

THE PREDATION STRATEGIES AND BIONOMICS OF THREE
SPECIES OF NOTONECTA (HETEROPTERA/HEMIPTERA).

BY

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ABSTRACT

Through an examination of literature on predation strategies, three factors emerge as being considered the most important in contributing to the nature of such strategies. These are; a) the energetic aspects of the strategy (e.g. net energy gains from different types of prey); b) behavioural activities by which the predator is able to forage; and c) morphological constraints on both the energetic aspects and the behavioural activities.

Laboratory experiments are designed, (with particular interest paid to realism and predator standardisation), to examine how the above factors affect the predator strategies of three species of Notonecta, feeding on three prey types, singly and in combination and in two environments. Simple models are constructed to attempt to identify the main factors affecting prey selection in a multiprey situation, and a morphometric study is undertaken to examine the dynamics of locomotion and prey catching. Factors affecting the control of handling time are also examined.

Comparisons are made between the strategies of the three British Notonecta species and with data for foreign species available from the literature.

On the basis of the predation strategies described from the laboratory results and on other aspects of the bionomics of this genus (such as oviposition behaviour, development rates etc), a prediction of the range of habitat types, which each species under study should be able to exploit, is drawn up. These predictions are then compared to actual distribution and habitat selection found from field sampling and described in the literature, with the aim of elucidating, to some extent, the ecological problems of species diversity and co-existence within this genus.

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CHAPTER I

I.1.

Introduction

It has been pointed out by several authors (e.g. Werner 1977) that one of the fundamental problems in Ecology is to identify and relate those factors which determine the number of species that can coexist in an area. Interspecific competition, as one factor, limits the similarity of co-existing species, but one frequently observes apparent violations of the ecological principle that two species cannot compete indefinitely for the same limiting resource (Gause's rule).

Many studies, testing such concepts as competitive exclusion, coexistence, character displacement etc., have shown that the species involved differ in their ability to utilise common resources. MacArthur and Levins (1967) have suggested that the success of a species invading between two residents on a particular resource axis is related to the differences in mean utilisation of this resource. This has led to Niche theory and the conclusion that there is usually no complete sharing of all resources of one sympatric species by another, because under the pressure of competition, initial small differences in resource utilisation are intensified through evolution, so that the two species come to use different portions of the once common resource.

The species of Notonecta are very similar ecologically (Gittleman 1973), and thus provide a useful tool for examining overlapping resource utilisation, niche separation and thus species coexistence. Studies by Taylor (1968) and Streams and Newfield (1972) suggest that the habitats and environmental resources used by six species of Notonecta in New England appear to overlap rather broadly. It is not uncommon to find three or four of the species present in the same pond. Sim-

ilarly, three, or sometimes all four of the British species have been found in the same pond (pers. observation.). Taylor, and Streams and Newfield do find that the microhabitats in which the species are usually found, tend to be separated. However, the authors conclude that although spatial and temporal differences tend to separate the species, there appears to be sufficient overlap in the feeding areas of several of the species, to permit significant competition between them. They further suggest that differences in feeding behaviour or prey preferences may further reduce such competition, although this has not been critically examined.

The only literature describing species separation and distribution of the British species of Notonecta to date, does so on the basis of selection of oviposition sites, life histories and of the common habitat type (e.g. Brown 1943; Walton 1943; Southwood and Leston 1959). These attempts have generally proved incomplete as one often finds populations of several of the species reproducing in the same, small, more or less homogenous pond.

As Emlen (1966) points out, the efficient exploitation of available food is a vital requirement of all animals, and a study of feeding and food preferences, therefore, should be of vital importance in ecology. Very rarely, have the differences in foraging efficiency of morphologically similar species been quantified in relation to a set of resources that change in a recognisable manner (Werner 1977). There are several studies which describe and quantify the feeding response of individual Notonecta species (e.g. Wiese 1971, 1972, Wolda 1961 etc.,) or species specific predator/prey interactions (e.g. Fox and Murdoch 1978, Lawton et al 1974, Toth and Chew 1972). There has however, been very little comparative research on the foraging efficiency of a guild of Notonecta species in relation to habitat selection, competition and

coexistence. The small guild of British Notonecta (four species) provides an ideal opportunity for such a study.

In the examination of a feeding strategy, attention should be paid to behavioural and morphological complexes which allow a given animal to gather food in a particular environment (Schoener 1971). The net value of different types of prey to the predator, in terms of some currency (e.g. energy, dry wt. etc.,) should also be examined. As Emlen (1966) points out, the value of food to an animal can be basically determined by its calorific yield per unit time to that animal. A more appropriate, and accurate, form of currency would be the net energy gain (net profit) per unit time, taking into account the cost to the predator of catching and handling the particular food type. It is likely, then, that natural selection will favour the development of feeding preferences and strategies that will, within the physical and nervous limitations of a species, maximise (or optimise) the net energy intake per individual of that species, per unit time available for feeding (Emlen 1966).

In order to examine and compare predatory strategies, one must examine a number of factors:-

- 1) The energetic aspects of the strategy (e.g. net energy gains from different types of prey) which may allow the prediction of the 'optimal' solution to a multiprey situation, if the net energy gain is the major factor involved in food preferences.
- 2) Behavioural activities by which the predator is able to forage for different prey and in different environments.
- 3) Morphological constraints on a) the behavioural aspects, in terms of what the predator can and cannot physically do, and b) the energetic aspects, in terms of types and sizes of prey it is physically able to catch, the ease of catching and handling these items and the costs

thereby incurred.

By combining such a study with other aspects of the bionomics of the species, including oviposition behaviour, life histories and development, a prediction of the range of habitat types, which each species of predator should be able to exploit, can then be formulated. One would expect differences between the species, which might allow coexistence in the more complex real world habitat, to become apparent in this overall description of their theoretically 'best' habitat. In other words, predictions of the circumstances in which several species may be able to coexist, can be made, and these predictions can be tested against the actual distribution and habitat selection in the field.

If the predicted and observed distribution patterns are similar, then perhaps, one has gone some way to elucidating the major influences in the ecological problem of species diversity and co-existence within this genus.

I. 1.1. The energetics of feeding strategies.

Analysis of the energetics of feeding has been almost totally concerned with optimisation problems. Feeding is treated as a device, whose performance, as measured by net energy yield/feeding time (or other similar "fitness" units) may be maximised by natural selection (Emlen 1966 ; Krebs 1974, 1978; MacArthur and Pianka 1966; Schoener 1971; Werner and Hall 1976 etc.,).

The usual function used to quantitatively describe food intake relates E , the total net energy yield from feeding to T , the total time spent feeding, during some longer time period P (Schoener 1971). Given an environment with several available prey species, a predator foraging optimally should be able to rank the different kinds of prey in terms of $\frac{E}{T}$. As foragers often search for all items simultaneously,

the ranking function need not include search time and energy costs, and can be written as below (Schoener 1971).

$$\frac{E}{T} = \frac{\text{(Available potential energy from prey-energy costs of pursuit handling and eating prey)}}{\text{Pursuit time + handling and eating time.}} \quad (1)$$

This description assumes that digestion is simultaneous with other feeding behaviour.

Similar functions have been used by Emlen (1966), Estabrook and Dunham (1976) and Rapport (1971) in the analysis of optimal diets. Although definitions of optimal diet based on maximising some measure of food value per unit time are the most often used, other criteria can be equally valid e.g. a diet that minimises total search, pursuit or handling time per food item captured (MacArthur and Pianka (1966)); one that maximises food value per unit of energy used in foraging (Tullock (1971)); or a diet controlled by ease of catching or ease of handling prey (see Schoener (1971)).

Optimal diets in which predators rank different prey according to the $\frac{E}{T}$ values, have three properties (Pyke, Pulliam and Charnov (1977)). Firstly, the decision as to whether or not to eat a food type is dependent only on the relative abundance of the food types of higher rank, a less profitable prey never being specialised on, regardless of its abundance. Secondly, it is predicted that, as the abundance of the most profitable prey type increases, the number of less profitable food types included in the diet will shrink i.e. increasing food abundance should increase specialisation. (Alternatively, as the abundance of preferred prey falls, so more, less preferred, prey should be included, but in their rank order). The final property is that a food type is either completely included in, or completely excluded from, the optimal diet (i.e. there should be no partial preferences, unless the theory is extended to include dietary constraints

or random variations in the food abundances (Pyke et al (1977)). Work such as that of Charnov (1976), Goss-Custard (1977) and Werner and Hall (1974), have shown that an animal's diet can be predicted on the basis of such theoretical arguments.

There are, however, several defects in such models of optimal diets (Hassell and Southwood (1978)). Firstly, they assume that prey exist in a homogeneous environment. Hassell and Southwood suggest that such models could be made more realistic by being based on some heterogenous distribution of prey as are optimum foraging models. Secondly, studies on free flying blood sucking insects and pollen and nectar gathering social bees, have shown that relative abundance of different food types does affect their inclusion in the diets (for references see Hassell and Southwood (1978)). Finally, the current optimal diet models make no allowance for the forager's need to sample the environment, and assume that a forager can unfailingly rank different prey types. (For a further critique of optimal foraging theory and models, see Maynard-Smith (1978)).

Two types of predator have been described on the basis of their attack strategy (Schoener 1971). Type I predators incur expenses in time and energy in feeding from pursuit, handling and eating the prey, and not from search. At the same time as monitoring the environment for food, such a predator will simultaneously look for mates, territorial invaders (where appropriate) and its own predators. Overall, it expends no more energy searching for food than on other activities. This is the classic 'sit and wait' predator, an apt description of Notonectids. Type II predators incur costs in time and energy for search as well as the other costs listed above. Search costs involve foraging in different areas, and optimal foraging would require the predator to order the feeding areas by their probable profitability.

The degree to which net food energy does increase the predator's fitness depends on several factors; e.g. age, metabolic requirements, storage of food, growth and reproduction. Feeding strategies are often restricted by the way the predator controls its metabolic expenditures to meet seasonal changes in thermal conditions and food supply. For example, diapause, hibernation and daily torpor are all devices to reduce metabolic energy consumption during unfavourable conditions. Generally, fitness can be quantified in several ways. Positive relationships between food intake and reproductive output are common, e.g. increase in the weight of reproducing individuals affecting egg production; increase in clutch or litter size; increase in size of newborn young or egg; and increase in the number of broods or litters per season, or in oviposition rate (Schoener 1971). It will be shown later that varying food levels for reproducing female Notonecta affects number of eggs laid, age at which eggs are laid and numbers of generations per year.

The profits an animal acquires in feeding must be weighed against the loss of time to participate in other important activities associated with fitness, such as search for mates or predator avoidance (Schoener 1971). Animals not grouped into localised pairs or harems, or with low population densities, may be subject to a decrease in mating success which might be directly proportional to time spent feeding. Animals below a certain size are subject to a positive relationship between conspicuousness, such as occurs when feeding, and the chance of being eaten themselves. Other competing activities such as grooming, preening and play are likely to be less important (Schoener 1971).

Schoener also suggests that predators may be classed according to the manner of maximising their fitness. Energy maximisers are described as animals whose fitness is maximised by maximising net energy intake

for a given feeding time. Females and animals with variable clutch sizes are good examples of this class of predator. Time minimisers are animals whose fitness is maximised when time spent feeding to gather a given energy requirement, M , is minimised. Animals with a relatively fixed reproductive output may be approximated by this case.

The parameters of the net energy/Time equation (1) have been discussed by Schoener (1971) and are considered the most important parameters in the analysis of foraging strategies.

a) Search time. The search time between two items of food, T_s , can be simply expressed as some constant over D , the density of items. With random search, this constant depends on both the predator's and the prey's speed, the search area of the predator and the diameter of the prey. NE , the reciprocal of T_s , gives the expected number of items encountered/time. As Notonectids are a Type I predator, this parameter need not be considered further.

b) Pursuit time. This represents time from detection of a food item to contact. For predators feeding by touch, this value is nil. For stationary prey, this time is the initial distance divided by predator speed, V_p . For a moving prey, the distance is multiplied by $\frac{V_p}{(V_p - V_i)}$; V_i being the prey speed. Other factors, such as acceleration and fatigue, may complicate this picture somewhat.

c) Search and pursuit energy. The simplest assumption on expenditure of energy during activity, is that it is proportional to W^λ , where W is the body weight, and λ a power index derived from respiration/weight correlations amongst several different types of animal, and commonly clusters about 0.75 (Schoener 1969). Active metabolism can be up to twenty times basal, but Schoener reports most data available demonstrates six to fourteen times, and food search may cost little more than rest.

d) Handling and eating time and cost per item. Handling and eating time vary for different predators and prey types and sizes. The energetic cost per item usually falls below pursuit costs. Apart from feeding and handling, costs may be incurred in transporting the prey item to some location for consumption or storage (this is often important as it can reduce risk of predation, where positions chosen for consumption reduce the feeders conspicuousness).

e) Pursuit and Capture Success. This will be examined in section I. 1.2.

f) Potential calorific content of food. This term can be expressed as $Ca i^t$, where Ca is some constant proportional to the number of calories the animal can extract from the food item per unit volume, and i^t gives some measure of the effective volume of the prey, i being prey length, t is some value between 2-3.

g) Relative abundance of kinds of food items. This is important in the construction of optimal diet models, although for theoretical purposes, it might be arbitrarily set.

I. 1.2. Behavioural aspects of feeding strategies.

I.1.2.1. Introduction

Whereas Schoener has examined foraging strategies in terms of the optimisation of gains and costs in relation to fitness, Holling (1959, 1961, 1966) considered such strategies from a more behavioural standpoint, breaking down the whole process of predation into a series of components, the effect of each one having an effect on the overall strategy. Holling (1961) classified the five main factors, which were thought to affect the predation process, into two categories. He termed basic components those factors which were universally present in predator/prey interactions i.e. a) Prey density, and b) Predator density. The remaining three factors, namely, c) characteristics of

the environment (e.g. number and variety of alternate foods, environmental complexity etc.,) d) characteristics of the prey (e.g. defence mechanisms, distributions etc.,) and e) characteristics of the predator (e.g. attack techniques etc.,), he termed the subsidiary components.

I. 2.2.2. Components of Predation.

It is necessary, at this point, to briefly introduce the term 'Functional Response'. This term was first proposed by Solomon (1949) and later used by Holling (1959) to describe the change in the capture rate of a predator with varying prey density. This usually shows an increasing prey capture rate with increasing prey density, and indicates the general impact of the predator on the prey population. Hassell, Lawton and Beddington (1976) note that the mathematical description of this response is normally defined for the case where predators search at random for a homogenous, randomly distributed prey population. Most mathematical descriptions of this response also assume that the instantaneous attack rate and handling time remain constant for all captures at each density. Holling described how the components of predation affected the functional response of Hierodula crassa on various insect prey items. Ten such components were described:-

i) The rate of success of search for prey by the predator. This component has many variables and is affected by them in a number of ways.

a) Size of reaction area of a predator for a certain prey, either in two (e.g. terrestrial predators) or three (aquatic predators) dimensions. This area can be measured by determining the maximum distances over which the predator will show at least an orientation response to the prey presented from different directions. The size of prey, its speed of movement and the predators hunger level will all affect the size of the reaction area. It will be reduced with small prey, slow prey and a low predator hunger level, and increased with large, rapidly moving prey and higher hunger levels. (Environmental complexity can also

affect its size).

b) Speed of movement of the predator and prey will affect search success. Hunger generally increases the rate of movement of a predator when searching.

c) Actual success in capturing prey by the predator, when prey enter its reaction area. This is further subdivided into three categories, chronologically describing the attack procedure.

cl) Recognition success of the prey item by the predator. This is given by -
$$\frac{\text{Number of recognised encounters}}{\text{Total number of encounters}}$$
 This will be affected by acuity of perception of the predator, prey camouflage effectiveness, and the clarity of the environment.

c2) Pursuit success, which is given by -

$$\frac{\text{Strikes made}}{\text{Total number of pursuits initiated}}$$

Where the pursuit is successful, the predator gets close enough to initiate a strike.

c3) Strike success, which is given by -

$$\frac{\text{Number of successful strikes}}{\text{Total number of strikes initiated}}$$

These subcomponents are important, as most attempts to describe the functional response of a predator use more than one replicate. There is likely to be a broad spectrum of variability between different individual predators in these behavioural phenomena, so that considerable variation between individuals in overall response is likely.

ii) The time the predator is exposed to prey. This is basically subdivided into the time associated with feeding behaviour, and the time associated with non-feeding behaviour. (For experimental purposes, one would try and reduce non-feeding behaviour as much as possible, by carefully selecting experimental animals e.g. predators should not be selected just prior to, during or just after moulting, oviposition etc.)

iii) The handling time. This involves the time spent for the pursuit, capture and eating of the prey, as well as the digestive pause after feeding. Handling time is affected by factors such as size of prey and hunger of predator, (and it is another likely cause of variation between predators).

iv) Hunger. This component is possibly the most important, as it affects every other component in feeding behaviour in some way. For example, it affects the area of search, speed of movement, rate and success of attack and the handling time. After eating, there is usually a digestive pause, during which it is presumed that the hunger threshold is below the attack threshold, so no search is initiated. (The threshold is some physiological state of the predator; see later).

All the above components will depend on the level of satiation of the predator. Obviously, the amount of food required to reach satiation will depend on the size of the predator and the length of previous food deprivation (as well as the general nutritional state of the predator). It is quite common amongst invertebrates, for the weight of food required to reach satiation to increase at a decelerating rate with time of food deprivation, levelling off at some value corresponding to the volume of the gut (Holling 1966).

v) Learning processes in the case of H. crassa and many other invertebrates will involve the development of a specific search image (Holling (1966)). Such search images will develop as a result of experience, (although the ability and rate of development of such a search image will vary between individuals) and is likely to improve the predators ability at recognising and catching prey.

vi) Inhibition by the prey, will include energetic defence, such as inhibiting further attack for a certain period of time after contact with the prey; escape; and sensory satiation and confusion at high

prey densities.

These six components change with prey density, whereas the next three components are affected by predator density.

- vii) Exploitation, where the predators compete for the same resource, thus as predator density increases, the chance that any one predator will discover an unattacked prey item decreases, which in turn decreases the attack rate.
- viii) Interference between predators. Meetings between predators decreases the time available for search, and the efficiency of search, and so tends to decrease attack rate.
- xi) Social facilitation is the opposite of viii), as it is possible for an initial stimulation for greater activity of the predator (hence a higher attack rate) to occur as predator density increases.

The last component concerns a response by the prey.

- x) Avoidance learning by prey. This is not very widespread in invertebrate prey, but quite common in vertebrates.

In natural conditions, the overall response by predators to prey will also be affected by the 'subsidiary' components listed previously. It would be impossible in the time available for this study, to examine predatory strategies under all environmental conditions, with all different prey distributions and types, over all predator stages. They must, therefore be examined under a selected range of conditions, with selected prey distributions and predator stages and such constraints must be taken into account when attempting to extrapolate the laboratory findings to field conditions.

I. 1.2.3. Simulation models of feeding behaviour

Both Holling (1966) and Johnson et al (1975) point to the importance of hunger amongst the various components, and if one assumes that feeding behaviour is determined by the interaction of hunger with

LEGEND TO FIG. 1

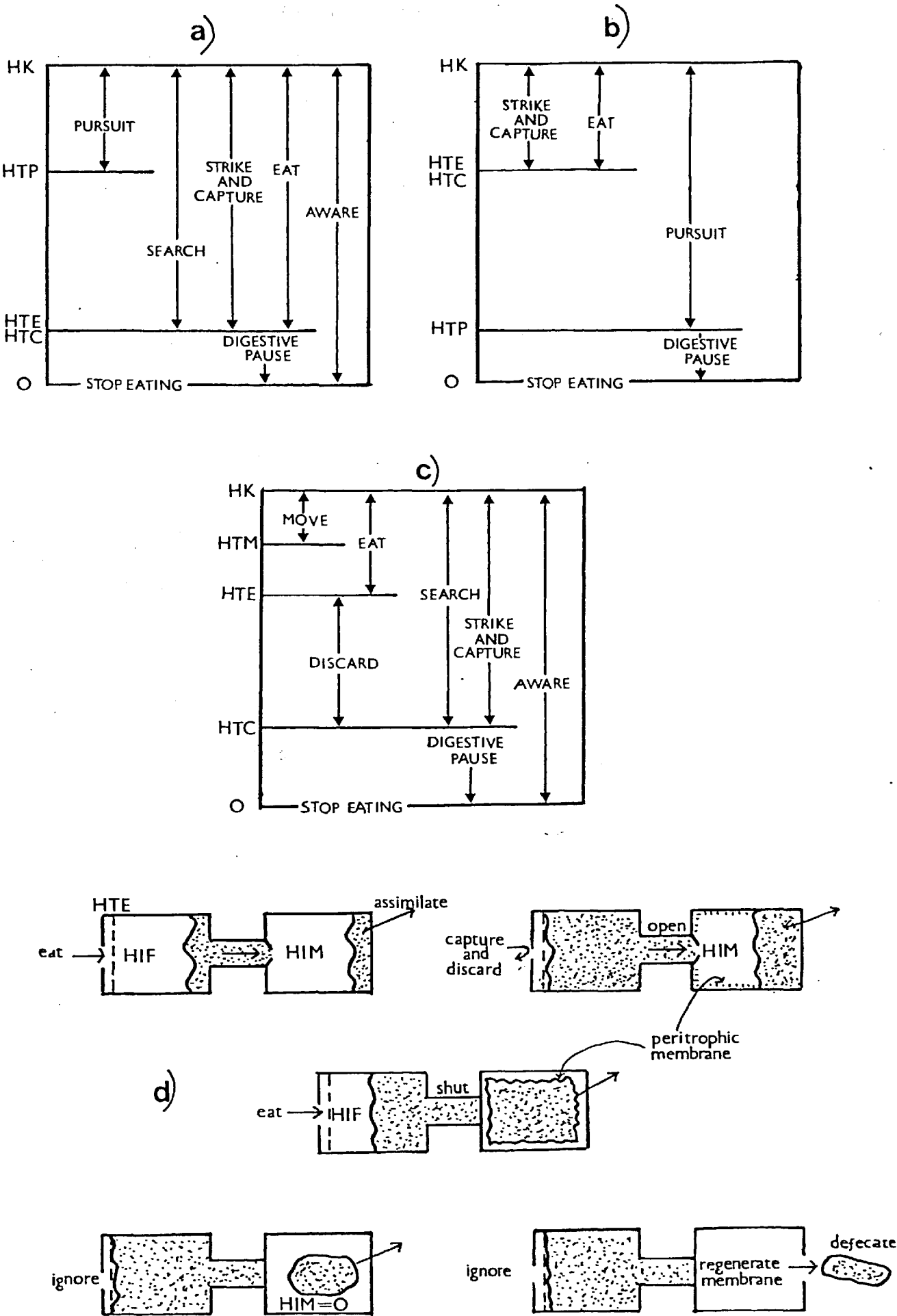
Diagrams showing the incorporation of feeding components into models of feeding behaviour (Johnson et al (1975))

- a) For the mantid H. crassa (after Holling (1966))
- b) For a beetle (after Johnson et al (1975))
- c) For a damselfly (after Holling (1966))
- d) For the damselfly Anomalagrion hastatum
(after Johnson et al (1975))

Key:

- O - Stop eating threshold
- HK - Gut capacity
- HTE - Threshold for eating
- HTC - Threshold for capture
- HTP - Threshold for pursuit
- HTM - Threshold for movement
- HIF - Hunger in foregut
- HIM - Hunger in midgut

FIG 1



hunger thresholds, switching on or off search, pursuit, capture and eating, then flow diagrams can be constructed, describing many different types of feeding behaviour incorporating the various components (Fig 1).

Such models assume that the emptiness of the gut, as a simple manifestation of hunger, provides the internal drive, motivating all components of feeding behaviour. Hunger declines during feeding, increases through the combined actions of defaecation and assimilation, and approaches a maximum value corresponding to the capacity of the gut. (Stretch receptors as described by Dethiers (1976) and Gelpein (1971) may provide the anatomical/physiological justification for these models). Johnson (1975) points out that if one assumes hunger is a unitary drive, and thresholds are arranged in a determinate hierarchy, then only qualitative descriptions of behaviour are necessary to specify a number of thresholds, as well as their relative magnitude (Fig. 1b). Holling also postulated the existence of a hunger threshold for eating greater than that for capture, to account for some predators pursuing and capturing prey, but not eating them (Fig. 1c).

Hunger is assumed to vary from 0 (stop eating threshold) to HK (the gut capacity). For the mantid H. crassa (Holling 1966) (Fig. 1a), the thresholds for eating (HTE) and for capture (HTC) are at a similar hunger level. Mantids will capture prey within reach if hungry enough to eat, but will not pursue flies unless much hungrier, as the threshold for pursuit (HTP) is a higher one. For a beetle (Johnson et al 1975) (Fig. 1b), the threshold for pursuit is lower than that for capture and eating, hence the predators behaviour of pursuing prey but not attempting to capture them. For a damselfly (Holling 1966), the threshold for capture is below the threshold for eating, (This is a 'sit and wait' predator, with little or no pursuit), hence the be-

haviour of capturing then discarding prey. The threshold for movement (HTM) is even higher, allowing for the changing of perch site in search of prey, and aggregative responses by predators to local concentrations of prey.

Johnson et al (1975) found data which conflicted with the proposition of Holling's model for Damsel fly predation, and postulated a different model. They describe a model which assumes a two compartment gut, where hunger in the foregut (HIF) affects the strike response and eating, and hunger in the midgut (HIM) affects only the strike response (Fig. 1d). It is also assumed there is no association of hunger responses with the hind gut. A strike can occur whenever the total hunger ($HIF + HIM$) exceeds a hunger threshold for capture (HTC), but eating can only occur if HIF exceeds a hunger threshold for eating (HTE) (Fig. 1d). Whenever the foregut became full ($HIF=0$), partially eaten prey would be discarded whether the midgut was 'hungry' or not. Discard of prey represents a temporary condition when the midgut is not yet full, but the foregut is too full to allow further consumption, thus the Damsel fly continues to capture prey, but does not eat. This two-compartment model of the gut, with separate proprio-receptors, does receive support from work on feeding in Phormia (Dethiers (1966), Gelperin (1971)).

I. 1.3. Morphological constraints on Predation

Whatever the ultimate causes determining the overall predation strategy, proximate causes for some aspects, such as size and type of prey selected and efficiency in locomotion, can be found in the physiological and structural features of the predator. As Holling (1964) suggests, for many measurements of the animals form, the optimum with respect to survival is usually near the mean, implying the population under study is nearly at equilibrium under natural

selection. One can then redefine the problem from one of 'how does prey size affect predation?', to 'how do the structures that the predators use to capture prey determine the size of prey captured?' (Holling 1964).

Generally, most work of this nature has been confined to the study of vertebrates e.g. rodents (Rosenzweig and Sterner 1970), fish (Werner 1977) etc.,. Of the little work on invertebrate morphology in relation to predation, the most famous example is that of Holling (1964), examining the relationship of preferred prey size with the size of the prey catching appendages in the mantid H. crassa. A somewhat similar study by Gittleman (1977) studied possible resource partitioning in the Notonectidae on the basis of relative sizes of the prey catching appendages and their mechanical functioning. He has also considered coexistence in the Notonectidae on the basis of relative locomotary efficiency (1974).

By comparing the form and mechanical functioning of prey catching and locomotary appendages within the British species of the genus Notonecta one can investigate the possibility of differential resource utilisation, and hence co-existence, amongst these superficially almost identical insects.

I. 2. General Biology of the Notonectidae

I. 2.1. Introduction

Although there are a number of reviews of aspects of the biology of the Notonectidae (e.g. Butler (1923) , Ellis and Borden (1970), Fox (1975), Toth and Chew (1972), Southwood and Leston (1959) etc), to date there has been no general review of the family as a whole. It is important, however, that such a review be attempted, since a detailed knowledge of the biology of a predator is extremely important in providing a basis to the understanding of its feeding strategy and habitat

selection.

The family Notonectidae forms part of the section Hydrocorisae, of the order Hemiptera. They are fairly large, actively swimming predators, found in a wide variety of freshwater habitats. Food intake and prey capture, described in more detail later, is carried out with the use of a piercing rostrum and raptorial fore and middle legs. Swimming is carried out by the posterior legs, which are provided with hairs, giving them an overall shape similar to an oar, hence the more popular name of Waterboatmen. These insects characteristically swim on their backs, which are keel shaped in section (Fig. 2A) and only for short periods do they turn up the 'right' way, for example when searching for perch sites or in capturing prey from such sites. Another obvious feature is the pair of large compound eyes, sited quite well forward on the head.

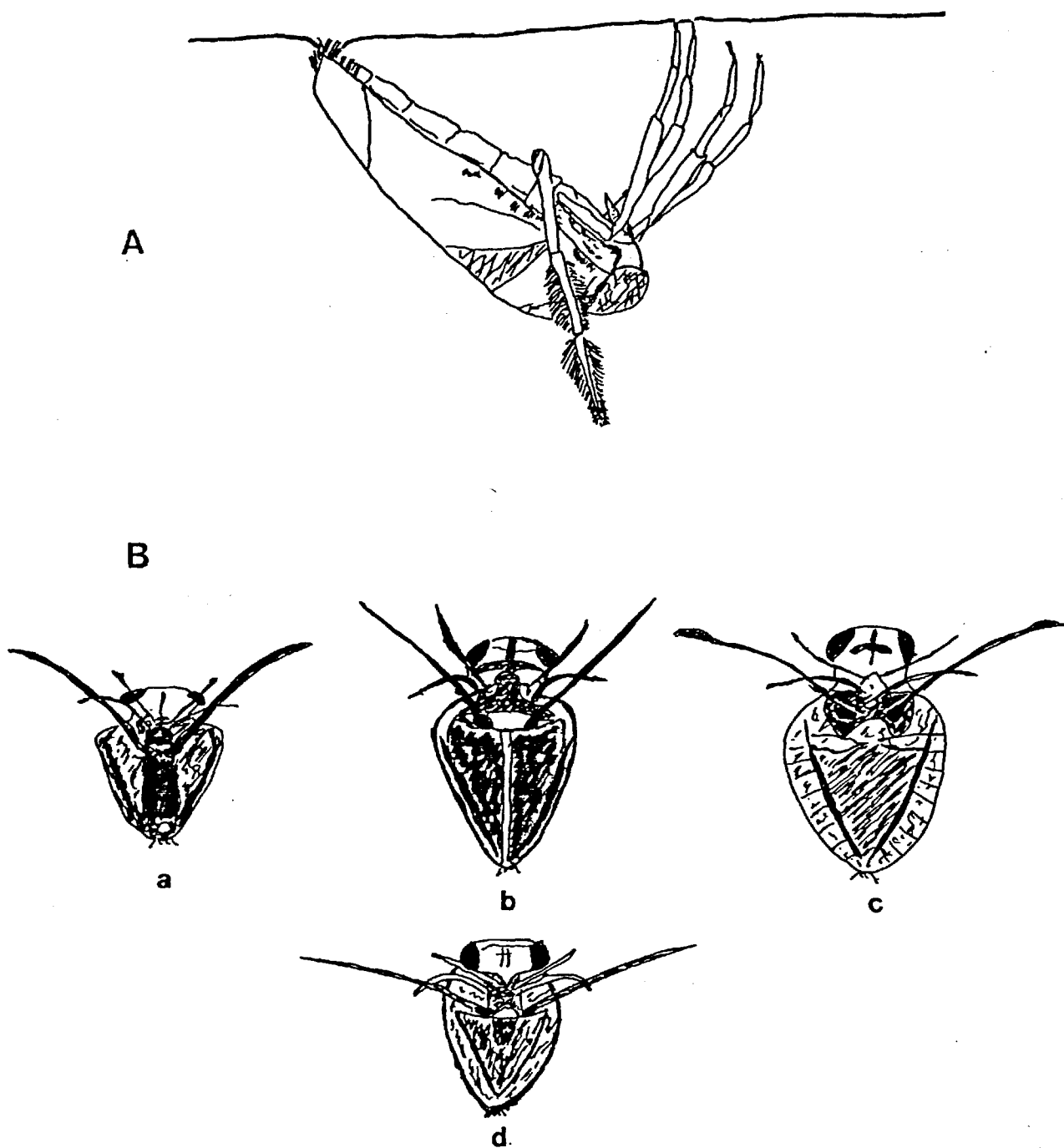
There are four species of the genus Notonecta found in Britain. These are Notonecta glauca (Linnaeus); Notonecta maculata (Fabricius); Notonecta viridis (Delcourt); and Notonecta obliqua (Gallen). The latter has two subspecies in Britain, the typical N. obliqua obliqua and N. obliqua delcourtii.

I. 2.2. Taxonomy of the British species.

The adults of the four species can be quite easily separated on the basis of their hemielytra colour (the sclerotised part of the forewings, which covers most of the abdomen of the adults).

N. glauca - This species has dark tan or buff coloured hemielytra, which sometimes have several fairly large dark blotches, these never, however, obscure the main tan or buff colour.

N. maculata - This species has much darker hemielytra, which are extensively mottled with dark brown or black dots, practically obscuring the ground colour. The first few segments of the abdomen,



LEGEND TO FIG. 2.

- A) Adult Notonectid hanging from water surface.
- B) 1st instar Notonecta nymphs (not to scale)
- a) N. glauca
- b) N. obliqua
- c) N. maculata
- d) N. viridis

on the dorsal side, have a deep orange colour, which is seen when the wings are opened.

N. obliqua - This species has almost black hemielytera, with two pale cream streaks, diverging from anterior to posterior, along both sides of the bug. This species is also the largest of the four. The sub-species delcourtii has additional pale yellow spots posterior to the streaks.

N. viridis (marmurea)- This bug is superficially similar to N. glauca, but the basic hemielytera colour is much lighter, tending towards a grey colouration. It is also the smallest of the four species, and has a characteristic black cross-marking along the sutures in the centre of the hemielytera. Southwood and Leston (1959) also refer to N. viridis as having pointed anterior angles to the pronotum, which embrace the eyes to some extent. All three pairs of legs are of a marked green colour.

Macan (1965a) separates the species on the basis of the genitalia.

Development in the Heteroptera is hemimetabolous, the young nymphs resembling the adult stage. In the genus Notonecta, the nymphs occupy the same habitats as the adults, and also eat similar food, although in the early nymphal stages, smaller items are taken. There are five nymphal stages, which are very difficult to identify to species level except in the first instar, where ventral abdomen colouration and size allow fairly easy identification (Fig. 2B).

I. 2.3. Life History.

The life histories of the British spp. have been described by Walton (1936) and Southwood and Leston (1959). N. glauca is reported to mate between December and late May, with oviposition mainly from early February to early May. The five instars occupy at least two months, but by late August, the new generation of adults has emerged.

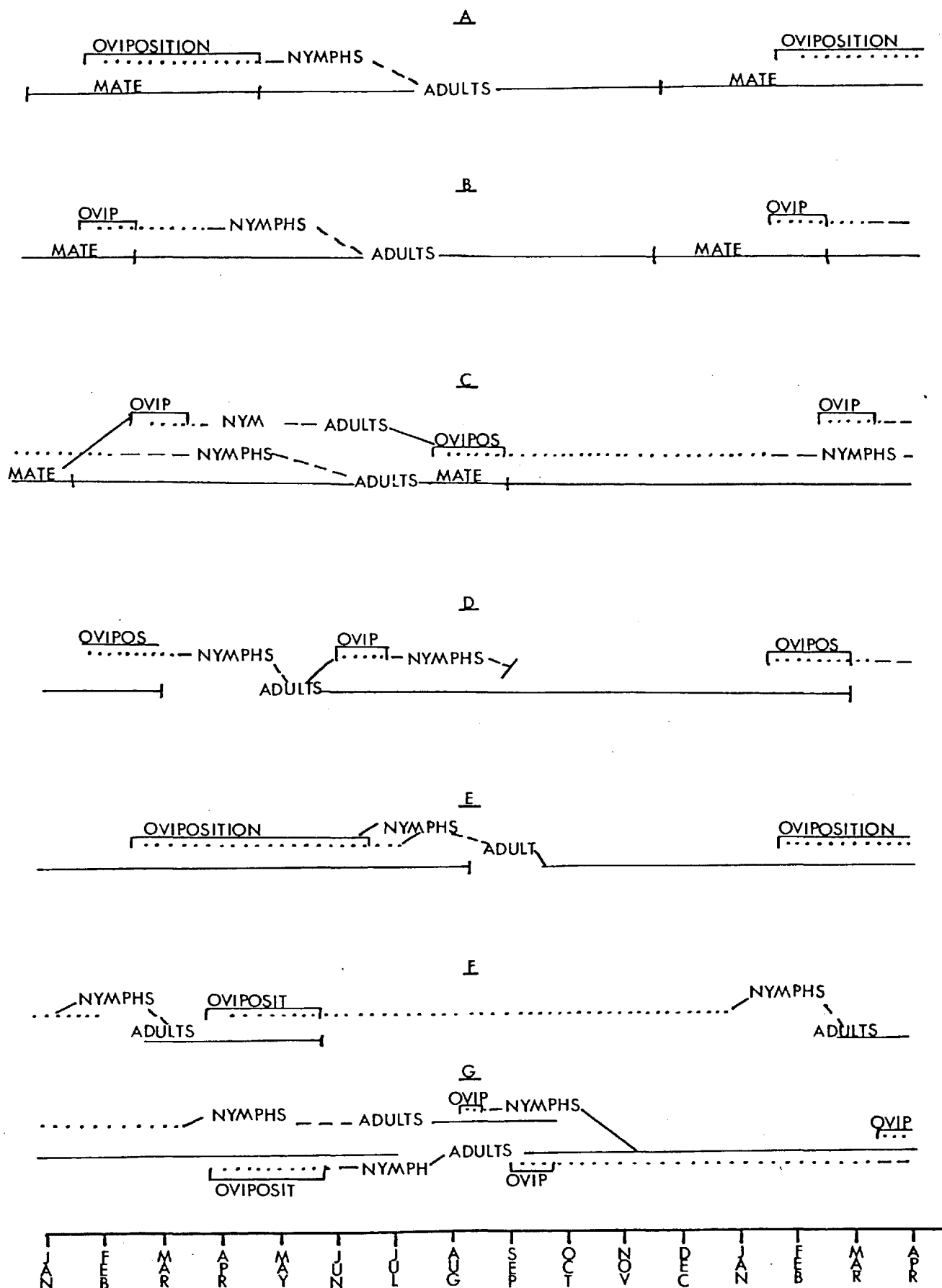
LEGEND TO FIG. 3

Life histories of the Notonectidae:

- A) N. glauca and N. obliqua (Walton (1936), Southwood
and Leston (1959))
- B) N. viridis (Southwood and Leston (1959))
- C) N. maculata (Walton (1936))
- D) N. undulata (Toth and Chew (1972))
- E) N. hoffmani (Fox (1975a))
- F) N. borealis (Rice (1954))
- G) Bueno elegans and B. martaritacea (Rice (1954))

FIG 3

LIFE HISTORIES OF THE NOTONECTIDAE



Only one generation is reported per year, with adults overwintering. N. obliqua has a similar life cycle to N. glauca, with oviposition occurring perhaps slightly earlier in the year (Fig. 3a). N. viridis is again similar, but the oviposition period is reported to be much shorter, occurring between February and March (Fig. 3b). These three species are normally uni-voltine. In N. maculata, the situation is rather more complex (Walton 1936), as there is a tendency for eggs to be laid at two distinct times in the year, August - October and March - April inclusive. These two lots of eggs develop in rather different ways. Those laid in the Autumn are of a form which undergoes a period of diapause, and do not hatch until March or April of the following year, and the nymphs develop relatively slowly to reach adulthood by late July or early August. The spring laid eggs, however, hatch in about three weeks and grow rapidly to become adults by the end of June (Fig. 3c). It is unclear as to which of these two adult cohorts then lay eggs in August or October, but it is unlikely that those reaching adulthood by late July or early August will have enough time to mature and lay eggs which subsequently overwinter. These adults will probably overwinter and lay eggs in the spring, whereas the adults matured from the spring eggs, probably lay eggs in August or October, which then overwinter, the adults either dying or possibly overwintering and producing another batch of eggs the next spring. This complex reproductive strategy may well be an adaptation to unstable habitats (a preferred habitat type (see Chapter VIII)), similar to the 'cohort-splitting' of terrestrial isopods (Sunderland, Hassall and Sutton (1976)).

Both N. glauca and N. obliqua, if brought into the laboratory in November, will lay eggs, and during the Autumn of 1976, in the sample ponds (see Chapter VIII), both species laid an extra batch of

eggs in November, which then hatched, but the nymphs failed to survive the winter. This may be either early oviposition of the spring eggs, or attempts at a second generation, taking advantage of the long summer and mild Autumn of 1976. During a similar period in 1977 and 1978, after poor summers, these extra batches of eggs did not appear in the field, but were laid in the laboratory. Obviously, temperatures and food availability play a large part in the control of oviposition and an examination of the life histories of some North American species helps to elucidate this.

Toth and Chew (1972) showed egg production by N. undulata was directly related to the female feeding level which controlled how long after ecdysis the first eggs were laid, and also described attempts at a second generation by this species (Fig. 3d). Fox (1975) noted that young female N. hoffmani normally did not reproduce until the following February, but if given sufficient food, they will reproduce in the late summer, a few weeks after moulting to adult. Fox concluded from laboratory studies that delay in the onset of reproduction was inversely related to the amount of food available, thus the one generation a year in the field shown by N. hoffmani, is a result of a relatively low food supply for the young adults (Fig. 3e).

Rice (1954) found four different types of life histories in ten species of N. American Notonectidae, and related them to the environmental temperature. One type shows only one generation a year, and is typified by adults overwintering; this includes N. irrorata, N. insulata, N. undulata and N. lunata. There are two types of female to be found in the autumn in this type of life cycle:- old females laying eggs and young immature females which will begin laying in the spring. The second type of life cycle is shown by N. borealis, which is univoltine with a long oviposition period, eggs being laid

up until the middle of July, when the adults die. The eggs spend four to eight months in diapause, overwintering, giving a life cycle (egg to adult) of 199 to 265 days, compared to 52-72 days in the previous four species (Fig. 3f). An intermediate strategy is shown by Bueno limnocantaris and B. macrotibialis. These species have eggs which can hatch after only 21 days in late August, and other which overwinter till next spring. The fourth type of life history is shown by B. elegans and B. martaritacea, which show overwintering as both adults and eggs and have two generations a year, one starting in the spring and the second in late summer, the eggs hatching after only nine days (Fig. 3g).

The two species described by Rice which show two generations a year are found in areas of higher temperature than the others, where food is either more abundant or available for longer periods. The species showing the longest egg-adult cycle is found in the coldest habitats, where water bodies are frozen for much of the year. The other species are restricted to one generation a year, although in some cases (e.g. N. undulata and N. hoffmani) they are physiologically able to have more, but restricted from doing so by a combination of low temperatures and low food levels.

This ability to change life histories by increasing the number of generations a year, shows the opportunistic nature of this family of water bugs, allowing them to exploit what seem to be inferior habitats.

I. 2.4. Egg classification.

British Notonectid eggs have been described by Walton (1936). They are oblong oval in form, always blunter at the anterior end, where the micropyle and its projecting peg occur. The chorion is two layers thick, hexagonally sculptured, and perforated with fine

holes. The embryo develops with its head to the anterior end.

N. maculata eggs are the largest eggs of the four British species and change noticeably in size during development. A new laid egg is 1.6mm in length and 0.6mm wide, and an egg showing eye spots (indicating it is almost fully developed) is 1.95mm by 0.8mm (an increase of about 100% in volume). When freshly laid, the fertilised egg is a pale orange-yellow, but quickly darkens to a brown. The micropyle peg is usually only a little rounded tubercle, sometimes downward curved. (Fig. 6a).

It is reported that the egg of N. glauca does not alter much in size during development. It does not usually exceed 1.7mm long, 0.5mm wide. When freshly laid, it is a pale yellow, slightly downward curving cylinder, with a small pointed micropylar peg, and it darkens slightly as it develops (Fig 6b).

N. obliqua eggs measure 1.9mm in length, 0.7mm in width, when showing red eye spots. They are pale yellow when freshly laid, and downward curving at both ends, but less so anteriorly. The egg darkens antero-dorsally as it develops, with a brownish tinge when fully developed (Fig. 6c).

N. viridis eggs are the smallest of the British species when freshly laid measuring 1.45mm by 0.5mm, and change very little in size during development. They become darkish brown after a couple of days, being yellowish-white inclining to a green tinge until then (Fig. 6d).

I. 2.5. Oviposition

The two sexes are not instantly recognisable, but by consideration of overall body shape, abdomen and the last abdominal segments, they can be separated (Fig. 4). Generally, the female appears wider across the anterior ventral abdomen (e.g. N. glauca $f \bar{x} = 0.499\text{cms}$ ($n = 25$),

FIG 4

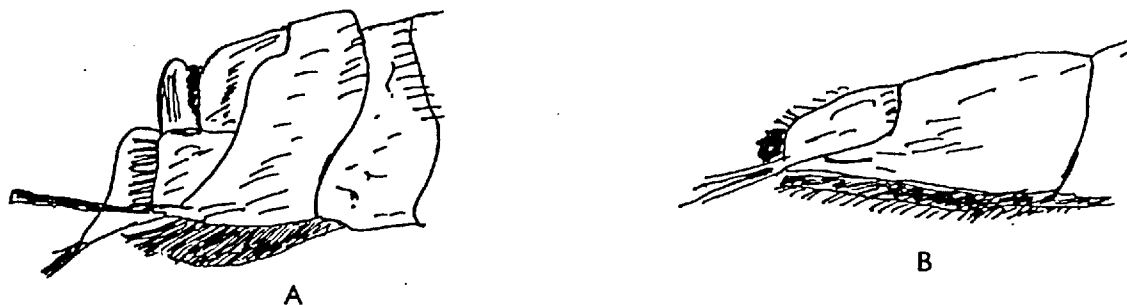


FIG 5

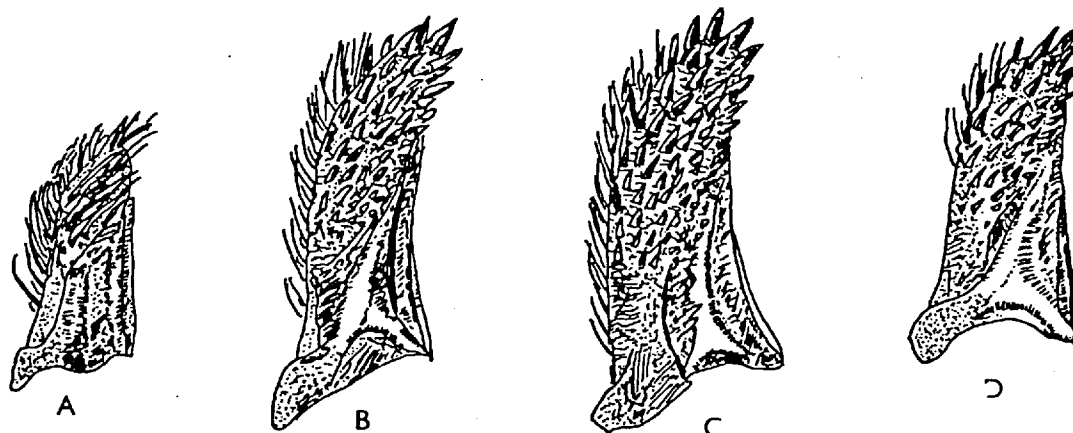
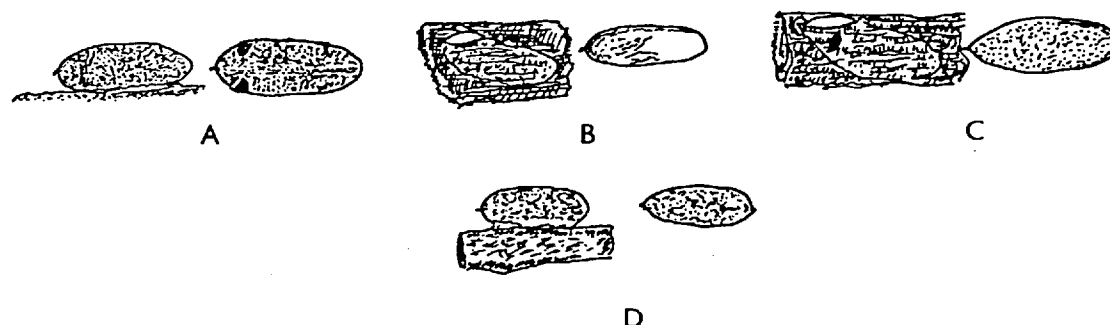


FIG 6



LEGEND TO FIG 4 Diagrams showing the terminal abdominal segments of
A) a female and B) a male Notonectid (side view)(after Macan (1965a)).

