Studies of *Notonecta undulata* Say,  
(Hemiptera:Notonectidae)  
as a Predator of Mosquito Larvae

by

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of

Biological Sciences

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Simon Fraser University

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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 microscope 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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Sincere appreciation is expressed to my advisor, Dr. J.H. Borden, for his helpful suggestions, valued criticisms and guidance.

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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.

\textit{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 ± 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 *N. undulata* showing pieces of rubber-mesh sink matting used for oviposition, cover and anchorage.

Fig. 2 Newly-laid egg of *N. 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.

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<tr>
<th>Characteristics</th>
<th>(1) Excavation Pool</th>
<th>(2) Excavation Ditch</th>
<th>(3) Swimming Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Burnaby, B.C.</td>
<td>Burnaby, B.C.</td>
<td>Coquitlam, B.C.</td>
</tr>
<tr>
<td>Date</td>
<td>24/7/68</td>
<td>24/7/68</td>
<td>8/5/67</td>
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<tr>
<td>Water Temp. (°C)</td>
<td>32.5</td>
<td>29.5</td>
<td>10.0</td>
</tr>
<tr>
<td>Water Hardness (ppm)</td>
<td>220</td>
<td>220</td>
<td>30</td>
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<tr>
<td>pH</td>
<td>7.0</td>
<td>7.0</td>
<td>6.0</td>
</tr>
<tr>
<td>Current</td>
<td>Slight</td>
<td>Slow</td>
<td>None</td>
</tr>
<tr>
<td>Macroflora</td>
<td>Few emergent grasses.</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Remarks</td>
<td>N. undulata plentiful; Mating observed; Late instars present; Adults active on surface film and flying from pool.</td>
<td>N. undulata rare in ditch leading from excavation pool.</td>
<td>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.</td>
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Key to symbols: *, present in low numbers; **, present in moderate numbers; ***, present in high numbers; and *****, present in unusually high numbers.
<table>
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<tr>
<th>Characteristics</th>
<th>(4) Placid Lake</th>
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<th>(6) Gwendoline Lake</th>
<th>(7) Silver Creek Park Pond</th>
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<td>Haney, B.C.</td>
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<td>6.0</td>
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<td>Slight</td>
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<tr>
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<td>Bog plants</td>
<td>Few emergent plants</td>
<td>Bog plants and emergent plants</td>
<td>Submerged, floating and emergent plants plentiful.</td>
</tr>
<tr>
<td></td>
<td>around margins.</td>
<td></td>
<td>along margins.</td>
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<td></td>
<td>Salelia larvae *</td>
<td>Salelia larvae *</td>
<td>Salelia larvae *</td>
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</tr>
<tr>
<td></td>
<td>Urodela adults *</td>
<td>Urodela adults *</td>
<td>Urodela adults *</td>
<td>Salmonidae *</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Gasterosteidae ***</td>
</tr>
<tr>
<td>Remarks</td>
<td>N. undulata rare; possibly related to high gerrid numbers. Mating not observed.</td>
<td>N. undulata absent; N. kirbyi plentiful. Practically no shallow areas around this habitat.</td>
<td>N. undulata rare; N. kirbyi plentiful. Mating not observed; No nymphs.</td>
