to leave the pans. This would result in a lower overall adult predation rate. In addition, the sex and reproductive

age of the test adults may have influenced the predation rate.

B. Effect of Prey Age Group on Predation Rate

(1) Prey Age Group 1 vs. Prey Age Group 2 to 4

Comparing the predation rates on first and second larval age groups (Fig. 16; B1:B2), more second than third age group larvae were killed by third and fourth instar predators (Fig. 11, 12). First, second and fifth instar and adult N. undulata do not appear to differentiate strongly between these prey groups.

Differences occur among the predation rates of all predator stages but the first, on first and third prey age groups (Fig. 16; B1:B3). The rate of predation by older predators (Figs. 12-14) was greater on the third age group than on the first but vice versa with the younger predators (Figs. 9-11).

Comparing first and fourth prey age groups (Fig. 16; B1:B4), one sees that all predator instars but the first differentiate between these 2 prey age groups. The second and third instar predators kill more younger prey than older prey where there are differences in the rates of predation (Figs. 10,11). On the other hand, the 3 older predator stages kill more older than younger larvae (Figs. 12-14).

(2) Prey Age Group 2 vs. Prey Age Groups 3 and 4

Comparing the predation rates on second and third prey age groups (Fig. 16; B2:B3), one observes that there are only a few differences. Second instar predators kill slightly

more third than second age group larvae at one density level.

On the other hand, third instar predators and adults kill more

second than third age group larvae at 2 and 1 density levels

respectively.  First, fourth and fifth instar predators did not

differentiate between these 2 prey stages.

There is a scattering of significant differences among

predator and density levels between the second and fourth age

group larvae (Fig. 15; B2:B4).  In all cases, second age group

larvae were taken most often (Figs. 9-14).  Here one finds the

first and only instance where first instar predators differentiated

between 2 prey age groups: they took more second than fourth age

group larvae (Fig. 9).  Fourth instar predators did not take

significantly more of any one age group than another (Fig. 12).

(3) Prey Age Group 3 vs. Prey Age Group 4

Between the third and fourth age group larvae (Fig.

16; B3:B4), none of the predator stages took more of one age group

than another (P = .05).  Second instars took slightly more third

than fourth age group prey at the 2 higher densities (Fig. 10)

whereas adults took slightly more fourth than third age group

prey at the second density level (Fig. 14).

C. Effect of Prey Density on Predation Rate

(1) Density 1 vs. Density 2

Comparing the first and second densities (Fig. 17;

C1:C2), there are slightly more differences as one proceeds

upwards in the predator stages until reaching the adults which, as the first instars, do not appear to differentiate between the 2 density levels. Also, the effect becomes more apparent with older prey age groups. In all cases where a significant difference occurred, the predation rate was lower at the lower density than at the higher density (Figs. 9-14).

(2) Density 2 vs. Density 3

When one compares the second and third density levels (Fig. 17; C2:C3), the trend observed in C1:C2 is not at all apparent. Each predator stage differentiated between the 2 densities at one prey age group level. Most of the differences occur when the predators are feeding on second and third age group larvae. In each case, the predation rate was lower at the lower density (Figs. 9-14).

(3) Density 1 vs. Density 3

The greatest difference occurs between the first and third density levels (Fig. 17; C1:C3). Proceeding from second to fifth instars it is apparent that there are a greater number of differences occurring in the predation rates at these 2 density levels. In each case, more larvae were killed at the high density level than at the low. Prey density has a less positive effect for both early instars and adults (Figs. 9-14).

### D. Implications

These results suggest the potential importance of

N. undulata in the natural or biological control of mosquitoes.
Individual backswimmers became increasingly efficient as they
developed from first to fifth instar in regard to the number
of prey they killed in a given period of time. Furthermore,
early age group larvae (B2, B3) were usually taken more often
than later age group larvae (B4); thus, greater numbers of small
larvae were required to satiate the backswimmer. In effect, by
concentrating their feeding on the earlier larval stages, the
backswimmers allow fewer mosquitoes to reach reproductive
maturity.