LEGEND TO FIG 5 The ovipositors of the female British Notonectids
(after Walton (1936)).

A) N. maculata B) N. glauca C) N. obliqua D) N. viridis.

LEGEND TO FIG 6 The eggs of the British Notonectids (after Walton (1936)).

A) N. maculata B) N. glauca C) N. obliqua D) N. viridis.

$m \bar{x} = 0.4725$ ($n = 8$) (sig. of diff = 0.1); N. maculata $f \bar{x} = 0.503$ cms
 $(n = 21)$; $m \bar{x} = 0.482$ cms ($n = 8$) (sig. of diff = 0.1); N. obliqua $f \bar{x} =$
 0.527 cms ($n = 27$) $m \bar{x} = 0.508$ cms ($n = 8$) (sig. of diff = 0.05), and the
 posterior end of the abdomen tends to be pointed in the female, but
 more angular in the male. The last abdominal segment appears to be in
 two parts on the ventral side, either side of the copulatory organs,
 in the male, each part is small and sharply pointed, in the female,
 larger and rounded.

Walton (1936) describes the female ovipositor as being provided
 with stout spines to which he ascribes the use of drilling holes in
 stems of plants, the usual mode of egg laying. The ovipositor is of
 a similar form in the four species of British Notonectids, but the
 numbers and types of spines on the ovipositor differ (Fig. 5). N.
maculata has a pair of only moderately long gonopophyses (first pair)
 with 43 long sharp spines on each valve, situated on an oval, raised
 portion of the valve (Fig. 5a). N. glauca has the longest, and re-
 latively most slender ovipositor valve of the four species with 56
 large, conical spines, tapering smoothly to a fairly sharp point (Fig. 5b).
 The basal spines are the shortest and bluntest, while the apical ones
 are the longest and sharpest. N. obliqua has a slightly shorter, but
 much more powerful ovipositor than N. glauca. The central part is
 very broad and solid, suited for strong muscle attachments. There
 are 66 stout spines (Fig 5c). N. viridis has a shorter, but relatively
 wider, ovipositor than the preceding two species, with 45 spines which
 are sharper and more slender (Fig. 5d).

The form of the ovipositors is well suited to the mechanism of
 oviposition. N. glauca buries its eggs the deepest into plant stems
 so would require the longest ovipositor. As its eggs are relatively
 small, little power is needed to scour out a hole, a single drill hole

probably being adequate. N. obliqua lays a much bigger egg, but it is not so deeply embedded. A wider, but shallower hole is required, so a shorter, broader and more muscular ovipositor is needed. This species also lays its eggs on supports. N. viridis still retains to some extent the habit of fixing eggs onto rather than into plant surfaces. It probably scrapes away a small depression in plant stems (when these are used), so it only requires a small ovipositor. The sharper spines could be used to scrape depressions on the surfaces of other solid objects. N. maculata retains the less advanced method of ovipositing, by laying directly onto objects by means of a waterproof glue. Walton (1936) reports that N. maculata never lays on soft plant tissue or other soft objects, but sometimes lays on twigs or branches if there are no stones etc., available in the habitat. Thus it would only require a short ovipositor with short spines.

Butler (1923) suggests that by laying eggs in plant stems, if the water level drops, the eggs will be protected from dessication, as in the plant they are furnished with moisture. N. maculata, which lays overwintering eggs in temporary ponds, is the most likely species to undergo dessication in the egg stage, but actually lays its eggs outside of plants. The eggs can undergo periods of dessication and survive, so it appears that Butler's argument is invalid.

Walton (1936) suggests that burying the eggs deep into the air-filled plant stem tissues, as in N. glauca, aids development by supplying additional oxygen. This is unlikely, as eggs have been laid in and successfully develop from, polystyrene tile pieces floating on the water surface, with no additional aeration, for all four British species (see Chapter II), and Ellis and Borden (1969a) reared N. undulata eggs laid in the mesh of 'vexar' strips. Eggs laid in plant stems by British species in the field, can be brought into the laboratory, removed from

the plants and still develop normally.

What seems a logical reason for this oviposition behaviour, is protection of the eggs from possible egg predators and parasites. By burying the egg in the most convenient soft object, namely plant tissue, the egg may be protected to a much greater degree than if left externally. There are no recorded egg predators or parasites of British Notonectid eggs, but Fox (1975a), working on N. hoffmani in California found evidence of egg predation, although the identity of the predator species was never discovered.

Several authors have suggested that habitat selection by the four British Notonectid species is mainly controlled by oviposition behaviour (e.g. Walton (1936), Brown (1943, 1948) etc.). Hence, N. glauca and N. obliqua prefer weedy habitats, N. viridis less weedy and partly stony habitats, and N. maculata concrete man-made ponds or oligotrophic ponds with stony substrates. Habitat selection will be considered in more detail in Chapter VIII.

I. 2.6. Prey Detection

A more detailed description of general predatory behaviour by this genus of bugs will be given later (Chapter IV), but the following section describes the location and functioning of the receptors involved in prey detection.

Wolda (1961) reports that N. glauca hangs upside down from the water surface, touching this surface with the tarsi of its four, short, prothoracic and mesothoracic legs, and with the tip of its abdomen. Small vibrations caused by a floundering insect which has fallen into the water, or in his experiments, by a thin steel wire touching the water surface, constitute adequate stimulation, to which the animal shows an orientation response. Gittleman (1973) and Murphey and Mendenhall (1973) generalise that N. glauca depend on the vibration

sense to locate their prey, and any surface disturbances in their habitats are likely to be caused by potential prey items. Their prey localisation behaviour can be elicited by artificially generated ripples in the frequency range 20 - 150 Hz, with ripples as small as 1 μ m in amplitude.

The use of vibrations to locate prey, as reported by the above workers, does not adequately account for all forms of prey detection. Notonectids can be observed searching for prey within the water column, or even along the bottom of the water body (Ellis and Borden (1970)). Southwood and Leston (1959) describing prey location by N. glauca, observed that although it goes immediately towards the source of an underwater disturbance, the final stage within an inch or two of the prey is by sight. They also suggest that, although N. maculata is principally a surface feeder, it is able to detect its prey by sight at a range of about 8 inches (although no experimental details were given). Personal observations have shown that N. glauca and N. obliqua will both respond to a bubble of air moving up and down a stationary pipette, where only a visual stimulus could elicit such a response.

As will be shown in later chapters, generalising on the predatory behaviour of all Notonectids is a gross oversimplification, as their behaviours vary as widely as their habitats. However, these references do indicate the two components in prey location in Notonectids, namely sight and wave detection, the importance of each varying with species and habitats. Gittleman (1973) has postulated that differences in the importance of these two components in detection and location of prey may allow coexistence between two, otherwise similar, species.

The location of the receptors for controlling orientation behaviour has received a fair amount of attention. Wolda (1961), reported that N. glauca responded to surface ripples after the pro- and meso-thoracic legs had been amputated proximal to the tibio-femoral joint,

indicating the presence of sensory receptors at this joint. Murphey and Mendenhall (1973), after amputating unilaterally, just proximal to the tibio-tarsal joints of the pro - and mesothoracic legs, found the variability of the turning response to prey was increased, but there was no circling movement, which should occur if all the receptors on one side are ablated. However, when the receptors distal to, or associated with the tibio-femoral joint were lesioned unilaterally, circling movements toward the intact side were observed. This supported the supposition that the receptors important to prey orientation behaviour are associated with the pro - and mesothoracic legs, and also implies that the main receptors are located at or distal to the tibio-femoral joint, and proximal to the tibio-tarsal joint. Even after all four tibio-femoral joints were ablated, the predator could still respond to a large stimulus, especially if posterior to the predator, indicating the presence of another receptor. This was found at the tip of the abdomen. A conspicuous row of hairs along the posterior lateral margins of each of the last three abdominal segments on either side was found to be the site of this receptor.

Murphey and Mendenhall conclude that orientation depends on the sensory input from all five points in contact with the surface film. The critical receptors are located near the tibio-femoral joint, the abdominal receptor is involved in control of turns to ripples arriving from posteriorly placed targets, the decision to turn left or right being based on a comparison between sensory inputs to hairs on the two sides of the abdomen. Murphey and Mendenhall (1973) suggest the CNS determines which receptor is nearest the target, and then initiates a turn in this direction. The prothoracic receptor (discovered by Wolda (1961)) is capable of eliciting small turns, but can be dispensed with and other interactions between remaining receptors will

lead to an almost normal input/output relationship.

Wiese (1971) reports that the range of frequencies perceived by the bug fits well with the spectrum of waves transmitted by the prey. The range of sensitivity extends from 5-300Hz (Wiese 1972). The threshold is lowest at 100-150Hz, where a $1\mu\text{m}$ amplitude enables a 50% response to a source of vibration. Thresholds of third instars are about two times that of the adult, and thresholds of fifth instars are intermediate. This is likely to be a pure scale problem, where small animals have a shorter base to their range finder (greatest distance between two receptors locating the prey).

Accuracy of location is maximal if the prey is situated in front of the predator, which gives the greatest base length of the range finder. Time differences of several milliseconds in arrival of waves at symmetrical receptors will occur when the prey is at an angle to the predator, allowing a decision as to direction of prey to be made. Accuracy of distance measurement will be lower to such stimuli, as the base length of the range finder will be smaller than in the forward direction.

The eyes of Notonectids are large and reniform, situated on the outerside and projecting a little way over the front margin of the prothorax. The visual field is described as extending through 246° in the horizontal plane and 360° in the vertical plane, the fields of the eyes overlapping so as to give binocular vision in front, above and below the head, (Hungerford (1919)). Ludke (1953) reports there are seven photo-receptive cells in each ommatidium of N. glauca. Bruckmoser (1968) found three different kinds of visual cells in the dorsal part of the eye; u.v. receptors with a maximum sensitivity of 350nm; violet receptors with a maximum sensitivity of 420nm; and yellow-green receptors with a maximum sensitivity of 567nm. The ratio was 1:6:6.

Bennett and Ruck (1970) found twelve cells on the dorso-posterior region of the eye of N. undulata and N. irrorata which were composed of three similar classes of cells in about the same ratio. These results suggest that the dorsal part and anterior part of the Notonectids eye contains cell types which could provide a basis for trichromatic colour vision. (Responses in the U.V. and violet ends of the spectrum seem to tie in with the necessities of life in water, where red is quickly filtered out by the medium.).

If an animal is presented with a continuous stimulus, a gradual decrease in responsiveness can occur, and such a phenomenon would affect the predators impact on a large prey population by affecting the capture success rate. Wolda (1961) found such decreases in responsiveness in N. glauca. Water vibrations were created in a series of tests by a thin steel wire. 900 stimulations in bouts of 25, then an hours rest, then another 500 stimulations were given on the left side of the animal, at the surface. Results showed that the probability of obtaining a response (a turn towards the stimulus) remained 100% for some time, then decreased to about 13% at the beginning of the fifth hundred stimuli, and remains relatively constant thereafter. The decrement curve of responsiveness in bouts of 25 is 'S' shaped, but after the hour rest, more responses were observed than before, indicating a recovery. The rate of recovery to response decrement is considerable during the first few minutes of the rest interval, and slows down afterwards, so that even after 24h, recovery is not complete.

In other tests, Wolda (1961) showed that the results were due to stimulus repetition, not response repetition. He also showed that response decrement to stimuli presented on one side is independent of the response decrement to stimuli presented at the contralateral

side of the animal. Responsiveness to left rear stimuli is at least, to a large extent, independent of a preceding series of left lateral stimuli, and there is evidence that the left rear response is weaker (as suggested by Murphey and Mendenhall (1973)). The decrement of both left and right responses did not prevent the occurrence of a large number of front stimuli responses. Left and right responses presented simultaneously gave no response at all. To left and front-right stimuli together, the usual response was a swimming forward movement. Such mechanisms could result in lowered success of capture at high prey densities.

I. 2.7. Prey capture and feeding.

Hungerford (1919) concludes that these predators not only free their front but also their middle pair of legs for service in retaining captured victims through remaining poised back downwards in the water and not having to cling to supports. Ellis and Borden (1970) maintain that the fore and middle legs are raptorial or grasping, being equipped with a series of spines and 'teeth'. The tarsi each have terminal claws that aid in seizing and manipulating struggling prey. Careful observations, however, reveal that the actual prey capture is accomplished mainly with the first pair of limbs, the second pair mainly aiding in the restraint of the struggling prey. With large prey, initial handling and subduing takes place at the surface with the bug, ventral side uppermost, the hind limbs being employed in providing additional support. They are angled back and act like an 'anchor' against the struggles of the prey. When the prey is sufficiently subdued, it is usual for the middle pair of legs to release their hold and resume monitoring the surface for vibrations, or to allow the predator to dive down and cling to some deeper perch site. Indeed in the capturing and handling of small prey, the second pair

of limbs are hardly ever used except near the end of feeding, when the prey is squeezed to complete extraction.

Hemipterans have a powerful rostrum, used for extracting juices of plants or animals on which they feed (Butler (1923)). Predacious hemiptera stab the prey, then inject salivary secretions which kill the prey. Following some external digestion of the prey tissues, they ingest the partially digested contents and discard the cuticular shell (Chapman (1969)). The venoms injected by heteropterans are produced in the salivary glands, which are enlarged and possess a muscular coat. Following penetration of the rostrum, the venom is forcibly injected by a powerful salivary pump, and is then transported round the body of the victim (in its haemolymph if an arthropod, or in the blood system in vertebrate prey such as tadpoles and fish fry etc.). Injection is followed by compulsive struggling of the prey, rapidly leading to tremors and death. Chapman (1969) reports that the venoms are non-specific, being toxic to a variety of insects, crustaceans and some vertebrates. Their action causes a general lysis of the tissues, so that nervous activity rapidly stops. Fox (1975a) reports that, associated with these venoms, are proteolytic enzymes which partially digest the prey tissues.

After capture, Ellis and Borden (1970) report the prey is manipulated by the fore legs and probed with the rostrum. As Butler (1923) points out, only the softer parts of the prey can be attacked, so it is likely that the probing by the rostrum is the searching for a vulnerable entrance point for the stylets. A good description of the functioning of the mouth parts of the heteroptera is given in Butler (1923).

Ellis and Borden (1970) report that in N. undulata, 3 or 4 seconds after capture, the stylets begin piercing deeply at one point in the

prey's body, and as the salivary fluid is injected, so the prey begins to turn a milky white. They suggest that when feeding on mosquito larvae, entry is gained to the prey in one of three main areas; the thorax-head area; the mid-abdominal area; and the posterior-abdominal area. From the initial point of entry, the stylets move posteriorly and anteriorly within the prey body cavity, and the prey is repositioned every 30 seconds as the probing continues. As one region is probed by the stylets, it gradually shrinks and loses its normal shape. When all regions have been probed, and the body fluids removed, the corpse is released. It is removed from the rostrum and pushed away by one of the fore limbs. The discarded prey item soon darkens, due to the action of residual digestive juices.

I. 2.8. Respiration

As Butler (1923) points out, the Notonectid body is velvety, and overspread with a glistening air film, which is conspicuous on the underside, but elsewhere hidden by the wings. Notonectids are inflated with air to such an extent, that they are very bouyant. The air stores are held by long hydrofuge hairs on the ventral surface and under the wings, and by small bristles over the dorsal surface of the fore wing in a thin film. Obtaining oxygen directly from the air necessitates some semi-permanent connection with the surface for a water insect, or frequent visits to the surface (Chapman 1969). The hindmost spiracles are large in Notonectids, as when the bug is at the surface, it is only the tip of the abdomen, possessing these spiracles, which makes contact with the air. The position of the air store is such that the body breaks the surface suitably orientated to renew its air supply. Observations with Notonectids, and their close relatives, corixids, (Popham (1952)), have shown that there is a conspicuous loss of bouyancy with continued submergence over 15°C, which may provide the stim-

ulus to return to the surface for replenishment of the air stores (Southwood and Leston (1959)). Popham (1962) examined the efficiency of the air stores as a physical gill in N. glauca and he concluded that at 10°C and above, the insect absorbs oxygen from the gas bubble at a faster rate than the oxygen diffuses into the gas stores from the water. At very low temperatures, the rate of oxygen consumption is small, and at $0 - 5^{\circ}\text{C}$, the insect can survive for an almost indefinite period submerged, which is important when ice forms on the surface. Thus the frequency Notonectids return to the surface depends on both activity of the bug and temperature of the environment.

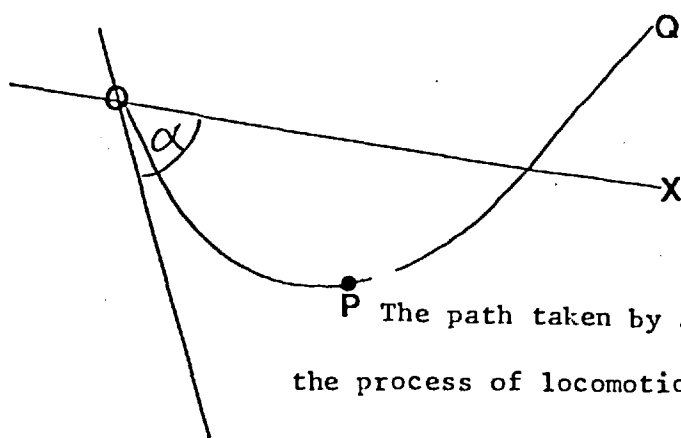
Respiration will be further discussed in Chapter III.

I. 2.9. Locomotion

Notonectids are practically unique in their habit of swimming on their backs. Their prey capture method and position of air stores are important factors involved with this habit, but which came first is open to debate. The bug 'rows' along in a series of short jerks, using the powerful hind legs. The hind legs are long, flattened, edged with hairs, and protrude from the body at an angle of approximately $30 - 45^{\circ}$ forwards from the thorax, and resemble two oars (Popham 1952). The greatest speeds are obtained during the leg kicks, where the legs are pulled back sharply towards the abdomen, through 135 to 150° of arc. While the legs are being returned to their original position, the resistance of the water retards the insect and may bring the bug to a standstill.

Because the insect is being raised by the bouyancy of the air stores, it can only progress along a horizontal path some distance below the surface if the kicks are of such a nature as to propel the insect downwards (Popham (1952)). In Fig. 7 the point O, represents the insect at the start of the kick. The line OPQ is the path taken

FIG 7

LEGEND TO FIG 7

The path taken by a Notonectid during one kick in the process of locomotion travelling in the horizontal

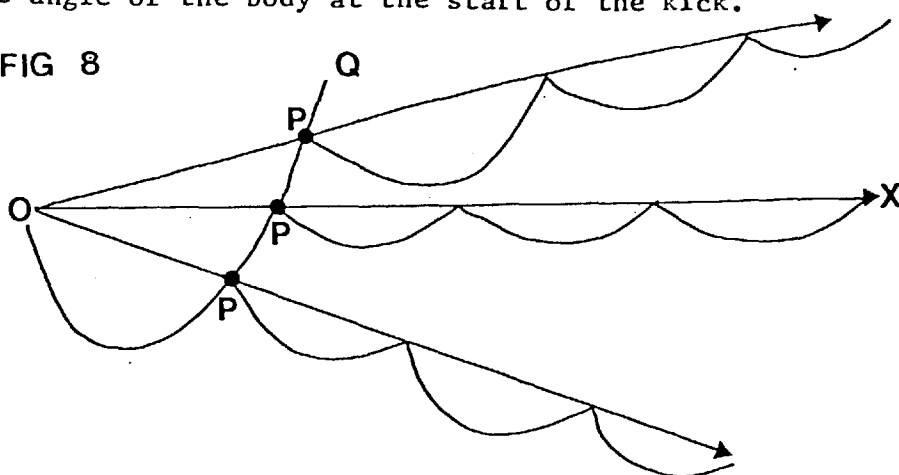
direction (after Popham (1952))

O represents the insect at the start of the kick.

OP - the path taken by the insect.

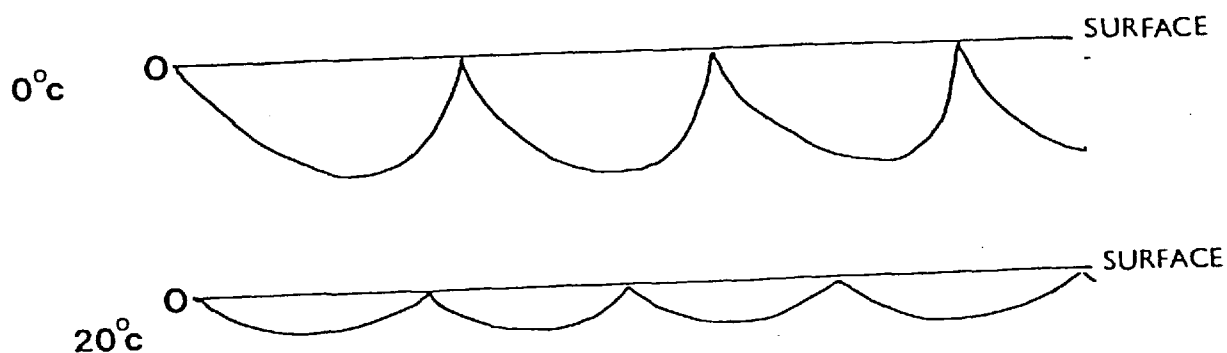
α - the angle of the body at the start of the kick.

FIG 8



LEGEND TO FIG 8 Diagram showing how the timing of the second kick (at P) can alter the path taken by the insect (after Popham (1952)).

FIG 9



LEGEND TO FIG 9 The effect of temperature on the path taken by the insect during locomotion along the surface (after Popham (1952)).

by the insect. The tangent to the curve OPQ at point O, makes an angle α with the line OX, and indicates the initial path of the insect. If the next kick takes place before the point P has crossed the OX axis, then the insect will swim deeper into the water. On the other hand, if the rate of leg beat is retarded so the next kick occurs after P has crossed the OX axis, the bug will rise to shallower water. Finally, if the next kick takes place when the point P reaches the OX axis, the insect will progress forwards along a horizontal path (Fig. 8).

The value of α varies from one species to another, and even between individuals. Generally, Notonecta starts with the dorsal surface of the body forming an angle of about 30° with the surface. As the hind legs move backwards, the inclination is increased to 55° , and the bug is driven down at this angle. As the temperature increases, the rate of leg beat increases, and the legs become more efficient as organs of locomotion (Popham (1952)) and this is associated with a decrease in angle α in order to compensate for this increased efficiency. For example, in the corixidae, at 2°C the legs move through 120° , whereas at 25°C they only move through 30 or 40° . This affects the depth to which each kick takes the bug (Fig. 9).

Further aspects of leg morphology and locomotory efficiency will be discussed in Chapter VI.

I. 2.10. Flight

Heteropterans have two pairs of wings. The upper (first pair) wings are composed of several regions, of which the basal membranes are stiff, and the apical ones membranous and flexible (Butler (1923)). These wings are known as hemielytera. The only species to have its flight examined in any detail is N. maculata (Walton (1935)). It is thought that only three senses are important in orientation of flight

by Notonecta. Firstly the sense of sight, secondly the sense equivalent to smell, and thirdly the sense of touch, detecting differences in air pressure.

Water bugs are unable to fly unless their wings are dry. During flight both pairs of wings vibrate fast, the front legs are tucked up and the long rear legs stretch out behind, helping to streamline the insect. On perceiving water, the insects fly towards it, close their wings and drop in. Walton concluded that N. maculata finds water by sight. When there is no other attraction, the greater number of bugs will either fly to the compass point of greatest illumination, or downwind, the line of least resistance.

N. maculata is described as a day flier by Southwood and Leston (1959) requiring temperatures around 20°C for flight, although this seems to be a little high, as this species tends to migrate in September, October or early November, when even daytime temperatures are low.

I. 2.11. Response to physical stimuli

Very little work has been done to examine the responses (taxes etc.,) of Notonectids to various physical stimuli.

Notonecta has a ventral light reaction which can be demonstrated by a simple test (Southwood and Leston (1959)). A glass tank is lit from below, and the bug swims the 'wrong' side uppermost i.e. with the ventral side downwards. This reaction is present in the late embryo. Chapman (1969), also reports an orientation by Notonectids upstream in lotic habitats, where the bugs will swim strongly as the current tends to drift them downstream. In this way, it tends to maintain its position. In a tank without any landmarks, or with the eyes blackened, Notonecta are unable to keep static and are swept downstream.

Further aspects of the biology of Notonecta such as habitat selection, prey selection, nymph development, learning, morpho-

metric measurements etc., will be discussed in later chapters.

In the design of an experimental procedure to compare the predation strategies of several predators, not only is it important to initially recognise the more relevant factors which should be observed and measured (as reviewed in section I.1.) but also to obtain a detailed knowledge of the biology of the animals in question (as reviewed in section I.2.) From this background information, one can organise the experimental procedure such that the maximum amount of both relevant and realistic information can be extracted in the time available for such a study.

CHAPTER II

GENERAL METHODS

II. 1.

Introduction

The general aim of this study is the examination of aspects of the predation strategies of Notonectids in terms of a) overall energetic gains from different prey types and in different environments; b) behavioural responses to the different prey types in different environments; and c) the morphological constraints on the predation strategy as a whole.

The nature of heteropteran predators and the physical factors of the habitats, make it necessary to bring such an analysis into the laboratory. The predators do not carry any easily recognisable prey feeding history in their guts, and it is more or less impossible to examine feeding behaviour by watching the predators or recovering prey carcasses in natural habitats, which are often weedy, cloudy and deep. One should endeavour, however, to make laboratory conditions as realistic as possible, whilst recognising the problems in experimentation that this brings in order that results will still be meaningful in natural situations. This means that considerable care must be exercised over decisions such as; what type of environment to use, how to run the experiments, which prey to use, how to standardise predators? These problems and their solutions are discussed in the following sections.

II.2.

Rearing of the PredatorsII.2.1. Introduction

Past feeding history can greatly affect the predatory activity of this bug, as it controls size, and hence predatory potential (Fox and Murdoch (1978)), maturity (Ellis and Borden (1970)) and hunger. If one uses predators from the field for experiments, one has no idea

of the past feeding history of the animal. Hunger can be controlled to some extent by starvation, but the overall predatory capabilities have been produced as an end product of development and past food levels, and unless predators of a certain size and age are carefully selected, a large variation in such capabilities can be expected. Rearing predators in the laboratory overcomes most problems associated with using field animals, in that past feeding history is known and can be controlled, predator age is known, and thus it is likely that there will be a reduction in variation between bugs. Laboratory cultures also allow two generations a year.

The disadvantages of laboratory rearing basically lie in the time and effort necessary to successfully rear such animals. Several workers (e.g. Williams (pers comm.), Lawton et al. (1974) etc), decided such efforts were not worthwhile, and so collected bugs from the field, but for detailed studies of the predation strategies large variation is a hindrance, and can mask many subtle and important changes of behaviour.

II.2.2. Maintenance of Breeding and Laboratory Cultures.

Successful rearing of Notonectids has been achieved by several authors (Ellis and Borden (1970), Fox (1975), Fox and Murdoch (1978), Leong (1963), Toth and Chew (1972)). In some techniques, very elaborate environments have been used, with aeration, controlled pH., filters etc., but these were found unnecessary for the British species.

Four or five pairs of adults were maintained in covered plastic bowls (approx. 75cm. diameter) in a room at 17° - 20°C. and fed every other day on several different prey types, depending on availability (e.g. Musca domestica adults, Daphnia magna, Gammarus pulex, Aedes aegypti larvae, Phormia larvae etc). Although, as reported in Chapter I, three of the species of the bug seem very catholic in selection of

oviposition sites in the field, all four species were found to successfully oviposit into or onto floating pieces of polystyrene tile. These 'egg pads' were then removed and transferred to other bowls for rearing. Ten or twelve pairs of each species gave sufficient offspring for experimental requirements, and in this system, two generations were produced each year. It was generally found that at least 75% of the eggs laid eventually hatched.

II. 2.3. Nymph Development

II.2.3.1. Nymph Mortality

Several authors report very high mortality in Notonecta nymphs during the first instar. In the laboratory, this has been ascribed to feeding levels (Leong (1963), Toth and Chew (1972)) and food type (Fox and Murdoch (1978)). The young nymphs must reach and break through the surface film of the water in order to obtain their air bubble, necessary for both respiration and locomotion, and from observations of this process, it appears that a large expenditure of energy is required, which, added to that needed to escape from the egg, must severely tax the nymph's energy resources. At this stage, as after every subsequent moult, the nymph undergoes a period when it is unable to feed. These problems appear additive, thus making this the most sensitive part of the life-cycle with respect to survival. Cannibalism is also an important source of mortality in early instars or moulting individuals (Fox 1975 (a) and (b), Macan (1965), Toth and Chew (1972)). Some workers believe that cannibalism is essential in the maintenance of population levels (Fox 1975 (b)), and could also explain observations by Larsen (1930), that ponds contained only one stage of N. glauca even though oviposition was seen to continue over long periods. Hence the nymphs must be reared singly in the laboratory in order to obtain sufficient numbers of adults.

II. 2.3.2. Effects of Food Level on Development

The food level available during nymphal development can affect both

FIG 10

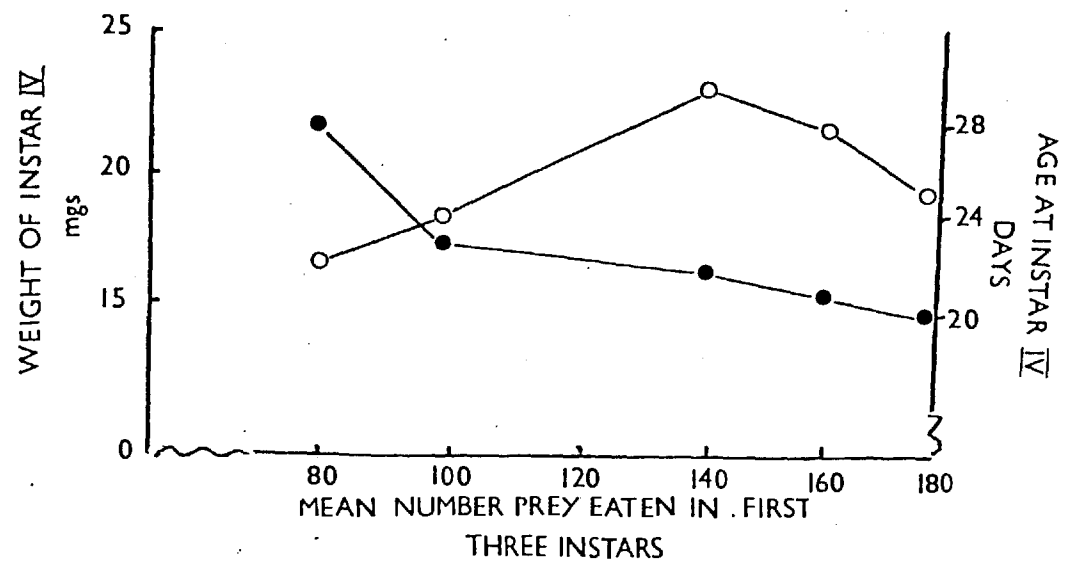
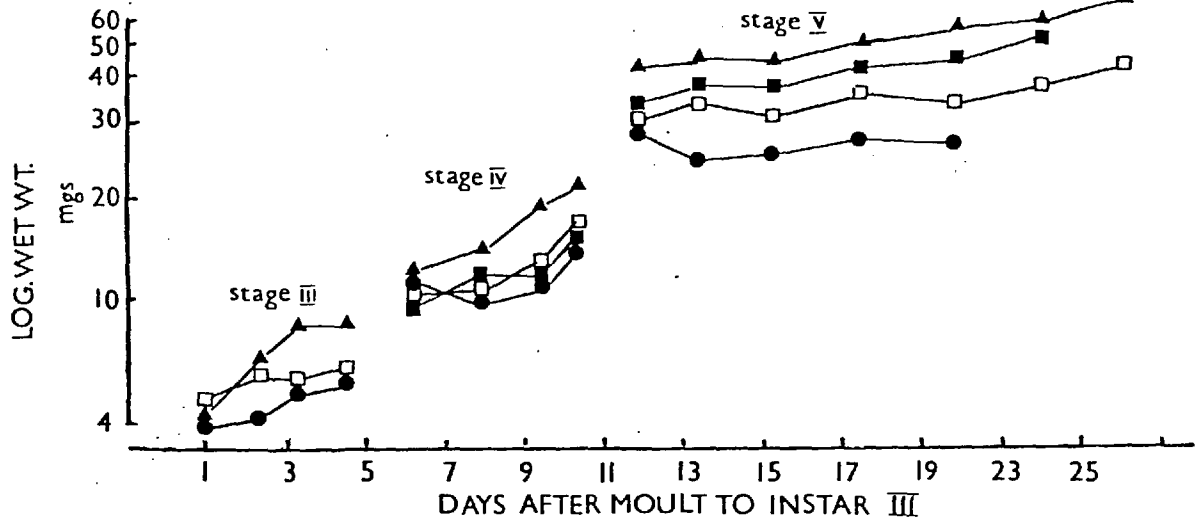


FIG 11



LEGEND TO FIG. 10

The effect of feeding levels (measured as mean number of prey eaten) on the time needed to become a IV instar nymph (● - age at IV instar) and the absolute size of that instar (O - weight of IV instar) (Fox and Murdoch (1978))

LEGEND TO FIG. 11

The effect of a fixed feeding level on the weight of the nymph and the duration of the instar (Toth and Chew (1972))

- Fixed feeding level of 1 4th instar larva/day
- " " " " 2 4th instar larvae/day
- " " " " 4 " " " "
- ▲ " " " " 8 " " " "

development and survival rates. Fox and Murdoch (1978) demonstrated that feeding levels influenced both the time needed to become a IV instar and the absolute size of that instar (Figure 10). Nymphs reared at the highest food level weighed about 21mg and averaged 21 days old when they moulted to IV instar, while those kept at the lowest level were about 17mg and 31 days old at the same moult. Toth and Chew (1972) found the effect of increased food level was more pronounced in later stages, when a fixed food supply at a low level became more restrictive as the size of the nymph increased (Figure 11), and from their results concluded that food supply affected survival more than it affected duration of the instars, when fixed levels were used.

From this, one can see that it is necessary to strictly control feeding levels and environmental temperature during the rearing of the nymphs, if any form of standardisation of the predators (and hence reduction in variance) is to be achieved. Such standardisation is necessary to allow direct comparison of the feeding strategies of the different species.

II. 2.4. Rearing Technique

The best rearing technique is the one producing the most adults in the shortest time from a given number of first instar nymphs, with a high synchrony of time of moult. Experiments on rearing nymphs to adults on different prey types, showed differences in development rates and subsequent adult feeding rates for some time after the final ecdysis (Tables 2.1 and 2.2). Overall, it was found that much reduced mortality occurs if first instar nymphs are fed on Daphnia than on fifth instar mosquito larvae, but this trend is reversed from the second instar onwards.

The most efficient method was found to be to leave the first instars to develop together in the same container with Daphnia as food. This allows natural mortality and cannibalism to 'weed out' the less viable individuals and gives an increased proportion of successful rearings.

Table 2.1. Rearing success of Notonecta nymphs on different diets.

DIET		REARING STAGES		REARING SUCCESS (NO. OF ADULTS)		AVERAGE TIME FROM III INSTAR → ADULT (DAYS)	
<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>
SMALL MOSQUITO LARVAE 10→15→20, 2nd or 3rd instars through time		FROM 1st INSTAR		0/12 ADULTS 2/12→3rd INSTAR NONE OVER 3rd.	0/12 ADULTS NONE REACHING 2nd INSTAR	/	/
<u>DAPHNIA MAGNA</u> 10 at 1st instar, 15 at 2nd, 20 at 3rd, 25 at 4th, 40 at 5th.		FROM 1st INSTAR		(1) 2/15 ADULTS 13.3% (2) 6/45 ADULTS 13.3%	(1) 0/5 ADULTS 0% (2) 0/19 ADULTS 0% 9/19 REACHED 5th	55.375 +4.72	/
MOSQUITO LARVAE 5th instars-REGIME AS ABOVE		FROM 1st INSTAR		(1) 6/110 ADULTS 5.45% (2) 1/31 ADULTS 3.23%	(1) 1/5 ADULTS 25% (2) 3/31 ADULTS 9.6%	41.857 +7.417	55.25 +17.05
AS ABOVE		—	FROM 2nd INSTAR	—	9/31 ADULTS 29%	—	61.889 +1.314
LARGE <u>DAPHNIA MAGNA</u> REGIME AS ABOVE		FROM 1st INSTAR		2/12 ADULTS 16.6%	0/12 ADULTS 11/12 REACHED 4th	76.0	/
UNCONTROLLED <u>DAPHNIA</u> DIET EXCESS <u>DAPHNIA</u> ≈50		FROM 1st INSTAR	—	12/50 ADULTS 24%	—	52.58 +3.00	—

Continued

Table 2.1. (Continued)

DIET		REARING STAGES		REARING SUCCESS (NO. OF ADULTS)		AVERAGE TIME FROM III INSTAR → ADULT (DAYS)	
<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. obliqua</u>
MIXED DIET MOSQUITO LARVAE + <u>DAPHNIA</u> <u>MAGNA</u> (M) (D) REGIME 15M) 1st and 2nd instars 15D) 20M) 3rd and 4th instars 20D) 25M) 5th instars 25D)		FROM 1st INSTAR		4/13 ADULTS 30.7%	4/15 ADULTS 26.67%	36.25 +10.5	36.0 +9.8
		FROM 1st INSTAR FROM FIELD		5/6 ADULTS 83.3%	4/10 ADULTS 40%	41.2 +4.6	38.0 +4.49
		FROM 2nd INSTAR		9/9 ADULTS 100%	37/40 ADULTS 92.5%	40.22 +1.27	
<u>N. MACULATA</u> AS ABOVE		FROM 2nd INSTAR		17/25 ADULTS 68%		FROM 2nd TO ADULT	44.5 + 3.55 DAYS

Diet	TIME 1st to 2nd	TIME 2nd to 3rd	TIME 3rd to 4th	TIME 4th to 5th	TIME 5th to Adult
Mixed Prey	<u>N. glauca</u> /	9+0.575	8.11+0.75	11+0.99	22.2+1.27
	<u>N. obliqua</u> /	7.86+1.49	7.86+1.09	10.14+3.5	17.43+3.32
Mosquito larvae only	<u>N. glauca</u> /	15.55+0.717	16.33+1.57	17.77+1.134	27.43+1.65
	<u>N. obliqua</u> /	13.55+1.158	16.33+1.22	18+1.35	27.89+1.31
<u>Daphnia</u> prey only	<u>N. glauca</u> 12.66+1.15	13.89+2.28	13.78+2.06	20.11+1.84	(7 out of 9 died 53.5
	<u>N. obliqua</u> /	12.33+1.15	15.66+0.813	(3 out 9 died) 26+4.58	All died

Table 2.2. Mean length of instars with different rearing diets.
(Days)

From the second instar onwards, individuals were reared separately in 200ml plastic beakers on a mixed diet of equal proportions of mosquito larvae and Daphnia. The food levels used were 15 mosquito larvae (M)/15 Daphnia (D) per two days for second instars, 20M/20D per two days for third and fourth instars, and 25M/25D per two days for fifth instars. Adults were then maintained on 30-35 mosquito larvae every two days.

Most success was obtained in rearing N. obliqua, N. maculata, and N. glauca, and as these are the predominant species found in this area, the experimental study was confined to a comparison of the predation strategies of these three.

II. 3. Standardisation of the predators for experimental purposes

II. 3.1. Introduction

The response a predator shows when presented with prey depends on many variables e.g. hunger, prey density, prey type, environmental complexity, predator experience, predator age, sex etc., (Schoener (1971)). To examine the effects of all of these variables in the predators response is a huge task, and well beyond the scope and time available for this study. It was therefore important to select which variables to examine, and which to hold constant during the experiments. In the examination of predatory strategies and their effect on habitat selection and coexistence, the effects of such variables as prey type, prey density and environmental complexity deserve consideration, and such variables as hunger, predator experience, predator age, size and sex should be kept constant.

Simple analysis of variance between feeding levels on seven occasions through one month, using unstandardised adult N. glauca of both sexes feeding on mosquito larvae, showed that within sample variance was greater than between sample variance ($F = 0.625$ n. sig - see Appendix I).

This demonstrates the need for both good standardisation of predators and large sample sizes.

II. 3.2. Selection of Standardised Predator life-history stage

The nymphal stages, as described in previous sections, are rather short, and the feeding levels fluctuate quite markedly during each instar, from low levels just after ecdysis, through maximum intake in the middle of the instar, to low levels again prior to the next ecdysis. This reduces time available for experimentation, thus making it difficult to obtain sufficient data without a complex rearing system to provide large numbers of similar age over long periods.

The adult, on the other hand, is much longer lived (8 to 18 months), and apart from a short period after ecdysis, maintains a relatively stable feeding rate until senescence in the male and oviposition in the female. The adult stage was therefore selected for the main experimental program.

II. 3.3. Standardisation with respect to Predator size and age within the selected stage.

Predators can be standardised with respect to these two variables by controlled rearing as described earlier (section II. 2.4.) and in this study predators showing similar development times from III instar were used. During monitoring of feeding levels through the adult stage, the effect of age of predator has not been found to be so important over the first few months of adult life (pers. observation), but after that, male senescence and female egg maturation and oviposition (even though unfertilised) do significantly alter feeding levels and introduce large daily variation. Thus not only were insects of similar developmental rate used, but they were only used for the first four months of adult life.

II. 3.4. Standardisation with respect to sex.

If one segregates the data on feeding rates shown in Appendix I,

with respect to sex, the variance within samples is much reduced though the between sample variance is still high. ($m - F = 10.3$ Sig 0.001, $f - F = 3.655$ Sig 0.05, Appendix II). Thus within sample variance can be reduced to a large extent by using predators of one sex. Differences in life history indicates that females should be used. The males are shorter lived (≈ 8 months at the most) and tend to go into a slow decline in feeding before they die. The female will generally live for over a year, and prior to egg maturation, feeding levels are relatively stable. The feeding strategy of the female is obviously the more important of the two sexes, as egg production and hence effective reproduction is directly tied to feeding levels (as discussed in Chapter I).

II. 3.5. Standardisation with respect to predators hunger.

As Holling (1966) pointed out, hunger is probably the most important of the components of predation, as it directly affects the nature of all other components. It is therefore essential that a method of standardisation be adopted which will ensure, to as great an extent as possible, that all predators are at a similar hunger level before any experiment, especially if the results are to be comparable.

The most widely used method of standardising a predator's hunger level involves starvation for a set period of time e.g. 24 h (Fox and Murdoch (1978)) or 48 h (Cook and Cockrell (1978), Williams (pers. comm.)). This method is used prior to short term experiments. During long term experiments, no starvation period is necessary, as the predators are given sufficient food to maintain a more or less stable level of satiation (Lawton et al (1974), Murdoch and Sih (1978)). During these types of experiments, the predators are much more likely to be under similar hunger levels to those in the field. These long

term studies however, only really demonstrate gross responses by the predator. If one requires an insight into the subtleties of predator behaviour, or measurement of energy expenditure, short term studies are preferable.

A pilot study was carried out to determine how the length of starvation affected the predators' subsequent feeding level and between predator variance. Predators were starved for 24, 48, 72 and 96 hours, and subsequently fed for 3h on fifth instar mosquito larvae. The numbers eaten, and amount of food removed (for details see Chapter III) were monitored for 16 predators. It was found that more prey were killed after 48, 72 and 96 hours than after 24 hours starvation, more food extracted from the prey after 72 and 96 hours, and also the coefficient of variation ($\frac{SD}{\bar{x}} \times 100\%$) was smallest after 72 hours, indicating this length of starvation appeared to give the least variable data (Table 2.3.) This length of starvation is too long to be realistic, so a shorter period was selected, which would require more replicates. This work does show, however, that short term, and more realistic starvation periods alone are not ideal, and the chances of bringing all predators to an absolutely standard hunger level prior to any experiment is likely to be remote.

If the predators are allowed to feed on an excess of prey after experimentation, and then starved prior to the next experiment, it is more likely that higher success in standardisation can be achieved. If this prey is not one used in experimentation, and is provided in excess, then predators which have undergone different feeding regimes in experiments, can even out any hunger differences at this time and reach similar levels of hunger prior to starvation for the next experiment.

The standardising technique used was therefore a combination of

Table 2.3 Effect of starvation time on predation rate of female N. glauca

		TIME OF STARVATION			
		24hrs.	48hrs.	72hrs.	96hrs.
$\bar{X}$	Number eaten	11.751	17.133	18.928	16.46
	Wt. extracted mgs.	0.829	1.722	2.777	2.544
SD	Number eaten	6.486	9.226	7.529	7.933
	Wt. extracted mgs.	0.788	0.881	1.148	1.245
$\frac{SD}{\bar{X}} \times 100$	Number eaten	55.195%	53.8%	39.77%	48.19%
	Wt. extracted mgs	95%	51.16%	41.34%	48.89%

Table 2.4 The effect on the number of prey killed by adult N. obliqua reared on mosquito larvae.

Predator	Food	No. killed after 3hrs.	No. killed after 24hrs.
1	<u>Daphnia</u>	0	10
2	<u>Daphnia</u>	1	5
3	Mosquito	3	6
4	Mosquito	9	13
5	<u>Daphnia</u>	0	17
6	<u>Daphnia</u>	1	13
7	Mosquito	4	9
8	Mosquito	8	15

satiation and starvation. After each test, the predator was given 70 Daphnia magna, the remainder of which were removed after a total of 24 hours feeding, including the experimental period. The predator was then starved for 24 hours. This technique was used in all the main experimental procedures.

II. 3.6. Standardisation with respect to Predator Experience.

Simple experiments were carried out to examine the feeding of predators on one prey when reared on another (using N. obliqua). A group of predators had been reared exclusively on mosquito larvae, at similar food levels. After 24 hour starvation period, half were given 20 Daphnia magna, and half 20 mosquito larvae. After 3 hours, the number of prey killed was recorded (dead prey being replaced during the 3h.) and this was repeated after 24 hours of feeding at this level (Table 2.4).

After 3 hours, there appears to be a reduced ability to detect and catch the novel prey compared to the normal prey. After 24 hours, similar numbers of both types were caught. However, each Daphnia item offers about half the calorific return of a mosquito larvae (Savan (1979)), so the results still demonstrate a poorer predatory efficiency on the novel prey. Two days later, more Daphnia were being taken than mosquitoes, and after three days, double the number of Daphnia were being eaten, indicating equal predatory efficiency on both.

When compared to later results (see Chapter VII), the time periods involved above do appear rather excessive, but they demonstrate that when subjected to a new prey, Notonectids are able to learn to capture this prey over a period of time. Similar increases in efficiency with time have been reported by Lawton et al. (1974). The above time values are only estimates, but they do indicate the necessity for allowing the predator a period of acclimatisation to a new prey type before experimentation.

The procedure adopted for the main experimental study was to allow the predators to acclimatise to a new prey type for five test periods before experimentation. Although apparently excessive, acclimatisation times for different prey types are likely to be different, and prolonged acclimatisation ensures standardisation of predator experience prior to testing on different prey types.

It should be pointed out, that when predators being fed on Daphnia in the study described above (Table 2.4), were returned to a diet of mosquito larvae, no loss in predatory ability on this prey was detected.

II. 4. Experimental Design

II. 4.1. Introduction

As was described briefly in the previous section, analysis of net energy gains to a predator and descriptions of behavioural responses both necessitate careful observations, thus the bulk of experimentation consisted of a series of short term, continuous observation studies. For each species of predator, the energetic and behavioural responses were monitored for varying prey type, prey density and environmental complexity.

In trying to make the artificial laboratory habitat as near natural as possible, lighting, temperature and environmental arena must be carefully selected. In considering predator responses, one must select prey types as close to natural prey as is possible, as well as realistic experimental times and prey densities. Also in considering the energetics of heteropteran predator feeding, the amount of food being extracted from any prey item must be ascertained.

II. 4.2. Lighting and Temperature

With poikilothermic predators, constant temperature conditions are necessary in order to obtain comparable results from different experiments. The selection of temperature was made on the basis of

the use of realistic natural temperatures, balanced against the practical problem of the availability of constant temperature room space. Lawton et al (1974) have worked with N. glauca at 8°C. This is the temperature corresponding to mean Winter/Spring conditions, and results in a lowered activity level by the bugs. This can be tolerated when undertaking long term experiments, but for short term experiments, such lowered activity is undesirable. Williams (unpublished) worked with N. maculata at 20°C, which is rather high. Temperatures more indicative of Spring or Summer are more desirable, and a temperature of 15°C was selected for most work. (When comparing results from different temperatures, it should be borne in mind that not only will the metabolic rate be altered, but so, also, will the effectiveness of the physical gill and efficiency of locomotion, giving a likely change in overall behaviour).