<td>N. undulata present in low numbers in this dammed-up creek. Mating not observed.</td>
</tr>
<tr>
<td>Characteristics</td>
<td>(8) Deer Lake</td>
<td>(9) Golf Course Pond</td>
<td>(10) Lost Lake</td>
<td>(11) Gravel Pit Pool</td>
</tr>
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<td>-----------------</td>
<td>--------------</td>
<td>----------------------</td>
<td>----------------</td>
<td>---------------------</td>
</tr>
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<td><strong>Location</strong></td>
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<td>Burnaby, B.C.</td>
<td>Coquitlam, B.C.</td>
<td>Haney, B.C.</td>
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<td>15/5/69</td>
<td>30/5/68</td>
<td>21/5/69</td>
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<tr>
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<td>24.5</td>
<td>24.0</td>
<td>22.5</td>
</tr>
<tr>
<td><strong>Water Hardness (ppm)</strong></td>
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<td>40</td>
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<td>10</td>
</tr>
<tr>
<td><strong>pH</strong></td>
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<td>6.6</td>
<td>6.0</td>
<td>6.0</td>
</tr>
<tr>
<td><strong>Current</strong></td>
<td>Slight</td>
<td>Slight</td>
<td>Very Slight</td>
<td>Slight</td>
</tr>
<tr>
<td><strong>Macroflora</strong></td>
<td>Submerged, floating and emergent plants plentiful.</td>
<td>Submerged, floating and emergent plants plentiful.</td>
<td>Submerged, floating and emergent plants plentiful.</td>
<td>Few emergent grasses.</td>
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<td>Notonectidae *</td>
<td>Notonectidae ****</td>
<td>Notonectidae ****</td>
<td>Notonectidae ***</td>
</tr>
<tr>
<td></td>
<td>Gerridae *</td>
<td>Gerridae *</td>
<td>Gerridae *</td>
<td>Gerridae *</td>
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<tr>
<td></td>
<td>Corixidae ***</td>
<td>Corixidae **</td>
<td>Corixidae **</td>
<td>Corixidae *</td>
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<tr>
<td></td>
<td>Dytiscidae **</td>
<td>Dytiscidae *</td>
<td>Dytiscidae **</td>
<td>Dytiscidae *</td>
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<tr>
<td></td>
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<td>Hydrophilidae *</td>
<td>Hydrophilidae *</td>
<td>Hydrophilidae *</td>
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<tr>
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<td>Noteridae *</td>
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<tr>
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<td>Gyrinidae *</td>
<td>Gyrinidae *</td>
<td>Gyrinidae *</td>
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<tr>
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<td>Trichoptera *</td>
<td>Trichoptera *</td>
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<tr>
<td></td>
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<tr>
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<td>Ephemeroptera *</td>
<td>Ephemeroptera *</td>
<td>Ephemeroptera *</td>
</tr>
<tr>
<td></td>
<td>Salmonidae *</td>
<td>Salietia *</td>
<td>Salietia *</td>
<td>Salietia larvae *</td>
</tr>
<tr>
<td><strong>Remarks</strong></td>
<td>N. undulata relatively rare; possible related to high number of corixids. Mating not observed.</td>
<td>N. undulata very abundant; Notonecta kirbyi low in numbers; Eggs and first instars of N. undulata present. Mating observed.</td>
<td>N. undulata very plentiful; Buenoa sp. also present; first and second instars present; mating observed.</td>
<td>N. undulata and N. kirbyi both plentiful. Mating observed; no nymphs.</td>
</tr>
</tbody>
</table>
### Table I. Survey of backswimmer habitats continued.