At some time in its life history, N. undulata feeds on
both larvae and pupae of A. aegypti. Bare (1926), although he
does not reveal the prey species, states that all stages of
N. undulata feed on all stages of mosquito larvae and on pupae.
Lee (1967) found that both adults and nymphs (of unspecified
instar) of N. undulata and Notonecta shooterii Uhler were able to
catch some first instar Culiseta incidens Thomson larvae, but
the rate of capture increased when older instars of mosquito
larvae were available. Although I have observed that first instar
and adult N. undulata do not readily feed on pupae and first
instar A. aegypti, respectively, they probably would feed on
mosquito species having either smaller or larger first instars
than A. aegypti, assuming size is the deciding factor involved
for all predator stages.

As a mosquito larval predator, the backswimmer might be rejected on the basis of its adult performance. The nymphal instars, however, greatly outweigh the adult deficiency. The need to investigate the effect of all predator stages on all prey stages is thus clearly demonstrated. Mukerji and LeRoux (1969), studying the effect of predator age on the functional response of the predator to prey size, also included the sex of each predator.

In nature, mosquito larvae would normally spend much of their time browsing in the shallows close to shore (Happold 1965) and, hence, would be afforded some protection from predation due to plant cover and camouflage. In the white-enamelled pans of this study, neither the backswimmer's vision nor maneuverability was impaired; hence, predation rates were probably slightly higher than in nature. The rates of predation may also have been high due to the lack of mutual interference (Lee 1967) between predators in their prey-catching activities. Behavioral observations of adults in my rearing aquaria also suggest that mutual aggression may be a factor in the natural situation.

An extensive field study might elucidate the temporal and spatial coordination (Turnbull 1960) of the developmental stages of both predator and prey species. A study of the interactions between backswimmer and mosquito populations could be made by artificially introducing the pest species and the predator species to one test plot and the pest species to a similar control

plot free from predation and then following the subsequent predator-prey interactions for several seasons (DeBach et al. 1951). Huffaker and Knight (1956) used this type of approach successfully in their study of the effects of predation on cyclamen mites in strawberry fields. A similar study with N. undulata might determine the backswimmer's effectiveness in a field situation. If the predator is at 'X' stage in its development when the prey is at 'Y' stage, laboratory data such as those of this study should enable the field investigator to make some reliable predictions as to the predator's effect on the prey population. If, for example, the majority of mosquitoes were 2 to 5 days old when most of the backswimmers were fifth instars one would expect, from the predator stage: prey age: prey density data, the backswimmers to destroy many larvae, other things being equal. If, on the other hand, the prey population were mostly composed of pupae when most of the backswimmers were first instars, one would expect the predators to have little effect on the mosquito population.

## EFFECT OF SATIATION ON PREDATION RATE

Methods

      To determine the number of mosquito larvae and the time required to satiate the predator, 10 starved (48 hours) adult N. undulata were offered 50 fourth age group larvae, hourly, for 10 hours. The number of larvae killed by each predator was recorded for each hour.

Results and Discussion

      The predation rate was highest in the first hour, and thereafter declined rapidly until reaching a plateau after the fourth hour (Fig. 18). In the first hour, the predation rate was significantly different (t tests, P = .05) from the remaining 9. The predation rate of hour 2 was different from all but that of hour 3. The predation rates of the remaining 7 hours were different from those of hours 1 and 2 but not from each other. This analysis suggests that the starved adults became satiated in approximately 3 hours (equivalent to about 30 fourth age group larvae per predator) and that, subsequent to the first 3 hours, the adults fed at a mean rate of 4 larvae per hour.