A constant lighting scheme of 16hours light, 8 hours dark was used, supplied from five, 8 foot fluorescent tubes, approximately four feet above the experimental arenas.

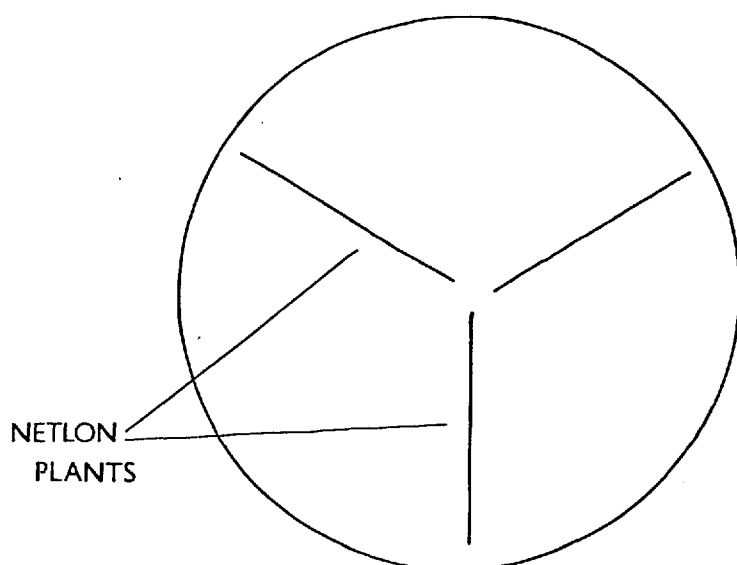
II. 4.3. Experimental Arena

Studies on the effect of arena size on predator feeding have been carried out using sit and wait predators, damselfly naiids, and showed that although small (unrealistic) arenas e.g. petri dishes, give low variability in results at certain densities, they also showed depressed feeding rates when results were compared to responses made in a larger (more realistic) arena with effectively similar densities of prey (Savan 1979). Predation in larger arenas, e.g. 2 gallon plastic buckets, although showing higher variability between predators, also gave higher feeding rates. In other words, it appears that gains by using small arenas in terms of lowered variance in results (necessitating fewer replicates e.g. Thompson (1975), (1978)), turn to losses in respect of reduced predator efficiency compared to the response made by predators

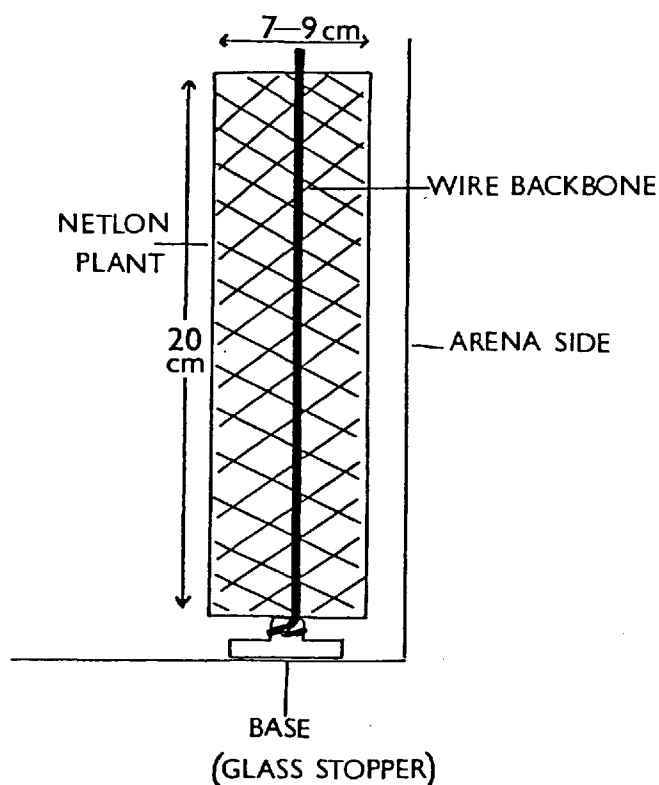
in more realistically sized arenas. If an attempt is to be made to extrapolate from laboratory results to predictions of responses in the field, it is obviously more important to offer more realistic conditions, allowing more natural responses by the predator, even though one is perhaps introducing higher variances into the data. Increasing replication can overcome high between-predator variation to a great extent, but no amount of juggling can alter the depressed predator responses in small arenas. Intuitively, it would appear sensible that the arena should be at least as big as the predators normal reaction area.

After considering the above arguments, the space available, and that differences between the predator species may be found in preferences for prey at different depths in the water body, a two gallon plastic bucket, filled to within 1½" of the top, was chosen as the experimental arena. Initially white buckets were used, (as by Williams (unpublished) for N. maculata), but pilot experiments indicated their unsuitability for N. glauca and N. obliqua. Blue buckets were found to be satisfactory.

Environmental complexity is likely to be utilised in different ways by the different species. Indeed, further pilot experiments indicated increased predation rates by N. glauca in a more complex environment when compared to a simple one. For these reasons, two environmental types were used in the study, a simple one, and a complex one. The simple environment consisted of the bucket on its own, filled to within 1½" of the top with tapwater (left to equilibrate for 24 hours at 15°C before use). The complex environment had in addition three netlon 'plants'. Each 'plant' consisted of a strip of green netlon, approximately 20cm. long, 7-9 cm. wide, held vertically with a wire backbone and supported on a glass stopper. They are arranged in the arena as shown in Figure 12.



CROSS SECTION OF COMPLEX ARENA

FIG 12LEGEND TO FIG 12

Diagrams showing the design of the 'plants' used in the complex environment, and the arrangement of plants in the arena.

II. 4.4. Experimental Time Period

In pilot experiments monitoring feeding levels over seven hours, it was found that between 60% and 70% of the feeding was done in the first three hours after presentation of the prey (using mosquito larvae fed to N. glauca and N. obliqua), the rest of the feeding was spaced fairly evenly over the other four hours. It was therefore decided to run each test for three hours.

II. 4.5. Prey Replacement and Weight of Food Extracted.

Simple pilot experiments indicated that low densities of small prey were fully exploited by the predators in a short space of time. In the examination of the predators response to prey density and construction of functional response curves, such results offer complications. The time period the experiment is viable for depends on how long it takes the predator to fully exploit low densities of prey. At this point, the experiment must be terminated, otherwise there will be a bias towards the high densities of prey. Experiments and descriptive mathematical equations describing the functional response, making allowances for exploitation, have been suggested by Rogers (1972), but this still limits experimental time periods. To overcome the problem posed by the use of low prey densities, the procedure of prey replacement can be used (Holling (1959), (1964) etc.,). Replacement techniques are varied; prey replaced as they are eaten; dead prey are replaced after a certain time; or dead prey are replaced after a certain percentage of exploitation (usually up to 10%). For this study, (which includes the use of low prey densities), prey are replaced as they are eaten. Prey replacement allows the maintenance of the prey density to which the predator was first introduced, and so allows the experiment to be carried out over any period of time without the associated problems of exploitation.

Unlike predators engulfing the whole prey, the number of prey killed by a heteropteran predator does not necessarily give an accurate description of the quantity of food ingested, as this type of predator can extract different amounts of food, depending on how long it spends feeding from each item. (This problem is more fully discussed in Chapter VII). For descriptions of the response by a heteropteran predator to prey, and for calculation of accurate net energy gains by the predator, both numbers of prey killed and weight of food extracted from each item must be monitored. Thus the carcasses of utilised prey items must be recovered, weighed, and by comparison to weights of similar sized live prey, the amount of food extracted by the predator can be ascertained. By relating the amount of food extracted to the time spent feeding on each item, the predator's rate of extraction of food for that prey type can be described (for further details see Chapter III).

II. 5. Prey Species Used.

II. 5.1. Introduction

One of the main differences one might expect between the predators feeding strategies, is in the utilisation of food resources distributed at different depths, i.e. in the use of surface and upper, mid water or bottom dwelling prey. In choosing the prey species for this study, this was the main factor considered. Within this constraint, the prey were chosen with respect to the ease of obtaining sufficient numbers either by rearing or capture from the field, as well as their general availability through the year. This unfortunately ruled out the use of naturally occurring prey, as the time and effort involved in catching and maintaining sufficient numbers would have been excessive, and the availability through the year sporadic. It was therefore necessary to select prey species not generally found in the predator's natural habitat,

but which were of a similar type, or showed similar behaviour to, those occurring naturally.

Although this imposes obvious disadvantages in the assessment of the predation strategy, there was no difficulty in getting the predators to feed on these prey. Predators were also successfully reared and maintained on them. Four prey types were used in this study; Musca domestica, L, adults as surface prey; Aedes aegypti (Linnaeus) fifth instar larvae as upper and mid-water prey; Gammarus pulex (Linnaeus) as bottom prey; and Daphnia magna (L) as a general standardising food.

II. 5.2. Prey rearing and collection.

Musca were reared by David Batt at the Silwood Insectory, and were then maintained in a 20°C C.T. room on sucrose and water from a gravity feeder. For obvious reasons, their wings were docked before use in the experiments. During an experiment, it is important that those flies not being fed on should remain alive. Flies trapped in the surface film will remain alive for over 20h, but at high densities flies are often drowned by the attempts of others to escape by climbing over them. In order to lessen this problem, several legs were also docked from each fly before use.

Gammarus were collected from the outlet stream of Silwood Lake, by 'kick-catching'. This entailed working upstream, dislodging stones etc., disturbing the animals, which were swept downstream into a net. They were maintained in plastic bowls at 10°C, feeding on stream debris and general laboratory waste from the rearing of predators.

Aedes larvae were reared from a culture maintained at 28°C, 70RH. Adult mosquitoes were maintained on 10% glucose solution and given a blood meal from a rabbit once or twice a week. Eggs were laid three days later on damp filter paper, dried, and in that state, could be stored for up to six months. When necessary, eggs were submerged in

water, and the larvae hatched after about a day. These were reared in plastic bowls (density approx. 1000/bowl), and fed on dried yeast, reaching the desired instar after four or five days. They were then removed to a 20°C room, where they could be held at this stage for several days. The adult culture was maintained by allowing other larvae to pupate, and returning the pupae to the stock cages.

Daphnia were obtained from a variety of sources (including local pet shops, Wraysbury Reservoir, and occasionally from local ponds). These sources were subject to climatic conditions and as a backup, Daphnia were reared in the laboratory. They were reared in plastic buckets at 10° or 15°C, being fed on Chlorella or animal waste with its associated bacteria.

II. 5.3. Prey vertical distribution in the water body.

Musca were obviously confined to the surface. The vertical distribution of the other three prey species was determined by time lapse photography. Various densities of prey were placed in a slim, rectangular, 1 litre glass tank. Covering the back of the tank was a piece of xylonite, divided into 49 sections (7 x 7). The tank dimensions were 15 x 15 x 5 cms. Using 30 seconds between frames, 20-36 frames were taken at each density of the three prey species, Aedes aegypti larvae at densities of 2, 9, 20 and 35 per arena; Gammarus pulex at densities of 2, 9, and 20 per arena; and Daphnia magna at a density of 30 per arena. The number of individuals in each section of the tank was recorded after examination of the negatives under a binocular microscope and summed over all frames at that density. The overall proportion of individuals found in each section was calculated and presented in the form of histograms (Figs 13, 14 and 15), showing both vertical and horizontal distribution in the tank.

For Gammarus, there is no doubt that the large proportion of

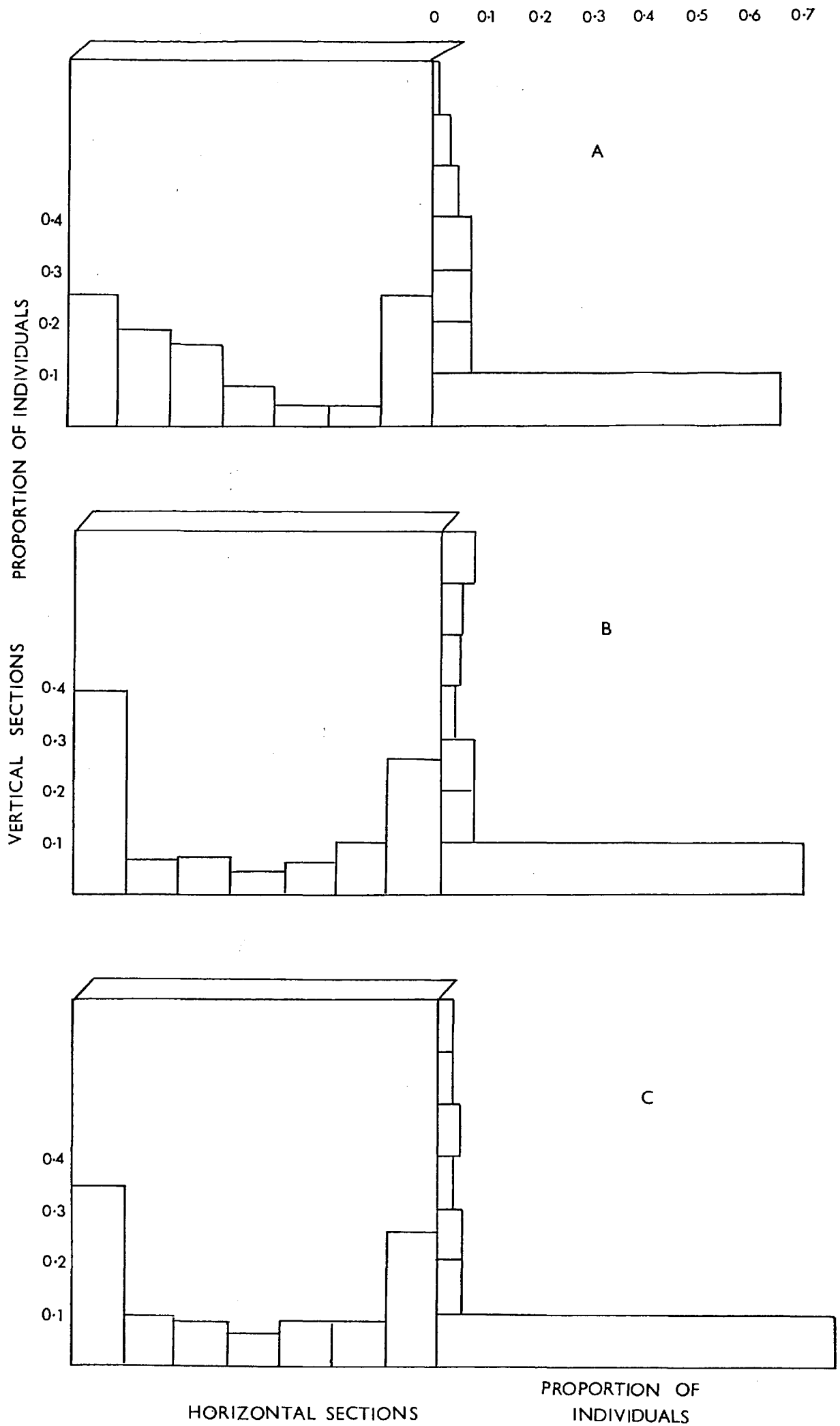
LEGEND TO FIG. 13

**Preference of position by Gammarus pulex in vertical
and horizontal planes as shown by time lapse photography**

A - with prey density 2 per arena

B - with prey density 9 per arena

C - with prey density 20 per arena



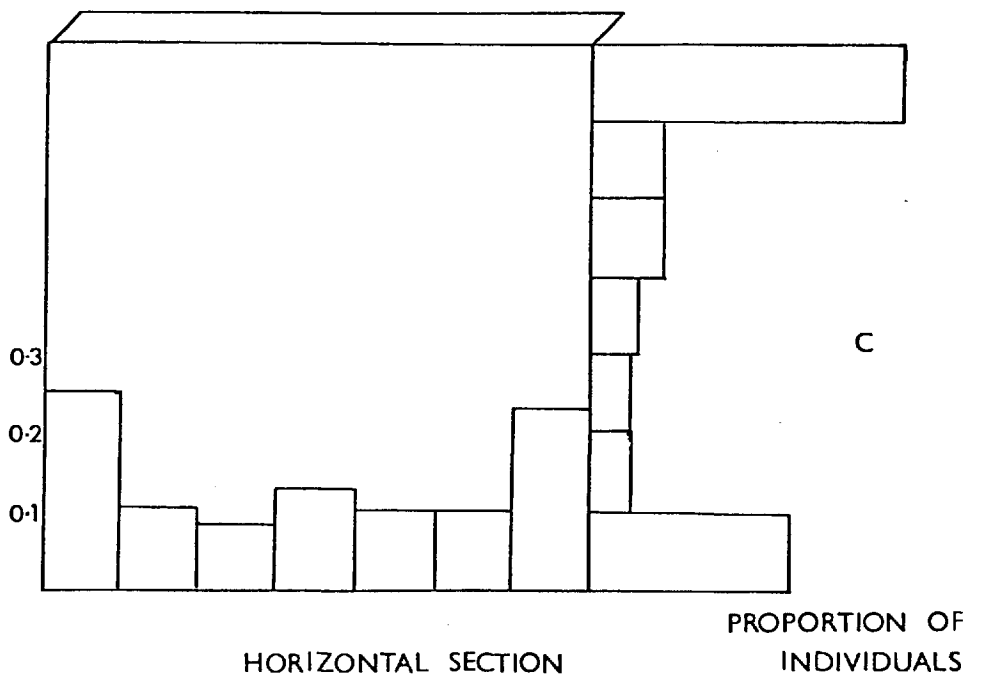
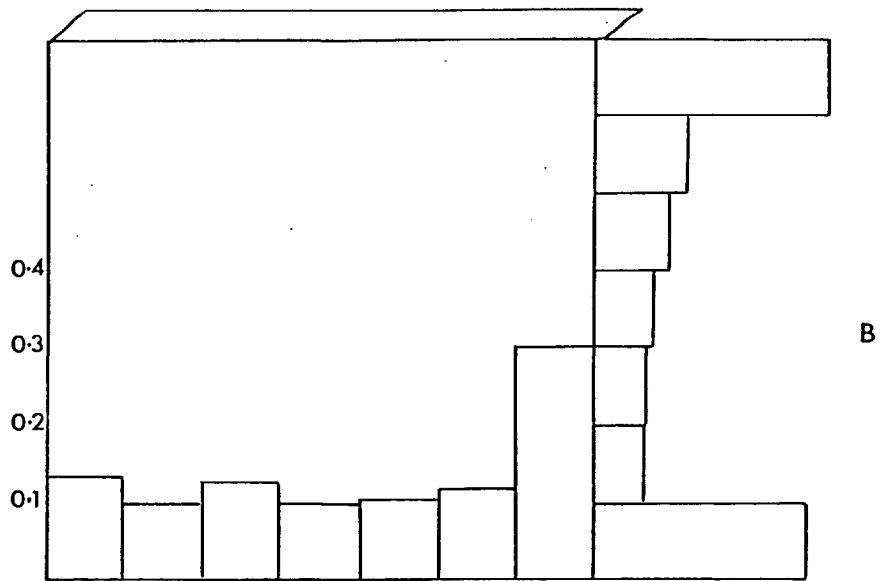
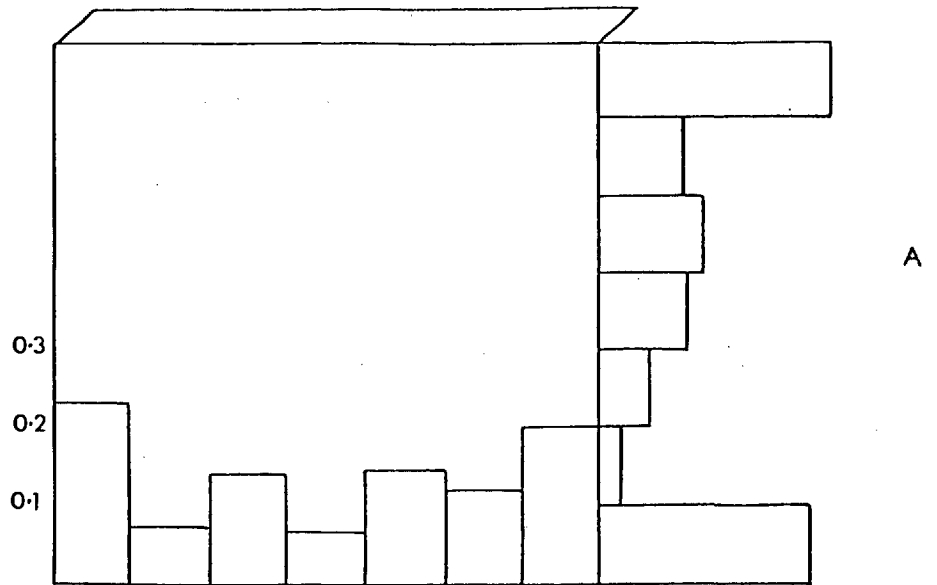
LEGEND TO FIG. 14

Preference of position by mosquito larvae (Aedes aegypti)
in horizontal and vertical planes as shown by time
lapse photography.

- A - with prey density 2 per arena
- B - with prey density 9 per arena
- C - with prey density 20 per arena

0 0.1 0.2 0.3 0.4

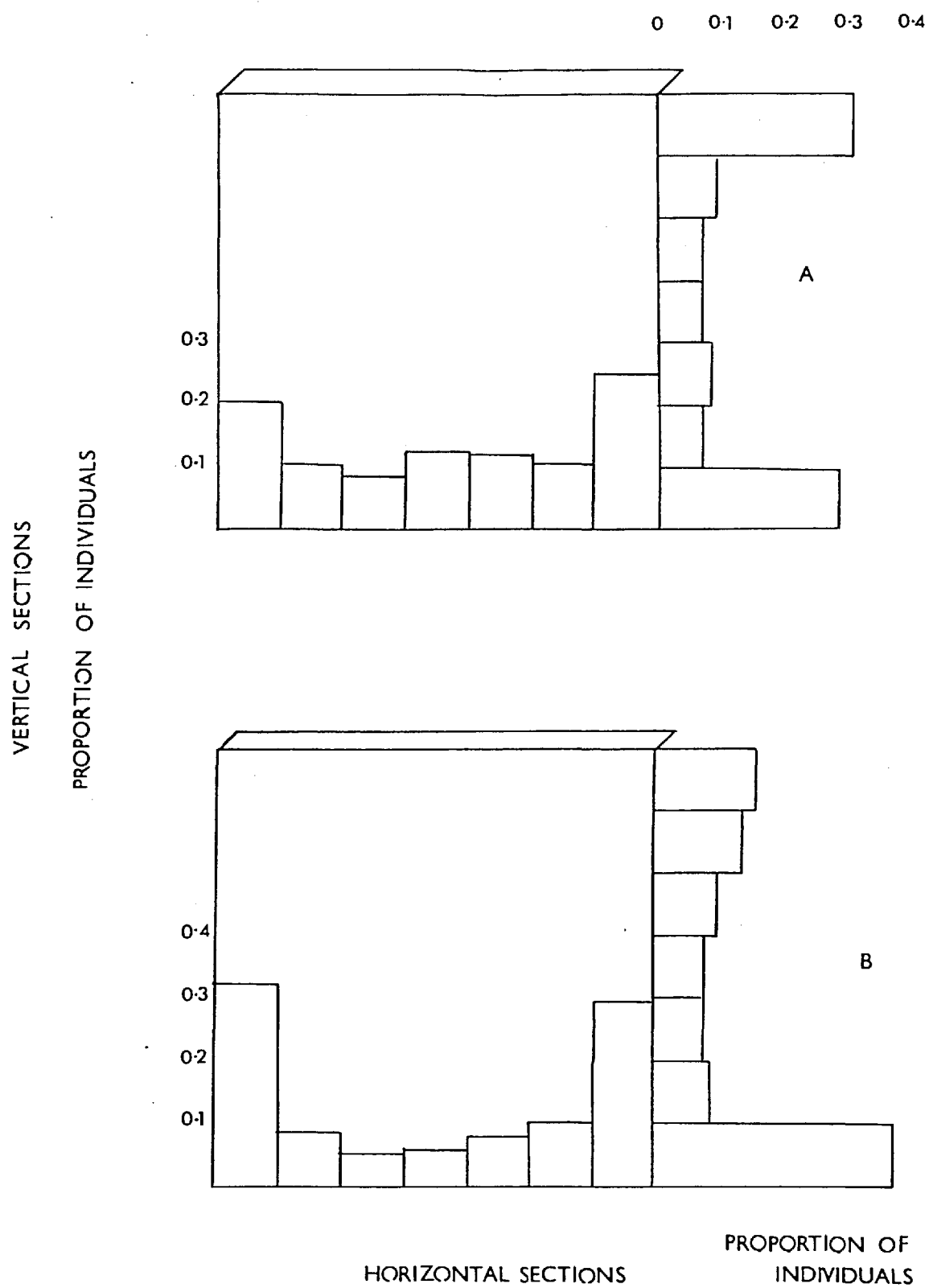
VERTICAL SECTIONS
PROPORTION OF INDIVIDUALS



LEGEND TO FIG. 15

- A - Preference of position by mosquito larvae at density 25 per arena.
- B - Preference of position by Daphnia magna at density 30 per arena as shown by time lapse photography.

FIG 15



individuals found at the bottom reflects a genuine preference as there is a general increase in numbers found as the depth increases, with low numbers at the surface and in adjoining areas. For mosquito larvae, there is a gradual decrease in numbers found with increasing depth, except for the uncharacteristic high proportion at the bottom of the tank. For Daphnia there is a more even distribution through the tank, except again for a high proportion at the bottom. For both mosquito larvae and Daphnia, this could be the accumulation of individuals which would go deeper if the tank was bigger. This can be tested by transforming the numbers of individuals in each vertical section to a log scale, and regressing the points against vertical position. If the area under the graph after the deepest section of the tank is sufficient to accommodate the proportion of individuals at the bottom of the tank, then one is justified in assuming this proportion is the product of summation of individuals which would have gone to deeper parts. As shown in Fig. 16, this is the case for Mosquito larvae and Daphnia. For Gammarus, the regression lines are positive (the surface value at density 9 appears anomolous), suggesting a strong preference for the bottom of the tank used.

From these results, it can be seen that the prey species used do have the desired qualities of vertical distribution, Gammarus preferring the deeper areas and bottom, Mosquito larvae the surface and upper layers, and Daphnia, being used as a general prey, showing a much more even distribution in the water body. One should also note the apparent edge effects shown by the prey species, which may complicate distributions somewhat. Leclezio (1979) also noted some aggregation of Gammarus and mosquito larvae round a 'plant' (as used in this study) which had been added to the tank.

LEGEND TO FIG. 16

Correlations between log number of individuals per section and vertical section for prey distribution data (sections 2cm squares).

A) With Gammarus pulex at density 2 per arena

regression for sections 1-7 $Y = -0.4089 + 0.298x$ $r = 0.889$

B) With Gammarus pulex at density 9 per arena

regression for sections 2-7 $Y = 0.382 + 0.196x$ $r = 0.753$

C) With Gammarus pulex at density 20 per arena

regression for sections 1-7 $Y = 0.405 + 0.22x$ $r = 0.834$

D) With Daphnia magna at density 30 per arena

regression for sections 1-6 $Y = 2.2407 + (-0.0617x)$

$r = 0.873$

E) With mosquito larvae at density 2 per arena

regression for sections 1-6 $Y = 1.586 + (-0.1636x)$ $r = 0.909$

F) With mosquito larvae at density 9 per arena

regression for sections 1-6 $Y = 1.936 + (-0.118x)$ $r = 0.895$

G) With mosquito larvae at density 20 per arena

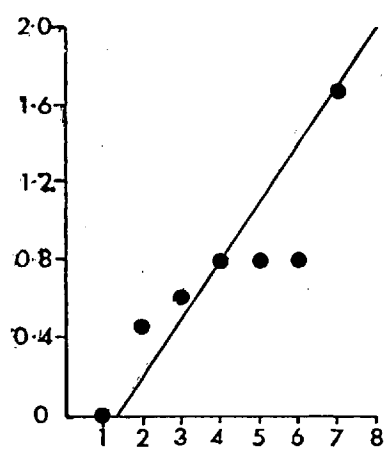
regression for sections 1-6 $Y = 2.316 + (-0.145x)$ $r = 0.837$

H) With mosquito larvae at density 35 per arena

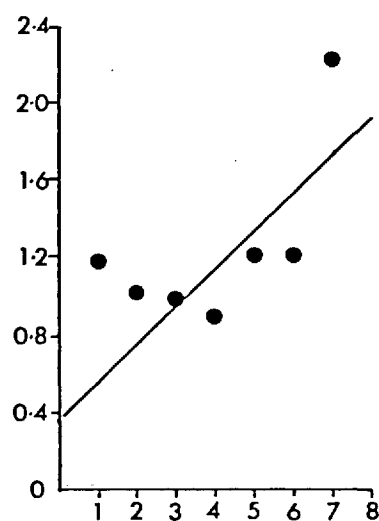
regression for sections 1-6 $Y = 2.355 + (-0.0947x)$

$r = 0.724$

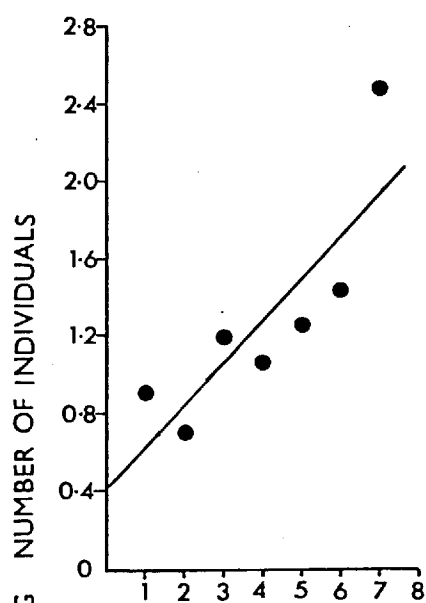
FIG 16



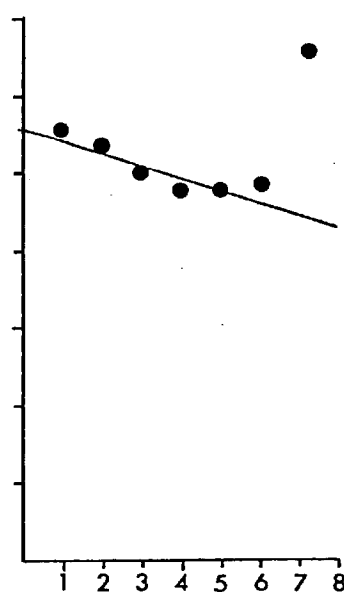
A



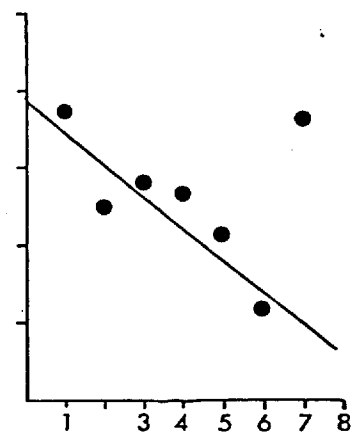
B



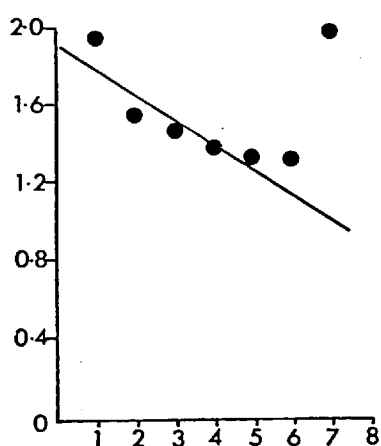
C



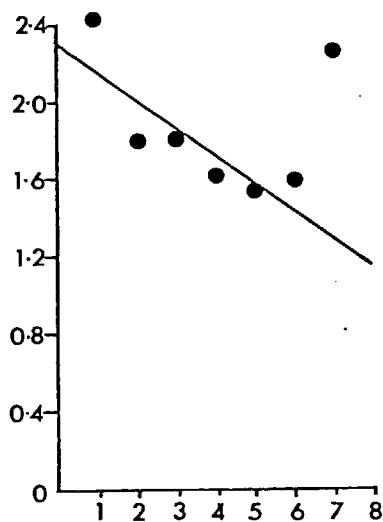
D



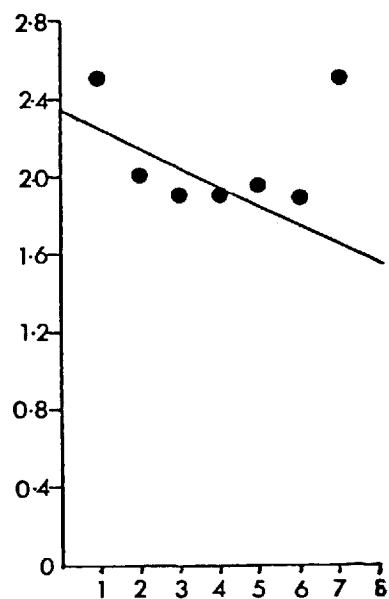
E



F



G



H

VERTICAL SECTION
SURFACE-DEPTH

II. 5.4. Prey Densities

The densities selected for this study were 2, 5, 10, 15, 20 and 25 per arena for Musca and Gammarus, and 2, 5, 10, 30, 50, and 70 per arena for mosquito larvae. A density of 70 Daphnia per arena was used in the standardisation procedure described in section II. 3.5.

II. 6. Experimental Procedure

The main experimental work consisted of a continuous observation study on three species of Notonecta, using six prey densities, three prey types and two types of environment. During one experimental 'Unit' a study was made with one predator species in one environment, using all densities and prey types. Thus the overall study consisted of six such units. For each unit, nine female predators, reared in the laboratory as described earlier, were used. The nine predators were divided into three groups of three, each group being tested on the different prey types in a different order, and each member of the group being tested with the range of prey densities in a different order. Each group of three predators were observed together.

In each experimental unit, 54 separate tests were carried out. Each 'test' consisted of a 3h observation experiment (10.00-13.00 hours or 14.00 - 17.00 hours) on three predators, followed by the removal of the prey and the addition of 70 Daphnia. The Daphnia were then removed after 21hr (making 24 hrs including the 3h experiment), and the predators were then starved for 24h prior to the next test. A 'set' of six tests were carried out for each group of predators on each prey type. Prior to each set, predators were introduced to the new prey type, being offered the new prey type for 3h, no observations being carried out, then given Daphnia and starved as in a normal test. For each new prey, five such periods were given. Densities used for these periods were 10 Gammarus, 10 Musca or 30 mosquito larvae per

Table 2.5

a) Experimental Test Schedule

OBSERVATIONS WITH PREY	Oh → 3h or PRESENTATION OF NEW PREY	3h → 24h 70 <u>DAPHNIA</u> GIVEN TO PREDATORS	24h → 48h PREDATORS STARVED	NEXT TEST
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b) Experimental Unit Schedule

5 Introductory Tests to New Prey 10 Days	6 Observation Tests 12 Days	5 Introductory Tests to New Prey 10 Days	6 Observation Tests 12 Days	5 Introductory Tests to New Prey 10 Days	6 Observation Tests 12 Days	8 Preference Observation Tests 16 Days
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TOTAL DAYS = 82

c) Prey Type Order

	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
Predator Group A Tests 10-1 Day 1, 3, etc.	1st	3rd	2nd
Predator Group B Tests 2-5 Day 1, 3, etc.	2nd	1st	3rd
Predator Group C Tests 10-1 Day 2, 4, etc.	3rd	2nd	1st

d) Prey Density Order within each group of three predators

Predator a	25, 2, 10, 15, 20, 5	
b	10, 15, 2, 20, 5, 25	<u>Gammarus</u> and <u>musca</u>
c	10, 25, 5, 2, 15, 20	
a	70, 2, 10, 30, 50, 5	
b	10, 30, 2, 50, 5, 70	mosquito larvae
c	10, 70, 5, 2, 30, 50	

arena. The experimental schedule is shown in Table 2.5.

A new batch of predators were used for each experimental unit. This system gives data consisting of nine replicates with each prey type at each density for each environment. During the observation experiments, various behaviours are monitored for each of the three predators in the group using a fifteen channel, digital event recorder (Savan 1979). The behaviours monitored are described in Chapter IV.

At the end of each experimental unit, 3h observation tests were carried out to examine the prey preferences of the predators in each environment, when presented with eight different mixtures of the three prey species together. Each test was carried out as for single prey experiments, except for the omission of feeding on Daphnia, the predators being starved from the end of one test, to the beginning of the next, 45h. later. Nine replicates for each of the eight different density combinations of the three prey species were obtained. Further details are given in Chapter V.

Methods involved in respirometry, calorimetry and field sampling will be discussed later (Chapters III and VIII).

Chapter III

Energy Strategies

III.1. Introduction

As was discussed in Chapter I, in the analysis of foraging strategies, a 'currency' must be chosen, which translates the ultimate currency of natural selection (changes in gene frequency measured as inclusive fitness) into a shorter term, measureable objective, which can then be subjected to cost-benefit analysis (Krebs (1978)). Most authors have chosen net rate of food intake (in terms of net energy gains) as the currency which must be maximised during the foraging period (e.g. Emlen (1966), Estabrook and Dunham (1976), MacArthur and Pianka (1966), Krebs (1978), Schoener (1971) etc). The derivation of such cost-benefit functions for different prey types then allows the prediction of optimal diets and prey selection, if it is assumed that predators can rank prey in terms of energy gained per unit time. Such assumptions then lead to relationships like that of Schoener (1971) (Equation 1, Chapter I). This approach ignores the question of how the predator allocates its time between, foraging and other activities, and whether an alternative goal other than maximising energy gain during foraging, such as minimising risk of predatory attack, might predominate (Krebs (1978), Sih (1979)). Also some predators may be restricted by lack of certain nutrients rather than energy levels in prey (e.g. Royama (1971)), but this is not usually considered so important in optimal diet and prey selection theory.

Two arguments are put forward in favour of using net rate of food intake as a short term index of maximal fitness. The first is for predators where food availability affects survival (i.e. food limited), and the second, for predators not food limited, but where feeding competes for time with other activities (such as avoiding enemies, mating, defending territories etc.), so maximisation of the rate of food intake min-

imises time required for feeding (Krebs (1978), Schoener (1971)). In the case of Notonecta, the 'sit and wait' strategy allows monitoring for mates, natural enemies etc., to be carried out simultaneously with feeding, so foraging does not necessarily compete with these activities for time. However, as has been discussed in earlier chapters, food intake directly affects growth, development and reproduction, so it appears that this bug could be food limited, and any strategy increasing reproduction, by increasing food intake, must increase fitness in the Darwinian sense. (see Schoener (1971), Krebs (1978)). This is strong support for the maximising of food intake as a possible goal for this predator.

In the simplest terms, the partitioning of energy assimilated from food can be as follows:-

$$\begin{array}{lcl} \text{Energy content of} & = & \text{Energy content of tissues} + \text{Energy degraded and} \quad (1) \\ \text{food assimilated} & & \text{produced in growth and} \quad \text{lost as heat of} \\ & & \text{reproduction} \quad \text{respiration} \end{array}$$

In the case of Notonecta, consumption includes only digestible food from the prey item, the undigestible remains are left as the carcass. If one assumes that all digested food is then assimilated, the energy content of food assimilated can be approximated to the energy content of food ingested (Gross energy gain). (Even in chewing predators, e.g. damselfly larvae, assimilation efficiency of ingested food is very high, (Lawton 1970)). Growth and reproduction result from net energy gains to the predator, and increases in both will result in an increase in fitness (Schoener (1971)). It is this value that a predator should attempt to maximise in the selection of an optimal diet based on net energy gains. Energy lost through respiration includes basic metabolic needs as well as energy required for activity in prey location and capture, which can be approximated simply by energy loss during foraging. These are the losses to the predator that an efficient foraging strategy can minimise. Rearranging Equation 1, we have:-

$$\begin{array}{lll}
 \text{Energy content of tissues} & = & \text{Energy content of} - \text{Energy degraded (2)} \\
 \text{produced in growth and re-} & & \text{food assimilated} \quad \text{and lost as heat} \\
 \text{production (NET ENERGY GAIN)} & & \text{(GROSS ENERGY GAIN)} \quad \text{through respiration} \\
 & & \text{(ENERGY LOSS)}
 \end{array}$$

or, in the case of Notonecta, as discussed above,

$$\begin{array}{lll}
 \text{NET ENERGY GAIN} & = & \text{ENERGY CONTENT OF} - \text{ENERGY LOST IN} \quad (3) \\
 & & \text{FOOD CONSUMED} \quad \text{RESPIRATION}
 \end{array}$$

in a given period of foraging time.

In the following sections, methods used in obtaining estimates of energy gains and losses from the experiments will be discussed, and the results and estimation of net energy gains from different prey types and densities, and in different environments will be reported.

III. 2. Energy Gains

III. 2.1. Calorimetry

III. 2.1.1. Introduction

An assessment of the energy available to a predator from prey items can be made by using a calorimeter to measure the calorific value per unit weight of food. This will allow comparisons between different prey types and an assessment of energy gain from a certain weight of food consumed.

The most accurate calorific value is one expressed as calories per mg. ash free, where allowances are made for incombustible parts of the prey, contributing to its weight, but not its calorific value. Such allowances, where appropriate, are important when dealing with the sucking predators, as only the digestable parts are consumed. For the prey species used in this study, the incombustible remains from mosquito larvae and Musca adults are practically negligible. Chapman (1969) reports that insect cuticles contribute generally less than 10% of the dry weight of the insect, and have similar calorific values to the rest of the body. Thus for these two prey types, allowances for unused prey parts are unnecessary in the calculation of energy value per gm. dry weight of body

tissue. Gammarus on the other hand, leaves quite a sizeable amount of incombustible residue after calorimetry. The cuticle, obtained by soaking preweighed Gammarus individuals in caustic potash, was found to contribute 39.03% to the total prey weight, and left 57.53% ash by weight when burned in a calorimeter, so it was estimated that, of the total weight of the individual, 22.45% was incombustible ash, and the calorimetry results for Gammarus were adjusted to take this into account. It was assumed that the combustible parts of the cuticle had a similar calorific value to the rest of the animal.

III. 2.1.2. Procedure

A microbomb calorimeter (Phillipson (1964)) was used to measure the energy content of the materials. Standard calorimetry practice was followed, the calorimeter was calibrated using thermochemical standard benzoic acid (certificate number BCS 190J), the test materials were dried, milled, formed into pellets weighing between 15-30 mgs, and burned in oxygen in the microbomb. The output values were translated into calories from the calibration graph. These values are then expressed as calorific value per mg. of sample, ash free.

III. 2.1.3. Results

Several samples of each prey type were used, and the mean calorific values ($\pm$ 95% confidence limits) obtained are shown in Table 3.1. In the calculations of energy gains, the mean values were used.

III. 2.2. Food Extraction

III. 2.2.1. Introduction

The most frequently used method for measuring consumption, is the gravimetric technique, where food is weighed before and after the animal has fed, so that, in terms of dry weight,

$$\text{FOOD OFFERED} - \text{FOOD LEFT} = \text{FOOD CONSUMED (C)} \quad (4)$$

Obviously, where a large number of prey items of slightly different weight are offered simultaneously to a predator, any one may be eaten, and unless

TABLE 3.1.

Calorific values of prey species (cals/mg. dry weight ash free)

	Prey Species		
	<u>Aedes aegypti</u> larvae	<u>Gammarus pulex</u>	<u>Musca domestica</u> adults
mean calorific value	4.04 cals/mg	3.884 cals/mg	4.854 cals/mg
SD.	0.161	0.259	0.249
Confidence limit (95%)	<u>+0.149</u>	<u>+0.198</u>	<u>+0.15</u>
Samples	7	9	20

all individuals are weighed and marked before hand, and a relationship derived between wet and dry weight, it would be difficult to ascertain the initial weight of the prey item, and a mean value for the sample would have to be used. A less time-consuming (and perhaps more accurate) method, would be to obtain a relationship between some physical measurement of the prey item, and dry weight, then the initial weight of the carcass utilised can be ascertained by measurement of the remains. The dry weight after feeding can then be subtracted from the estimated initial weight, giving the weight of food eaten. The weight extracted can then be related to the handling time on that prey type by the predator, and an extraction curve against time can be found.

III. 2.2.2. Procedure

The part of the animal chosen for measurement must not be affected by the predator's feeding methods (i.e. a part which does not shrink as food is removed from the carcass). For Gammarus, a convenient measurement was the width of the tergite of the 4th abdominal segment from the tail, which was linearly correlated with dry weight. The collar width of mosquito larvae (first thoracic segment behind the head) was found to be linearly related to dry weight, and was not affected by predator feeding. This method was found to be unreliable for Musca, and hence the alternative method of obtaining a relationship between wet weight and dry weight was used, individuals being marked and weighed before experiments. The marking was done with small spots of a cellulose based paint, the flies being immobilised with CO₂ before being weighed on a 'Cahn' electrobalance (Model Number 8832). The regressions for Gammarus and Musca were re-examined before each 'set' of experiments but it was found necessary to standardise mosquito larvae more frequently than this (after each test), as the weight of these changed slightly from batch to batch despite being reared at standard density with excess food.

In such procedures, the prey carcasses must be recovered after

feeding in order to find the amount of food removed. Such recovery must be made as quickly as possible in order to avoid leakage of body contents into the water, and also because of scavenging by Gammarus and mosquito larvae. Removal of carcasses can, however, disturb the predator during experiments, especially in the simple environment. The complications described above can be avoided by deriving a standard extraction curve for each predator on each prey type, following the procedure below.

- 1) Carcasses were removed only during experiments in the complex environments, where there was minimal disturbance to the predator.
- 2) The carcasses were then washed quickly in distilled water to remove contamination from the water in the experimental arena.
- 3) The carcasses were freeze dried, weighed on a 'Cahn' electrobalance, and the appropriate measurements made under a binocular microscope using a graticule eyepiece.
- 4) The weight of food extracted from each item was then computed.
- 5) These weights were then related to the time spent feeding on that item (the handling time) in the form of an extraction curve, such curves obtained for each predator species feeding on each prey type.
- 6) The weights of food extracted from each item in all tests were then estimated, using the extraction curve, on the basis of the handling time for that item (as measured by continuous observation).

Energy gains could then be derived simply by multiplying the estimated total weight of food extracted during each test by the appropriate calorific value per mg. for that particular prey type.