#### Backswimmer Habitat

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>(12) Rolley Lake</th>
<th>(13) Jewel Lake</th>
<th>(14) Hatzic Slough</th>
<th>(15) Kanaka Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Mission, B.C.</td>
<td>Haney, B.C.</td>
<td>Hatzic, B.C.</td>
<td>Mission, B.C.</td>
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<td>Date</td>
<td>26/5/69</td>
<td>21/5/69</td>
<td>27/6/69</td>
<td>27/6/69</td>
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<tr>
<td>Water Temp. (°C)</td>
<td>16.0</td>
<td>23.5</td>
<td>22.5</td>
<td>22.0</td>
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<tr>
<td>Water Hardness (ppm)</td>
<td>10</td>
<td>10</td>
<td>30</td>
<td>20</td>
</tr>
<tr>
<td>pH</td>
<td>6.1</td>
<td>6.0</td>
<td>6.2</td>
<td>6.0</td>
</tr>
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<td>Current</td>
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<td>Very slight</td>
<td>Slight</td>
<td>Slight</td>
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<td>Macroflora</td>
<td>Submerged, float-</td>
<td>Bog plants abun-</td>
<td>Emergent grasses,</td>
<td>Submerged and</td>
</tr>
<tr>
<td></td>
<td>ing and emergent</td>
<td>dant, emergent</td>
<td>plentiful.</td>
<td>emergent plants</td>
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<tr>
<td></td>
<td>plants abundant.</td>
<td>and submerged.</td>
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<td>abundant.</td>
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<td>Notonectidae *</td>
<td>Notonectidae *</td>
<td>Gerridae *</td>
<td>Gerridae **</td>
</tr>
<tr>
<td></td>
<td>Gerridae *</td>
<td>Gerridae ***</td>
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<td>Corixidae **</td>
<td>Corixidae **</td>
<td>Dytiscidae *</td>
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<td>Dytiscidae *</td>
<td>Noteridae *</td>
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<td>Trichoptera *</td>
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<tr>
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<td>Cyprinidae **</td>
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<td>Chironomidae **</td>
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<td>Trichoptera *</td>
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<td>Odonata ***</td>
<td>Odonata **</td>
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<td></td>
<td>Salietia ***</td>
<td>Salietia *</td>
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<td></td>
<td>Urodele *</td>
<td>Ephemeroptera *</td>
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<td></td>
<td>Salmonidae *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ictaluridae **</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Remarks</td>
<td>N. undulata scarce.</td>
<td>N. undulata absent.</td>
<td>N. undulata absent.</td>
<td>N. undulata absent.</td>
</tr>
<tr>
<td></td>
<td>Mating not ob-</td>
<td>N. Kirbyi in low</td>
<td>Water was very</td>
<td></td>
</tr>
<tr>
<td></td>
<td>served.</td>
<td>numbers.</td>
<td>turbid.</td>
<td></td>
</tr>
</tbody>
</table>
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 backswimmer 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 backswimmer 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 temperature 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 then 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 temperature 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 *N. undulata*. 
Fig. 6 Lethal temperature apparatus used to determine the upper temperature tolerance of *N. 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, respectively (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.
First Instars (mean = 25.7 ± 2.8°C)
Fifth Instars (mean = 25.9 ± 3.1°C)
Adults (mean = 26.9 ± 2.7°C)
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 temperature, 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 *N. 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.
EXPOSURE DURATION (HR.)

PERCENT MORTALITY

KEY (°C)
- 34
- 35
- 36
- 37
- 38
- 39
- 40

EXPOSURE DURATION (HR.)
Survival at water temperatures up to 34 °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 preference 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* (*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.
-28-

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. Corresponding standard deviations are shown.
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. aegypti* 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. 'A1:A2') the significance level is shown by a shaded square (see 'key to significant differences'). Line graph inserts in each figure represent the mean predation rates when the interactions of each of the 2 other factors are blocked. Symbols are as follows: A1 to A6 represent the 5 nymphal instars (A1 to A5) and adults (A6) of *N. undulata*; B1 to B4 represent the 4 larval age groups of *A. aegypti* (1 - 3, 4 - 6, 7 - 9, and 10 - 12 days old, respectively); and C1 to C3 represent the 3 prey densities (5, 10 and 50 larvae per 1000 ml, respectively).
KEY TO SIGNIFICANT DIFFERENCES

PREDATOR INSTAR

PREY AGE GROUP.

PREY DENSITY

Mean Number Killed/Hour

Predator Stages

Prey Stages

Mean Number Killed/Hour

Prey Stages

Predator Stages

Prey Density

1 2 3 4 5 6


A1:A5 A2:A6

A1:A6

PREDATOR INSTAR

PREY AGE GROUP.

PREY DENSITY

Mean Number Killed/Hour

Predator Stages

Prey Stages

Mean Number Killed/Hour

Prey Stages

Predator Stages

Prey Density

1 2 3 4 5 6

B1:B2 B1:B3 B1:B4

B2:B3 B2:B4 B3:B4

1 2 3 4

1 2 3 4

1 2 3 4

1 2 3 4 5 6

C1:C2 C2:C3 C1:C3

5 10 50

5 10 50

5 10 50

5 10 50
(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 killing 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 significantly 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 significantly 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 lowering 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 vs. 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 vs. 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 (B5, 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 *N. undulata* which were starved for 48 hours prior to being offered, 50 fourth age group *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 N. undulata. Response decrement, a decrease in responsiveness when repeatedly presented with a stimulus, may, however, tend to reduce the predation rate of N. undulata as in Notonecta 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, N. 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 *N. undulata* to be an insatiably 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 ephemerid 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.
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 ensnared 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 characteristics 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 backswimmer habitat survey.
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 backswimmer 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 obtaining 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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