      These results indicate that due to the effects of starvation, the predation rates obtained in the predator stage: prey age:prey density trials are, at least for the adults, probably slightly higher than would occur naturally. Since the predators in those trials were starved for only 24 hours, however,

Fig. 18   Mean hourly rates of predation over 10 hours by

adult $\underline{N}$. undulata which were starved for 48 hours

prior to being offered, 50 fourth age group $\underline{A}$. aegypti

larvae hourly.   Vertical bars are standard deviations.
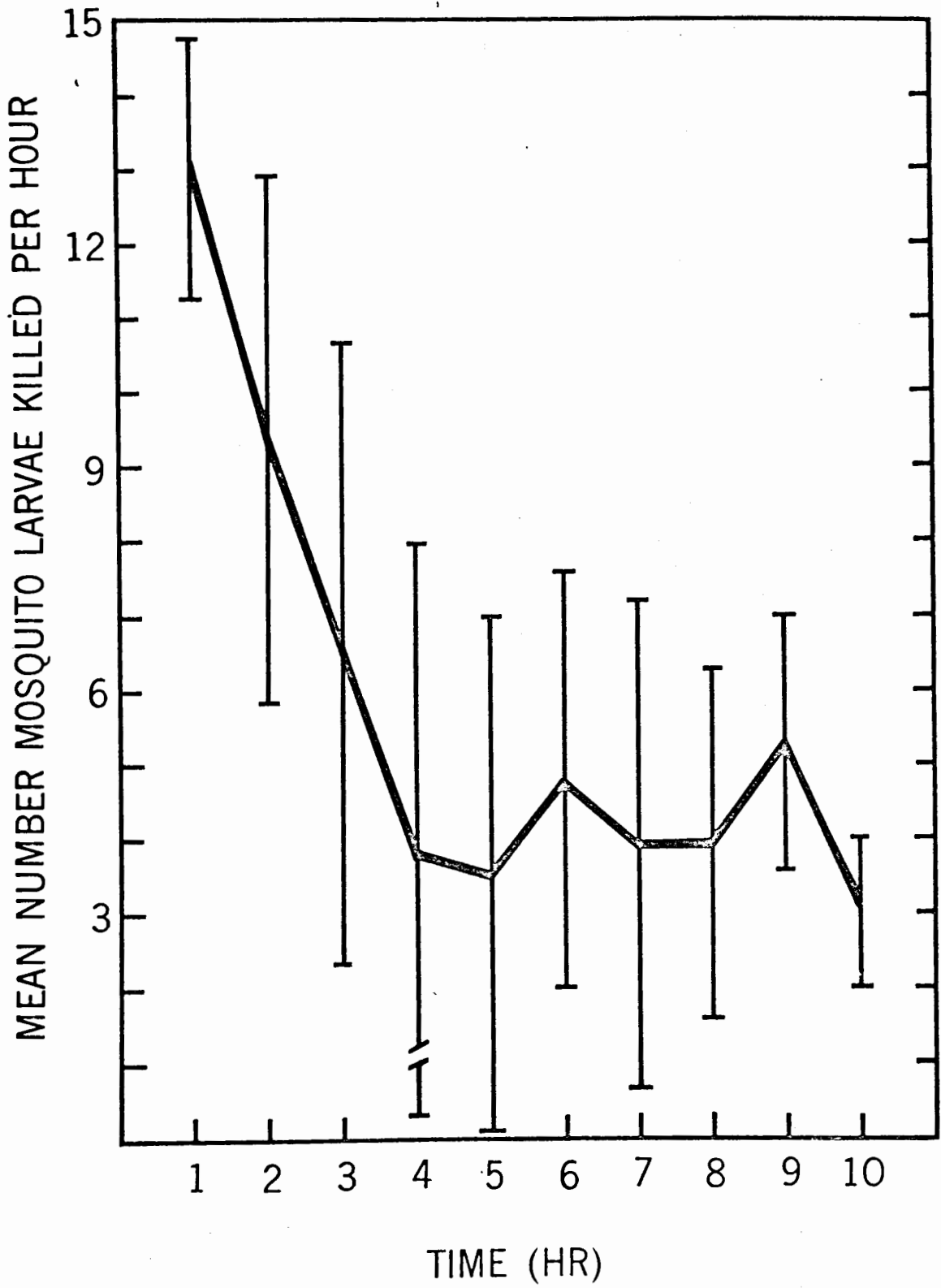
the effect might not be so pronounced.