III. 2.2.3. Results

Examples of the prey dry weight correlations are shown in Fig. 17. The extraction curves were formed by obtaining the mean weight of food extracted from pooled data during a certain interval of time, e.g. for

LEGEND TO FIG. 17

- A. Example of correlations between wet weight and dry weight of Musca adults -

$$Y = -0.677 + 0.35x \quad r = 0.944 \quad (\text{sig } 0.001)$$

- B. Example of correlations between collar width and dry weight of mosquito larvae -

$$Y = -0.175 + 0.1x \quad r = 0.864 \quad (\text{sig } 0.001)$$

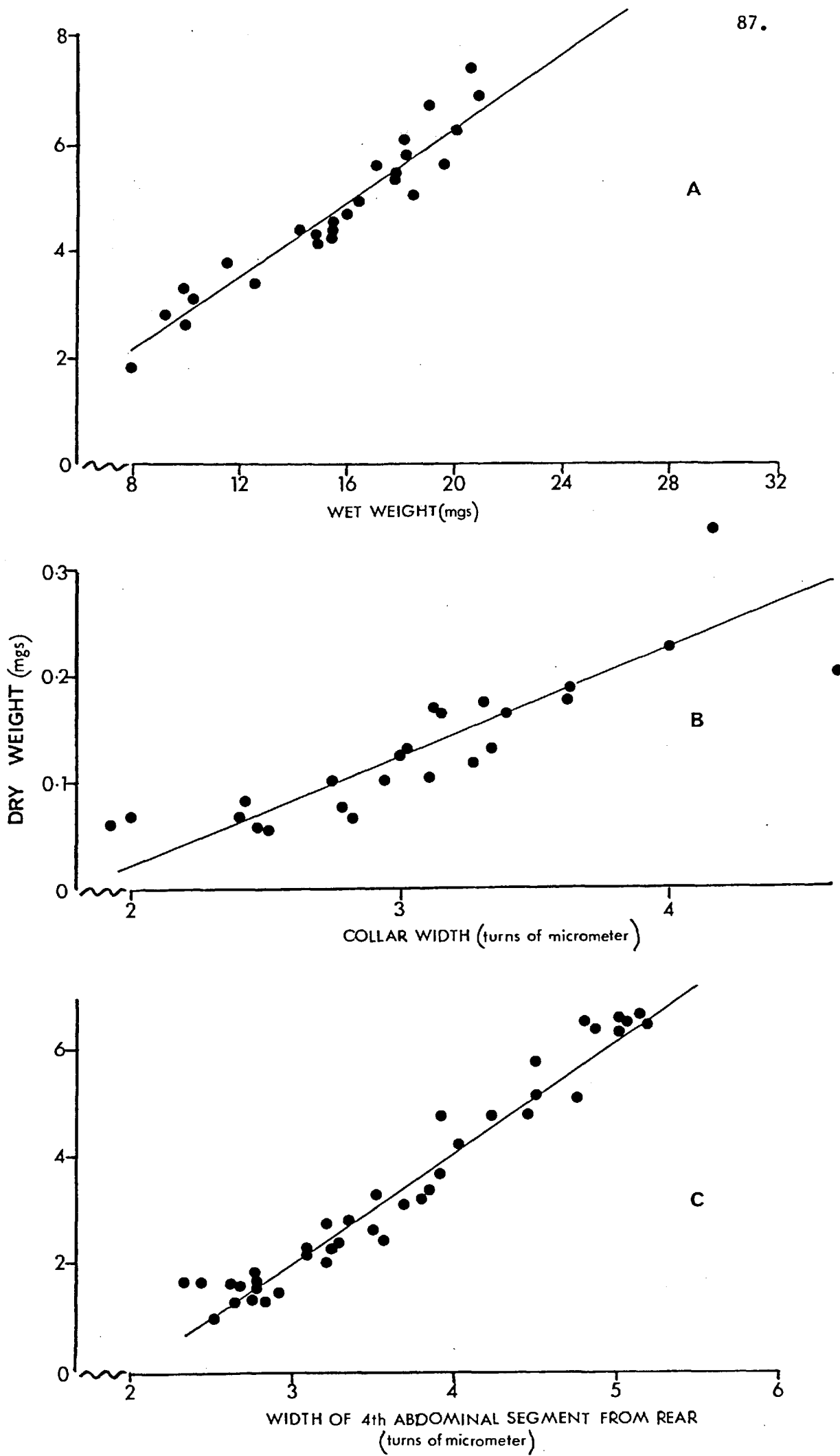
- C. Example of correlations between width of 4th abdominal tergite from the tail and dry weight of Gammarus pulex -

April 1978

$$Y = -4.311 + 2.097x \quad r = 0.967 \quad (\text{sig } 0.001)$$

FIG 17

87.



LEGEND TO FIGS 18, 19, 20

Graphs showing extraction curves with time for the three predator species feeding on each of the three prey types.

95% confidence limits shown. Curves fitted by eye.

Fig. 18 Musca domestica prey

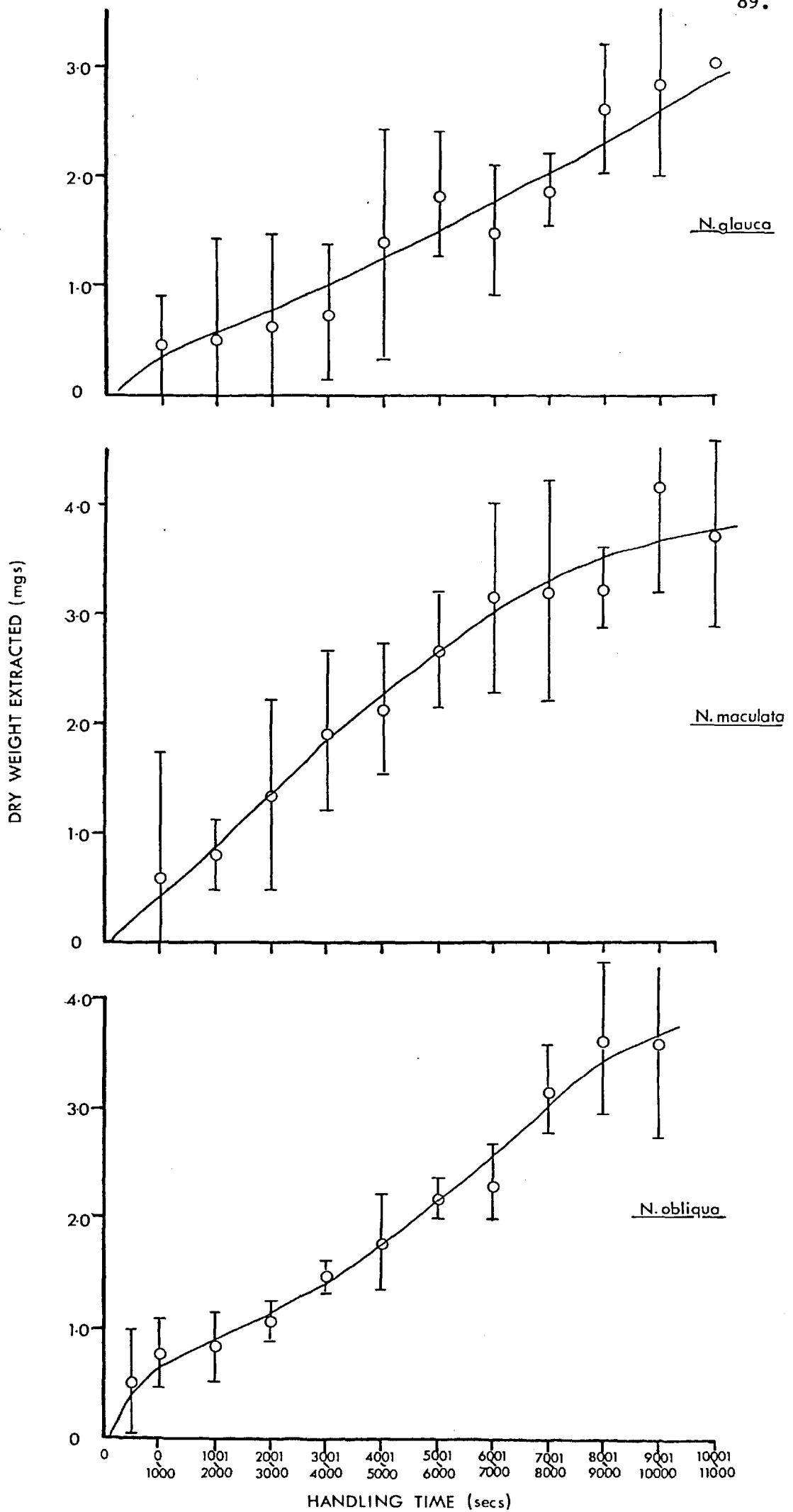
Fig. 19 Gammarus pulex prey

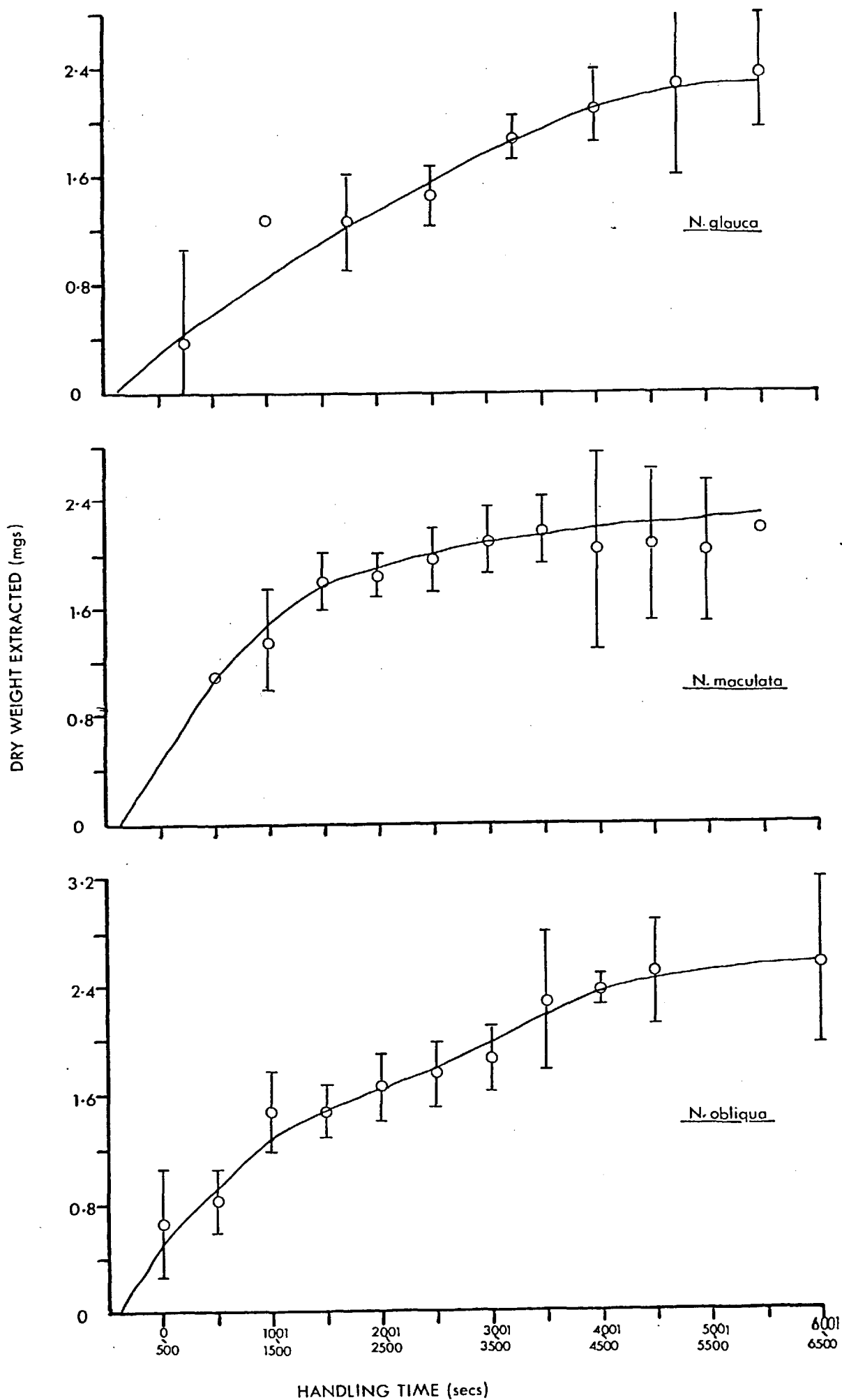
Fig. 20 Mosquito larvae (Aedes aegypti) prey

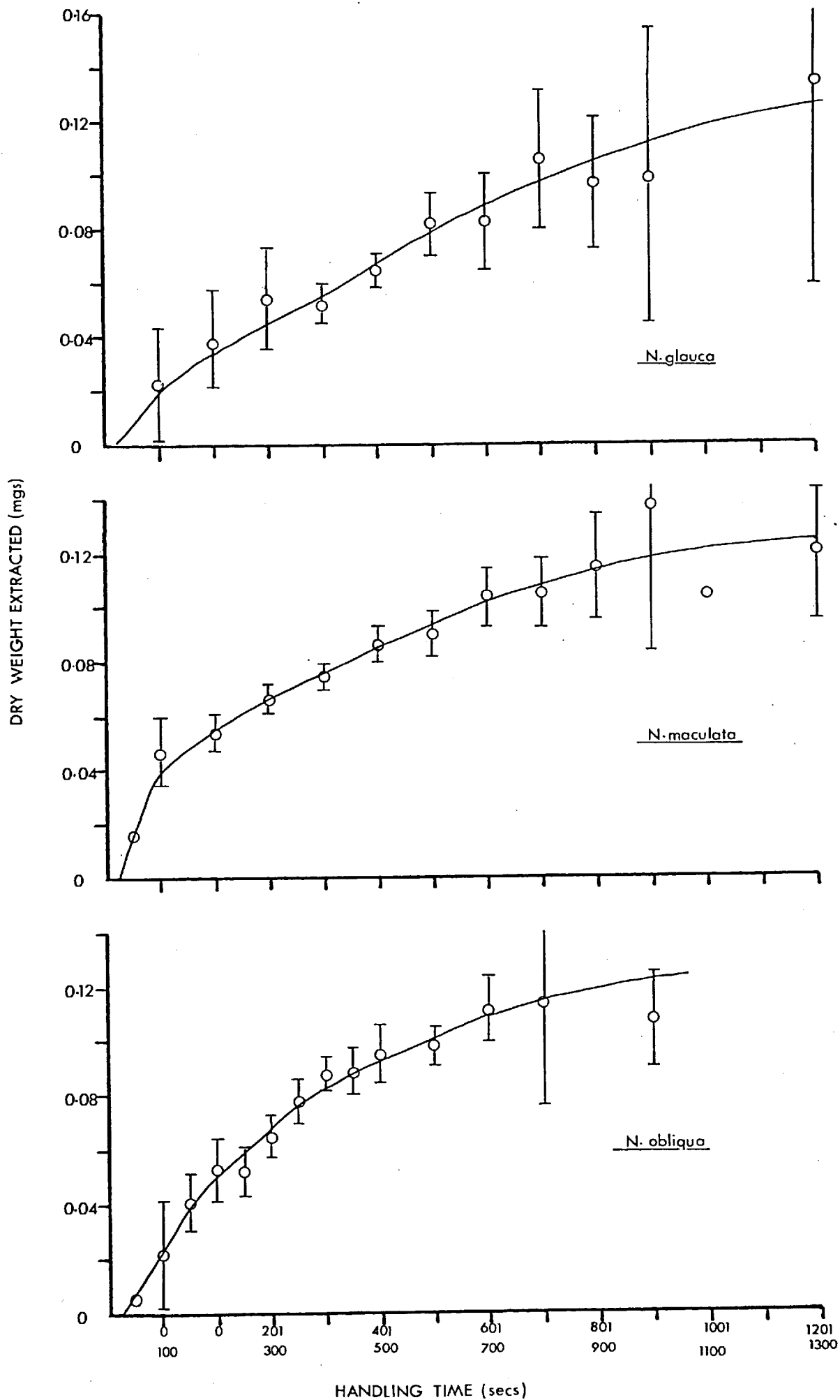
FIG 18

MUSCA PREY

89.







Musca, the mean weight extracted for handling times between 0 - 1000 seconds, 1001 - 2000 seconds etc., were computed (Figs 18, 19 and 20). In all cases, the curve eventually reaches an asymptote, as the available food material in the prey items gradually declines and becomes progressively harder to extract (see Chapter VII for further discussion). It is encouraging to note that the asymptotes are very similar for each predator species, even though the curves and associated rates of extraction are very different (Fig. 21).

Attempts were made to find some relationship between leaching of prey contents and time of exposure to water after being pierced, but no such relationships were found (J. Lawton (pers. commun.).

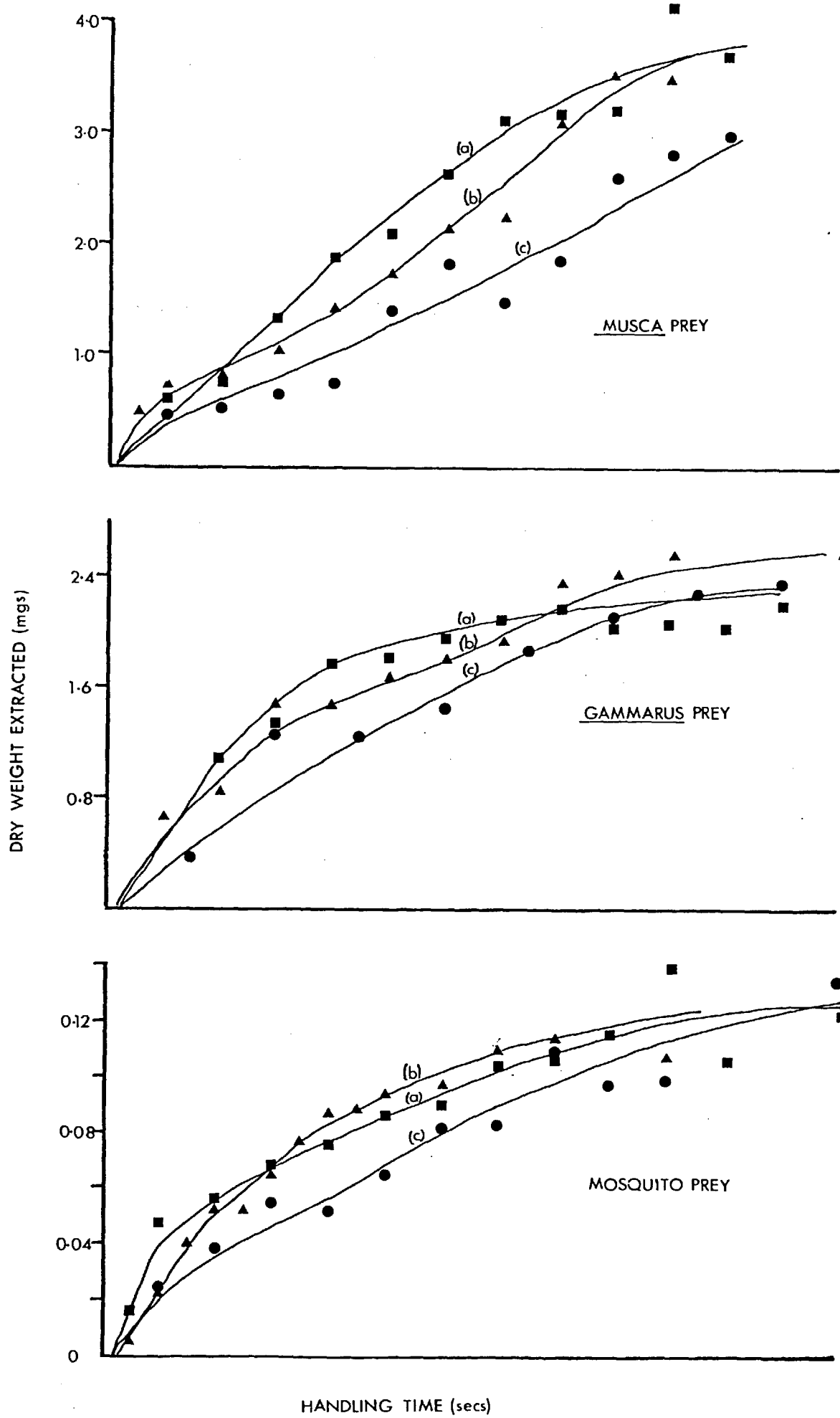
Comparison between the shape of the extraction curves of the three species shows quite marked differences in the ability to remove food from the prey items. For all three prey types, N. glauca shows the slowest extraction rates, the asymptote (indicating total exploitation of the prey) being reached much later than in the other two predator species; 1300 seconds for mosquito larvae; 6500 seconds for Gammarus; and well over 10,800 seconds for Musca. N. obliqua and N. maculata reach the asymptotes at similar times; 1000 seconds for mosquito larvae; about 5000 seconds for Gammarus; and about 10,000 seconds for Musca prey. However, the shapes of the curves and rate of reaching the asymptotes are different. For both of the larger prey (Gammarus and Musca), N. maculata shows higher extraction rates, and a rather extended slow phase of extraction to the asymptote, compared to N. obliqua, which shows initially slower rates of extraction, but has a relatively short, slow phase to the asymptote. For the smallest prey type, N. maculata initially shows the fastest extraction rate, but after this period N. obliqua appears to extract more food, with a slow phase of extraction before the asymptote. These differences may well be explained to some

LEGEND TO FIG. 21

**Comparison between the extraction curves with time
of the three predator species with each of the
three prey types.**

Curves fitted by eye.

- **N. maculata** (a)
- ▲ **N. obliqua** (b)
- **N. glauca** (c)



extent by differences in rostrum size and bore diameter, and crop capacity.

III. 3. Energy Losses

III. 3.1. Introduction

The respiratory rate is a useful and sensitive measure of the organism's metabolic expenditure of energy (Grodzinski, Klekowski and Duncan (1975)). Metabolism as a whole can be affected by various factors including body size; developmental stage; reproductive state; nutritional state; composition of diet; state of acclimation to temperature; environmental factors; state of stress (to immediate handling or other forms of disturbance); and state of activity (Grodzinski et al (1975)). For consideration of losses occurring in a foraging strategy, the important factor to examine is the state of activity, providing all other factors can be standardised (see Chapter II). Losses can then be considered as consisting of two main factors, the standard metabolism and activity during search, attack, pursuit and capture of prey i.e. active metabolism. Standard metabolism losses will occur through the whole experimental period and will be added to by any activity occurring during this time (This assumes that feeding costs are similar to standard metabolism). If one can derive a relationship between percentage time active and total respiratory losses, then the losses during any period of time can be predicted simply by a value of total time active (assuming that all activity is at the same level). Standard metabolism can be derived by extrapolating back to zero time active.

The usual method of measuring the respiratory rate of an aerobic animal is through the measurement of the rate of oxygen consumption, which in turn gives a measure of the energy expenditure involved in normal metabolic processes (Duncan and Klekowski (1975)). There are several different techniques for the measurement of oxygen consumption,

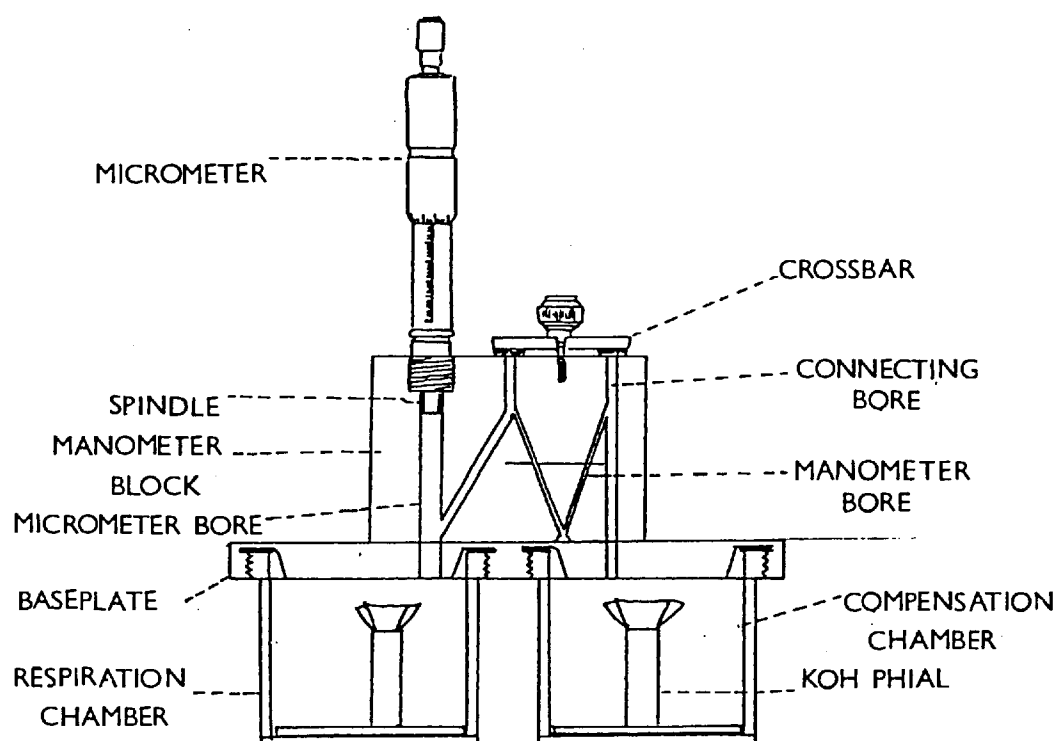


FIG 22

LEGEND TO FIG 22.

A diagram of the Spencer-Davis respirometer.

ranging from manometric, through chemical analyses to the use of oxygen electrodes. After due consideration, it was decided that the use of manometric, constant pressure, respirometry techniques offered the most straightforward and convenient methods for short term measurements of oxygen consumption. The most suitable sized respirometer described in the literature, which would allow room for activity of Notonecta, and at the same time monitor the small changes in pressure due to oxygen consumption likely in a poikilothermic invertebrate, was the Spencer-Davis Constant Pressure Respirometer for medium sized animals (Spencer-Davis (1966)), which was successfully used for limpets and beetles, and has been used for Notonecta (Williams (Unpublished)).

III. 3.2. Procedure

The construction of this respirometer is described by Spencer-Davis (1966), and basically consists of a drilled perspex block containing the manometer, a micrometer head as the measuring device and the use of wide mouthed respiration chambers (Fig. 22). Modifications to the original design included enlargement of the chambers to a height of 10cm, with an approximate volume of 300mls, and positioning of the KOH containers in the centre of the chambers.

The standard method for the measurement of oxygen consumption is given by Spencer-Davis (1966). In the procedure for this study, the KOH (CO₂ absorber) is held in small plastic phials (approx. volume 1ml), cemented onto a removable perspex disc, which sits on the floor of each chamber. A 20% solution of KOH is added, and a roll of filter paper, the end of which is cut vertically and then opened out like the 'petals of a flower', is placed into the phials, increasing the surface area available for CO₂ absorption. Water, at environmental temperature is then put into the two chambers, up to a level of 1cm below the top of the KOH phials (60mls volume). A female bug, starved for 24 hours,

is then placed in the respiration chamber, and the two chambers screwed into the manometric block. The whole unit is then immersed into a water bath, the level of which covered the two chambers completely. The unit is then left to equilibrate for 10 minutes and the connecting bores then closed to the atmosphere by the crossbar. The unit is left for twenty minutes, then the manometric fluid on the respiration chamber side was positioned at a level marked on the manometer block by adjustment with the micrometer. Any leakages became apparent during this time period, as they will show themselves in a large movement of the fluid in either arm of the manometer. If this occurred, the unit was dismantled, resealed and the above procedure repeated.

The oxygen consumption was measured for one hour, with occasional stimulation of the bug to activity, and the total time of activity during the hour being measured on a stop watch during continuous observation. The initial reading of the micrometer was noted, and the level of the fluid in the respiration chamber arm of the manometer was repositioned to the starting pointing every 15 minutes. The difference between the final micrometer reading and the initial one gave the volume change in the respiration chamber during the time period. Williams (unpublished) also monitored the O_2 level in the water in the respiratory chamber using micro-winkler techniques, but found no change during the hours measurement. This is probably due to the large surface area/volume ratio of water in the wide-necked chambers in this respirometer, which allows rapid equilibrium between O_2 concentration in the air and water as oxygen is consumed by the bug from the water. For each measurement made, values of mls of O_2 consumed and percentage time active were obtained, which could then be analysed by linear regression. Respiratory rates were measured at $15^{\circ}C$ for all three species.

LEGEND TO FIG 23

Relationships between mls O₂ consumed per hour at 15°C and percentage time active for the three predator species.

A) N. glauca $y = 0.0235 + 0.00538X$ $r = 0.8973$ (sig. 0.001)

B) N. maculata $y = 0.04277 + 0.00477X$ $r = 0.842$ (sig. 0.001)

C) N. obliqua $y = 0.03195 + 0.009016X$ $r = 0.841$ (sig. 0.001)

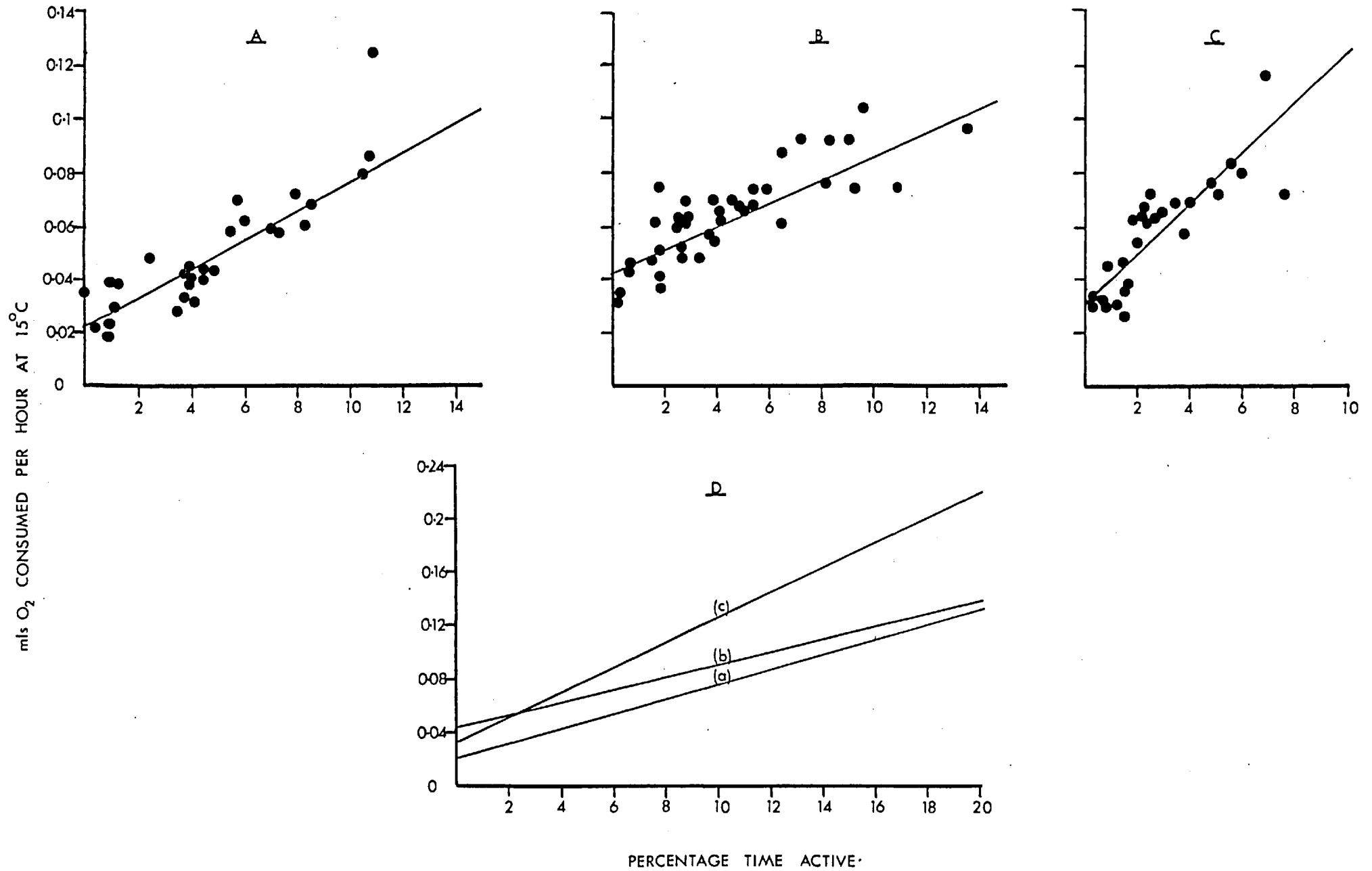
D) Comparison between regression lines for all three predator species.

a) N. glauca

b) N. maculata

c) N. obliqua

FIG 23



III. 3.3. Results

The graphs in Fig. 23 show the linear relationships between mls of O₂ consumed per hour and percentage time active, for the three species at 15°C. The volume of O₂ consumed during any 3 hour test can simply be estimated by reading off the percentage activity shown by the bug from the above graphs, and multiplying the O₂ consumption by three. This value includes the combination of resting standard metabolism and active metabolism, but is made on the basis of an assumption that all activity is at the same level. Although this is an oversimplification, it was deemed justified on three counts;

a) Assessment of oxygen consumption during different levels of activity would be extremely difficult, requiring many more data points and complex analysis.

b) The proportion of time spent in activity is, on the whole, relatively small (see Chapter IV), and even though active metabolism is much greater than standard metabolism, any differences between levels of activity are unlikely to have a great effect on the assessment of net metabolic costs.

c) For purposes of this study, a comparison between the predation strategies on different prey types and between different predators is required, and so long as all data is treated in the same way, such oversimplifications are unlikely to affect the overall considerations.

One would expect that the respiratory rate of N. obliqua would generally be the highest, as it is the largest of the three species, and similarly one would expect N. glauca to have the lowest rate as it is the smallest. These predictions are generally borne out by the results. What should be noted, however, are the actual slopes of the curves. A steep slope indicates greatly increased energy expenditure

with activity, whereas a shallow slope indicates a much lower increase. N. obliqua shows the steepest slope and N. maculata the shallowest. This seems to indicate that N. maculata might be the most efficient swimmer of the three, requiring the least energy for locomotion and N. obliqua might be the least efficient, with N. glauca between the two. (This fits in with the general conclusions on the morphometric studies in Chapter VI). However, at rest (or at very low activity levels), N. maculata shows the highest basal respiratory rate, N. glauca again the lowest, with N. obliqua inbetween. This appears to indicate the largest standard metabolic rate is found in N. maculata. Further discussion of these results is on page 261- Chapter VI.

In the conversion of mls of oxygen consumed to energy expenditure, the value of 5 cal per ml consumed was used. This approximates to the normal values found in the literature of between 4.8 and 4.95 (e.g. Prus (1975)).

III. 4. Net Energy Gains

III. 4.1. Introduction

The net energy gains to each predator species can be calculated as described in Section III. 1. (Equation 4). Results are shown in the form of graphs relating energy gain in the presence of each prey type with prey density, in each of the two environments. Due to varying sizes of the different prey species, and the use of different densities with each prey type, a comparison of the efficiency of feeding by each predator species, on each prey type can be made by correlating net energy gain with prey biomass presented. Biomass is calculated by multiplying the mean individual dry weight of the prey species by the density (see Appendix III for relevant data). The raw data for energy gains, energy losses and net energy gains are given in Appendix IV. The data for net energy gains are given for each predator species in turn.

III. 4.2. Statistical Analysis

Confidence limits at the 95% level were calculated for each data point. In addition, each set of data (comprising the net energy gains at six prey densities of one prey type in one environment for one predator species) was subjected to an analysis of variance. The mean values of the data points in each set were then compared using the fixed range test (LSR) (Parker (1973)). Both the analysis of variance and fixed range test gave a general idea of the statistical range of the data, but both were found to have rather low sensitivity in comparing means whose confidence limits did not, or only partially overlapped. In these cases, the 'T' test was used.

The data at each density for each prey type was compared between the two environments using the 'T' test. The results of the statistical analyses are given in the figure legends for each set of data.

III. 4.3. Results

III. 4.3.1. Introduction

The experimental design allows an analysis of the net energy gains to the predators from three points of view:-

- a) The effect of prey density of each prey type in both environments on the net energy gains.
- b) The effect of environmental complexity on the net energy gains at each prey density.
- c) The effect of prey type on the net energy gains for each predator species.

Feeding efficiency can be examined not only by comparing the sizes of the energy gains, but also by examining the ratio of mean net energy gain and handling time (as in Schoener (1971) see Chapter I) for each prey density of each prey type in both environments (Table 3.2) (N.B. as pursuit time is so small relative to handling time, and is so similar

TABLE 3.2

		COMPLEX ENVIRONMENT						SIMPLE ENVIRONMENT					
		25	20	15	10	5	2	25	20	15	10	5	2
<u>Musca</u> Prey	<u>N. glauca</u>	0.0053	0.0055	0.0053	0.0054	0.0055	0.0055	0.0051	0.0047	0.005	0.0051	0.0048	0.0044
	<u>N. maculata</u>	0.008	0.0081	0.008	0.0079	0.008	0.0082	0.0079	0.0082	0.0079	0.0074	0.0075	0.0074
	<u>N. obliqua</u>	0.0073	0.0073	0.0076	0.0074	0.0074	0.0072	0.0073	0.0072	0.0072	0.0075	0.0075	0.0073
<u>Gammarus</u> Prey	<u>N. glauca</u>	0.0075	0.0077	0.0076	0.0076	0.0072	0.0075	0.0044	0.003	0.0045	0.0032	-0.0031	-
	<u>N. maculata</u>	0.0087	0.0096	0.0097	0.0096	0.0108	0.0088	0.0122	0.0114	0.0128	0.0117	0.012	0.0103
	<u>N. obliqua</u>	0.0103	0.0103	0.0099	0.0096	0.0097	0.0094	0.0099	0.0106	0.0111	0.01	0.0113	0.0097
Mosquito larvae		70	50	30	10	5	2	70	50	30	10	5	2
	<u>N. glauca</u>	0.00195	0.00197	0.00195	0.00184	0.00186	0.0011	0.0012	0.00115	0.00145	0.001	0.0011	-0.0004
	<u>N. maculata</u>	0.0027	0.0031	0.0029	0.0025	0.0024	0.002	0.0039	0.0038	0.0034	0.0032	0.0033	0.0027
	<u>N. obliqua</u>	0.003	0.0029	0.0029	0.0026	0.0025	0.001	0.0033	0.0033	0.0032	0.0032	0.003	0.0027

Table 3.2. Ratio of mean net energy gains and mean handling time ($\frac{E}{T}$ Schoener (1971))
for each density of each prey type.

for each prey type, it can be omitted (see Chapter IV for relevant data).)

III. 4.3.2. Net Energy Gains by *N. Glauca* (Figs 24, 25, 26, 27 and 28).

a) Effect of prey density

The density of *Musca domestica* did not affect the net energy gains in either environment ($F = 0.172$ simple environment; $F = 0.735$ complex environment). Such a result is not totally unexpected, as the size of the prey and stimulus it produces at the surface is likely to elicit a response by a hungry predator from any position over a large area at the surface. The long handling time on this prey would also reduce any density effect. In both environments however, there is some indication of a lower net energy gain at the lowest density, although this is not significant.

A density affect is apparent with *Gammarus pulex* prey. In the simple environment this is confined to a significant difference between the lowest and highest densities (i.e. 2 and 25 per arena). This is probably due to the large confidence limits around the data. With prey densities 2 and 5 per arena, the mean values show a net energy loss, the others a net energy gain. In the complex environment, the density effect is slightly clearer, the lowest density showing the lowest net energy gains, and there is no significant differences between the other densities.

The data for mosquito prey shows the clearest density effect. In the simple environment, the lowest density has significantly the lowest value (a net energy loss). No significant differences were found between data at the other densities, although the large confidence limits obscure the general trend of increasing mean net energy gain with increasing prey density up to density 30, with a slight drop in mean values through densities 50 and 70 per arena. In the complex environment, the prey density effect separates out the results into three levels. The lowest level at density 2, the next level including densities 5 and 10, and data

LEGEND TO FIG. 24

Net energy gains by N. glauca feeding on six densities of Musca domestica, compared between simple (□) and complex (■) environments. 95% confidence limits shown.

Simple environment - analysis of variance for data of all 6 densities

$$F = 0.1725 \text{ (n.sig)}$$

Complex environment - analysis of variance for data of all 6 densities

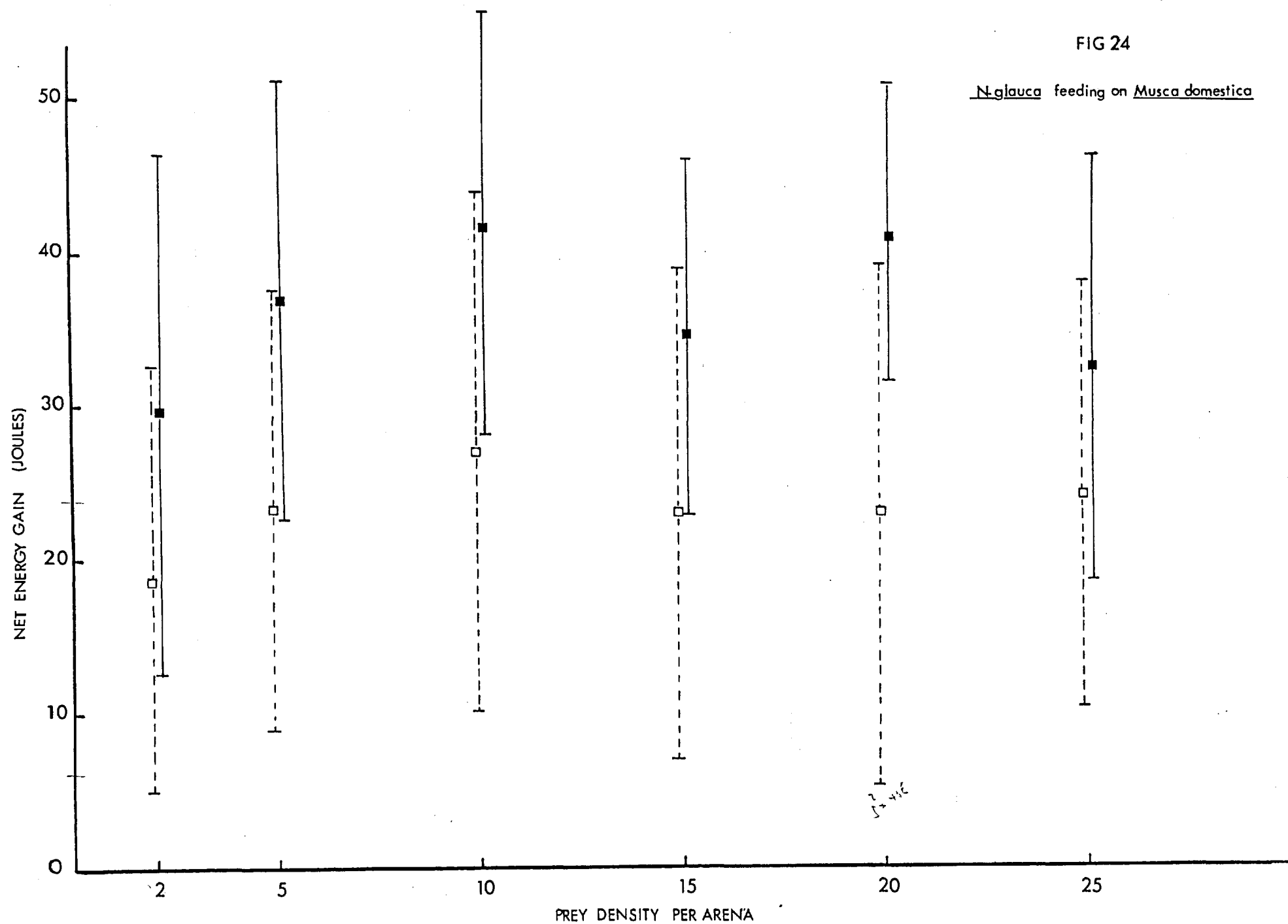
$$F = 0.735 \text{ (n.sig)}$$

Comparison between simple and complex environments.

T test:	Density	25	20	15	10	5	2
	T =	0.972	2.049	1.318	1.538	1.438	1.15
	significance =	n.sig	0.1	n.sig	n.sig	n.sig	n.sig

FIG 24

N. glauca feeding on Musca domestica



graphical

LEGEND TO FIG. 25

Net energy gains by N. glauca feeding on 6 densities of Gammarus pulex, compared between simple and complex environments. ■ complex. □ simple. 95% confidence limits shown.

Simple environment - analysis of variance for data of all

6 densities: F = 0.571 n.sig

Comparison by means of T test (sig. 0.05)

Density -	<u>25</u>	<u>20</u>	<u>15</u>	<u>10</u>	<u>5</u>	2
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Complex environment - analysis of variance for data of all

6 densities: F = 2.792 sig. 0.05 LSR = 5.29

Comparison by means of T test (sig. 0.05)

Density -	<u>15</u>	<u>5</u>	<u>20</u>	<u>25</u>	<u>10</u>	2
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Densities underlined not significantly different.

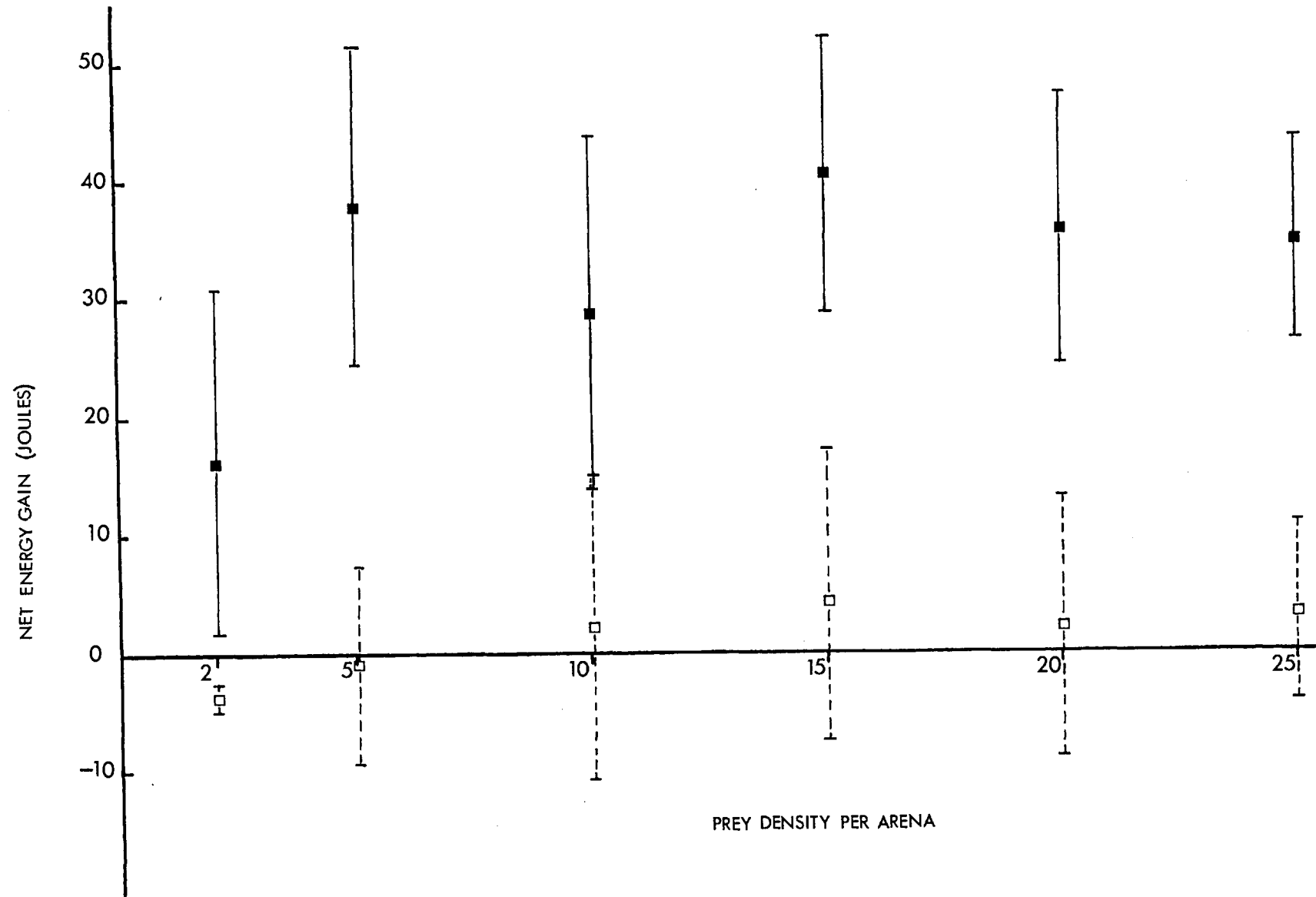
Comparison between simple and complex environments.

T test.

Density	25	20	15	10	5	2
T =	6.244	4.86	5.174	3.082	6.0	3.15
Significance	0.001	0.001	0.001	0.01	0.001	0.01

FIG 25

N. glauca feeding on Gammarus pulex



LEGEND TO FIG. 26

Net energy gains by N. glauca feeding on 6 densities of Aedes aegypti mosquito larvae, compared between simple (□) and complex (■) environments. 95% confidence limits shown.