The precipitous decline over the first 4 hours and subsequent leveling off of the predation rate of the starved adults is typical of many predators. In a similar study, stickleback exhibited changes in the predation rate that were both short term and cyclic (Beukema 1968). Holling (1966) observed that, as flies were killed by mantids, there was a resulting decrease in mantid hunger which, in turn, caused a decline in the number of flies attacked per hour until hunger stabilized.

There was no evidence that learning (Beukema 1968) played a role in the satiation of $\underline{N}$. $\underline{undulata}$. Response decrement, a decrease in responsiveness when repeatedly presented with a stimulus, may, however, tend to reduce the predation rate of $\underline{N}$. $\underline{undulata}$ as in $\underline{Notonecta}$ $\underline{glauca}$ L. (Wolda 1961). Although response decrement was not examined in this study of satiation (even though the effects of response decrement and satiation on backswimmer predation rate are similar), the predator stage:prey age:prey density trials indirectly substantiate Wolda's (1961) findings. The predation rate at high densities is less than one would expect from the rates at lower densities. Thus, $\underline{N}$. $\underline{undulata}$ may be less responsive if it repeatedly encounters prey.

Any mathematical model involving backswimmer predation

should account for the effects of such variables as satiation

and response decrement on the feeding rate (e.g. Holling 1966,

Beukema 1968). It should not, as in some instances (e.g.

Nicholson 1933, Larkin 1966), assume $\underline{N}$. $\underline{undulata}$ to be an in-

satiable or random searcher.

## PREY PREFERENCE

Methods

To test N. undulata for its prey preferences, laboratory-reared adults (N = 20) were offered the following prey types, one of each to a backswimmer: A. aegypti larvae and pupae, Chaoborus nyblaei Zettorsfedt larvae and pupae, small ephermerid nymphs, large ephemerid nymphs, bloodworm larvae (Chironomidae) and small corixid nymphs. Care was taken that only organisms (except A. aegypti) from backswimmer habitats were offered in preference tests because Thompson (1951) has argued that captive predaceous insects will often eat organisms that they would seldom come across in nature. The pans were examined every 30 minutes and the dead prey, if any, were removed and recorded as to whether they were killed first, second, etc. Usually, all prey were killed within 7 to 10 hours. Controls were set up without the backswimmers because C. nyblaei larvae are known to prey on mosquito larvae (James 1950) but in no instance were any control larvae killed. The A. aegypti larvae were all fourth instar and, therefore, may have been too large for the midge larvae to ingest. As a check against conditioning for mosquitoes in the laboratory-reared backswimmers, six additional replicates under identical conditions were set up using only freshly-caught N. undulata adults. All backswimmers were starved for approximately 24 hours prior to all trials.

## Results and Discussion

The adults exhibited a definite preference for A. aegypti larvae and pupae (Fig. 19). A. aegypti larvae were taken first by 55% of the backswimmers, second by 35% and third by 10%. Overall, second choice were A. aegypti pupae which were eaten first by 25%, second by 25%, third by 5%, fourth by 20% and seventh by 5%. Corixid nymphs appeared to be third choice, overall, and were followed by C. nyblaei pupae, C. nyblaei larvae, large and small mayfly nymphs and bloodworm larvae. N. undulata exhibited no marked preference between small and large mayfly nymphs. The last in the order of preference were bloodworm larvae. They were taken last 35% of the time and seventh 20% of the time. Freshly-caught backswimmers, starved for 24 hours and offered the same prey types, produced almost identical results. Thus, there appeared to be no conditioning of the laboratory-reared backswimmers for mosquito larvae and pupae. Although N. undulata feeds on a variety of terrestrial and aquatic invertebrates and even some vertebrates (Essenberg 1915), its preference for aedine larvae and pupae over other types of aquatic insects offered suggests that the backswimmer is not as general a feeder as is commonly assumed.

Observations on the behavior of the prey types may elucidate backswimmer prey selection. A. aegypti larvae, in white-enamelled pans, normally rest at the surface or on the

Fig. 19  Prey preference of adult N. undulata (N = 20) when

offered a choice of 8 aquatic insect types.  Percent

killed refers to the frequency with which a prey type

was killed first, second ..... seventh or eighth.

PERCENT KILLED

AEDES AEGYPTI LARVAE

CHAOBORUS NYBLAEI LARVAE

AEDES AEGYPTI PUPAE

LARGE MAYFLY NYMPHS

CORIXID NYMPHS

SMALL MAYFLY NYMPHS

CHAOBORUS NYBLAEI PUPAE

BLOODWORM LARVAE

ORDER IN WHICH PREY KILLED
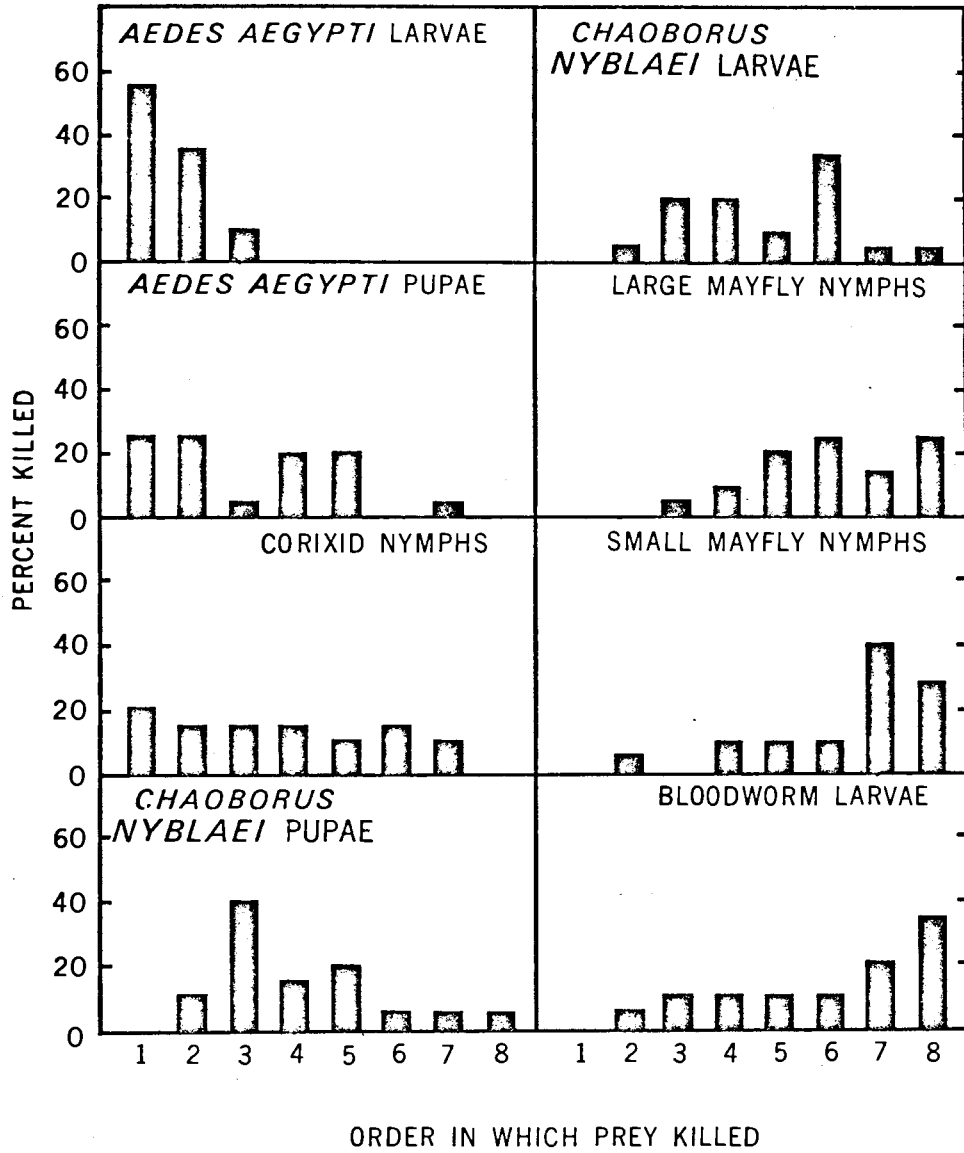
bottom. While on the bottom they usually browse for particulate food. They must surface every few minutes for air. When disturbed by a backswimmer swimming nearby they invariably wiggle away as fast as possible. If at the surface when disturbed they move downwards in the water column. Pupae rest at the surface most of the time. When disturbed they swim rapidly downwards and away from the source of disturbance, moving slightly faster than the larvae.