Simple environment - analysis of variance for data of all 6 densities

$$F = 5.956 \text{ (LSR 1.475) Sig. 0.05}$$

Comparisons by T test between means

$$\underline{30} \quad \underline{50} \quad \underline{70} \quad \underline{5} \quad \underline{10} \quad 2 \quad (\text{sig. 0.05})$$

Complex environment - analysis of variance for data of all 6 densities

$$F = 8.247 \text{ (sig. 0.01) (LSR = 1.323)}$$

Comparisons by T test between means

$$\underline{70} \quad \underline{30} \quad \underline{50} \quad \underline{5} \quad \underline{10} \quad 2 \quad (\text{sig. 0.05})$$

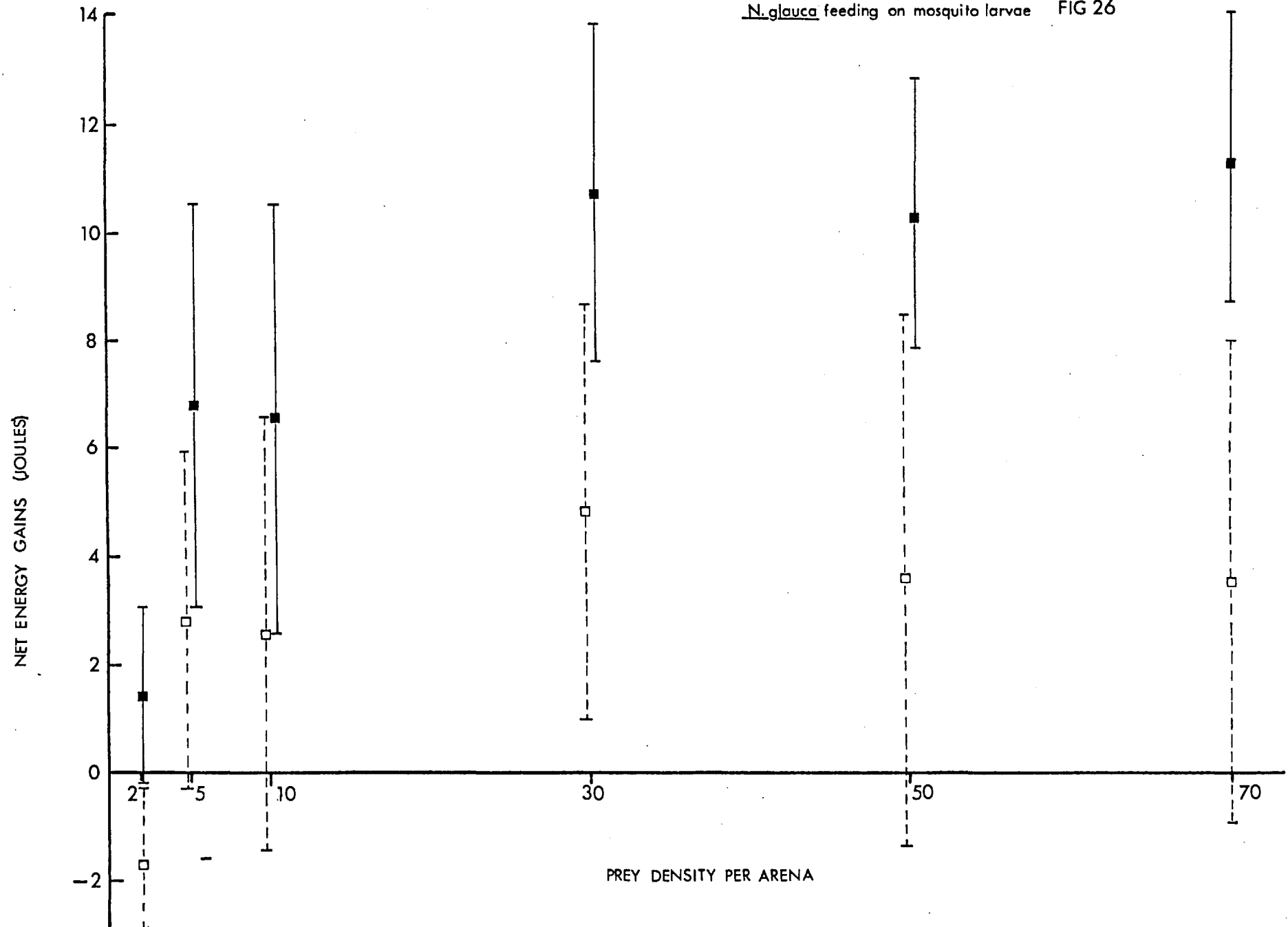
Densities underlined not significantly different.

Comparison between simple and complex environments

T test

Density	70	50	30	10	5	2
T =	3.466	3.08	2.155	1.65	1.862	3.395
Significance	0.01	0.01	0.05	N.sig	0.1	0.01

N. glauca feeding on mosquito larvae FIG 26



from densities 30, 50, and 70 show the largest net energy gains, although there are no significant differences between these latter three densities.

b) The effect of Environmental Complexity

For all prey types there is an obvious trend for larger net energy gains in the complex than in the simple environment. This is most marked with Gammarus prey, significant differences found at all densities. Similarly, with mosquito larvae, the differences are significant for all densities except density 10, although the mean value for net energy gain is more than double in the complex than in the simple environment. At the low densities of these two prey types, there are net energy losses in the simple environment. The data with Musca prey shows no significant differences except at density 20 ($P = 0.1$).

It should also be noted that the confidence limits for data from the simple environment are generally larger with both mosquito and Musca prey than in the complex environment.

c) The Effect of Prey Type

The efficiency of predator feeding on the different prey types can be compared by considering the net energy gains in the presence of similar total biomasses of the prey species (Figs. 27 and 28), where higher net energy gains indicate more efficient feeding. In the simple environment, N. glauca is clearly most efficient in feeding on Musca prey at all levels of biomass of food presented. At low levels of biomass, this predator appears more efficient at feeding on mosquito prey than on Gammarus, but at higher biomass levels, where there are no data on mosquito larvae, net energy gains on Gammarus increase to the levels found on mosquito larvae at low density. In the complex environment, a markedly different picture becomes apparent, with no differences between Musca and Gammarus prey. N. glauca is least efficient feeding on mosquito larvae at the

LEGEND TO FIGS 27 and 28

A comparison of the net energy gains by N. glauca feeding on each prey type plotted against total biomass presented in both environments.

95% confidence limits shown.

▲ Musca

△ Gammarus

● Mosquito larvae

Fig. 27 Complex environment

Fig. 28 Simple environment

FIG 27 N. glauca feeding in the complex enviroment

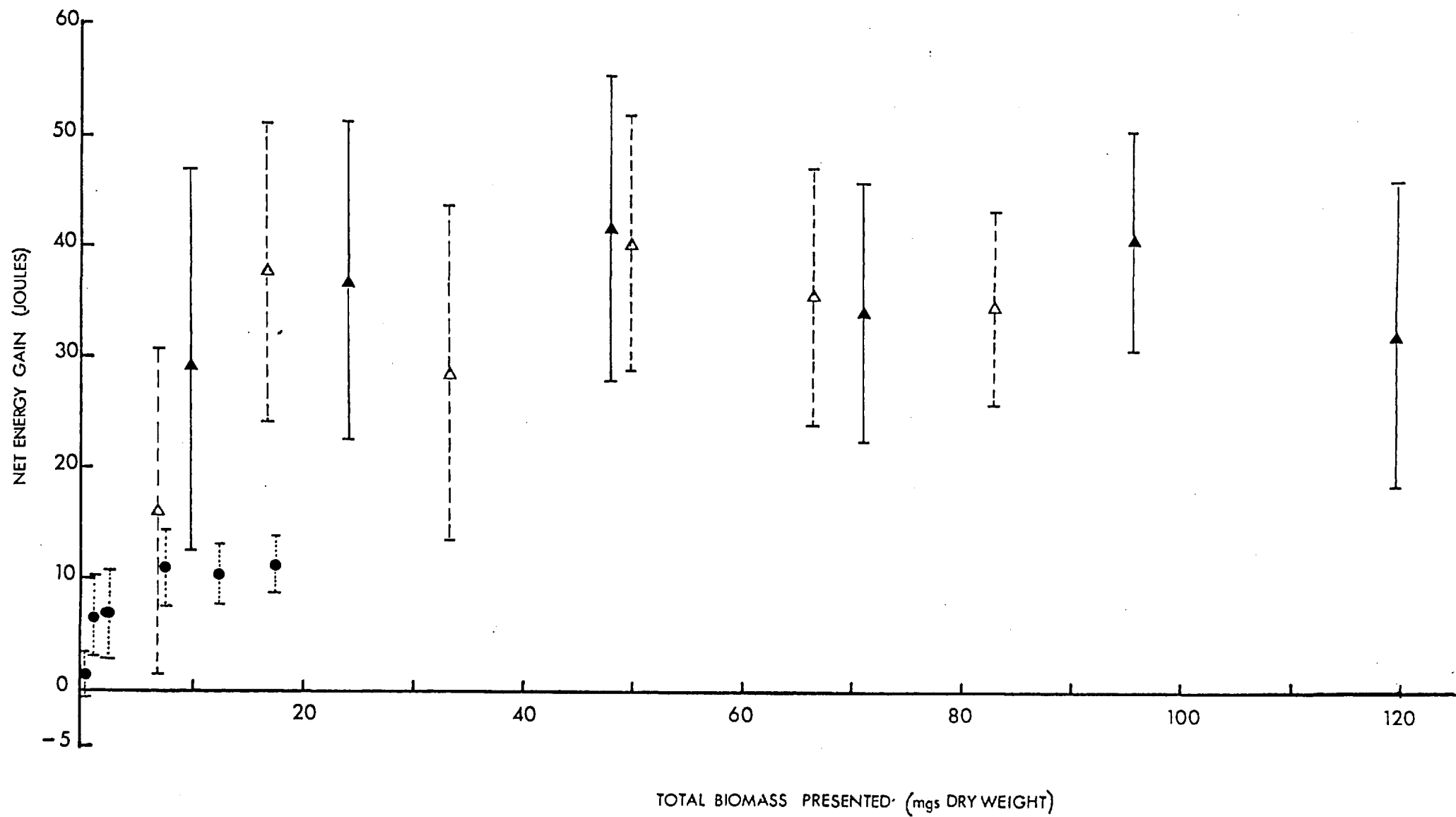
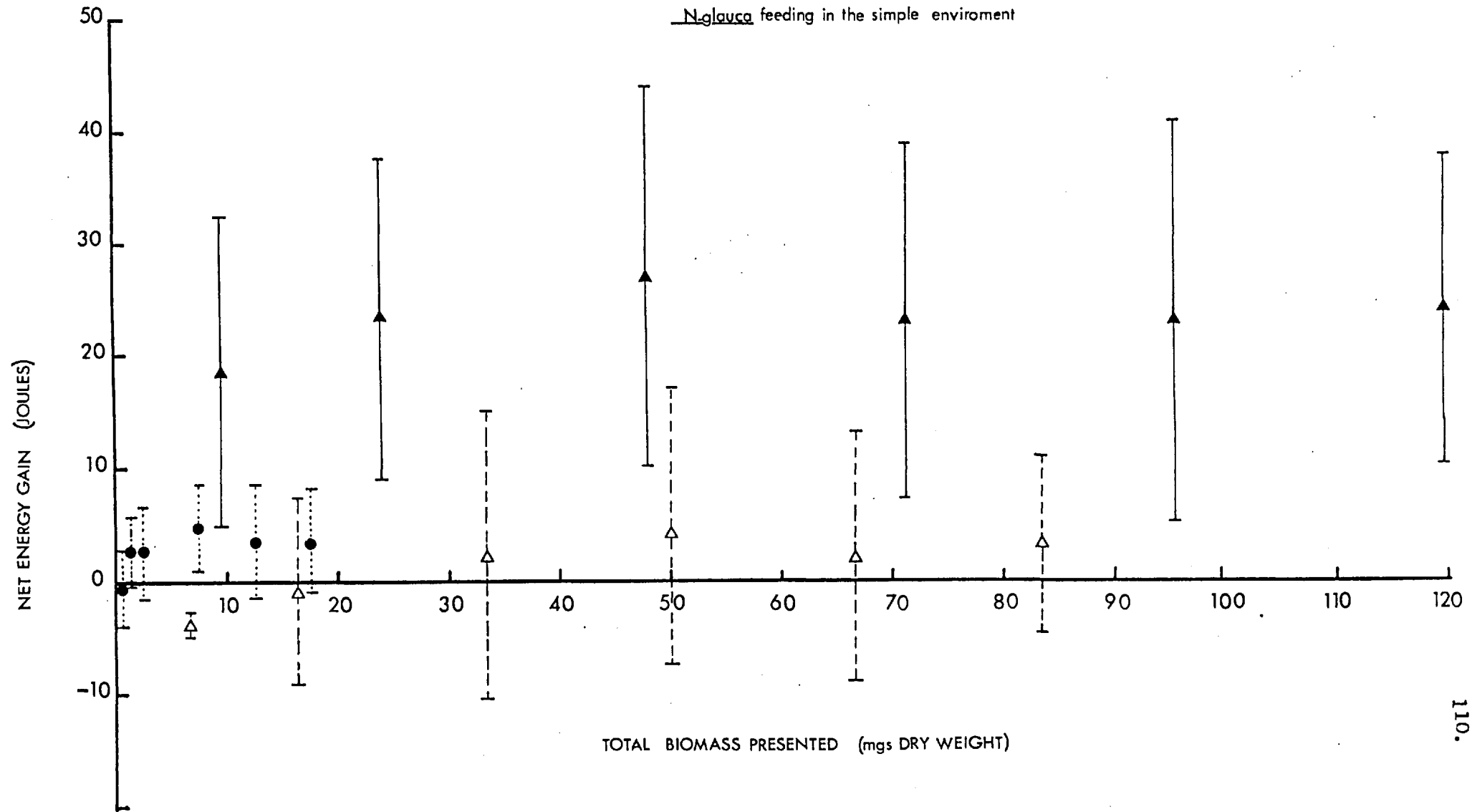


FIG 28

N. glauca feeding in the simple enviroment



biomasses presented of this prey.

$\frac{E}{T}$ values (Schoener (1971)), support the conclusions of section b) and c) (Table 3.2.).

III. 4.3.3. Net Energy gains by *N. maculata* (Figs. 29, 30, 31, 32 and 33)

a) The Effect of Prey Density

Generally, the effect of prey density is similar to that for *N. glauca*. With *Musca* prey in the complex environment, no differences are apparent ($F = 0.5664$), but in the simple environment, it appears that net energy gains with density 2 are larger than with densities 25, 20 and 5 per arena, but not with densities 10 and 15. There are no significant differences between data from the other five densities. This points to the possibility of confusion effects on the predator when presented with high densities of this prey in the simple environment.

There appears to be little density effects for *N. maculata* feeding on *Gammarus* in the simple environment, although the net energy gains at prey density 2 are the lowest. In the complex environment, this difference is more marked, with significant values between density 2 and densities 10 and 20.

As with *N. glauca*, the density effect is most marked with mosquito prey. There is a general trend for increased net energy gains with increased prey density for data from both environments. In the simple environment, the data with density 2 shows the lowest values, the data for densities 10 to 70 per arena the highest (there being no significant differences between these sets of data). In the complex environment, the differences are even more marked, with largest net energy gains at densities 30, 50 and 70 per arena, and a significant decrease in net energy gains with decreasing density through 10, 5 and 2 per arena.

b) The Effect of Environmental Complexity

The reverse effect of environmental complexity is apparent with *N.*

LEGEND TO FIG. 29

Net energy gains by N. maculata feeding on 6 densities of Musca domestica prey in simple (□) and complex (■) environments. 95% confidence limits shown.

Simple environment - analysis of variance for data of all 6 densities.

$$F = 0.982 \text{ (n.sig)}$$

Comparison of means by T test

$$\frac{2 \quad 10 \quad 15 \quad 25 \quad 20 \quad 5}{\text{---}} \text{ (sig 0.1)}$$

Complex environment - analysis of variance for data of all 6 densities.

$$F = 0.5664 \text{ (n.sig)}$$

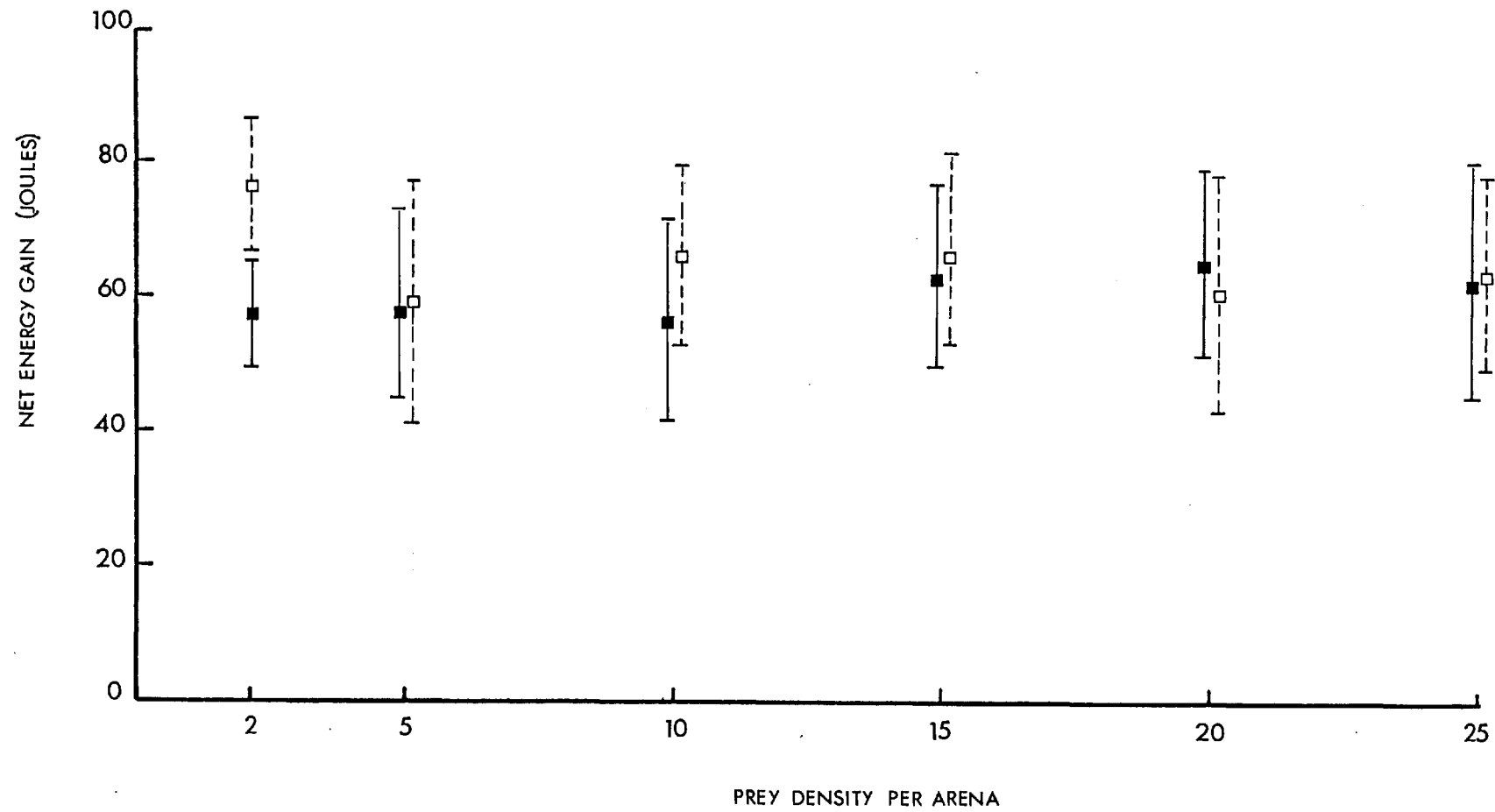
Comparison of simple and complex environments for 6 densities

T test

Density	25	20	15	10	5	2
T =	0.096	0.493	0.365	1.14	0.118	3.416
Significance =	n.sig	n.sig	n.sig	n.sig	n.sig	0.01

FIG 29

N. maculata feeding on Musca domestica



LEGEND TO FIG. 30

Net energy gains by N. maculata feeding on 6 densities of Gammarus pulex in simple (□) and complex (■) environments. 95% confidence limits shown.

Simple environment - analysis of variance of data for all 6 densities

$$F = 1.180 \quad \text{n.sig}$$

Comparison of means by T test (sig. 0.05)

<u>15</u>	<u>25</u>	<u>20</u>	<u>10</u>	<u>5</u>	2
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Complex environment - analysis of variance of data for all 6 densities

$$F = 2.433 \quad (\text{sig. } 0.05) \quad (\text{LSR} = 8.058)$$

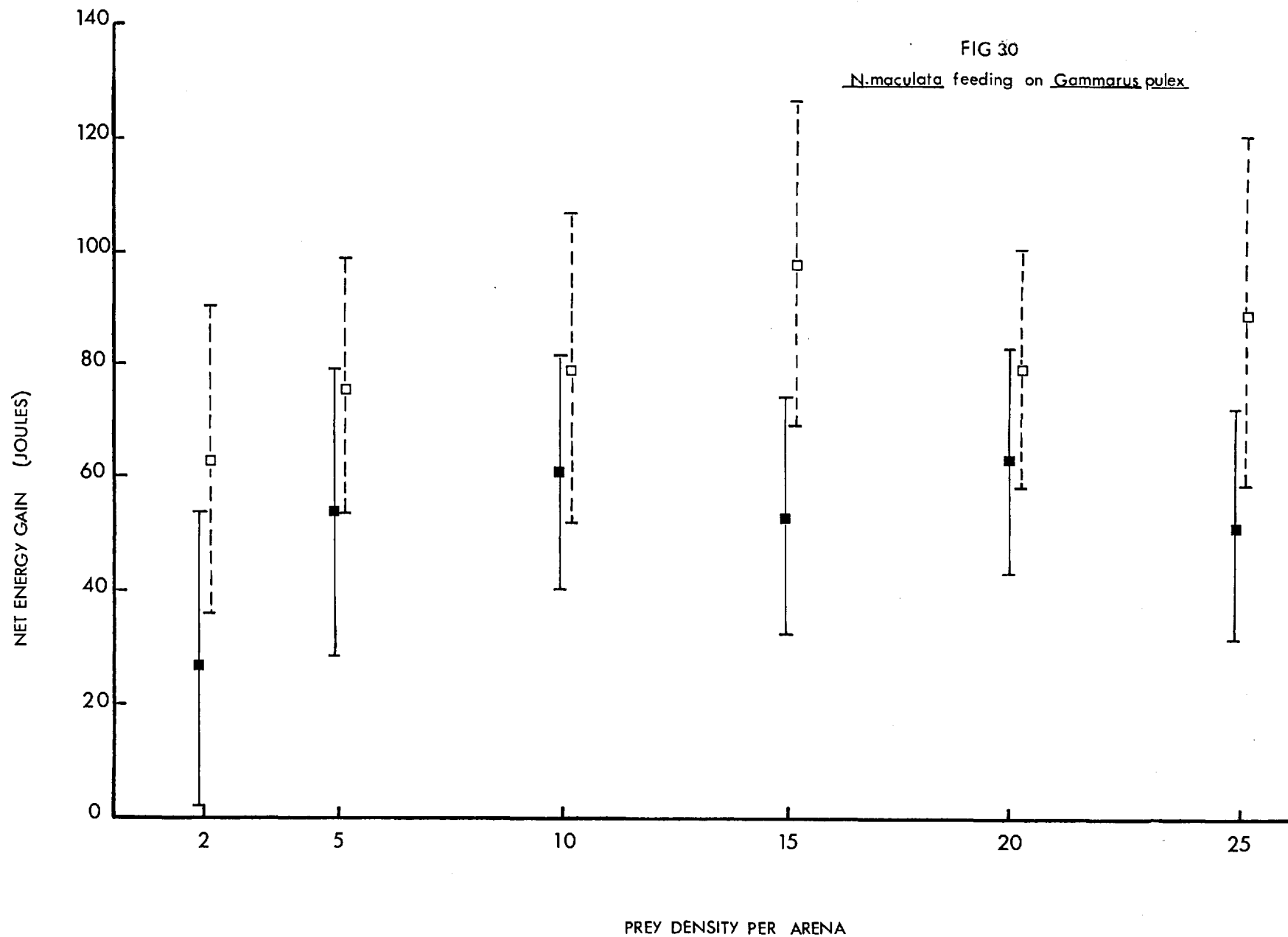
Comparison of means by T test (sig. 0.05)

<u>20</u>	<u>10</u>	<u>15</u>	<u>25</u>	<u>5</u>	2
-----------	-----------	-----------	-----------	----------	---

Densities underlined not significantly different.

Comparison of simple and complex environments at each density
T test

Density	25	20	15	10	5	2
T =	2.34	1.29	2.89	1.23	1.577	2.174
Significance	0.05	n.sig	0.02	n.sig	n.sig	0.05



LEGEND TO FIG. 31

Net energy gains by N. maculata feeding on 6 densities of Aedes aegypti larvae in simple (□) and complex (■) environments.

95% confidence limits shown.

Simple environment - analysis of variance for data of all 6 densities

$$F = 5.235 \text{ (sig 0.01) (LSR = 2.946)}$$

Comparison of means by T test (sig. 0.05)

<u>70</u>	<u>50</u>	<u>30</u>	<u>10</u>	5	2
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Complex environment - analysis of variance for data of all 6 densities

$$F = 12.489 \text{ (sig. 0.001) (LSR = 1.734)}$$

Comparison of means by T test (sig 0.05)

<u>50</u>	<u>30</u>	<u>70</u>	10	5	2
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Densities underlined not significantly different.

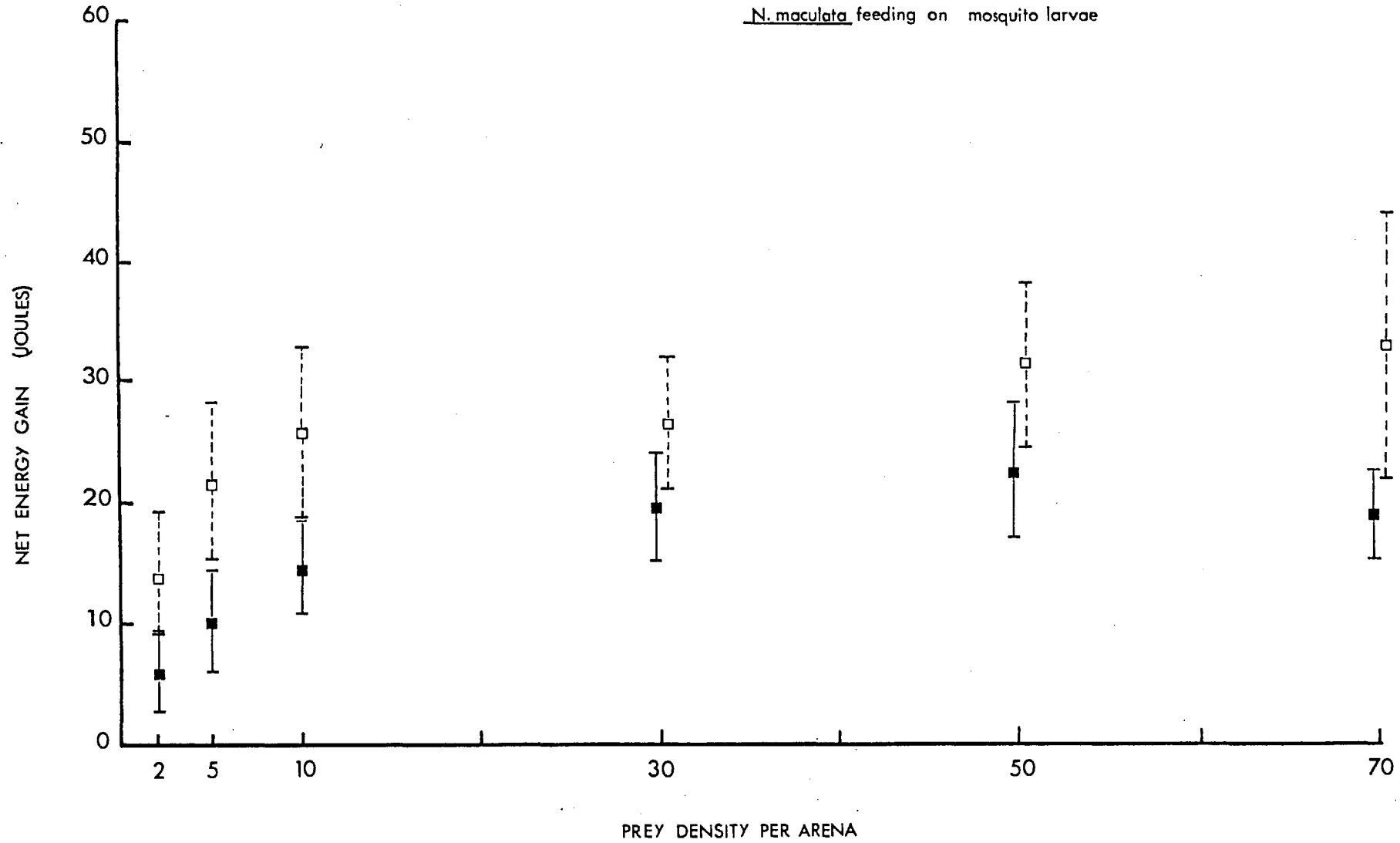
Comparison of simple and complex environments

T test

Density	70	50	30	10	5	2
T =	2.748	2.266	2.24	3.21	3.46	2.988
Significance	0.02	0.05	0.05	0.01	0.01	0.01

FIG 31

N. maculata feeding on mosquito larvae



LEGEND TO FIGS 32 and 33

A comparison of the net energy gains by N. maculata on each prey type plotted against total prey biomass presented in the two environments.

95% confidence limits shown.

▲ Musca prey

△ Gammarus prey

● Mosquito prey

Fig. 32 Simple environment

Fig. 33 Complex environment

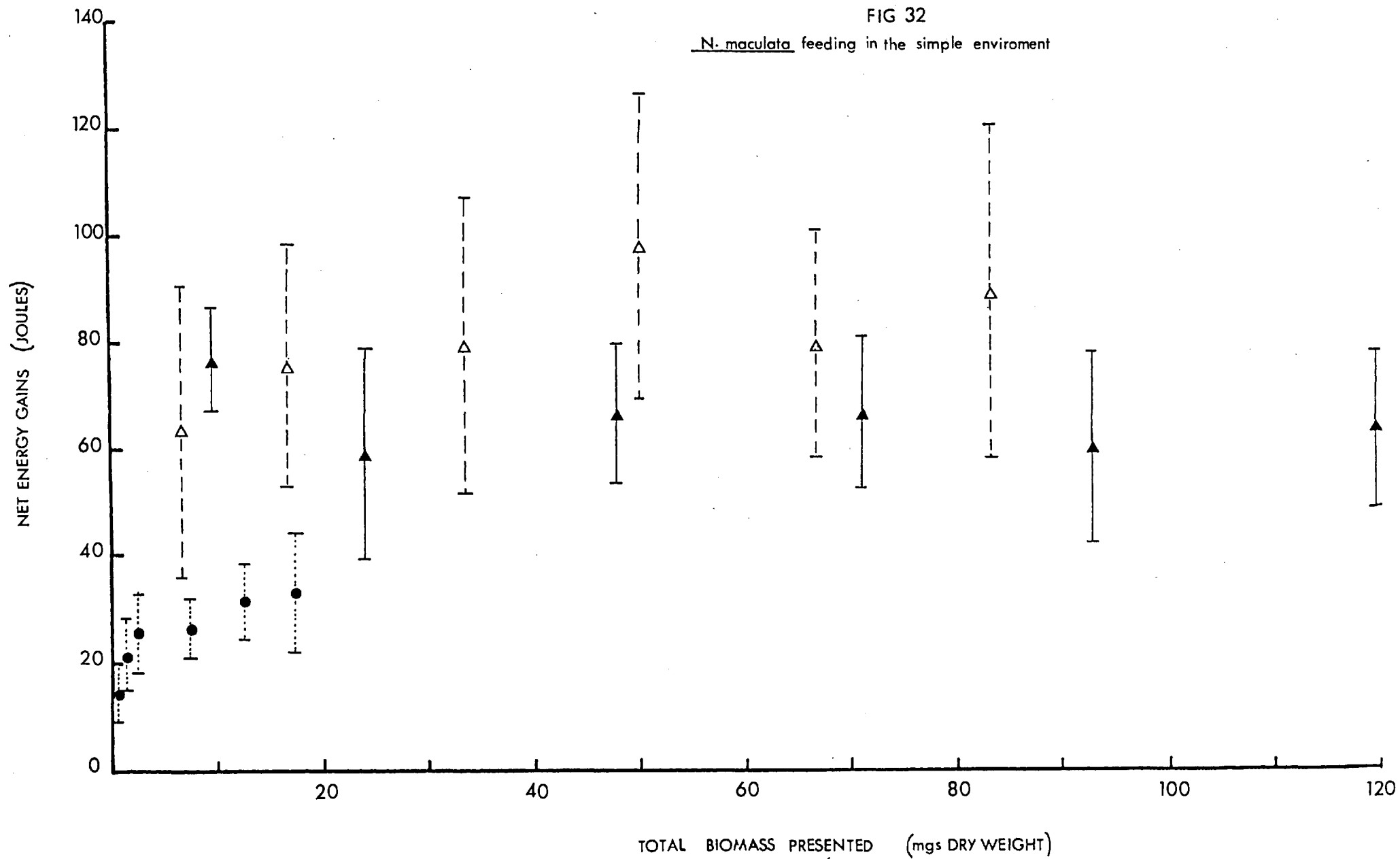
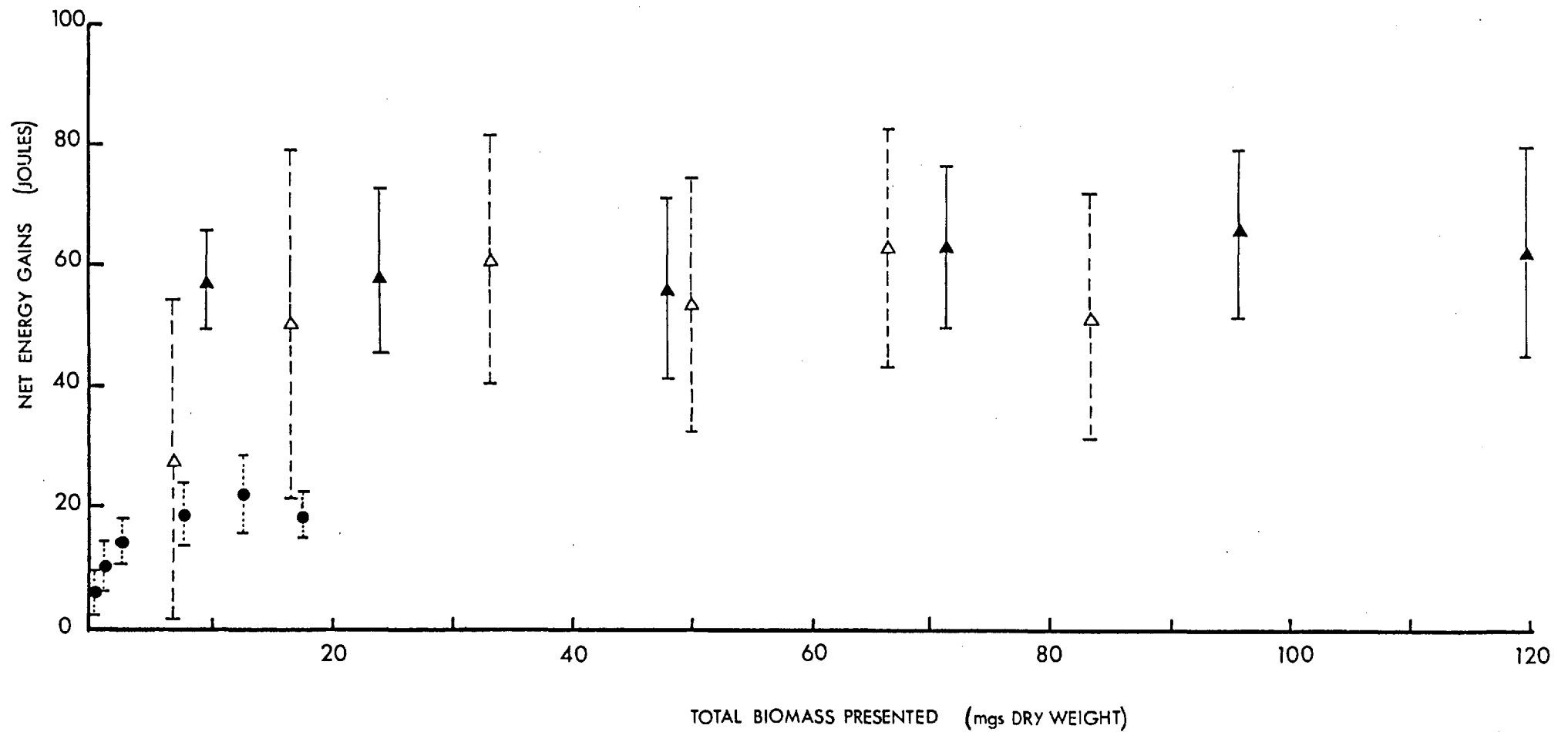


FIG 33

N. maculata feeding in the complex enviroment



maculata than was found with N. glauca, as there is a general trend for larger net energy gains in the simple environment than in the complex one. This is most marked for mosquito prey, where values for net energy gains at all densities are significantly larger in the simple environment. With Gammarus prey, significant differences were found at densities 25, 15 and 2 per arena, although the same trend is apparent for the other densities. The data with Musca prey shows no differences except at density 2. The data for the other five densities is virtually identical in the two environments.

c) The Effect of Prey Type

In the complex environment, there is very little difference in the efficiency of N. maculata feeding on Musca or Gammarus in situations where large values of prey biomass are presented (i.e. ≥ 15 mg dry weight). With low biomass values (10mg), N. maculata tends to be more efficient feeding on Musca, and there is little difference between Gammarus and mosquito larvae as food. The $\frac{E}{T}$ values tell a slightly different tale (Table 3.2), being largest at all densities for Gammarus prey and smallest for mosquito larvae.

In the simple environment, a slightly more complex picture is found when considering net energy gains. The predator is again least efficient feeding on mosquito prey. At low prey biomass values (7-20 mg dry weight), there appears to be little difference in efficiency between feeding on Musca and Gammarus by N. maculata. At biomass values above this, there is a general trend for larger net energy gains feeding on Gammarus prey. The $\frac{E}{T}$ values again show Gammarus as the most efficient prey and mosquito larvae the least efficient.

III. 4.3.4. Net Energy Gains by N. obliqua (Figs. 34, 35, 36, 37 and 38).

a) The Effect of Prey Density

The effects of density of Musca prey are similar to those of N. glauca.

LEGEND TO FIG. 34

Net energy gains by N. obliqua feeding on six densities of Musca domestica compared between complex (■) and simple (□) environments.

Simple environment - analysis of variance between all six densities

$F = 0.56$ (n.sig)

Complex environment - analysis of variance between all six densities

$F = 3.3298$ (sig. 0.05)

T test comparison between means

15 5 10 25 20 2 (sig. 0.05)

Densities underlined not significantly different.

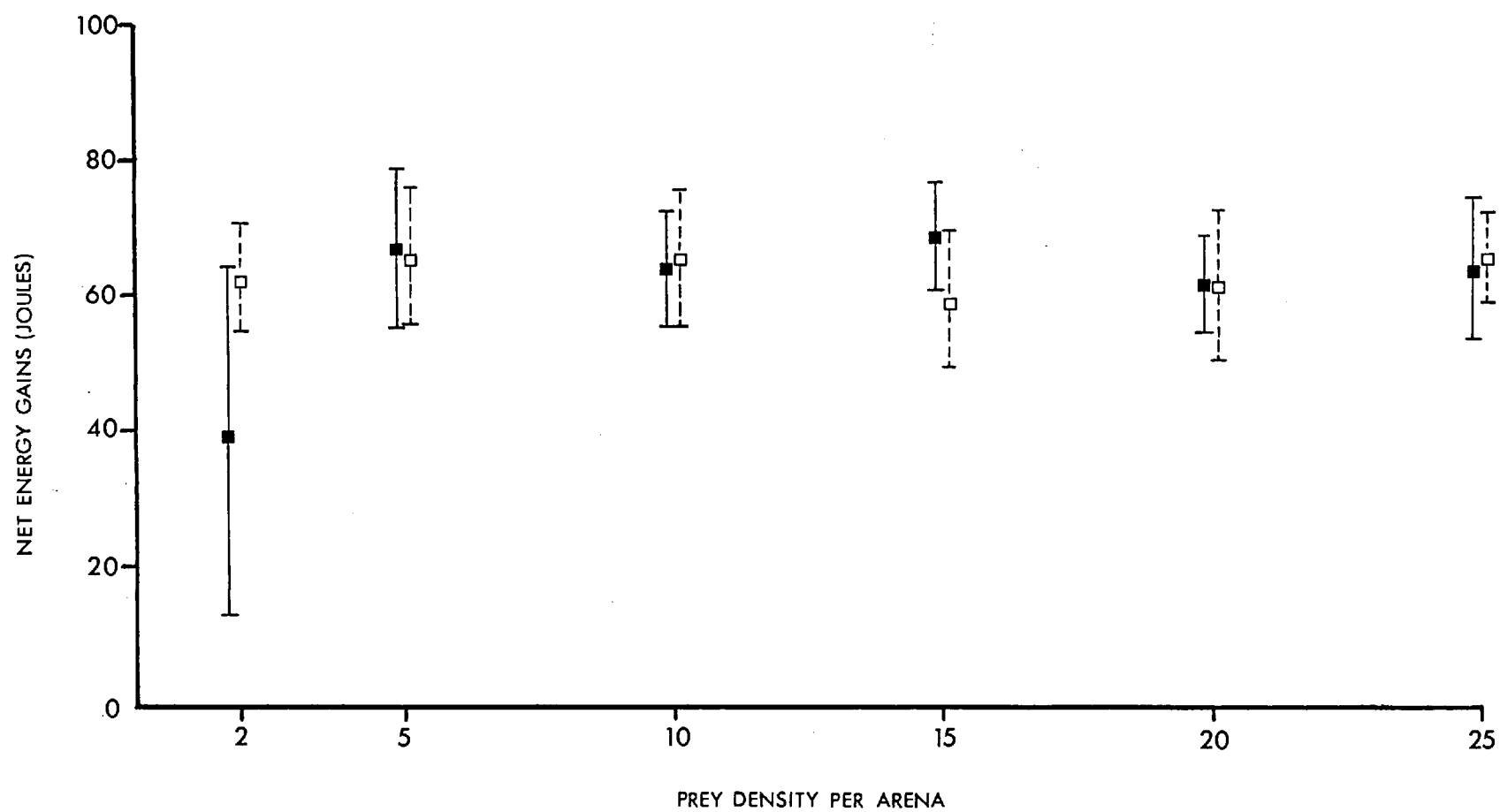
Comparison between simple and complex environment

T test

Density	25	20	15	10	5	2
T =	0.326	0.024	1.757	0.218	0.174	1.971
Significance	n.sig	n.sig	0.1	n.sig	n.sig	0.1

FIG 34

N. obliqua feeding on Musca domestica



LEGEND TO FIG. 35

Net energy gains by N. obliqua feeding on six densities of Gammarus pulex prey, compared between complex (■) and simple (□) environments.

Simple environments - analysis of variance between all six densities

$$F = 6.578 \quad \text{sig } 0.01$$

T test differences between means

<u>15</u>	<u>25</u>	<u>20</u>	10	5	2	(sig 0.05)

Complex environments - analysis of variance between all six densities

$$F = 1.14 \quad \text{n.sig.}$$

T test differences between means

<u>15</u>	<u>25</u>	<u>10</u>	<u>20</u>	<u>5</u>	<u>2</u>
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Densities underlined not significantly different.

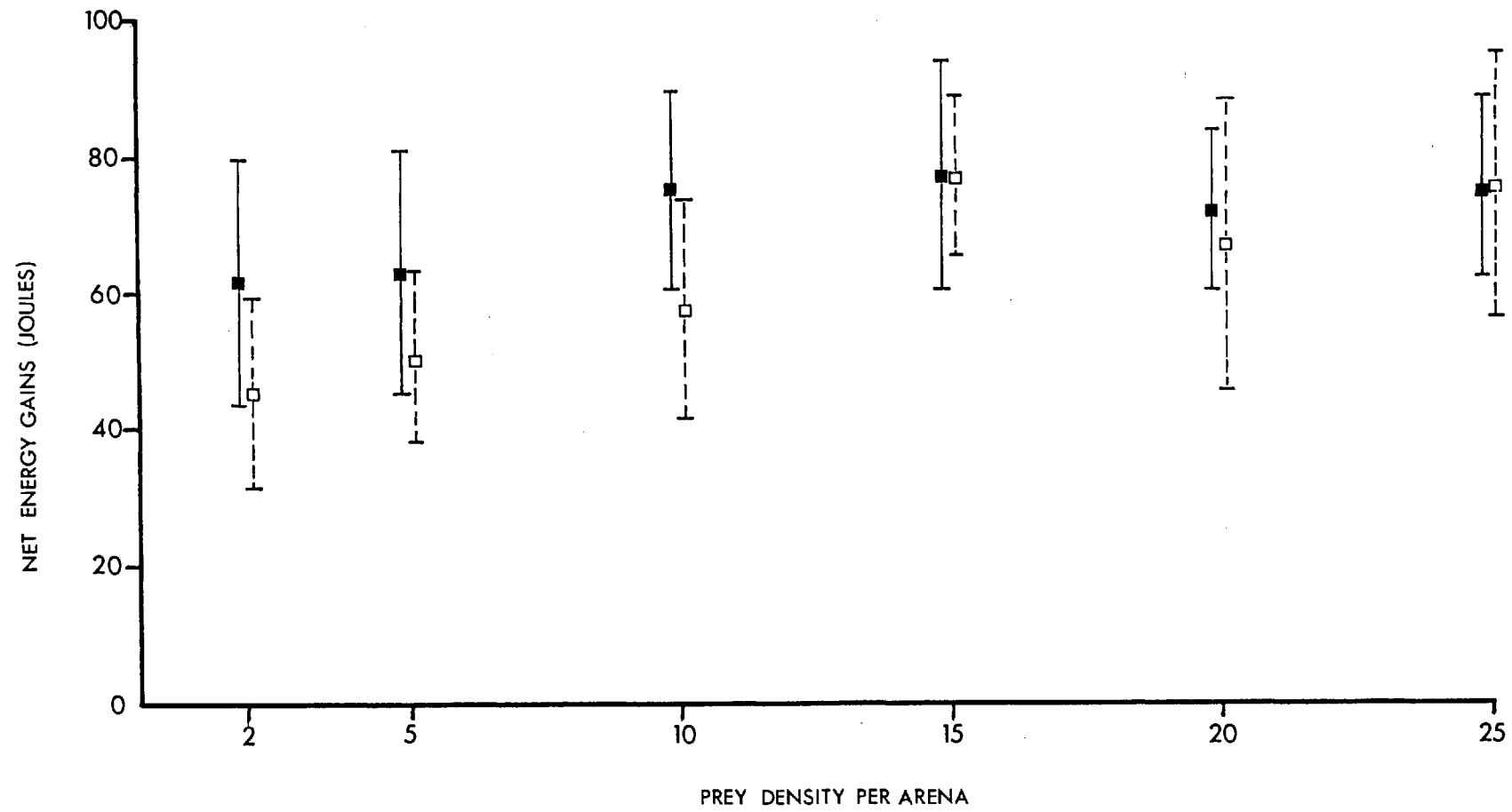
Comparison between simple and complex environment.

T test

Density	25	20	15	10	5	2
T =	0.05	0.463	0.018	1.89	1.368	1.66
Significance	n.sig	n.sig.	n.sig	0.1	n.sig	n.sig

FIG 35

N.obliqua feeding on Gammarus pulex



LEGEND TO FIG. 36

Net energy gains by N. obliqua feeding in six densities of mosquito larvae compared between complex (■) and simple (□) environments.

Simple environment - analysis of variance between all six densities.

$$F = 29.93 \text{ (sig 0.01) (LSR = 1.199)}$$

T test comparison between means

$$\underline{70} \quad \underline{30} \quad \underline{50} \quad \underline{10} \quad \underline{5} \quad 2 \quad (\text{sig. 0.05})$$

Complex environment - analysis of variance between all six densities

$$F = 15.18 \text{ (sig. 0.01) (LSR = 1.821)}$$

T test comparison between means

$$\underline{50} \quad \underline{70} \quad \underline{30} \quad \underline{10} \quad \underline{5} \quad 2 \quad (\text{sig. 0.01})$$

Densities underlined not significantly different.