C. nyblaei larvae are larger than mosquito larvae. They normally rest about midway in the water column and do not surface for their air. This species is almost transparent and thus difficult to see unless it is moving. The larvae move very fast when disturbed. Pupae are larger than mosquito pupae and, again, normally rest at the surface swimming downwards only when disturbed. They do not appear to be as fast as mosquito pupae.

Corixids rest either at the surface or at the bottom of the pan. They must surface for air every few minutes thus exposing themselves more often than the C. nyblaei larvae by their frequent movements up and down the water column. They are reasonably fast swimmers but slightly awkward in comparison to the backswimmers.

Mayfly nymphs spend nearly all their time on or near the bottom of their container. They browse along the bottom slowly and intermittently. When disturbed by a backswimmer they rush away along the bottom. The smaller nymphs are not as fast

nor do they usually move as far away when disturbed.

The bloodworm larvae which were approximately the same size as the mosquito larvae spent most of their time resting on the bottom of the pan, surfacing only occasionally to replenish their oxygen supply. Their swimming behavior as they move vertically in the water column is snake-like in appearance.

Several factors are involved in prey selection, i.e., prey size, mobility, defence or avoidance behavior, palatability, abundance and the extent to which the predator and prey habitats overlap. As Turnbull (1960) and Young (1967) point out, each of these is part of a complex and the degree to which the predator responds to this complex will determine the preferred prey. Prey abundance was constant in the prey preference study, one of each prey type to each predator. It is assumed that all prey species were palatable since all were killed.

Size is often considered of major importance in prey selection. Solitary wasps prey most often on smaller sized species and smaller individuals of larger sized species of bumble-bees (Mason 1965). Size may determine the frequency with which a prey organism becomes ensnarled in a spider's web (Turnbull 1960). Young (1967) suggested that the susceptibility of aquatic prey to the larvae of Dytiscus marginalis L. may involve such factors as width of the prey in relation to the distance between the mandibles of the larvae, and the relative motility of predators

and prey. The prey captured by mantids is partly determined by
the handling capacity of the predator's grasping forelegs (Holling
1966). However, when two prey types of almost equal size (A. aegypti
larvae and bloodworm larvae) were offered to N. undulata adults,
one was first choice and the other was last. Size may be more
important intraspecifically to N. undulata. The prey killed in
nature will depend on which instars of both prey and predator occur
simultaneously in the same habitat.

Prey mobility (spatial movements related to searching,
feeding, etc.) and motility (speed attainable to avoid capture)
appeared to be important in the selection of prey by N. undulata.
For example, although mayfly nymphs are normally slow moving while
browsing for food and, thus, less likely to attract a predator
they will swim away rapidly when disturbed by a backswimmer.
A. aegypti larvae, on the other hand, normally are active browsers;
when disturbed, however, they cannot swim away as fast as the
mayfly nymphs. Thus, because the mosquito larvae are exposed
more often to backswimmer predation than mayfly nymphs and cannot
escape as readily, they are the 'preferred' prey. Turnbull (1960)
found a somewhat similar situation in the selection of prey by
spiders. An ideal prey was one which among other things, was
highly mobile but not a strong or adroit flyer. This increased
its chances of becoming ensnarled in the spider web.

Perhaps even more important in prey selection by

N. undulata is to what degree do the predator and prey share the same micro-habitat. Since N. undulata spends much of its time at the surface film, it comes into contact most often with organisms regularly found at that level in the water column, such as mosquito larvae which frequently surface to replenish their oxygen supply. Turnbull (1960) observed a similar phenomenon in his study of spider prey; the normal activities of the prey species must bring it into those parts of the community occupied by the spiders' webs for it to be available in significant numbers.

Although N. undulata exhibited a marked prey preference, it will also feed on a wide range of other common aquatic insects. Therefore it possesses one of the fundamental characterisitcs of a biological control agent, i.e., an agent of control must have, first, a predilection for the prey species and, second, be able to subsist on other prey when the pest species is scarce (Beirne 1962). Huffaker and Knight (1956) observed a similar situation in their study of predaceous mites which could survive on other organisms when their regular prey were at very low densities.

The backswimmer's preference for mosquitoes may explain why mosquito larvae and pupae were only rarely found in the back-swimmer habitat survey.

## PREDATORY BEHAVIOR

### Methods

To study the predatory behavior of N. undulata two approaches were taken. The first was with an Ampex VR 5000 video-tape recorder and a television camera equipped with a 25 mm lens. The backswimmer and its prey were confined to a perspex observation cell which was narrow enough to minimize depth of field problems yet wide enough to allow free movement of the backswimmers and their prey. This arrangement allowed immediate re-play of the video-tape to determine whether or not the desired information was recorded. Video-taping predatory behavior was of limited value. Its main drawback was of a technical nature: the backswimmer's rapid movements could not be photographed close-up without restricting normal swimming behavior. Nevertheless, the video-tape did show some important aspects of the backswimmer's gross predatory behavior patterns.

In the second approach, adult backswimmers, starved for at least 24 hours, were placed in a 50 ml preparation dish. Fourth age group larvae and pupae of A. aegypti, were offered one at a time, and the predatory behavior was observed through a dissecting microscope.

### Results and Discussion

There were four general situations in which the back-swimmer catches prey, each depending primarily on the location of

the prey. In the first situation, the backswimmer catches prey
while swimming along the bottom. It often flushes out prey
animals which are browsing on bottom sediments or just resting
on the bottom. The prey animals react to the backswimmer's
presence by swimming away as fast as possible. Their movement
alerts the backswimmer which then attempts to seize them. Often
the backswimmer is unsuccessful in this form of attack.

In the second situation, prey organisms are attacked
while moving somewhere in the water column. They are either
surfacing for air or diving to browse on the substratum (e.g.
Aedes larvae). In this situation, the backswimmer often exhibits
a 'semi-stalking' behavior. If it is resting at the surface or
slowly buoying to the surface after diving and detects a prey
moving in the water column it may pursue and catch the prey. The
predator appears to be successful more often in this situation
than the former one.

In the third general situation, the backswimmer exhibits
a definite stalking behavior and seldom misses catching the prey
organism. The prey is either resting (e.g. Aedes pupa) or obtain-
ing its air supply (e.g. Aedes larva) at the surface. If the
backswimmer is resting nearby and the prey makes any movement the
backswimmer will align itself to the source of the vibrations
and slowly move towards it until it is within striking distance.
If the prey in turn detects the backswimmer it will immediately

begin to swim away, usually downwards. The backswimmer, with one or two strokes of its swimming legs, swims downwards and towards the prey where the prey is almost invariably grasped in its fore- and middle legs.

The fourth situation is similar to the third. Here the prey has been caught in the surface film and while struggling to free itself attracts the backswimmer. Its struggles (e.g. an adult mosquito emerging from its pupal skin) bring the backswimmer within striking distance and it is quickly seized. Only if the prey is much larger than the backswimmer can it escape and even then the escape is usually only temporary. Even large organisms weaken in time and will be grasped in the backswimmer's forelegs to be pulled beneath the surface and killed.

Events occurring immediately after an adult backswimmer captured a mosquito larva were followed in detail under a low power dissecting microscope. Observations were easy to make because the backswimmer, after capturing its prey, buoys to the surface with the prey held between its forelegs and against its venter, which is uppermost in the field of view.

N. undulata nymphs and adults have raptorial or grasping fore- and middle legs. The femur and tibia are equipped with a series of spines and 'teeth' and the tarsi each with two terminal claws (Bare 1929) that aid in seizing and manipulating struggling prey.