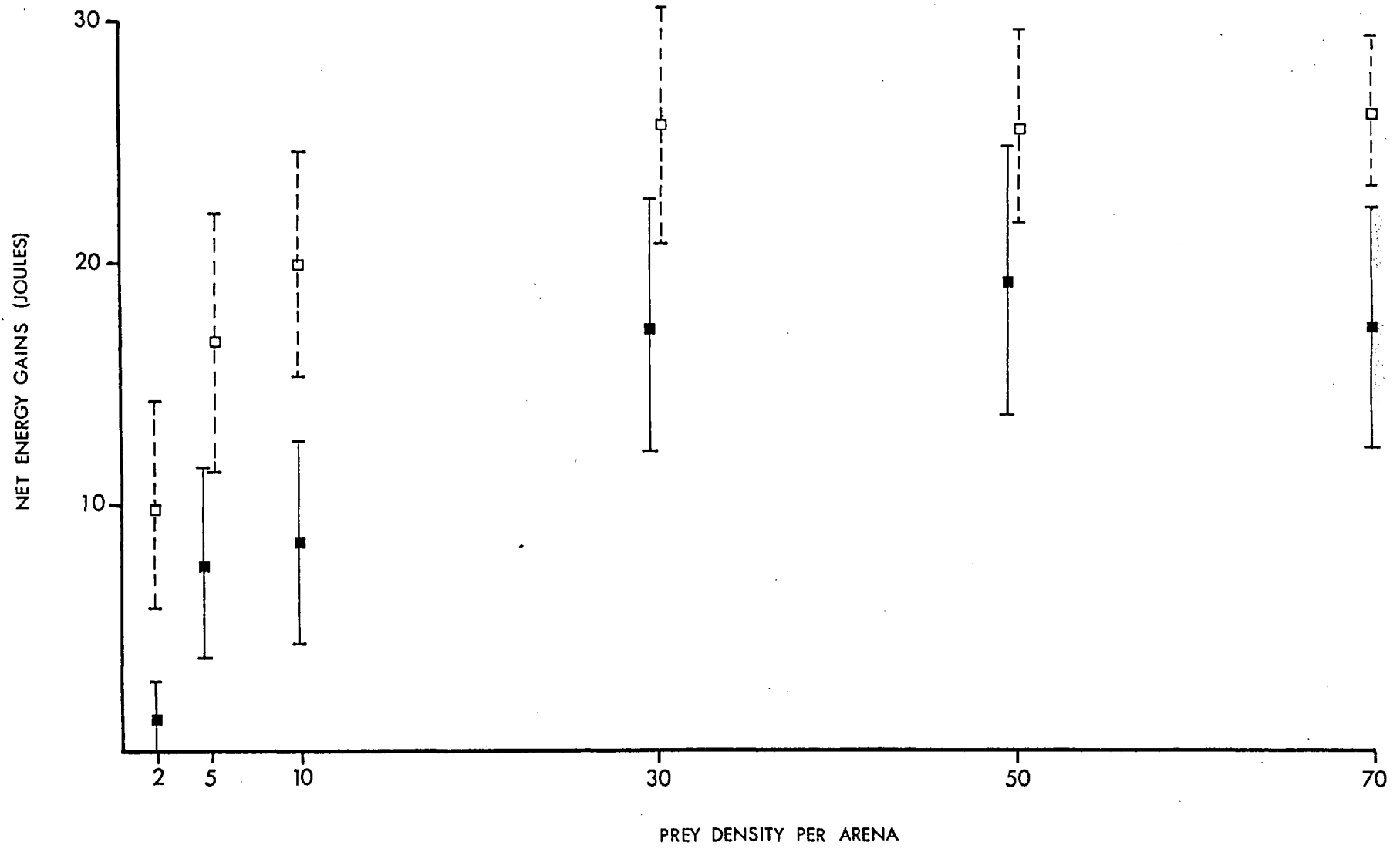
Comparison between simple and complex environments

T test

Density	70	50	30	10	5	2
T =	3.493	2.143	2.671	4.199	3.147	4.28
Significance	0.01	0.05	0.02	0.001	0.01	0.001

FIG 36

N. obliqua feeding on mosquito larvae



In the simple environment there is no effect at all ($F = 0.56$), but in the complex one ($F = 3.33$), net energy gains are significantly the lowest at density 2, with no differences between the other densities. The results for N. obliqua feeding on Gammarus prey are different from both of the other predator species. In the complex environment, due to large confidence limits, there is no significant effect of prey density, but the mean net energy gains at the lowest two densities have the lowest values. In the simple environment, this effect is more pronounced, with increases in net energy gains from densities 2 through to 15, then a slight drop for densities 20 and 25 per arena. Results with density 15 are significantly larger than for densities 10, 5 and 2, results for density 25 significantly higher than for densities 5 and 2, and those for density 20 significantly higher than for density 2. There are no significant differences between densities 10, 5 and 2.

As with the other two predators species, the clearest density effect is found with mosquito prey. In both environments, there is a progressive increase in net energy gains with increased prey density, up to density 30 in the simple environment, and density 50 in the complex one. In the simple environment there is no effect at higher densities, in the complex one, there is some evidence of a slight drop in energy gains at the highest density. In both environments, the data appears to be divided into three levels, density 2, densities 5 and 10, and densities 30, 50 and 70 per arena.

b) The Effect of Environmental Complexity

The results for N. obliqua appear to fall inbetween the other two species, where N. glauca achieved larger net energy gains in the complex environment, and N. maculata in the simple one. For N. obliqua, feeding on Musca, there is virtually no difference except for prey density 2 where larger net energy gains were made in the simple environment and

LEGEND TO FIGS 37 and 38

A comparison of the net energy gains by N. obliqua feeding on all prey types in both environments plotted against total biomass presented.

95% confidence limits shown.

▲ Musca

△ Gammarus

● mosquito larvae

Fig. 37 Complex environment

Fig. 38 Simple environment

FIG 37

N. obliqua feeding in complex enviroment

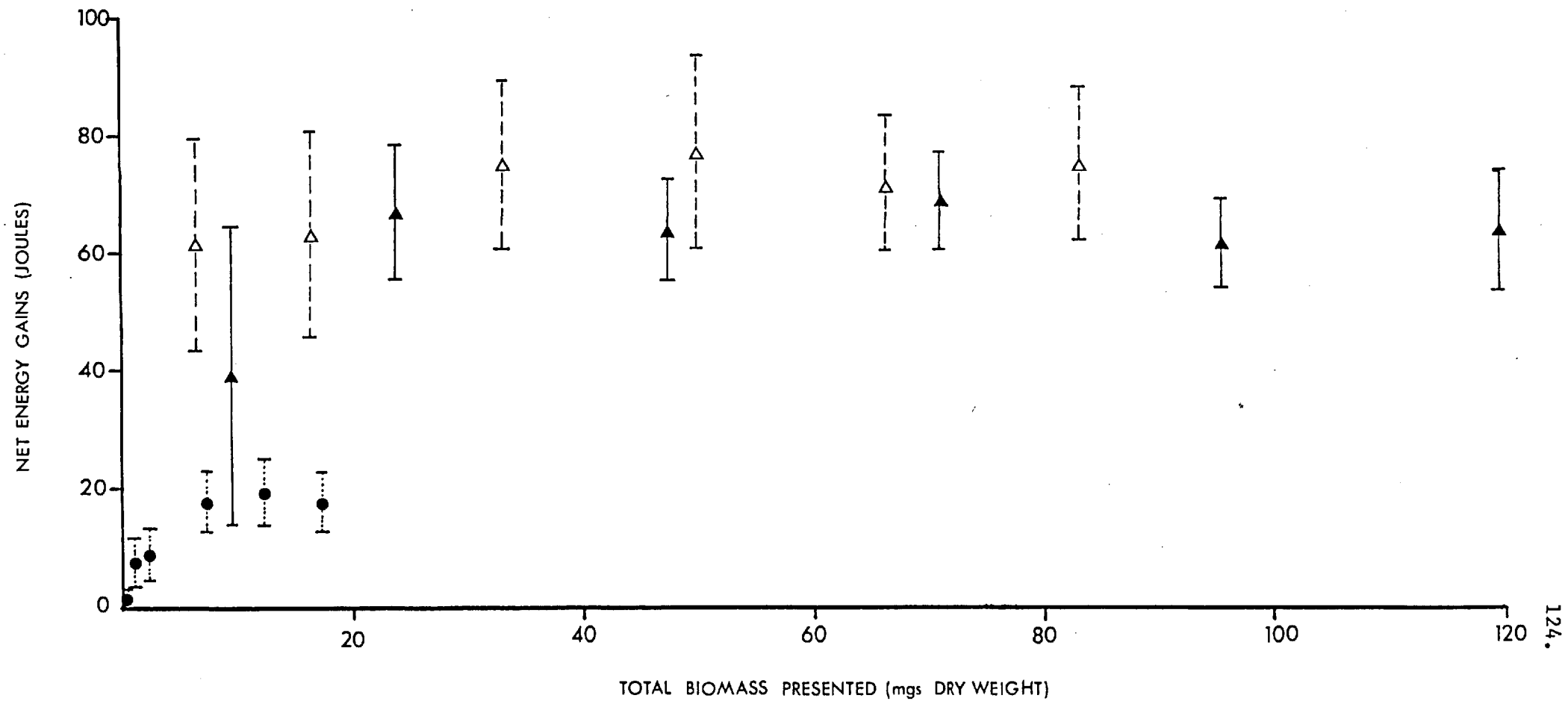
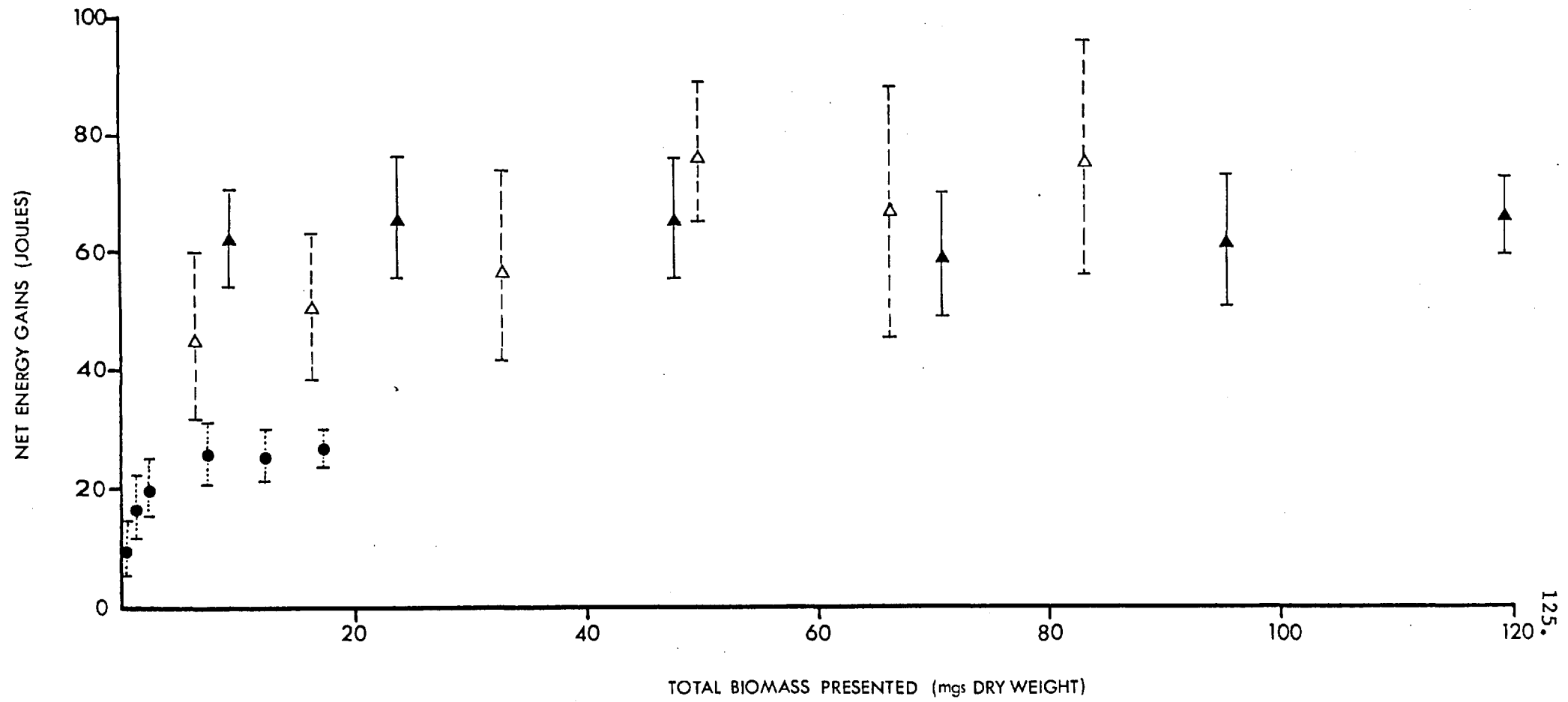


FIG 38

N. obliqua feeding in simple enviroment



at density 15, where the reverse was true. For Gammarus prey, there is no difference at the highest densities (15, 20 and 25 per arena), but at lower densities, there is a general trend for larger energy gains in the complex environment (only significantly so at density 10). The opposite is found with mosquito prey, where significantly larger net energy gains are made at all densities in the simple environment. The $\frac{E}{T}$ values (Table 3.2) are virtually identical for Musca in both environments and slightly larger for both Gammarus prey and mosquito prey in the simple environment.

c) The Effect of Prey Type

Different patterns emerge in the two environments. In the complex one, there is a general trend for more efficient feeding on Gammarus prey than on Musca, which is more marked at prey biomasses below 50 mg dry weight. (This is supported by the $\frac{E}{T}$ value). In the simple environment, at prey biomasses below 40 mg, N. obliqua appears to be more efficient feeding on Musca than on Gammarus, but at higher prey biomasses, this efficiency tends to switch, with slightly larger gains on Gammarus. $\frac{E}{T}$ values are largest for Gammarus at all densities. In both environments mosquito larvae offer the poorest food returns.

III. 5.

Summary

For N. glauca, there is no effect of prey density on net energy gains with Musca prey in either environment, significantly lower net energy gains are made in low densities of Gammarus, and increased net energy gains are made with increased prey densities of mosquito larvae up to a plateau at density 30. $\frac{E}{T}$ values are somewhat different, with no effects of density on Musca or Gammarus prey in the complex environment, but a tendency for lower values with decrease in prey density for mosquito larvae in the complex environment and all three prey types in the simple one. There is a general trend for increased feeding

efficiency in the complex environment both in terms of net energy gains and $\frac{E}{T}$ values, the differences most marked for Gammarus prey and least so for Musca. N. glauca is most efficient on Musca prey in the simple environment (in terms of net energy gains and $\frac{E}{T}$ values), and at low prey biomasses, more efficient in terms of net energy gains and $\frac{E}{T}$ values on mosquito larvae than on Gammarus. As biomass is increased, net energy gains on Gammarus reach those of mosquito larvae at the low biomasses, and $\frac{E}{T}$ values exceed them. In the complex environment, net energy gains on Musca and Gammarus are similar, but $\frac{E}{T}$ values are larger with Gammarus.

For N. maculata, there is again no effect of prey density of Musca in the complex environment, but in the simple one, larger gains are made at the lowest density, although $\frac{E}{T}$ values tend to be lower at the lower densities than at the higher ones. With Gammarus prey, again lower energy gains are made at low densities and increased energy gains occur with increased mosquito density up to a plateau, which is reached at a lower density in the simple (density 10) than in the complex (density 30) environment. $\frac{E}{T}$ values show similar trends. In contrast to N. glauca, N. maculata generally achieves larger energy gains in the simple than in the complex environment, this being most marked for mosquito prey and least so for Musca, these conclusions supported by $\frac{E}{T}$ values. In both environments N. maculata is least efficient feeding on mosquito larvae. In the complex environment, at low prey biomasses larger energy gains are made feeding on Musca than on Gammarus, with larger prey biomasses in the complex and low biomasses in the simple environment, there is little difference, and finally in high prey biomasses in the simple environment, N. maculata makes larger net energy gains on Gammarus. The $\frac{E}{T}$ values show feeding on Gammarus to be the most efficient under all conditions, and on mosquito larvae the least efficient.

As mentioned earlier, N. obliqua tends to lie between these two

sets of results. There is no density effect with Musca in the simple environment, but low densities of Musca offer the lowest returns in the complex one. There are basically no differences in $\frac{E}{T}$ values in both environments. There is a tendency for increased energy gains with increased Gammarus density in both environments, this being more pronounced in the simple environment. $\frac{E}{T}$ values tend to support this conclusion. As with the other two predators, energy gains increase with mosquito prey density, but with N. obliqua the plateau is reached at 30 per arena in the simple, and at 50 in the complex. (The differences between the prey densities at which the three predators reach a plateau of net energy gains feeding on mosquito larvae can be explained on the basis of size of reaction areas (see Chapter IV)). The effect of environmental complexity is also different from the other two predators. For Musca prey and high densities of Gammarus, there is little effect on energy gains, but for low densities of Gammarus larger gains appear in the complex environment, and for mosquito larvae, larger gains appear in the simple one. $\frac{E}{T}$ values again tend to support these conclusions, except there is a trend for larger values at low densities of Gammarus in the simple than in the complex environment. The trend is for larger energy gains feeding on Gammarus than on Musca in the complex environment, especially at lower prey biomasses, which is also found, but to a lesser degree, at high biomasses in the simple environment. At low biomasses in this environment, N. obliqua appears to make larger gains feeding on Musca, and in both environments, it is least efficient feeding on mosquito larvae. The $\frac{E}{T}$ values again show greatest efficiency of feeding on Gammarus prey under all conditions, and lowest on mosquito prey.

Comparing the energy gains made by the three predators, the general trend is for N. maculata to make the highest gains in the simple

environment, N. obliqua the highest gains in the complex one, and N. glauca to show the lowest gains in both environments.

Prey density effects can be explained on the basis of the prey size/handling time relationship in short term experiments, and the size of the predator's reaction area. Also the effects of prey refuges, search image formation and prey availability in the predators preferred areas of the environment, play a role (especially with mosquito larvae and Gammarus prey). The effects of environmental complexity will be due more to the morphology and behaviour of the predator, and the effects of prey type can be explained on the basis of prey size and the nature of the predators extraction curves (All of which are discussed in later chapters).

CHAPTER IV

BEHAVIOURAL STRATEGIES

IV. 1.

Introduction

One of the best ways an animal can exploit a habitat is to utilise a resource not being used to capacity by other organisms in the habitat. Notonectids have done this by utilising their abilities to feed at the water's surface, on organisms coming up to the surface from deeper areas, or terrestrial organisms falling onto the surface. There are very few other invertebrates which can utilise this resource (e.g. raft spider Dolomedes, the Amphibicorisae etc), and several species of fish, to which in fact, Notonectids offer a food source (Macan (1965)). Some Notonectid species also utilise additional sources of food, by apparently actively searching for food along the bottom, or intercepting organisms within the water column (Ellis and Borden (1970)). These authors described four general methods by which Notonectids obtain their food.

The first involves the Notonectid catching prey while swimming in an inverted position (i.e. dorsal side uppermost), along the arena bottom, often using a jerking, probing motion, which flushes out potential prey organisms. The prey are disturbed by this behaviour and swim away, the predator often pursuing them. Lawton, Beddington and Bonser (1974) also show that N. glauca uses this method to hunt Asellus, which walk slowly on the substrate. In both studies, no perch sites were available to the predator. From observations during this present study, this mode of prey capture appears to be spurious, as the probing action shown by the Notonectid in the inverted position is associated with search for a perch site. Similar actions were observed down the arena sides in arenas with very few available perch sites, and in most instances, chance meetings of prey by this method are ignored by the

predator. It is quite likely that a stationary prey item is treated as a potential perch site rather than food in such encounters. Active prey, such as Mayfly nymphs (Lawton et al (1974)) and Gammarus (pers. obser.) are very rarely caught by this method.

The second method of attack is by a Notonectid from its vantage point at the surface, or on a perch site within the water body, on a prey swimming past it. Ellis and Borden describe pursuit and capture of such prey as semi-stalking behaviour, and it is used in the capture of Aedes larvae (Ellis and Borden (1970)), Mayfly nymphs (Lawton et al (1974)) and Gammarus (pers. observ.)

The third method of capture occurs when the predator is at the surface and actively stalks a prey which has just risen to the surface for air or rest. The predator will orientate to the direction of disturbance of the water surface, and slowly stalk the prey. Depending on the distance, the prey is reached in one or several movements (Murphey and Mendenhall (1973), Wolda (1961)), and is then attacked in a swift lunge. Ellis and Borden report that the predator rarely misses a prey during this form of attack.

The fourth method involves exploitation of prey trapped in the water surface e.g. dipterans emerging from pupae or terrestrial insects falling onto the surface. The struggles of the prey, or the dark silhouette (Gittleman (1973)), attract the Notonectid, which follows a similar series of movements to those described above. Unless the prey item is large, this form of attack is usually entirely successful.

It is likely that each species of Notonecta specialises in different combinations of feeding behaviour mechanisms, which may allow exploitation of slightly different types of habitat or food resources. The three species of Notonecta under study are remarkably similar in form, and it is likely that any such behavioural differences between

them, will show themselves in rather subtle ways. The easiest way of assessing such differences is by continuous observations on the predators in the presence of food. A component analysis approach was used (Holling (1966)), recording various behavioural components associated with actual feeding as well as 'background' behaviour such as rest and other activity not necessarily associated with feeding. The behavioural strategy can be conveniently divided into three broad components; a) Use of time; b) Response to prey; and c) Use of space.

Table 4.1 lists the different behavioural activities monitored, either on the event recorder (E) or by simply noting activities (N).

Table 4.1

<u>Use of Time</u>	<u>Use of Prey</u>	<u>Use of Space</u>
Handling Time (E)	Success of pursuits (E)	Selection of perch sites (N)
Total Rest Time (E)	Success of attacks (E)	Time of rest at surface (E)
Activity not associated with feeding (E)	Success of captures (E)	Time of rest at depth (E)
Activity during Handling (E)	Types of attack sequence (E)	Handling time at surface (E)
Time for attack sequence (E)	Size of reaction area (N)	Handling time at depth (E)
	Functural response (E)	Position from where attack sequence initiated (N)

Behavioural activities monitored during continuous observation experiments on the event recorder (E) or noting activities (N).

A more detailed description and discussion of the activities is presented in the following sections. The data are presented for

each predator species feeding on each prey type at different densities in each of the two types of environment. In addition, two other experiments were carried out, one to examine the effect of the lighting regime on feeding levels, and the other to examine feeding on two types of Daphnia magna occupying different areas in the water column.

IV. 2. The Use of Time.

In order to examine extraction rates for each prey type, handling time must be measured for every prey item caught. Calculation of energy losses necessitates the measurement of total time active (as discussed in Chapter III), which includes not only activity involved in the pursuit of prey, but also general activity and activity during feeding. Allocation of time to feeding, activity and rest may well be different between the three species, and in different environments, so records of rest periods are also required.

IV. 2.1. Handling Time.

IV. 2.1.1. Introduction.

The original definition of handling time included time from first response to the prey, pursuit, attack, capture and subduing of the prey, feeding time on the prey and finally, a digestive pause during which no further feeding responses are elicited (Holling (1966)). In the present study, the main interest lies in how much food is extracted from each prey item, and for this, actual time spent feeding on the prey is the important measure, so in this study, handling time is defined as the time from capture to release of the prey item by the predator. It is also assumed that the predator has a similar rate of extraction during a feed on each item of each of the prey types.

IV. 2.1.2. Results

A convenient method of comparing handling times on different prey and between different predators is by plotting histograms of

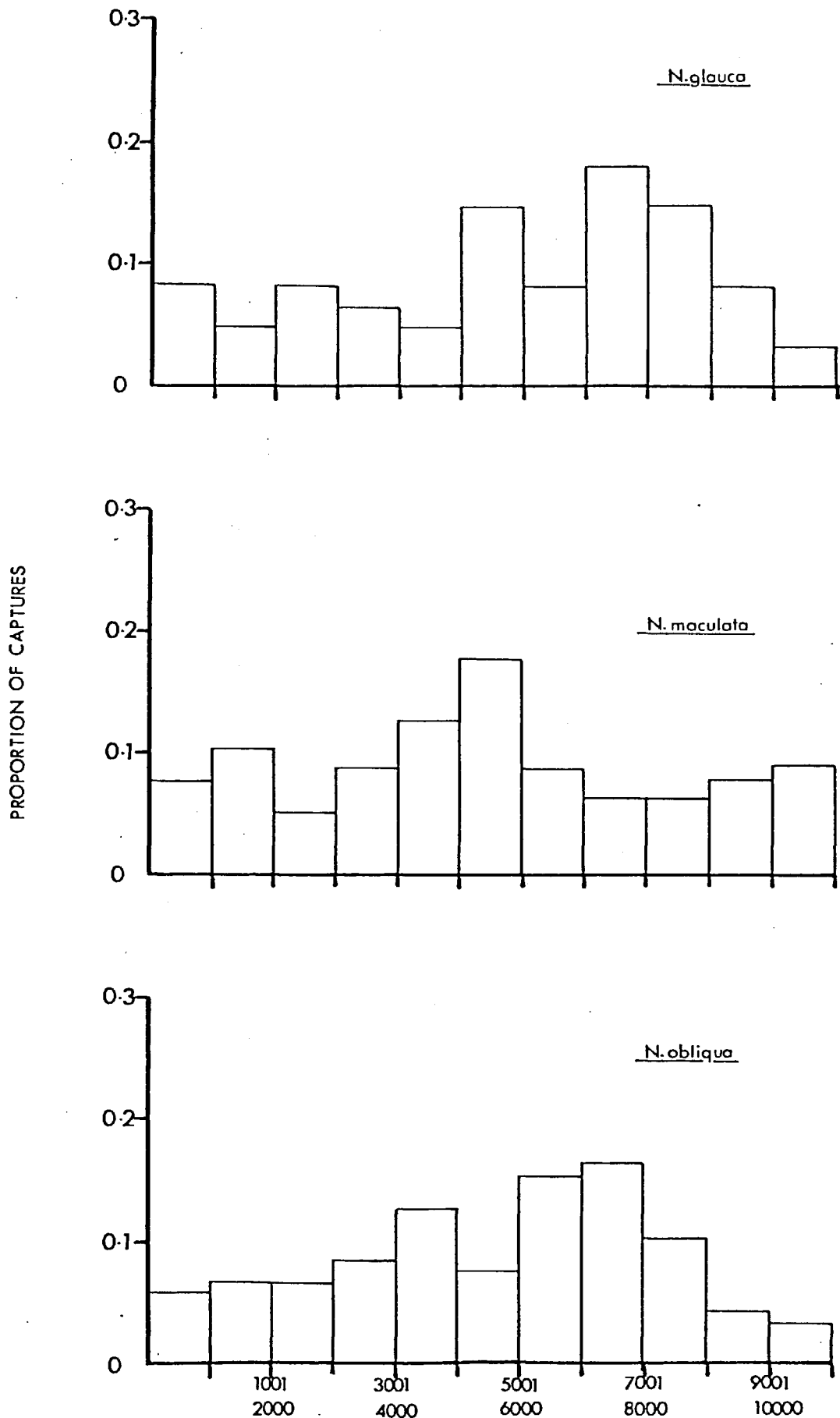
the proportion of total captures against handling time, giving a handling time distribution for each predator species on each prey type (Figs. 39, 40 and 41). These plots used pooled data for all densities of prey and all captures, in the complex environment.

The first obvious conclusion is that all three predator species have the longest handling times on Musca prey and the shortest on mosquito larvae, handling times on both Musca and Gammarus being in the order of ten times those of mosquito larvae. This is as expected on the basis of prey size (Chapter III). The distributions do appear different between the three predator species, which is shown when one compares the proportions of captures during each handling time period (see Appendix V).

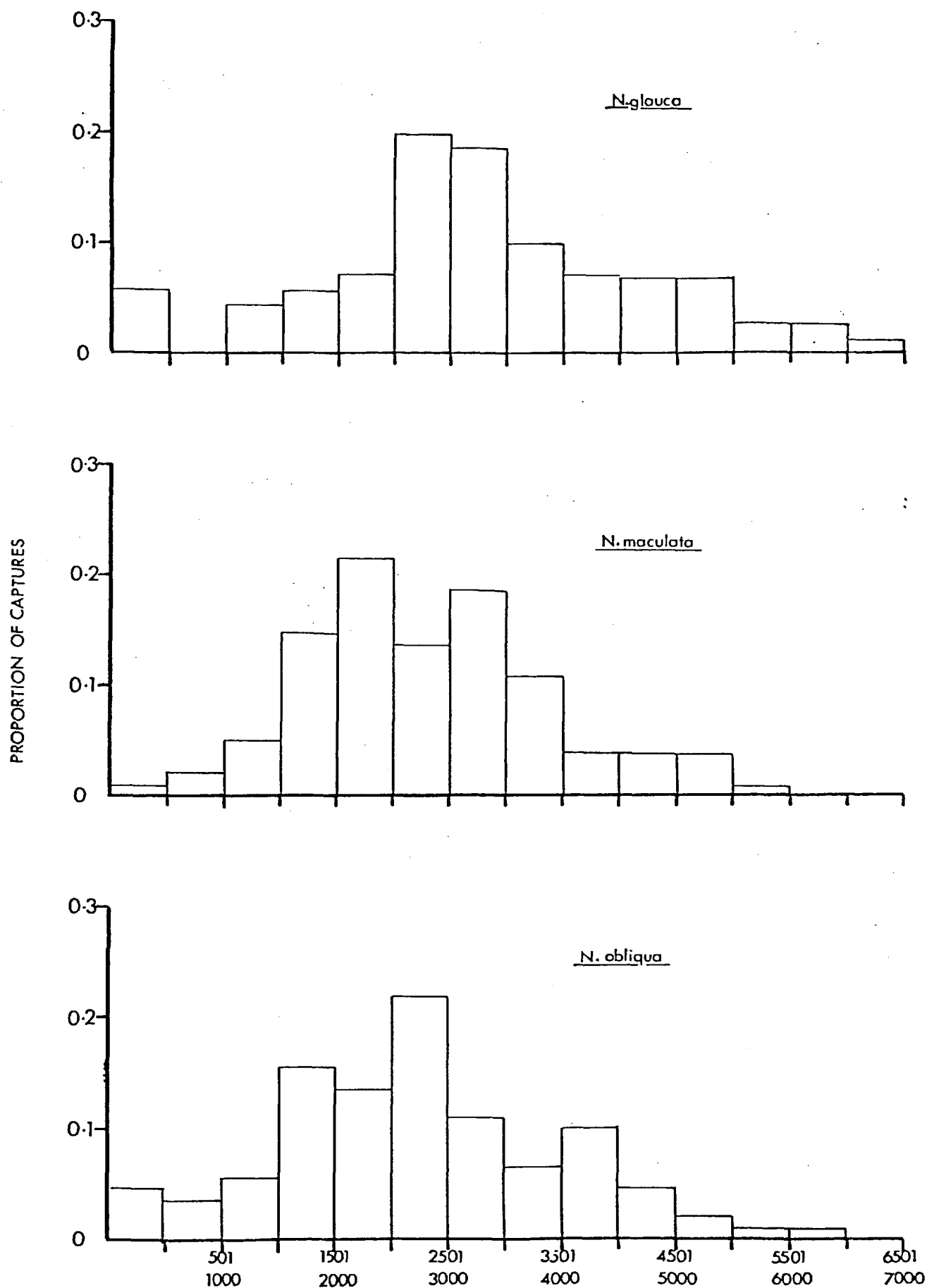
The difference is clearest with mosquito larvae. N. glauca shows smaller proportions of captures with handling times between 100 and 400 seconds, but larger proportions with handling times of 400 to 700 seconds than the other two species, indicating N. glauca has the longest handling time on this prey. N. maculata has a larger proportion of captures between 200 and 300 seconds handling time than N. obliqua, but the latter predator shows larger proportions of captures between 300-400 seconds and 500 to 600 seconds, indicating a slightly shorter handling time in N. maculata.

With Gammarus prey, the differences are rather small. There is still a trend for longer handling times to be found in N. glauca, where this species shows smaller proportions of captures than N. obliqua between 1500 to 2000 seconds handling time; and than N. maculata between 2000 and 2500 seconds handling time, but a larger proportion than N. obliqua between 3000 to 3500 seconds, and than both of the other species above handling times of 4000 seconds. There are no significant differences between the distributions of handling times

HANDLING TIME DISTRIBUTION FEEDING ON

Musca domesticaLEGEND TO FIG 39

Histograms showing the handling time distribution of captures by the three predator species feeding on Musca domestica (results pooled over all conditions).

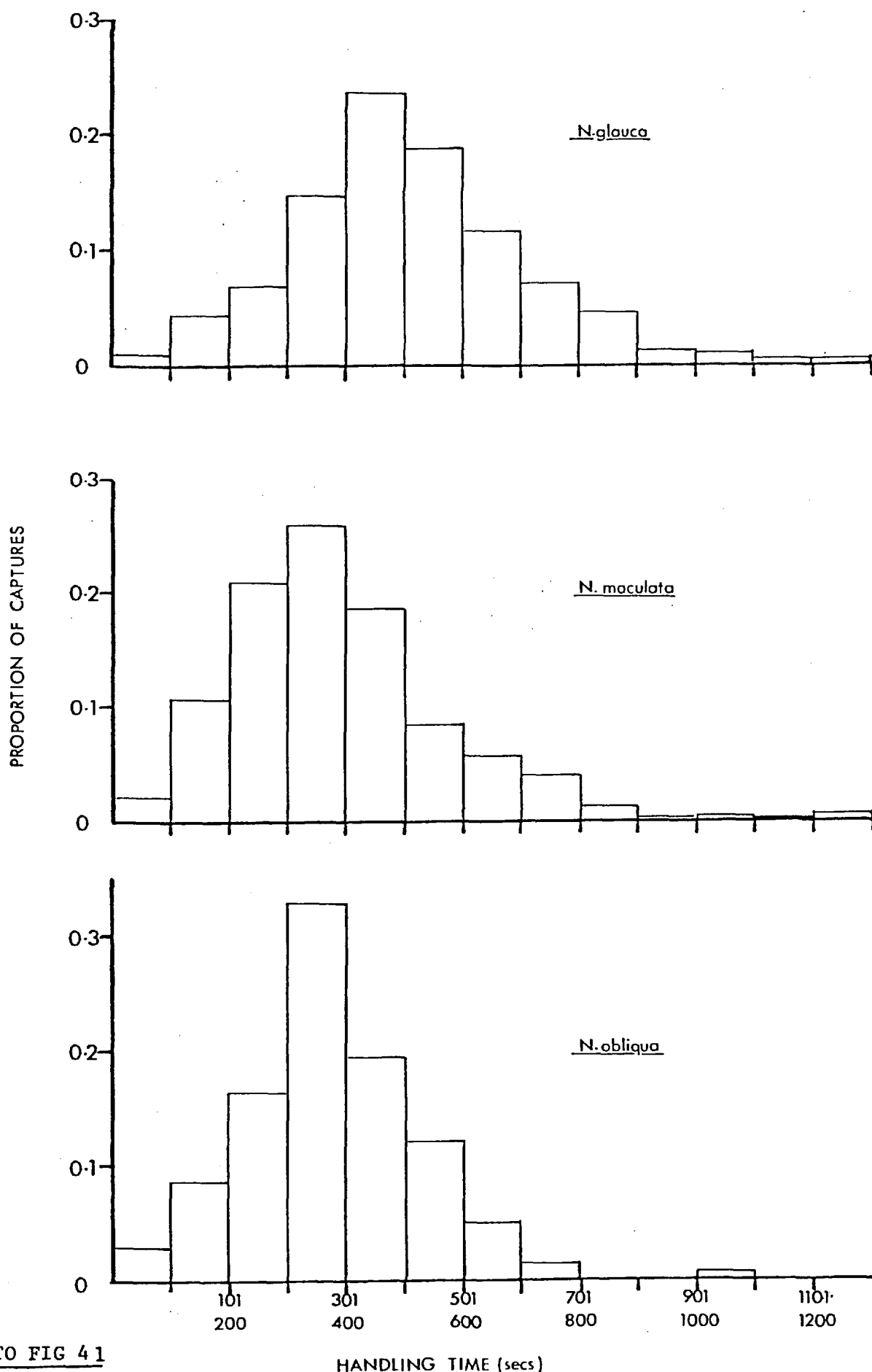
Gammarus pulexLEGEND TO FIG 40

HANDLING TIME (secs)

Histograms showing the handling time distribution of captures

by the three predator species feeding on Gammarus pulex (results pooled over all conditions)

FIG 41

HANDLING TIME DISTRIBUTION FEEDING ON
MOSQUITO LARVAELEGEND TO FIG 41

Histograms showing the handling time distributions of captures by the three predator species feeding on mosquito larvae (results pooled over all conditions).

of N. maculata and N. obliqua, although the mode of the distribution seems to be at a shorter handling time for N. maculata.

A similar picture is found with Musca prey. N. glauca again appears to show the longest handling times, N. maculata showing a greater proportion of captures between 4000-5000 seconds handling time, N. obliqua a greater proportion between 6000 to 7000 seconds, and N. glauca showing a larger proportion of captures between 7000 - 8000 seconds than N. maculata, and between 8000 - 9000 seconds than N. obliqua. There are again, no significant differences in the distributions of N. maculata and N. obliqua but the mode of the distribution for N. maculata appears to be at a shorter handling time.

It is interesting to note, that when one considers the modes of the above distributions in connection with the extraction curves described in Chapter III, similar quantities of food are predicted to be extracted by each of the predator species from each prey type (Table 4.2.).

Table 4.2.

The modes of the handling time distribution (Th Secs) and weight of food extracted (wt. ext. mgs. dry wt.) for the three predator species.

	<u>Musca</u>		<u>Gammarus</u>		<u>Mosquito larvae</u>	
	<u>Th</u>	Wt. ext.	<u>Th</u>	Wt. ext.	<u>Th</u>	Wt. ext.
<u>N. glauca</u>	6001-8000	1.6-2.15	2001-3000	1.36-1.8	401-600	0.055-0.078
<u>N. maculata</u>	4001-5000	1.6-2.2	2001-2500	1.68-1.82	201-300	0.054-0.065
<u>N. obliqua</u>	5001-7000	1.8-2.4	2501-3000	1.68-1.86	201-300	0.048-0.069

IV. 2.2. Time allocation.

IV. 2.2.1. Introduction

The allocation of time during the observation period has been divided

amongst the three main behavioural components; Rest; Activity (general activity, activity associated with prey capture and activity during handling) and Feeding (total time spent handling prey). In the consideration of the energetics of the feeding strategies, the two important components are total handling time and activity time, the remaining periods being classed as rest. As a general rule, larger net energy gains are reflected in larger proportions of time spent handling prey, the size of the gains being dependant on the prey items available, the general level of activity and the number of prey fed on.

IV. 2.2.2. Results

The results are presented in the form of histograms showing the mean proportion of time spent in each component activity, for each predator, in each environment in the presence of each prey type and prey density. An example, the results with mosquito prey, are shown in Figs 42, 43, & 44, the rest of the data, with Gammarus and Musca is given in Appendix VI. Table 4.3 also shows division of activity periods into mean values of activity not associated with feeding, activity associated with prey capture, and activity during handling. Comparisons between results have been made using T tests on the original data (Appendices VII and VIII.)

As a general observation, the description of Notonectids as 'sit and wait' predators is substantiated here by the low proportion of time spent active by these bugs.

a) N. glauca

Generally a greater proportion of time is spent feeding on Musca than on either of the other two prey, this being most marked in the complex environment. A larger proportion of time is spent feeding on mosquito larvae than on Gammarus in the simple environment, but

Table 4.3 : The mean values of time active in each of the three categories for the predators, with the three prey types, shown for the two environments (Time in seconds) G-N. glauca M-N. maculata O-N. obliqua

COMPLEX ENVIRONMENT										SIMPLE ENVIRONMENT								
	Activity not Feeding			Attack Time			Activity During Handling			Activity not Feeding			Attack Time			Activity During Handling		
<u>Musca</u>	<u>G</u>	<u>M</u>	<u>O</u>	<u>G</u>	<u>M</u>	<u>O</u>	<u>G</u>	<u>M</u>	<u>O</u>	<u>G</u>	<u>M</u>	<u>O</u>	<u>G</u>	<u>M</u>	<u>O</u>	<u>G</u>	<u>M</u>	<u>O</u>
25	19.11	15.2	12.37	8.55	5.55	2.33	21.86	20.66	31.44	131.55	29	54.11	9.22	7.88	4.59	27.315	33	27.44
20	14.77	12.22	7	5.66	5.66	3.55	25.44	19.8	37.22	202.55	48.4	46.22	5	5.44	3	17.33	51.77	14.11
15	12.11	14	6.11	2.33	5.44	2.66	18	25.89	30.89	235.89	67	71.33	8.55	5.77	3.33	20.125	35.11	25.55
10	13.67	14.55	4.77	4.44	3.33	3.44	37.33	31.32	34.55	178.44	63.89	60.78	5.66	5	4.77	26.75	62.89	15.22
5	9.77	11.22	2.88	2.77	2.66	3.22	17.77	21.67	32.2	215.22	36	68.66	4.22	6.33	4.33	57.14	37.66	13.11
2	11.88	7.44	8.44	2.66	4.77	2	20.78	18.55	11.55	268.55	70	63.44	5.55	3.77	3.44	98.28	26.11	23
<u>Gammarus</u>																		
25	50.78	28.22	28.11	10	10.55	5.71	61.33	54.66	82.4	665.2	110.44	117.33	4.66	35.78	9.33	39.5	.83	57.66
20	40.77	22.9	30.44	10.66	11.44	6.66	43.55	58.3	78.66	870.9	121.33	81.11	2.44	20.55	8.33	-	135.55	15
15	32.78	26.7	29.11	10.11	12.44	8	66.44	51.55	91.89	955.2	103.33	111.55	2.88	19.88	6.77	-	215.55	25.66
10	42.78	39.3	19.66	8.78	12.44	7.22	30	55.22	73.78	819.11	115.66	139.5	2.44	16.55	8.44	-	108.22	79.22
5	29.66	39.66	31.66	6.77	16.66	6.33	45.77	24.62	54	774.7	139.22	139	2.88	24.78	8.77	-	108.22	63.66
2	32.22	28.78	26.77	4.89	8.88	7.33	17.33	33.5	47.66	739.2	118.66	152	0.55	11	4.77	-	212.89	44
<u>Mosquito larva</u>																		
70	25	18.11	28.9	23.33	34.33	24.89	35.11	49.22	70.89	443.11	87.88	68.22	14	66	45.33	230.22	117.78	133.44
50	21.66	27.89	32.77	20.22	42.89	28.77	23.22	50.11	69.55	502.9	113	67.8	12.88	72.89	45.44	156	85.55	43.22
30	21.77	24.22	46.22	21.22	37.67	27.4	25.22	57	61.66	308.44	101.89	47.11	16.11	71.67	47.55	177.5	135.44	42
10	31.11	32.67	42.55	16.22	32.44	14.5	16.22	33.22	27.33	392.55	64.11	76	11.66	66.33	33.78	186.71	117.11	25
5	24.89	31.55	36.44	16.55	21	13.2	14.33	20.33	17	350.44	58.77	51.55	12.44	55.41	34.33	210.44	72.44	66.11
2	42.88	52.55	33.55	7.77	16.89	6.66	7.44	19.22	11.11	402.2	172.44	71.55	5.33	46.33	18.9	51.55	146.77	9.89

LEGEND TO FIGS. 42, 43 and 44

Time allocation of the three main behavioural activities
in the presence of six densities of mosquito larvae
(70, 50, 30, 10, 5 and 2) in both simple and complex
environments during 3h experiments.

REST - Total rest time

ACT - Total time active including activity
associated with and without feeding.

HAND - Total handling time on prey.