After capture of a prey organism, the backswimmer manipulates it with its forelegs and probes it with its beak. Whether the backswimmer is searching for a vulnerable entrance point or simply making several preliminary injections of a paralyzing-digestive fluid is not clear. Within 3 or 4 seconds the stylets begin piercing deeply at one spot into the prey's body. A digestive fluid is probably injected as the stylets probe deeper since the body immediately begins to turn a milky white color. Probing usually begins in one of three general regions: the thorax-head area, the mid-abdominal area or the posterior-abdominal area. From these probing centers, the stylets move anteriorly or posteriorly within the prey's body cavity. When they are close to the body surface, the stylets can be clearly viewed as they move upon each other. The action of the stylets has been previously described (Snodgrass 1935). Occasionally the stylets break through the opposite body wall; they are immediately retracted into the prey before they begin to probe in a different direction.

The prey's body is repositioned about every 30 seconds as the probing continues. As one region is probed it gradually shrinks in size and loses its normal shape. When all regions have been probed and body fluids removed the corpse is released and pushed away. Soon after a prey is released and pushed aside it begins to blacken in color and, later, sinks to the

bottom. The former is probably due to the action of residual digestive fluid on the remaining tissues.

The length of time which the backswimmer feeds on a single prey organism appears to depend on the backswimmer's hunger level and/or the influence of nearby disturbances (e.g. other mosquito larvae). Response decrement (Wolda 1961) may have been another factor. Less and less time is spent handling successive prey as the backswimmer becomes satiated or as its response to the presence of prey decreases. The handling times of one previously starved backswimmer were 567, 470, 280, 230, 213, and 120 seconds.

This study of the backswimmer's predatory behavior indicates that N. undulata is well adapted for the perception, location and capture of small aquatic organisms (particularly mosquito larvae), whether they be benthic (browsing larvae), nectonic (swimming larvae or pupae) or hyponeustonic (resting larvae or pupae). Morphologically, the backswimmer is well equipped to manipulate and quickly subdue struggling prey.

## CONCLUSIONS

N. undulata occurs in several types of semi-permanent and permanent habitats under a variety of physical and biotic conditions (Table I). The backswimmer's response to environmental factors (e.g. temperature, Figs. 7, 8) and its related habitat preferences are similar to those of many North American mosquito species (Bates 1965, Happold 1965). The fact that aquatic stages of mosquitoes were seldom found in backswimmer habitats suggests that N. undulata may be more important as a predator of mosquitoes than previously considered.

Observations of predatory behavior, suggesting that N. undulata is well suited for the capture of the aquatic stages of mosquitoes, are supported by preference trials in which the backswimmer consistently chose mosquito larvae and pupae over 6 other prey types (Fig. 19). Its ability to survive on other organisms in the absence of mosquito larvae further supports the conclusion that N. undulata may be highly adaptable to local mosquito population conditions.

Several aspects of backswimmer predation on mosquito larvae were elucidated by the predator stage: prey age:prey density experiments. With the exception of the first instar, the nymphs killed more larvae than did the adults (Figs. 9-14). Thus, larval mosquitoes and nymphal backswimmers must be present at the same time for N. undulata to be most effective in controlling

mosquito populations. Since the backswimmers killed more younger than older larvae, they must kill more individual prey to obtain sufficient food. Therefore, they may have a more detrimental effect on adult mosquito population levels than predators which feed predominantly on either pupae or adults. However, because the effect of increasing prey density on the backswimmer's predation rate diminishes in magnitude from low to high density, N. undulata may not, in nature, be able to repress a rapid increase in larval numbers. Moreover, because mosquito larvae develop faster than backswimmers (Bates 1965), a large larval population could conceivably not be greatly suppressed by backswimmer predation.

This study suggests that, overall, N. undulata is very favorably adapted as a predator of the aquatic stages of mosquitoes and that it warrants detailed investigation in a natural situation to further elucidate its role in the existing mosquito predator complex.

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