Fig. 42 N. glauca

Fig. 43 N. maculata

Fig. 44 N. obliqua

FIG 42

N.gluca feeding on mosquito larvae

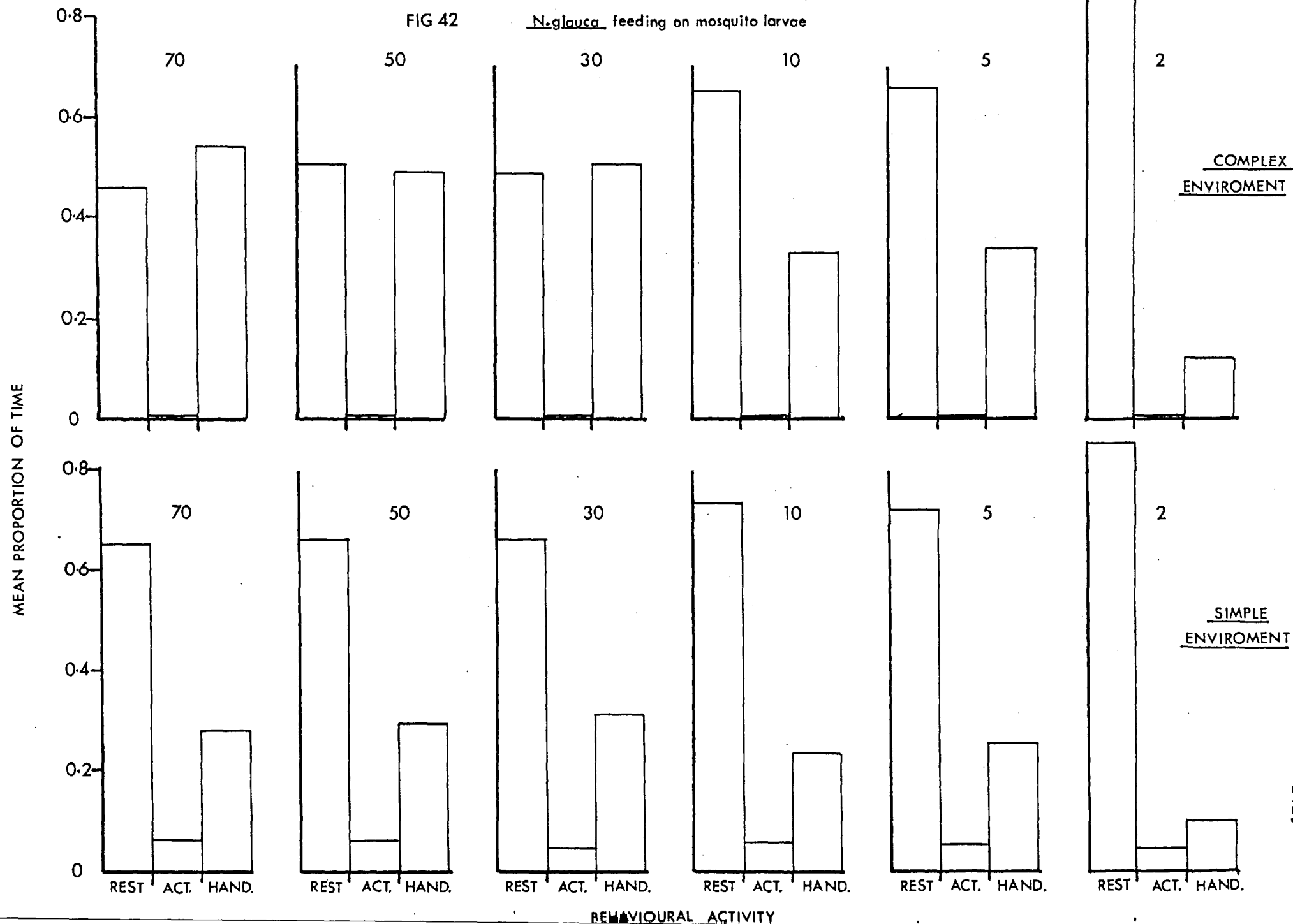


FIG 43 N. maculata feeding on mosquito larvae

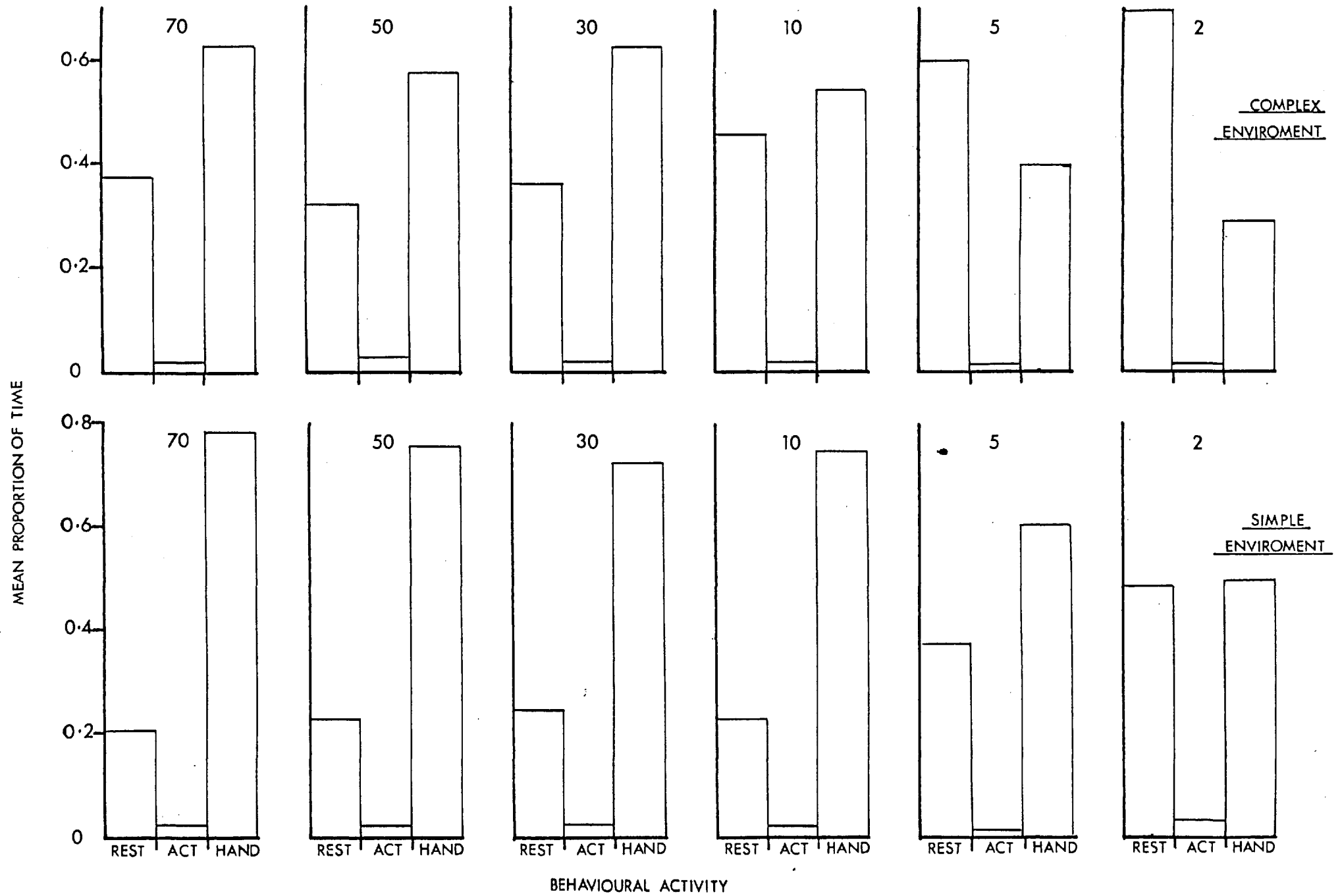
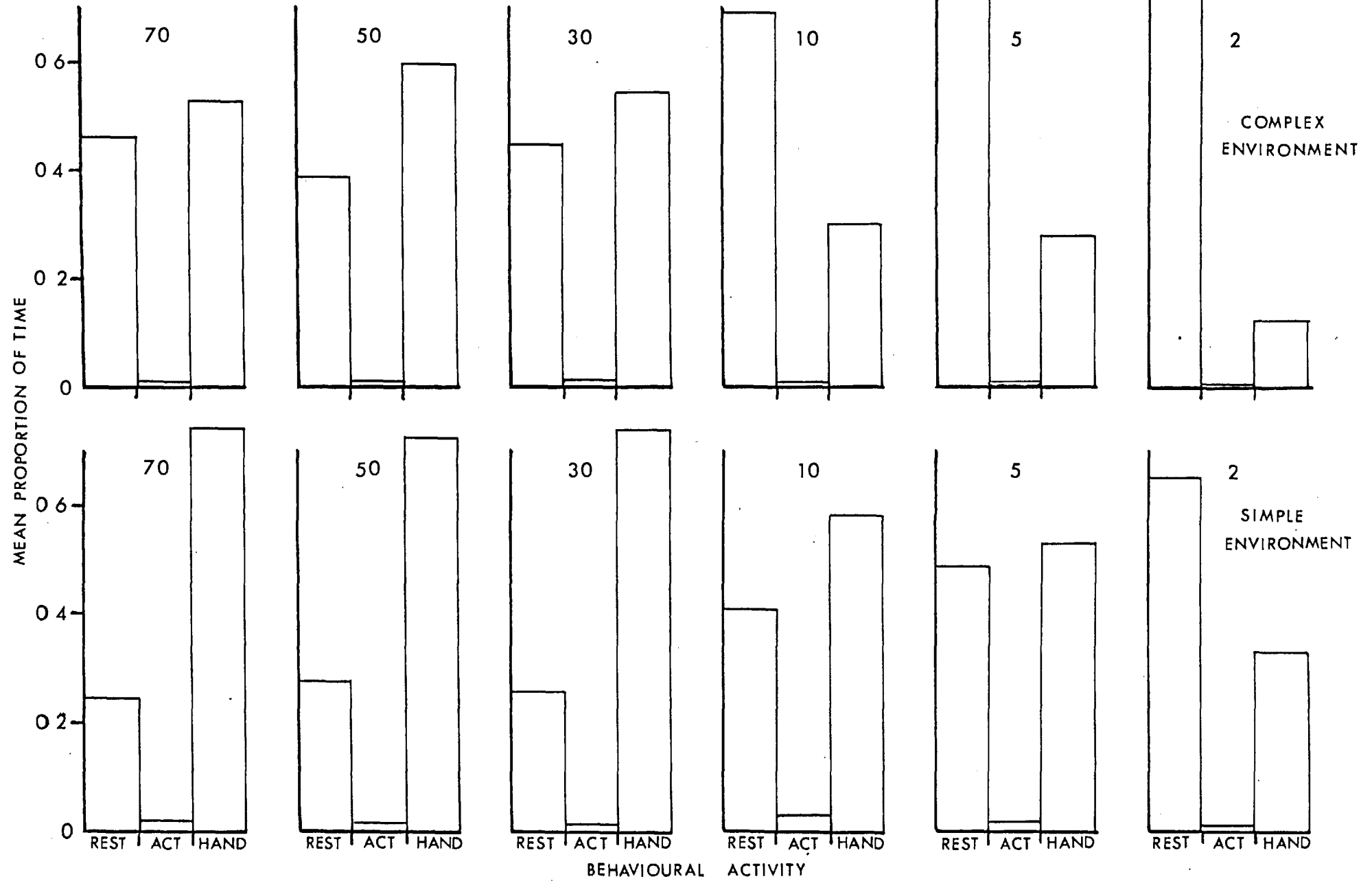


FIG 44

N. obliqua feeding on mosquito larvae



there is no difference in the complex one. The trend is for increased feeding time in the complex compared to the simple environment, this being most marked with Gammarus and least so with Musca.

The proportion of time active in the complex environment tends to be lowest in the presence of Musca. The trend is for higher activity levels to be shown in the presence of Gammarus, although only in a few situations is it significantly so. This increase in activity with Gammarus is due to an increase in activity not associated with feeding (see Table 4.3), indicating that there is considerable disturbance of the predators by this very active prey. In the simple environment, the proportion of time active markedly increases relative to the complex one. This increase appears least with Musca and greatest with Gammarus. The general increase is likely to be due to the search for perch sites within the water body and predator disturbance by the prey, which is likely to be increased in the simple environment. This conclusion is supported by the fact that with both mosquito and Gammarus prey, the predators increase in activity is due to an increase in activity not associated with attack and feeding and the effect is smallest in the presence of the least mobile prey i.e. Musca (Table 4.3).

b) N. maculata

In the complex environment, the general trend is for the greatest proportion of time to be spent feeding on Musca (although this is significant only at the lower prey densities), with similar values with mosquito larvae and Gammarus. In the simple environment there is no differences at all except at the lowest density, where again, feeding time is longest with Musca. The general trend is for increased feeding time in the simple compared to the complex environment, this being most marked with mosquito larvae, and least so with Musca, which is in contrast to the findings for N. glauca.

The lowest level of activity is found with Musca in both environments, there being little difference in activity levels with the other two prey types. There is again a general increase in activity in the simple compared to the complex environment, this being least marked with Musca. This increase is probably due to search for perch sites and predator disturbance with Gammarus prey and also in part due to an increased attack rate on mosquito larvae.

c) N. obliqua

In the complex environment, the trend is for the largest proportion of feeding time to be with Musca, and the smallest with mosquito larvae. In the simple environment, the trend is for the largest proportion of feeding time to be found with Musca (only significantly so at the lowest densities) and for larger (but not significant) proportions found with mosquito larvae than with Gammarus. There is an increased proportion of time spent feeding on mosquito larvae in the simple compared to the complex environment, no difference with Musca, but a trend for increased feeding on Gammarus in the complex compared to the simple environment (significantly so at the lower prey densities).

Lowest activity is again found in the presence of Musca in the complex environment, there being no difference with the other two prey. A similar trend is found in the simple environment, although large variation in the results has lowered the significance of differences. The effect of environmental complexity on the level of activity of N. obliqua is very much reduced from that of the other two species. There is a significant but small increase in activity in the simple environment with Musca prey, due to an increase in activity not associated with feeding, a similar but not significant effect with Gammarus prey, and virtually no effect at all with mosquito larvae.

IV. 2.2.3. Conclusions

It should be noted, that although proportions of time spent

feeding on different prey types might be similar, the energetic returns are very different. The data presented here should be considered in the light of the $\frac{E}{T}$ values shown in Table 3.2 (Chapter III.)

With Musca, the smallest proportion of time spent feeding is shown by N. glauca, this being more marked in the simple than in the complex environment. In both environments there is little difference in proportions between N. obliqua and N. maculata, although the general trend is for larger values with N. obliqua. With Gammarus a similar picture is found in the complex environment, but in the simple one, the trend is for larger values to be found for N. maculata than for N. obliqua (the differences not significant though), and again smallest values are found for N. glauca. With mosquito larvae, the results are essentially the same in both environments. N. maculata shows larger proportions of time feeding than N. glauca at all prey densities, and than N. obliqua at low prey densities, there being little difference at high ones. In the complex environment, N. obliqua shows similar proportions of time feeding to N. glauca, but in the simple one, N. glauca clearly shows the lowest values.

With regard to activity levels, in the complex environment, there are very few significant differences (Appendix VIII(b)) between the predators. In the simple environment, N. glauca clearly shows the highest level of activity, and although there are few significant differences, the general trend is for N. maculata to show higher activity levels than N. obliqua. The increase in activity in the simple compared to the complex environment is also greatest with N. glauca, and least with N. obliqua.

IV. 3.

Responses to Prey

Some differences in predation strategies are likely to occur in relative success of the three species at capturing different prey types in different environments. As discussed in Chapter I, an attack

sequence takes the following form:

orientation to prey $\curvearrowright$ Pursuit $\rightarrow$ Attack - Capture

the nature of this sequence depending on the relative distances of predator and prey, i.e. the necessity of pursuit of the prey. The functional response of the predator to each prey type also gives an indication of the predators ability to exploit the prey type in the environment in question. Differences may also be found in the relative sizes of the reaction area of the predators.

IV. 3.1. Attack component Success

IV. 3.1.1. Introduction

In the attack sequence, Holling (1966) described the first category of successful response as the recognition success of the prey items by the predator. To assess this component, the total number of possible encounters must be monitored, and for predators with such a relatively large reaction area and high prey densities as those being studied, this would be an impossible task.

The first component that can be assessed in this study is the pursuit success, a successful pursuit enabling the predator to get close enough to initiate an attack (or strike). This second component is a rapid lunge over a short distance, and if successful, enables the predator to get close enough for an attempt at prey capture with the raptural limbs. A successful capture is made when the prey is grasped, and only rarely does a prey subsequently escape.

The success of this chain of events is dependent on the weakest link; for example, if capture and pursuit successes are 100%, but attack success only 50%, then only half the total of successful encounters will result in a successful capture. The relative successes of these various components can, then, greatly affect the eventual outcome of the predator's strategy. As an example, the results for

N. glauca are presented here, those for N. maculata and N. obliqua are given in Appendix IX . Statistical analysis of the results is given in Appendix X .

IV. 3.1.2. Pursuit Success (Fig 45 , Appendix IX).

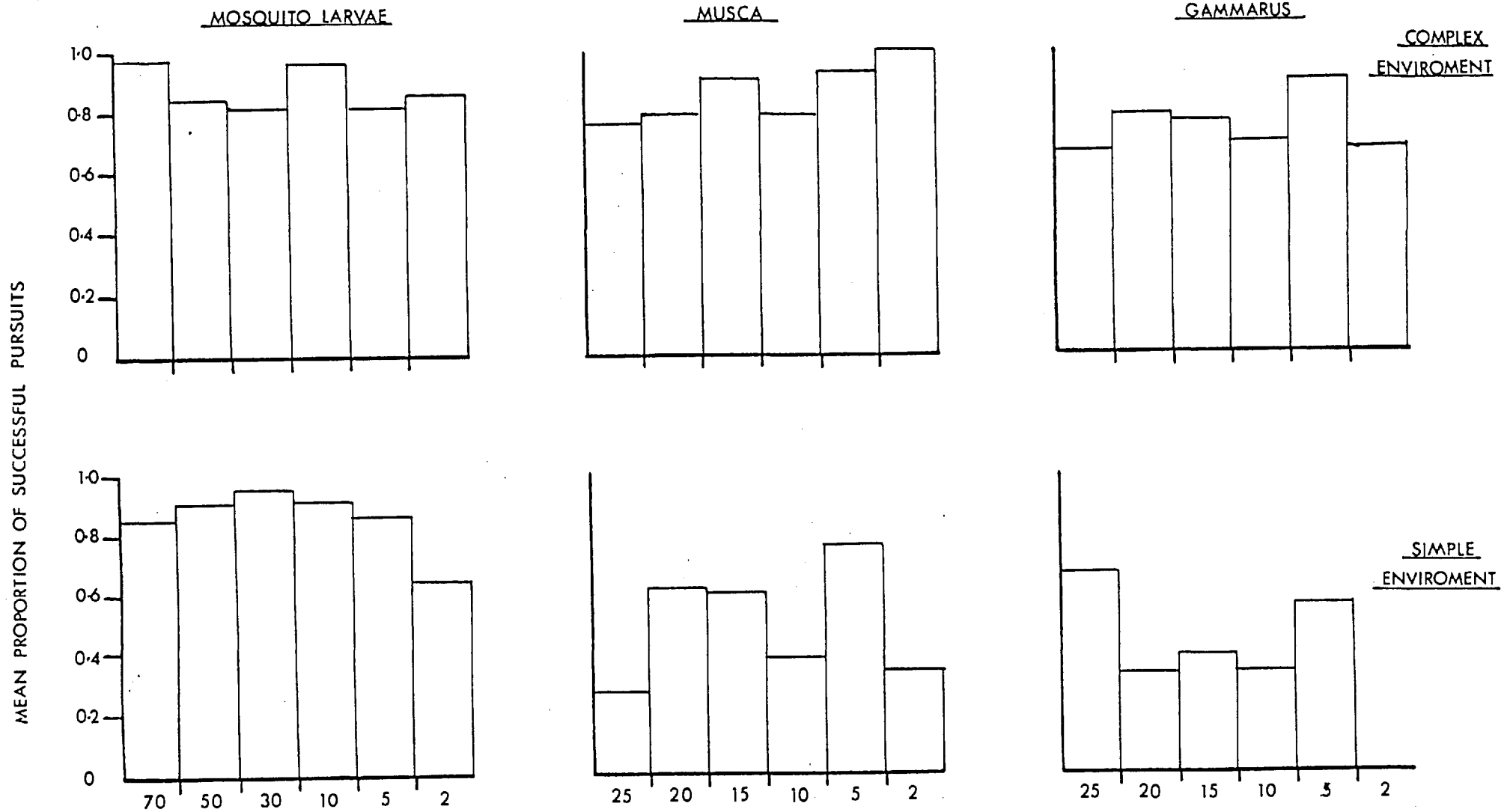
For N. glauca in the complex environment, there is little difference in pursuit success on the three prey types, although the general trend seems to show lowest success on Gammarus prey. In the simple environment, the largest success is found with mosquito larvae, there being little difference with the other two prey types, although again, the trend is for lowest success with Gammarus. The effect of environmental complexity on pursuit success is most marked with Gammarus and Musca where there is reduced success in the simple compared to the complex environments, but there is virtually no effect with mosquito larvae.

For N. maculata in the complex environment there is again very little difference in pursuit success with the three prey types, but in the simple one, the trend is for reduced success with Gammarus prey. There appears to be no effect of environmental complexity on pursuit success.

The pursuit success of N. obliqua seems unaffected by both prey type and environmental complexity.

The pursuit of prey is likely to contribute the largest energy loss in the attack sequence, so in an efficient strategy, unsuccessful pursuits should be limited. One would expect the lowest pursuit success to be found with Gammarus, being the most active prey, and this is the general trend with both N. glauca and N. maculata. Musca are generally stationary, so it would be expected that pursuit success would be very high. However, as Ellis and Borden (1970) point out, predators tend to stalk such large prey, with a series of short movements towards the prey. Each stage of this type of pursuit except the final one

FIG 45

N. glauca pursuit success

LEGEND TO FIG 45

PREY DENSITY PER ARENA

Histograms showing the mean proportion of successful pursuits ($\frac{\text{Successful pursuits}}{\text{Total pursuits}}$) for N. glauca feeding on six densities of each of the three prey types, in both simple and complex environments.

must be termed unsuccessful, and this is likely to affect the general measure of pursuit success with this prey. Mosquito prey are small, and not very fast moving, so one would expect a high pursuit success.

In the comparison of the pursuit successes of the three predators, very few significant differences are found. However, in the complex environment, the general trend seems quite clear, with the highest pursuit success being shown by N. obliqua (being most marked with Gammarus and least so with mosquito larvae) and the lowest pursuit success appears to be shown by N. maculata (being most marked with Musca). In the simple environment, the trend again appears to show highest success by N. obliqua, but lowest success by N. glauca with large prey, and by N. maculata with small prey.

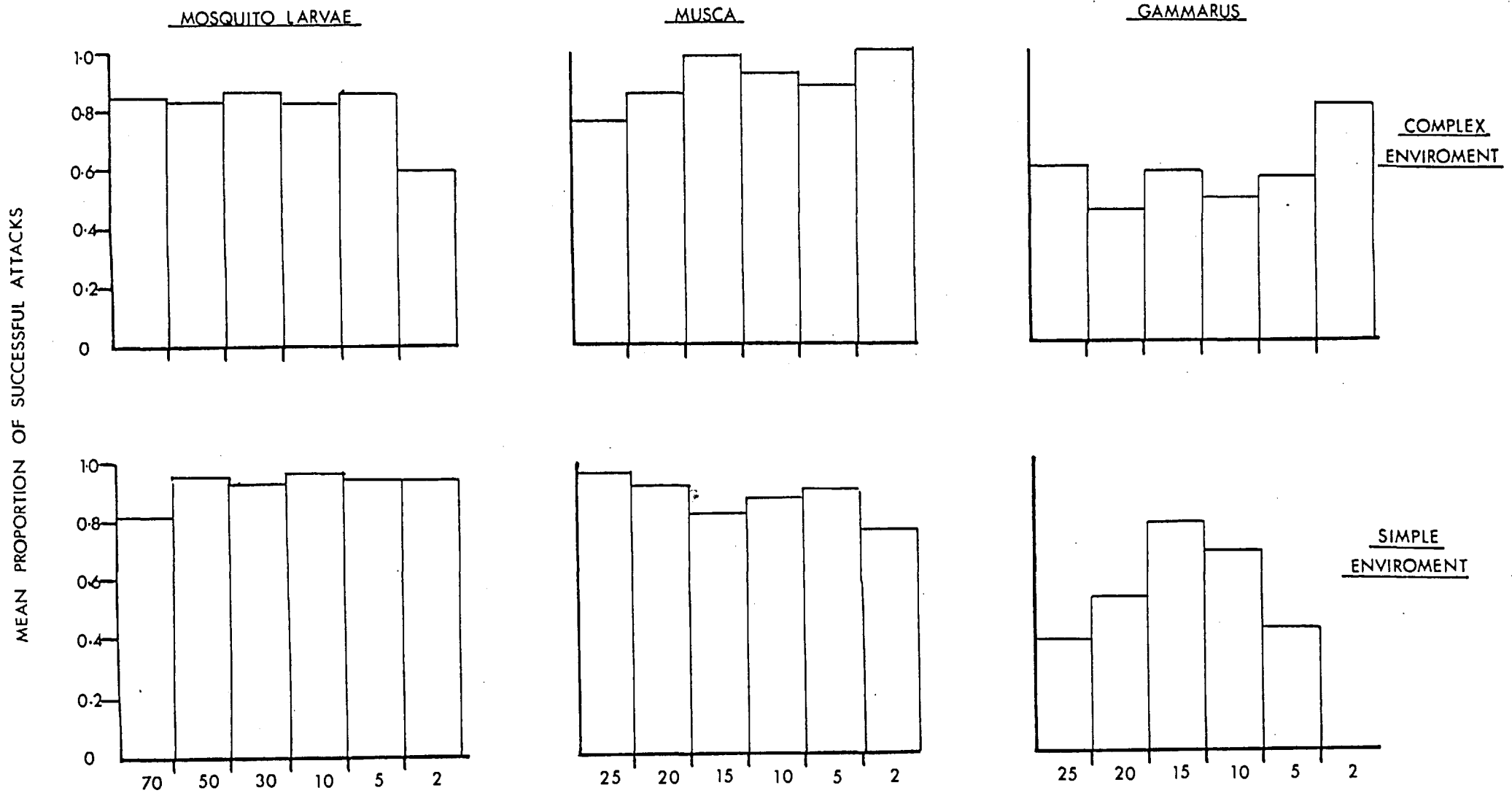
IV. 3.1.3. Attack Success (Fig 46 , Appendix IX)

For N. glauca in both environments, the lowest attack success appears to be with Gammarus. There is no significant difference between attack successes with the other two prey types, but in the complex environment, the general trend is for greater success with Musca, but in the simple one, the trend is for greater success with mosquito larvae. There is no effect of environmental complexity except with mosquito larvae where higher attack success is apparent in the simple than in the complex environment.

A similar picture is found with N. maculata. In both environments, lowest attack success is found with Gammarus, and there is no significant difference between attack successes on the other two prey but the general trend shows success is greater on Musca than on mosquito larvae. There is no effect of environmental complexity with Musca and mosquito larvae, but with Gammarus, lower attack success is found in the simple environment.

N. obliqua shows 100% attack success with Musca prey in the complex environment, which is significantly higher than with the other

FIG 46

N. glauca attack success

LEGEND TO FIG 46

PREY DENSITY PER ARENA

Histograms showing the mean proportion of successful attacks ($\frac{\text{Successful attacks}}{\text{Total attacks}}$) for N. glauca feeding on six densities of each of the three prey species in both simple and complex environments.

two prey. The general trend is for lower attack success on Gammarus than on mosquito larvae, but the differences are not significant. In the simple environment, the differences are much smaller and less significant, but the trend is still for greater attack success on Musca, and little difference between successes with the other two prey, although success with Gammarus appears lowest. There is no effect of environmental complexity on attack success with the three prey species.

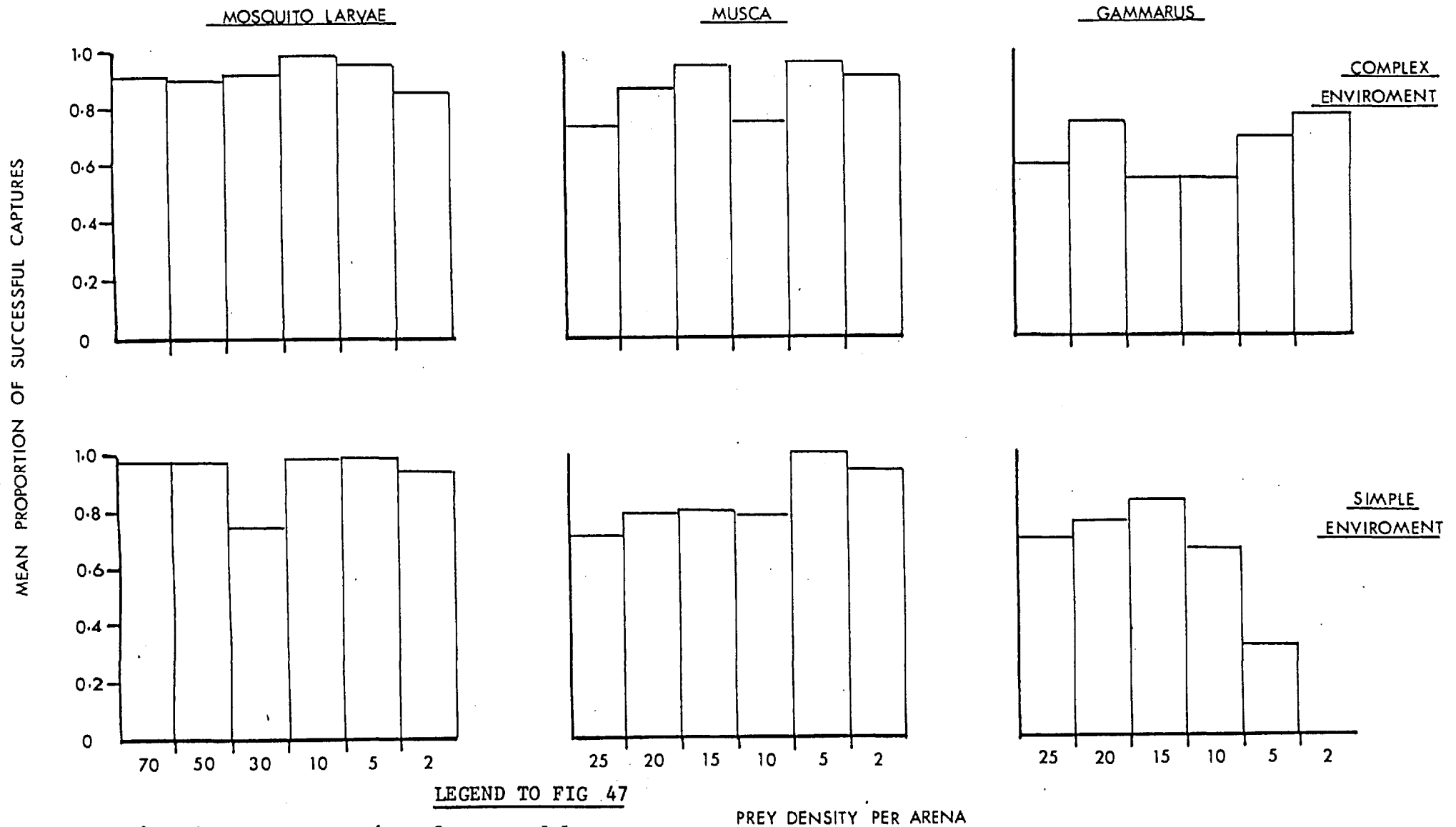
On the basis of prey mobility, it is expected that highest attack success would be found with Musca prey, being the least active, and lowest success would be found with Gammarus, and the above results generally bear out this prediction.

Comparing the attack success of the three predators, in the complex environment, with large prey (i.e. Musca and Gammarus), the general trend shows highest success with N. obliqua and lowest with N. glauca (although very few of the differences are significant) and there is no trend with the smallest prey (i.e. mosquito larvae). In the simple environment, there are again few significant differences, but the general trend again shows highest attack success by N. obliqua with large prey, and lowest by N. glauca, but with small prey, the trend is for greatest success by N. glauca, and lowest by N. maculata.

IV. 3.1.4. Capture Success (Fig 47 , Appendix IX)

In the complex environment, the capture success by N. glauca is lowest with Gammarus, there being no difference in success on the other two prey. In the simple environment lowest success occurs with Gammarus, no significant difference between the other two was found, but the general trend shows greater success with mosquito prey. There is no significant effect of environmental complexity on the capture success by N. glauca with the three prey types.

FIG 47

N. glauca capture success

Histograms showing the mean proportion of successful captures

PREY DENSITY PER ARENA

$\left(\frac{\text{Successful captures}}{\text{Total captures}} \right)$ for N. glauca feeding on six densities of each of the three prey species in both simple and complex environments

N. maculata shows lowest capture success in the complex environment with Gammarus and although there is little difference in success with the other two prey, the trend is for greater success with mosquito larvae than with Musca. In the simple environment, though the differences are much smaller, the success with Gammarus is still lowest. Again, although there are no significant differences, the trend is for higher success with mosquito larvae than with Musca. There is no significant effect of environment but with both Gammarus and mosquito larvae, there is a tendency for increased capture success in the simple compared to the complex environment.

There are few significant differences in capture success with prey type by N. obliqua in either environment, the success being over 95% in most cases, but the general trend in both environments is for slightly lower capture success with Gammarus than with the other two prey, this difference being significant in the complex one.

On the basis of prey size and activity, it is expected that the greatest capture success should be with mosquito larvae, and the lowest with Gammarus. This is generally the case, although N. obliqua has very high success values for all prey types.

Comparing the capture success of the three predators in the complex environment, N. obliqua generally shows a significantly greater success than the other two predators. There is little difference between capture success of N. glauca and N. maculata, but the trend is for lowest success by N. glauca with Musca and mosquitoes, and with N. maculata with Gammarus. In the simple environment, there are few significant differences with all three prey types, but the general trend seems to show greatest success by N. obliqua, and lowest by N. glauca.

By comparing the success with each component of the attack sequence

for the predators, some indication of the limiting component can be found (i.e. the component with the poorest success value, which limits the capture rate the most). For N. glauca in the complex environment, very few significant differences between the components are found, but the trends seem to show that attack success limits capture rate with Gammarus and mosquito larvae, whereas with Musca, the limiting component appears to be pursuit success. In the simple environment N. glauca tends to be limited in capture rate by pursuit success, this being clearest with Musca.

For N. maculata in the complex environment, there are again few significant differences between component successes, but the trend appears to show capture rate with Musca and mosquito larvae is limited by pursuit success, and with Gammarus by capture success. In the simple environment, capture rate with Musca and mosquito larvae tends to be limited by pursuit success again and capture rate with Gammarus seems equally limited by pursuit and attack success.

N. obliqua shows similar limiting components to N. glauca in the complex environment, capture rate tending to be limited by pursuit success with Musca and attack success with Gammarus and Mosquito larvae (but only with Gammarus is the trend generally significant). A similar trend is found in the simple environment, but few differences are significant.

A summary of the limiting components is given in Table 4.4.

Table 4.4.

	Complex environment			Simple environment		
	Mosquito prey	<u>Musca</u> prey	<u>Gammarus</u> prey	Mosquito prey	<u>Musca</u> prey	<u>Gammarus</u> prey
<u>N. glauca</u>	attack success	pursuit success	attack success	pursuit success	pursuit success	pursuit success
<u>N. maculata</u>	pursuit success	pursuit success	capture success	pursuit success	pursuit success	pursuit/attack success
<u>N. obliqua</u>	attack success	pursuit success	attack success	attack success	pursuit success	attack success

The limiting components with regard to capture rate for the three predators in simple and complex environments.

IV. 3.2. Type of attack sequence

IV. 3.2.1. Introduction

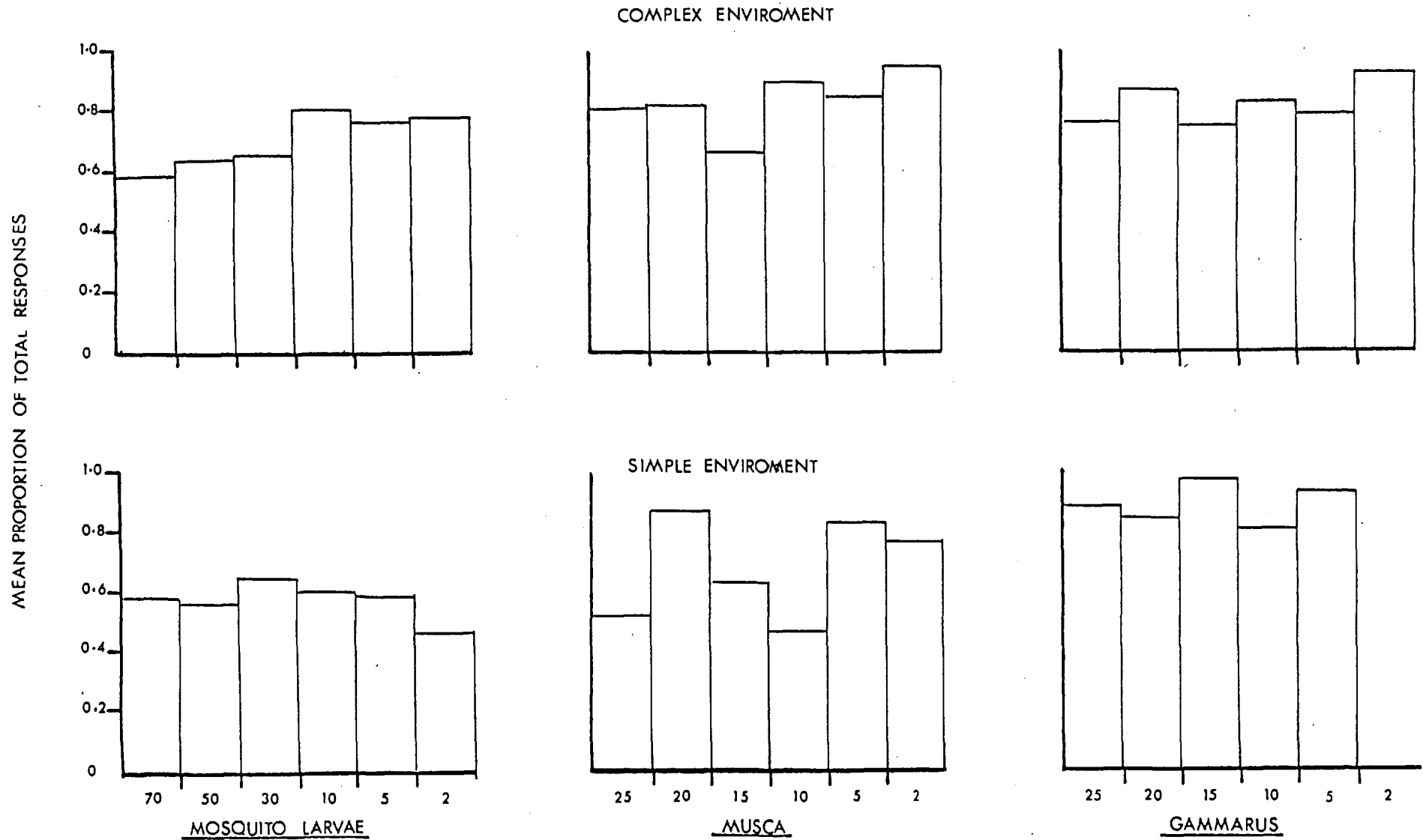
The type of attack sequence depends on whether the prey is pursued or not. As Holling (1966) and Charnov (1976) found for the mantid, it is likely that a sit and wait predator will pursue a prey item further, or at a greater distance at high hunger levels (as measured by food level in the gut). One might expect a higher proportion of pursuit-attacks at low prey densities, especially where density affects the predators consumption (as is the case with Notonecta feeding on mosquito larvae and to some extent Gammarus), or purely in terms of random encounters, where at high prey densities, it is more likely that a prey item will swim near enough to the predator for a direct attack. Statistical analysis is given in Appendix XI.

IV. 3.2.2. Results (Figs 48, 49, and 50).

The high variance in the results for N. glauca tend to mask the general trends, as the differences are not significant. These trends show a general increase in the proportion of pursuit-attacks with decreasing density of all prey types in the complex environment, and with Musca in the simple, and also show a tendency for lowest proportions of pursuit-attacks to be found with mosquito larvae, and highest with Musca in the complex and Gammarus in the simple environment. There also appears to be a reduction in pursuit-attacks with Musca in the simple compared to the complex environment.

For N. maculata in the complex environment, there is again very little difference between prey densities or prey types in the proportions of pursuit-attacks. The general trend seems to show larger proportions with Gammarus and increased proportions of pursuit-attacks with decreasing mosquito larvae density. A similar pattern is observed in the simple environment, although the trend is for lowest proportions to be found with mosquito larvae, which again shows a trend for increasing

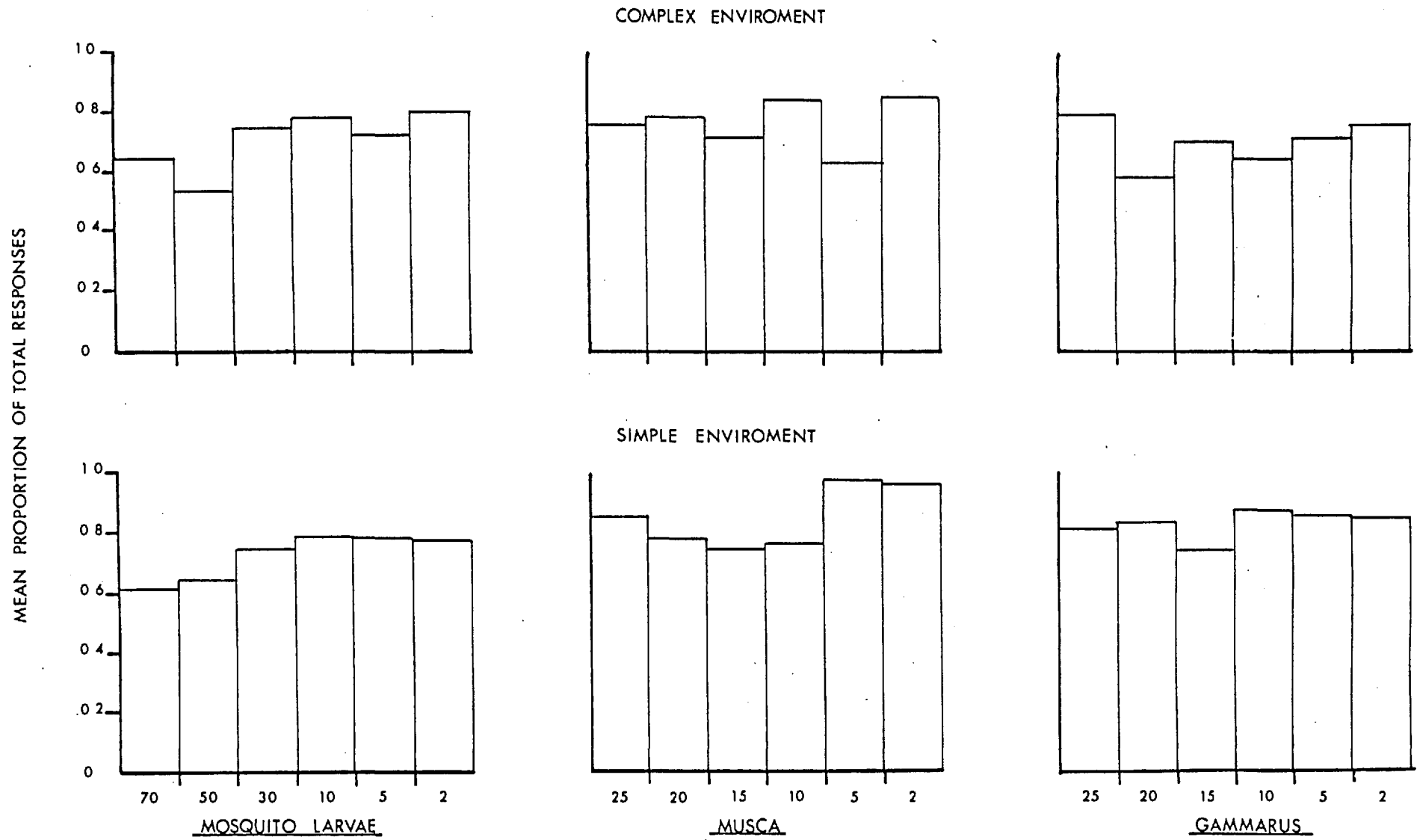
FIG 48

Proportion of pursuit-attacks by N. glaucaLEGEND TO FIG 48

PREY DENSITY PER ARENA

Histograms showing the mean proportion of responses in the pursuit-attack mode by N. glauca feeding on six densities of each of the three prey types in both simple and complex environments.

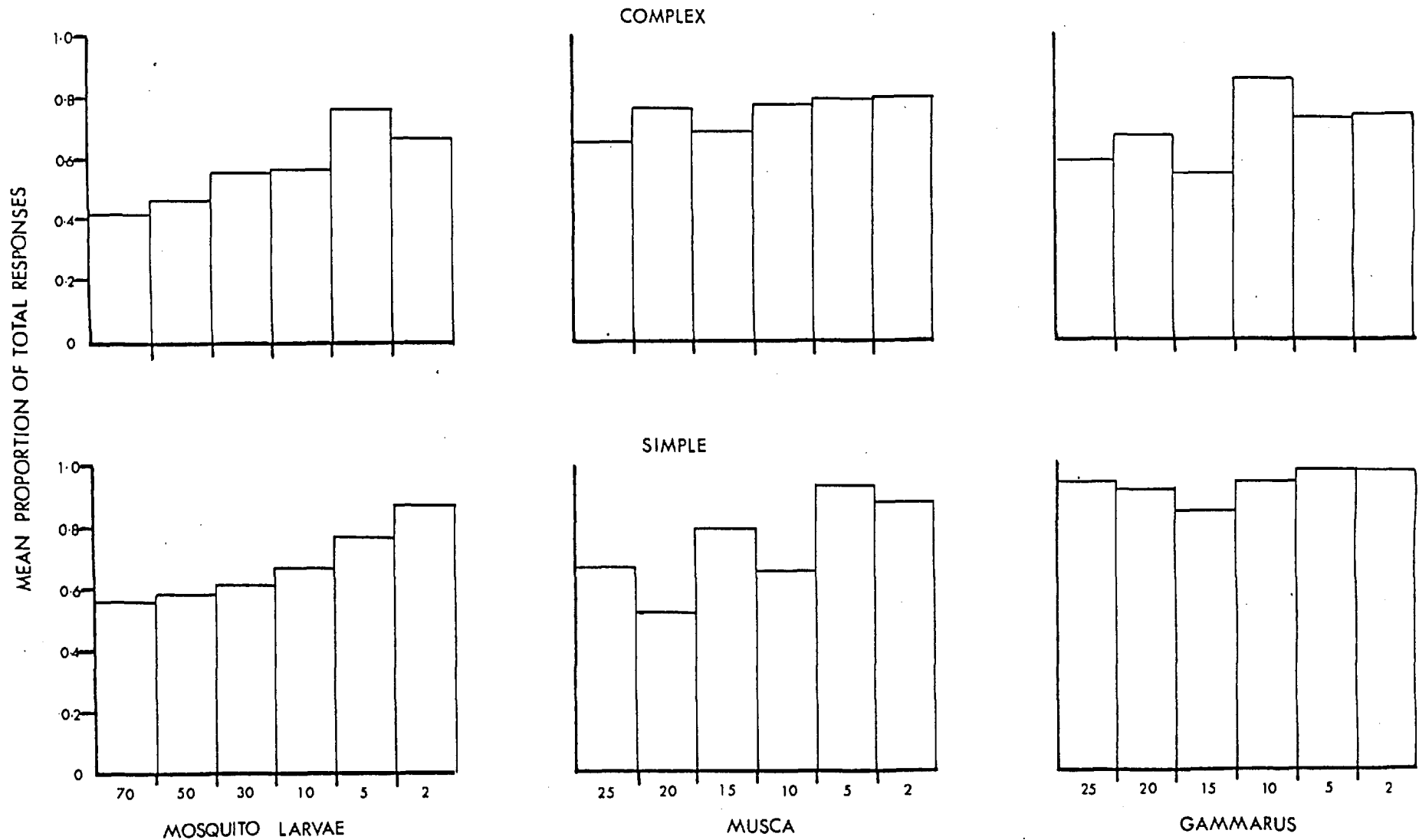
FIG 49 Proportion of pursuit-attacks by N. maculata



LEGEND TO FIG 49

istograms showing the mean proportion of responses in the
ursuit-attack mode by N. maculata feeding on six densities of each of the three prey types in both simple and complex environments.

FIG 50 Proportion of pursuit-attacks by N.obliqua



LEGEND TO FIG 50

PREY DENSITY PER ARENA

Histograms showing the mean proportion of responses in the

pursuit-attack mode by N. obliqua feeding on six densities of each of the three prey types in both simple and complex environments.

values with decreasing density. There is also a trend for higher proportions of pursuit-attacks with Gammarus, mosquito larvae and to a lesser extent with Musca in the simple compared to the complex environment.

With N. obliqua, once again, there are few significant differences, but like N. glauca, there is a trend for increased proportions of pursuit-attacks with decreasing prey density, and for the lowest values to be found with mosquito larvae. In the simple environment, there is still the trend for increased proportions of pursuit-attacks with decreasing prey density with Musca and mosquito larvae, which is very marked in the latter case, and also for results with mosquito larvae to show the lowest values (significantly so compared to Gammarus). The proportion of pursuit-attacks with Gammarus also increase in the simple environment compared to the complex one.

Some aspects of these results may be explained by consideration of the prey behaviour. Musca prey are confined to the surface, and are practically immobile when trapped in the surface film. Unless a predator surfaced directly next to a prey, a pursuit would be necessary to bring the predator to within striking distance of the prey. This may explain the generally high level of pursuit-attacks made by the predators on this prey. The relatively high prey densities and high activity level of mosquito larvae increases the likelihood of these prey coming close enough to the predator to allow a direct strike when compared to the other prey types, so may explain the general trend for lowest proportions of pursuit-attacks to be found with this prey. The general increase in proportions of pursuit-attacks with Gammarus in the simple compared to the complex environment may be explained on the basis of relative predator and prey positions in the simple environment, where the predators tend to be more confined

to the surface, whereas the prey prefer the arena bottom. In the complex environment, the increased availability of perch sites allows greater overlap in predator/prey positions.

A comparison of the proportions of pursuit-attacks between the three predators reveals very little difference, due mainly to the large variation in the data. However, broad trends seem to show the largest proportions found by N. glauca and the smallest by N. obliqua in the complex environment, and the largest proportions with Musca by N. maculata and with Gammarus by N. obliqua in the simple one. In this environment, with Musca and mosquito larvae, N. glauca tends to show the lowest proportion of pursuit-attacks, but with Gammarus, N. maculata tends to do so.

IV. 3.3. Functional Responses

IV. 3.3.1. Introduction

The functional response describes a relationship between the predators rate of capture and the density of the prey (Murdoch (1973)). Holling (1959) described four major types of response, but only Types II and III are thought to be common for invertebrates (Hassell, Lawton and Beddington (1976)). In a Type II response, the rate of capture (described in terms of numbers of prey eaten or killed), increases at a decreasing rate to a plateau, and in a Type III response, the capture rate initially increases at an increasing rate, but at a certain density level changes to a decreasing one. This type of response is often thought to be the result of predator learning, prey refuge effects or changing rates of attack during the experimental period. Holling (1959) and Mori and Chant (1966) describe another type of response, which is dome shaped. Initially, the rate of capture increases with prey density at a decreasing rate, but after some density level, the rate of capture starts to decrease. This is usually att-

ributed to confusion effects on the predator at high prey densities. Reviews of the functional response and associated mathematical models are given in Hassell et al (1976a) and b)) and Savan (1979). The mathematical approach to these responses has not been considered here, as the two basic components, handling time and attack rate, have been found to vary through successive captures, and so violate the assumptions made in these models (see also Savan 1979).

Because the shape and general level of the response curves will depend on the length of the handling time on the prey as well as the attack rate, there will be marked differences in the functional responses on the three prey types. The functional response does indicate the general attack rate, and so comparisons of the curves on each prey type between the predators will show differences in the predators overall feeding behaviour.

IV. 3.3.2. Results (Figs 51, 52 and 53)

The functional response of N. glauca with mosquito prey is of a Type II; the plateau being reached with about 10 prey killed in the complex environment, and 8 in the simple one at density 30. The general shape of the response with Gammarus appears to be domed in both environments, indicating some possible confusion effects at high density. There is no response with Musca prey.

The functional response with Gammarus for N. maculata is of a Type II, although the differences between successive densities are not quite significant. With mosquito larvae, there is a Type II response in the simple environment with a plateau being reached at a density of about 30 per arena with 35 prey killed, but in the complex environment it appears to be of a domed nature, the peak at a density of 50 prey per arena with about 20 prey killed. There is again essentially no response with Musca prey.

LEGEND TO FIG. 51

The functional response of N. glauca feeding on six densities of each of three prey types in simple (□) and complex (■) environments.

- A - Musca domestica prey
- B - Gammarus pulex prey
- C - mosquito larvae (Aedes aegypti) prey

95% confidence limits shown.

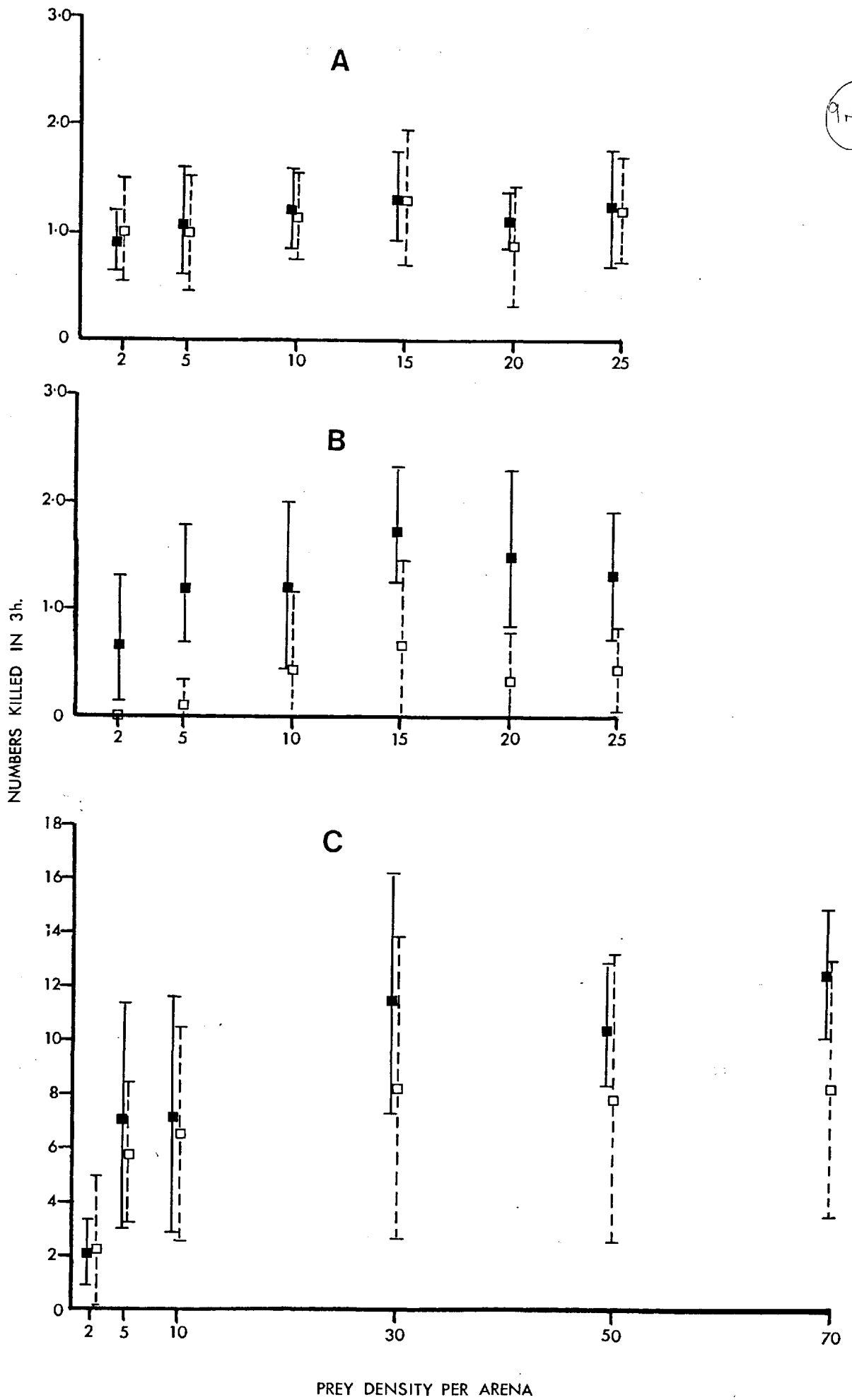
Comparison of densities by T tests (sig 0.05) and analysis of variance of data from all densities. (Densities underlined not significantly different).

<u>Musca</u>	Complex	<u>15</u>	<u>25</u>	<u>10</u>	<u>20</u>	<u>5</u>	<u>2</u>	(F = 0.845)
	Simple	No significant differences (F = 0.177)						
<u>Gammarus</u>	Complex	<u>15</u>	<u>20</u>	<u>25</u>	<u>10</u>	<u>5</u>	<u>2</u>	(F = 3.786 sig. 0.01)
	Simple	<u>15</u>	<u>25</u>	<u>10</u>	<u>20</u>	<u>5</u>	<u>2</u>	(F = 1.009)
Mosquito	Complex	<u>70</u>	<u>30</u>	<u>50</u>	<u>10</u>	<u>5</u>	<u>2</u>	(F = 7.66 sig. 0.01)
	Simple	<u>30</u>	<u>70</u>	<u>50</u>	<u>10</u>	<u>5</u>	<u>2</u>	(F = 1.3)

FIG 51

N. glauca functional response

164.



LEGEND TO FIG. 52

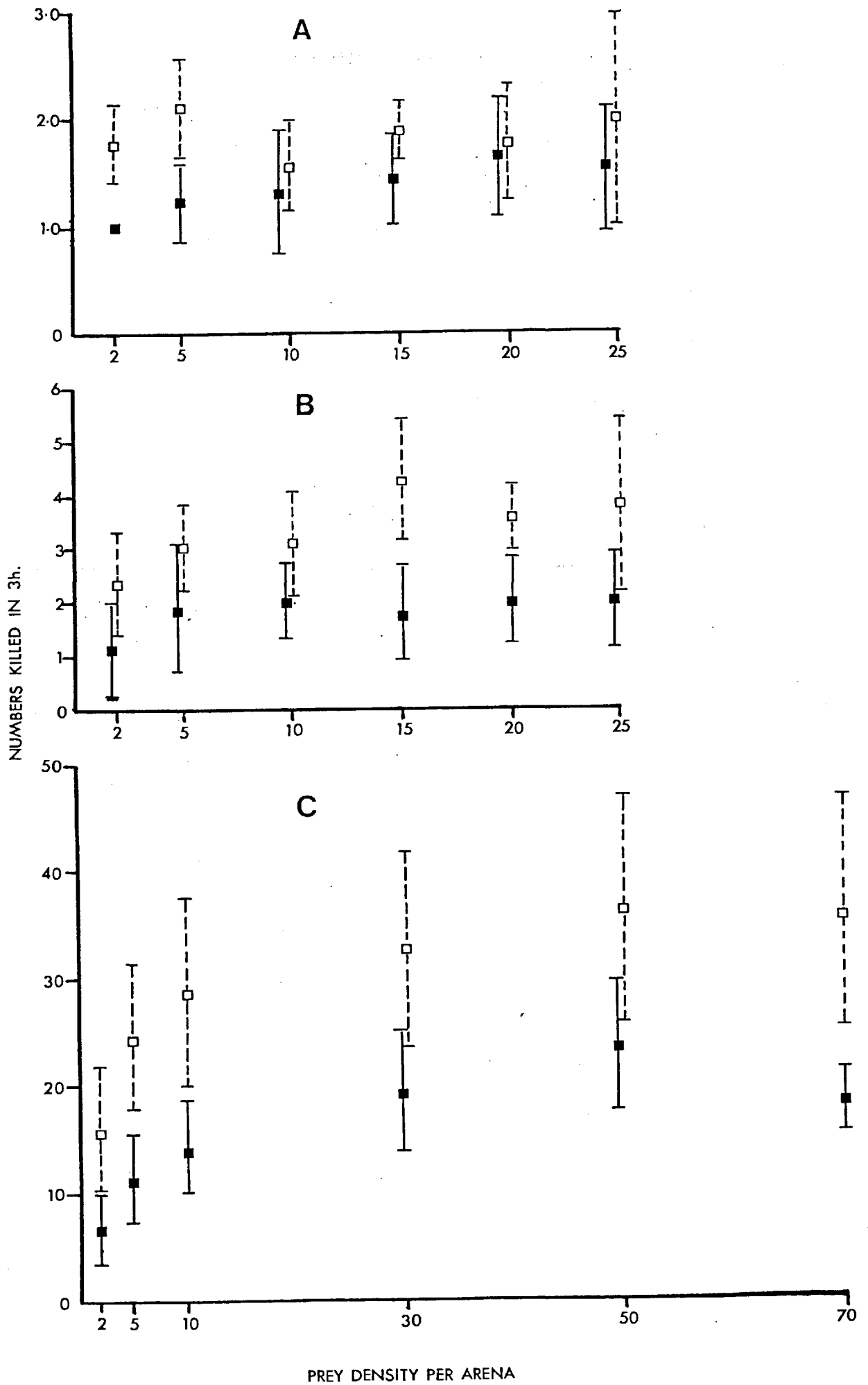
The functional responses of N. maculata feeding on six densities of each of the three prey species in simple (□) and complex (■) environments.

- A - Musca domestica prey
- B - Gammarus pulex prey
- C - mosquito larvae (Aedes aegypti) prey

95% confidence limits shown.

Comparison of densities by T tests (sig 0.05) and analysis of variance of data from all densities. (Densities underlined not significantly different).

<u>Musca</u>	Complex	<u>20</u>	<u>25</u>	<u>15</u>	<u>10</u>	<u>5</u>	2	(F = 0.56)
	Simple	No significant differences						
<u>Gammarus</u>	Complex	<u>25</u>	<u>20</u>	<u>10</u>	<u>5</u>	<u>15</u>	<u>2</u>	(F = 0.787)
	Simple	<u>15</u>	<u>25</u>	<u>20</u>	<u>10</u>	<u>5</u>	2	(F = 2.558 sig. 0.05)
mosquito	Complex	<u>50</u>	<u>30</u>	<u>70</u>	<u>10</u>	<u>5</u>	2	(F = 8.346 sig. 0.01)
	Simple	<u>50</u>	<u>70</u>	<u>30</u>	<u>10</u>	<u>5</u>	2	(F = 4.37 sig. 0.01)



LEGEND TO FIG. 53

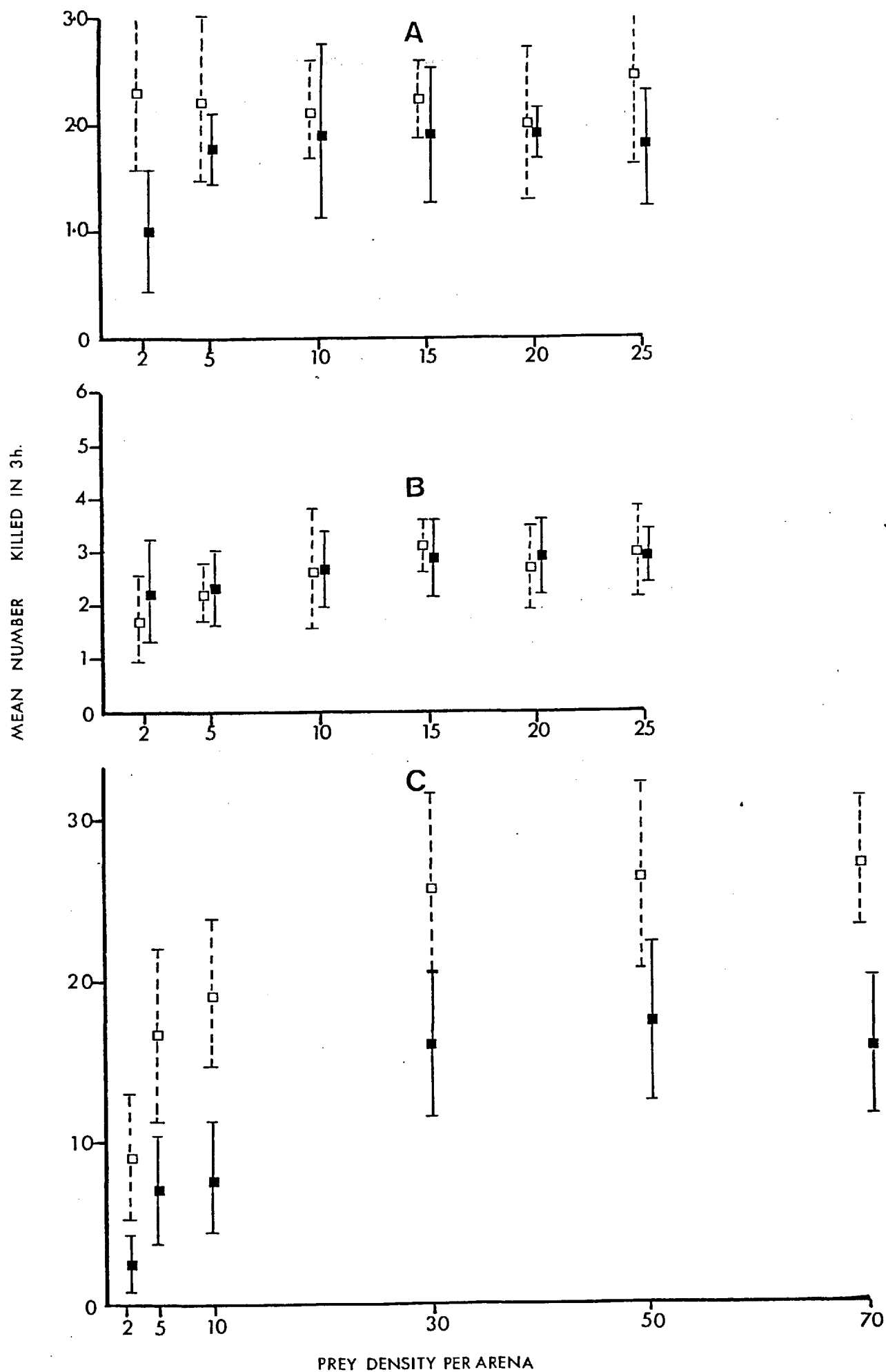
The functional responses of N. obliqua feeding on six densities of each of the three prey species in the simple (□) and complex (■) environments.

- A - Musca domestica prey
- B - Gammarus pulex prey
- C - mosquito larvae (Aedes aegypti) prey

95% confidence limits shown.

Comparison of densities by T tests (sig. 0.05) and analysis of variance of data from all densities. (Densities underlined not significantly different).

<u>Musca</u>	Complex	<u>20</u>	<u>15</u>	<u>10</u>	<u>25</u>	<u>5</u>	2	(F = 0.8)
	Simple	No significant differences						
<u>Gammarus</u>	Complex	No significant differences						
	Simple	<u>15</u>	<u>25</u>	<u>20</u>	<u>10</u>	5	2	(F = 3.8 sig. 0.01)
mosquito	Complex	<u>50</u>	<u>30</u>	<u>70</u>	<u>10</u>	<u>5</u>	2	(F = 8.6 sig. 0.01)
	Simple	<u>70</u>	<u>50</u>	<u>30</u>	<u>10</u>	<u>5</u>	2	(F = 9.2 sig. 0.01)



Responses by N. obliqua with Gammarus, Musca in the complex environment and mosquito larvae in the simple one are also of a Type II, but the response with mosquito larvae in the complex environment appears to be slightly domed with a peak at 50 prey per arena with about 18 prey killed. There is no response with Musca in the simple environment.

With Musca prey, there is little difference in capture rate between the three predators, although the general trend is for slightly higher rates with N. obliqua, and lower rates with N. glauca.

With Gammarus prey, the trend again shows lowest capture rate by N. glauca, and highest by N. obliqua in the complex, but by N. maculata in the simple environment.

With mosquito larvae, the trend is for highest capture rates by N. maculata in both environments, and generally lowest rates by N. glauca.

IV. 3.4. Reaction Areas

IV. 3.4.1. Introduction

The reaction area is the volume of water around the predator in which the predator will respond to a prey item. The size of the area depends on several factors including the prey size, speed of movement, contrast to the rest of the environment, and the predators sensory acuity, hunger levels and behavioural state (Holling (1966)).

In this study, the direction and distance of the predator from the prey item which elicited a response was recorded (a response being defined as at least an orientation movement). As the environmental arena does not lend itself to the use of grids for measuring distances, distances and direction of prey from the predator when a response occurred were judged by eye. Although the ideal method of representing a reaction area is in the form of a three dimensional picture,

this was found too difficult an exercise given the available data. Instead, the reaction area has been considered for three general situations. Firstly, responses to prey at the water surface (in two dimensions) were divided into four main divisions; Forward; Rear; Left; and Right. Secondly, responses from the water surface down into the water body were originally described in terms of distance along the surface and down from the surface. It was found however, that very few responses to prey below the surface were made in any direction other than in the forward direction from the surface, so the reaction area from the surface down into the water body was considered in terms of only two dimensions again, forward and down. Thirdly, a similar record was kept for responses from a perch site within the water body. Responses could be made in all four directions, as well as up and down from the perch, but again few responses were found in any direction other than the forward direction, so the reaction area can again be considered in two dimensions forward and up or down from the perch site.

As the reaction areas with each prey are likely to be different, they are considered separately for each predator. In each situation, the data is transformed to proportions of total responses in that situation. Data is pooled for all prey densities and all replicates. The results have been presented in several ways, depending on the relative positions of predator and prey. For responses at the surface, the main method of presentation is through a contour map, the lines of which join distances at which equal proportions of total responses are made in each of the four directions, the bug being the central point. The full data is presented in the form of histograms where the proportion of total responses is plotted against distance from the bug in each direction, and in the form of a graph showing cumu-

lative proportion of total responses in each direction plotted against distance from the bug.

As Musca prey are confined to the surface, estimation of reaction areas to prey within the water body is confined to mosquito larvae and Gammarus. For responses from the surface and from perch sites, proportions of total responses at different distances from the predator are represented by the height of bars at the appropriate position on simple graphs.

In the description of the reaction areas, the most accurate methods are to determine the limits of responses (in terms of distances from the predator) by the predator, using artificial stimuli (e.g. Wiese (1971), Wolda (1961)). In these situations, only one stimulus is given at a time, and the predator scored as to whether a response was made or not. In this study, the predator is being subjected to several stimuli from different directions in many cases, produced by actual prey items, and is being scored on the basis of the proportion of responses being made to stimuli distances and directions from it. Although the results from such an analysis may not define the extreme limits of prey detection, they will indicate the likelihood of the predator responding to prey at certain distances from it, and will allow a comparison to be made between the three predators.

IV. 3.4.2. Results

Data is presented for each situation described above, as proportion of total responses from that situation rather than as proportions of total responses made. Data in section IV.4.4. shows how the total responses are divided amongst the general situations described here. As an example of the results, the data for N. glauca is included here, and those for N. maculata and N. obliqua are shown

in Appendices XII, XIII and XIV.

a) Responses at the surface (Figs 54, 55 and 56; Appendix XII).

The most obvious result demonstrated by all three predators feeding on all three prey types is that the greatest proportion of responses is made in the forward direction, and generally the lowest are made to stimuli from the rear. Stimuli from the forward direction are not only received through the tactile sense organs, but also reinforced through the visual organs. The separation of the eyes of Notonectids shows that it is likely that they have binocular vision (as described for Robber flies, Oldroyd (1964)), which would increase accuracy of prey location in the forward direction. The assessment of prey distances would also be the most accurate in the forward direction (Wiese (1971), (1972)) due to the base length of the range finder system. Stimuli from the rear are only picked up by the tactile sense organs (the abdominal one being the most prominent), and those from the left or right, by the tactile organs and one eye. There appears to be little difference in proportions of responses elicited towards stimuli to either side of the predator. It appears that responses to prey are made most frequently when stimuli are received by the two sensory systems in combination.

Another general observation is that the largest reaction area is shown in the presence of Gammarus prey. The reaction area with Musca tends to be larger than that for mosquito larvae, except in the forward direction. These trends can be explained in terms of prey movement and strength of stimulus given out. Gammarus is the most active of the prey species and also causes large disturbances of the water body and surface while moving. Mosquito larvae, although being the smallest prey, and so produce the smallest disturbances of the water surface, are more active than Musca. It is expected, there-

LEGEND TO FIG 54

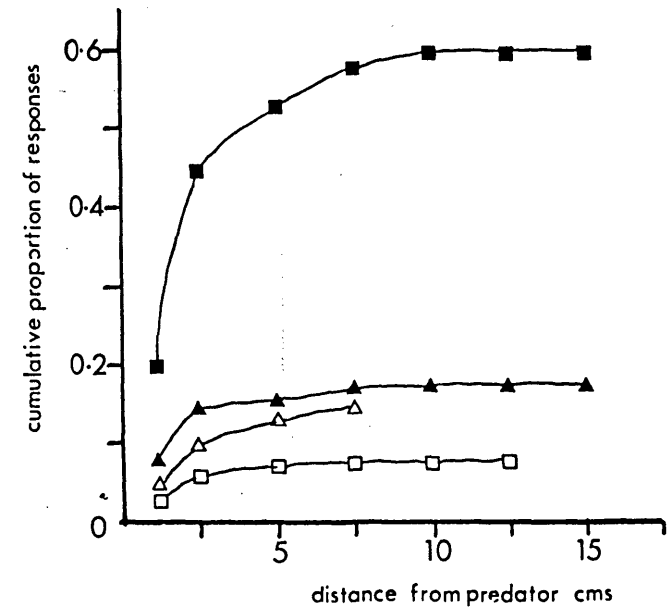
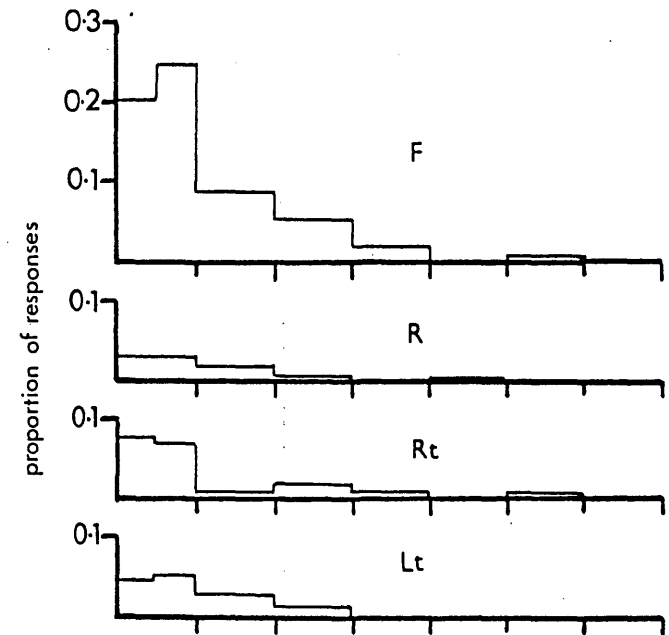
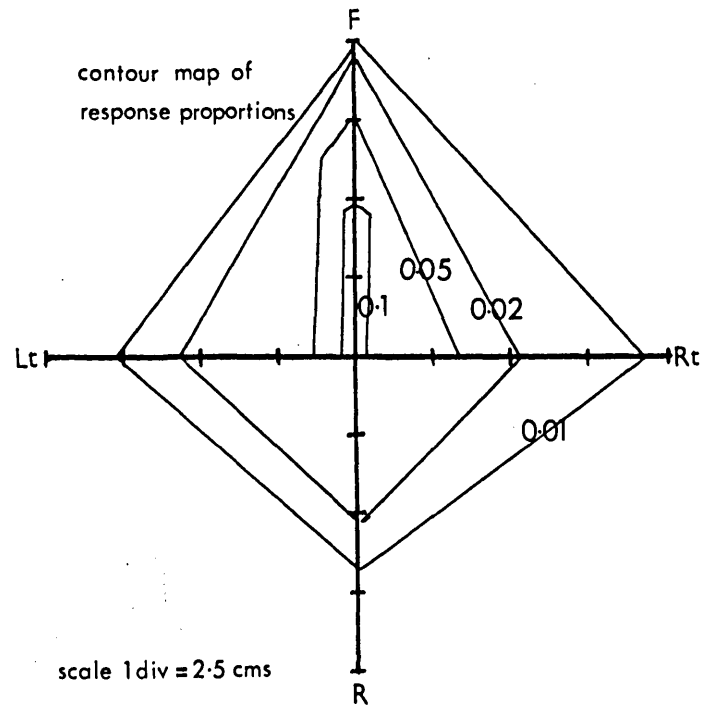
Reaction area of N. glauca at the surface with Musca domestica prey.

F = Forward, R = Rear, Rt = Right, L = Left

- A) Proportion contours - figures represent proportion of total responses and contours join **distances** from predator at which equal proportion of responses are made.
 - B) Proportion of total responses made at different distances from the predator in each direction.
 - C) Cumulative proportion of responses with distance from predator in each of the four directions
- Forward, Rear, Right Left.

FIG 54

N. glauca with Musca at the surface



LEGEND TO FIG 55

Reaction area of N. glauca at the surface with Gammarus pulex prey.

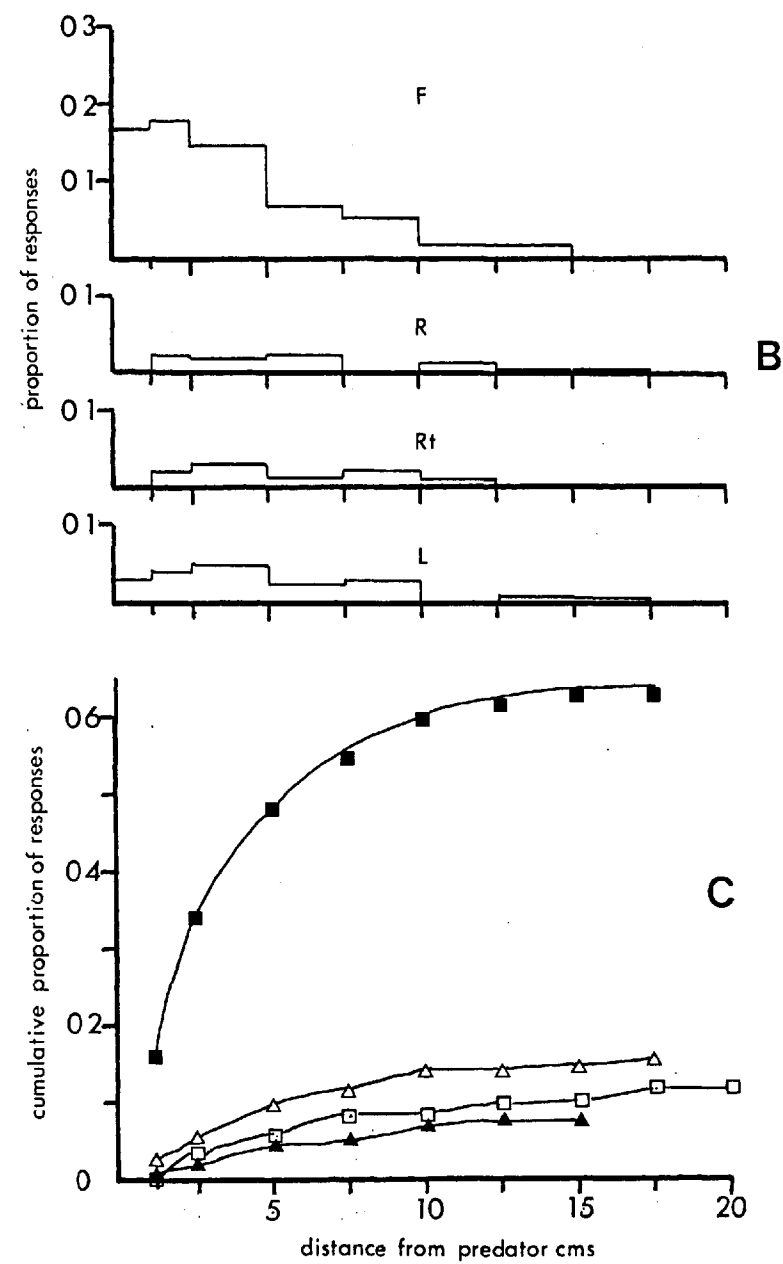
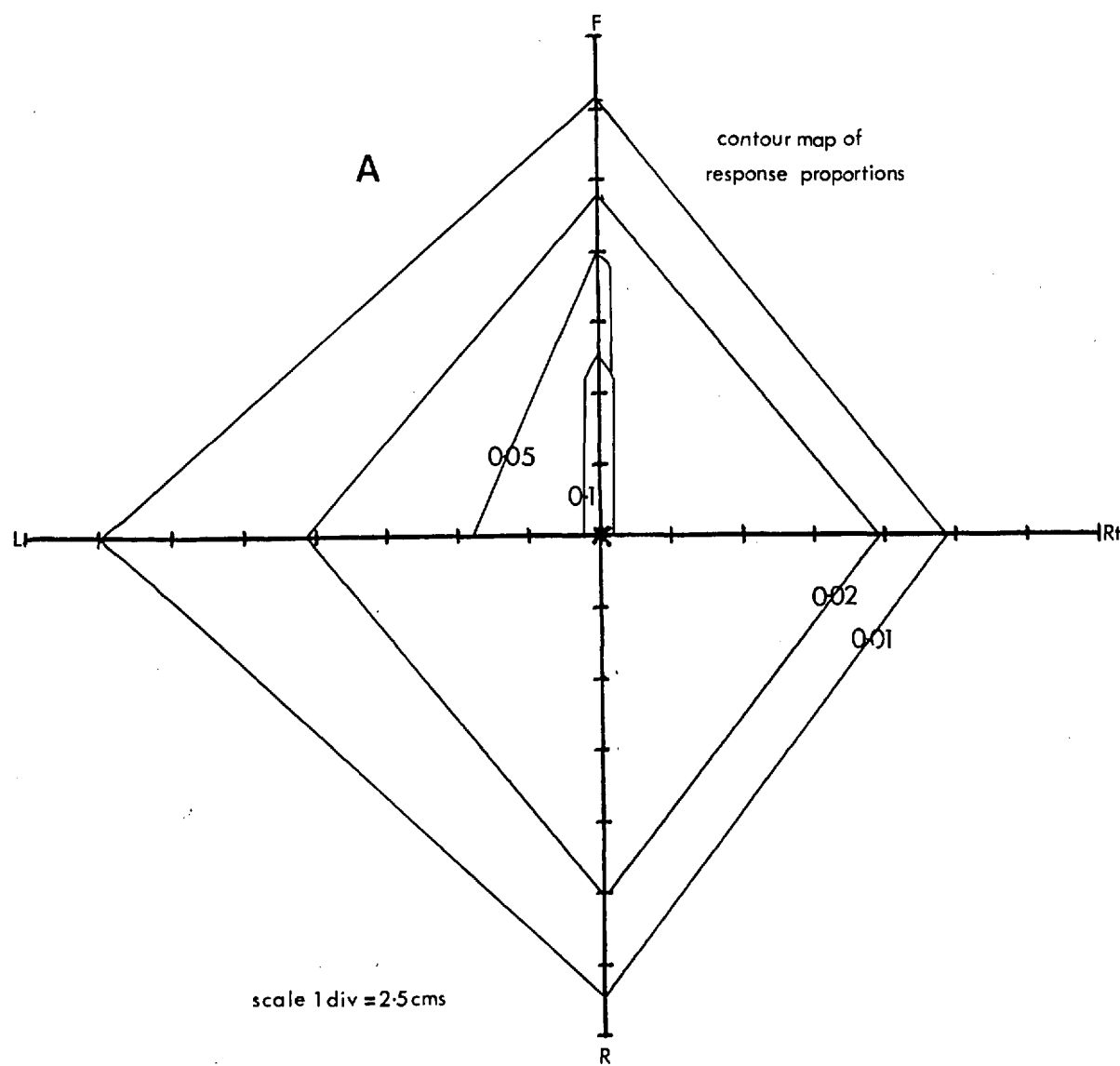
F = Forward, R = Rear, Rt = Right, L = Left

- A) Proportion contours - figures represent proportion of total responses and contours join distances from predator at which equal proportion of responses are made.
- B) Proportion of total responses made at different distances from the predator in each direction.
- C) Cumulative proportion of responses with distance for predator in each of the four directions

Forward, Rear, Right Left.

FIG 55

N.glauca with Gammarus at the surface



LEGEND TO FIG 56

Reaction area of N. glauca at the surface with mosquito larvae.

F = Forward, R = Rear, Rt = Right L = Left

A) Proportion contours - Figures represent proportion of total responses and contours join distances from the predator at which equal proportion of responses are made.

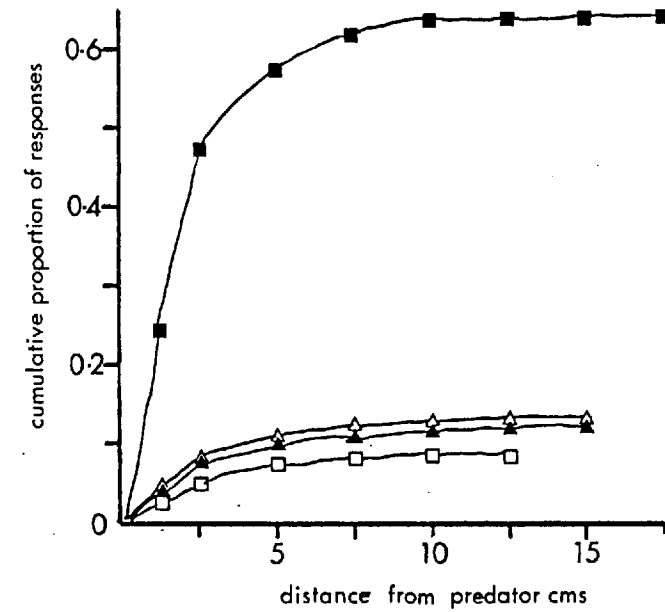
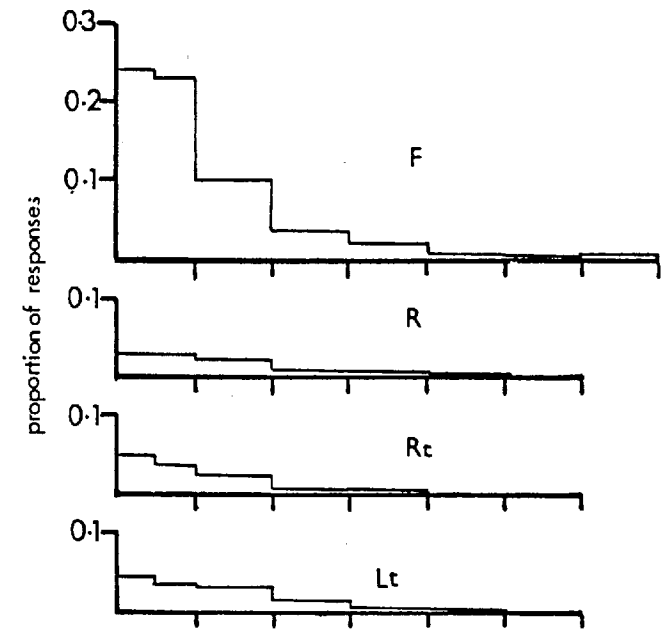
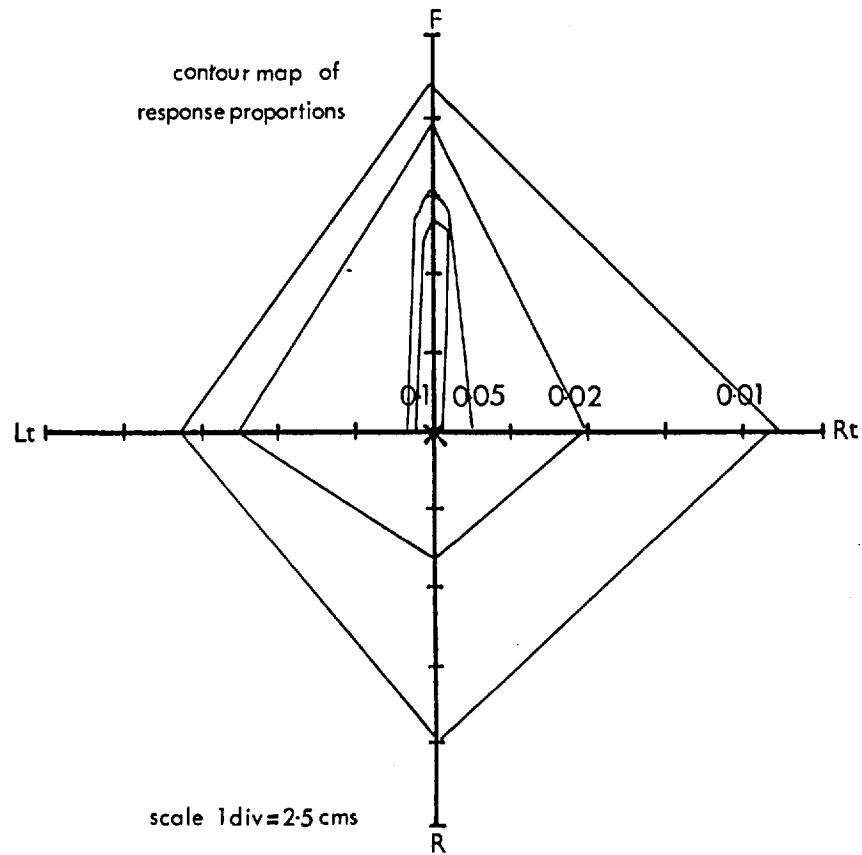
B) Proportion of total responses made at different distances from the predator in each direction.

C) Cumulative proportion of responses with distance from the predator in each of the four directions

Forward, Rear, Right Left.

FIG 56

N.glauca with mosquito larvae at the surface



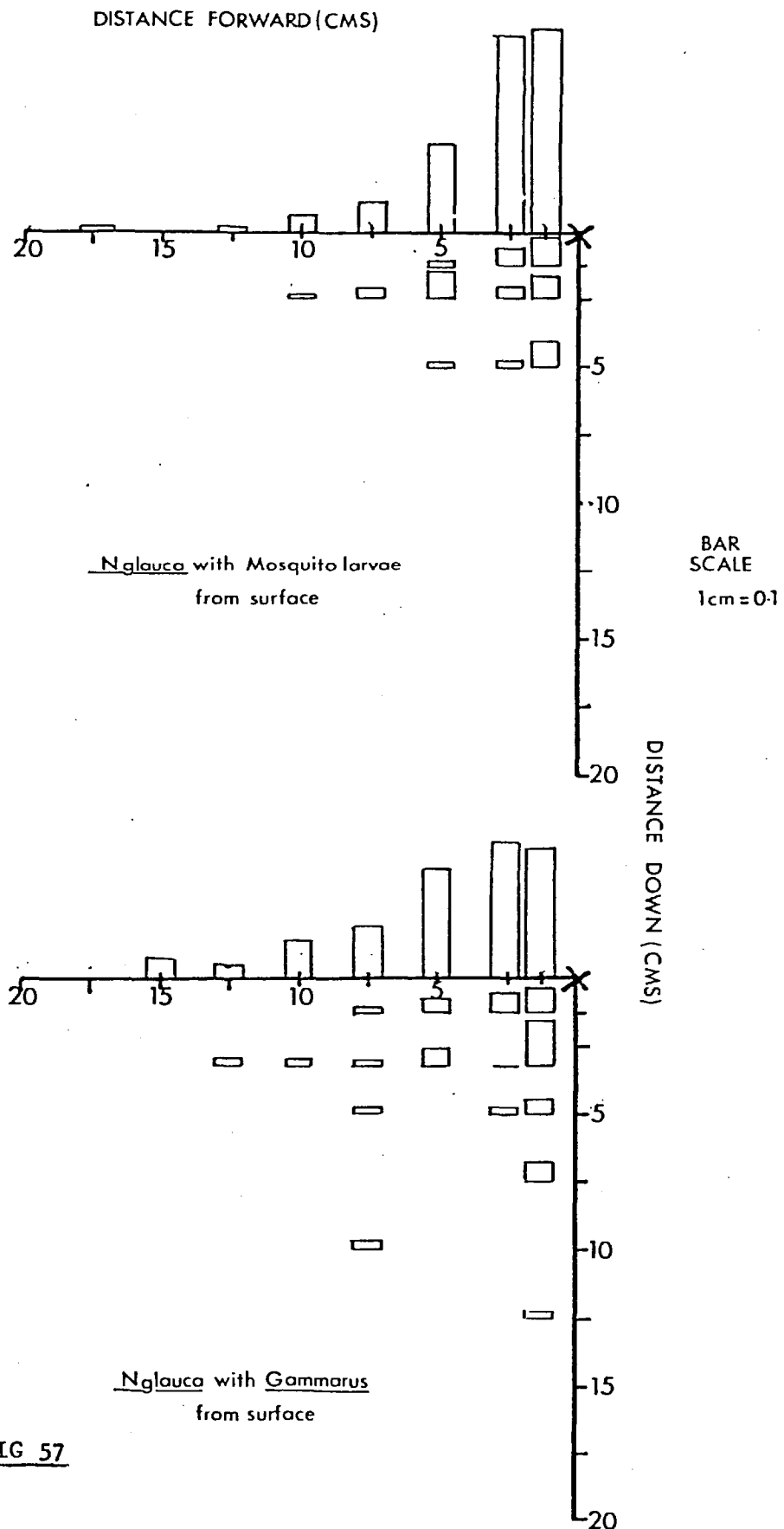
fore, that more responses will be made to Musca at a greater distance from the predator when the predator's tactile senses are most important i.e. rear, left or right, but where the visual senses are important, the greater movement of mosquito larvae should allow recognition at distances where the tactile organs might be unresponsive.

Comparing reaction areas of the three predators at the surface, with both Gammarus and Musca, N. maculata shows the largest area i.e. N. maculata responds to prey at greater distances than either of the other two predators. N. glauca also appears to have a larger reaction area than N. obliqua, with Gammarus and Musca. Similar reaction areas are found for all three predators with mosquito larvae.

With Musca, the patterns of responses are similar for all three predators, whereas, with mosquitos, similar proportions of responses are made by N. glauca and N. maculata in each direction, but N. obliqua shows a greater proportion of responses in the forward direction than the other two. With Gammarus, the responses of the predators are different. N. maculata shows the lowest proportion in the forward direction compared to the other predators, N. obliqua and N. glauca showing similar proportions. Both N. maculata and N. glauca show similar proportions of responses in the other directions, but N. obliqua shows a very low proportion of responses to stimuli from the rear and right.

b) Responses from the surface (Fig 57 Appendix XIII)

Responses in this situation are more or less confined to the forward plane. Attacks on prey in the water body requires accurate assessment of distance, which is best estimated through binocular vision and differential stimulation of the tactile receptors on the first two pairs of limbs, which will only occur from stimulation in the forward direction.



LEGEND TO FIG 57

Reaction area from the surface of N. glauca feeding on mosquito larvae and Gammarus.

Height of bars indicate proportion of total responses made at that distance from the predator (marked X)

With mosquito larvae, practically all responses are made within 5cms of the predator. For all three species of predator, the majority of the responses are made at the surface. Of the three predators, N. maculata responds to mosquito prey at the greatest distance, N. glauca at the shortest. As expected, the proportion of total responses decreases with distance from the predator both forwards and downwards.

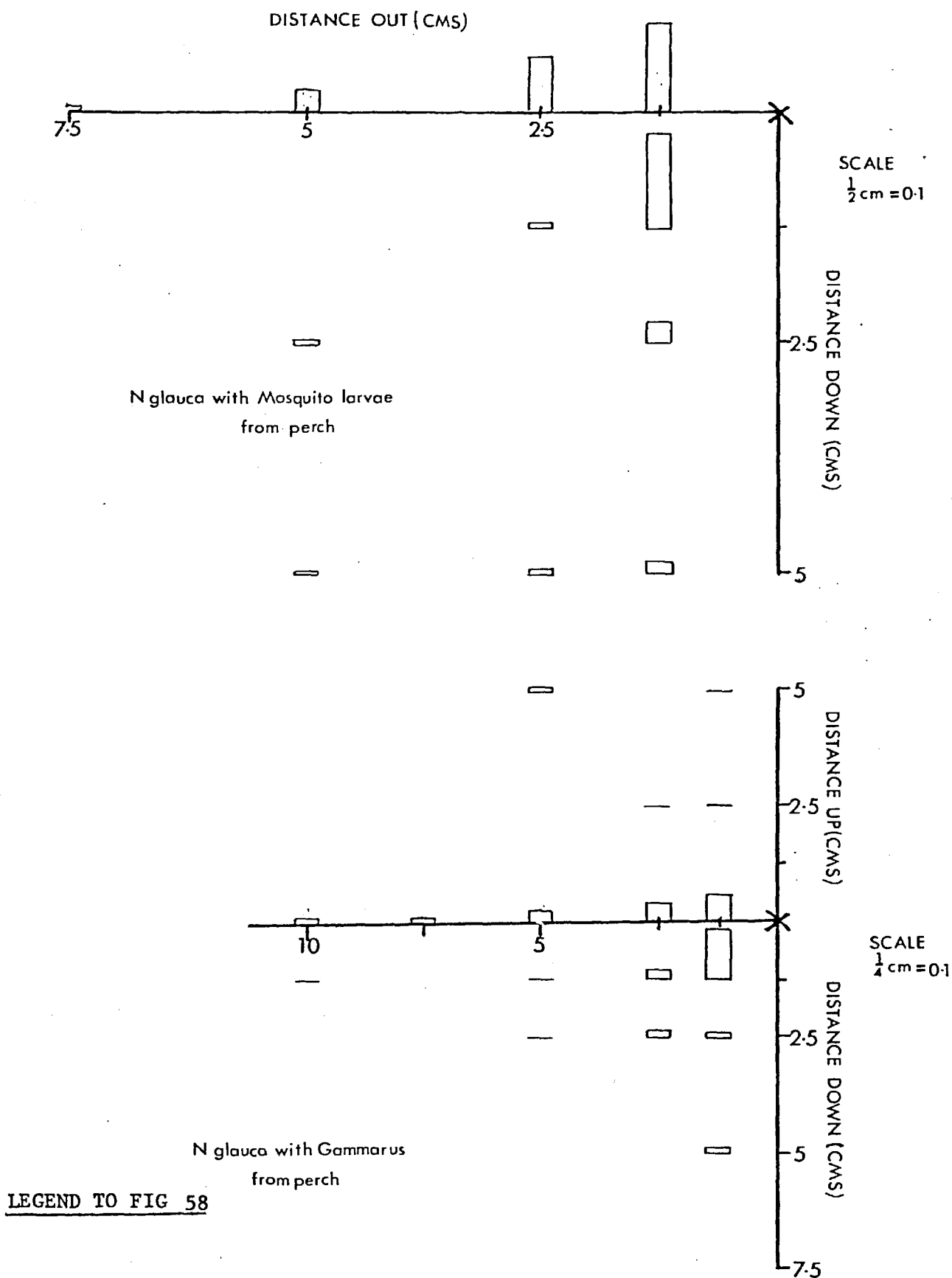
With Gammarus, all three predators respond to stimuli at a greater distance than with mosquito larvae. There is generally a decrease in proportion of responses with distance from the predator, although both N. maculata and N. obliqua show quite substantial responses to prey almost directly below i.e. forward 1cm, down 20cm.

N. maculata shows a slightly larger reaction area than N. obliqua but N. obliqua shows a larger proportion of responses to prey below the surface than N. maculata.

c) Responses from perch sites in the waterbody (Fig 58 Appendix XIV)

As with responses from the surface, most responses from perch sites are confined to the forward plane. All three predators respond over shorter distances from a perch site than from the surface.

Of the three predators, N. maculata again shows the largest reaction area in this situation. N. glauca shows the greatest proportion of responses within 2.5cms in the forward direction (horizontally out) and 1cm in the downward direction for both mosquito larvae and Gammarus. N. obliqua shows the greatest proportion of responses either within 2.5cms in the forward direction, or 2.5cms downwards. For both N. maculata and N. glauca, the reaction area with Gammarus is larger than that with mosquito larvae, with N. obliqua, there is little difference.



LEGEND TO FIG 58

Reaction area from perch sites of N. glauca feeding on mosquito larvae and Gammarus.

Height of bars represents proportion of total responses made at that distance from the predator (marked X).

IV. 4.

Use of SpaceIV. 4.1. Introduction

In the studies examining the distribution of Notonecta species, emphasis has been placed on describing the type of habitat selected in terms of the physical factors such as pH, depth, presence and type of vegetation etc., (e.g. Streams and Newfield (1972), Taylor (1968), Walton (1939), (1943) etc). Very little work has been carried out to see how the various species utilise the space within the habitats, in terms of preferred resting positions in the water body, and selection of perch sites in these areas. The little work that has been done, was confined to considerations of the distributions of various instars within the habitat, pointing out that nymphs normally progressively move away from the shallow edge regions towards the pond middle as they develop through the instars (e.g. Fox (1975(a)), Macan (1965)).

In the present study, the use of the habitat by adult females is examined in a number of ways; namely proportion of rest and handling times at the surface or at depth; selection of perch sites within the water body and on the plants themselves; and finally the positions from which attack sequences are mounted.

IV. 4.2. Proportion of time at surface and depthIV. 4.2.1. Introduction

These values were obtained during the continuous observation experiments, where the total rest time or handling time was proportioned into time spent at the surface and time spent at perch sites within the water body. Data with mosquito prey is presented here for all three predators, and results with Gammarus and Musca is given in Appendix XV. Proportions and percentages follow a binomial distribution, and when comparing such data, statistical tests usually

require a large sample, so that a normal approximation can be used (Bailey (1959) Parker (1973)). This unfortunately precludes any analysis on the prey density data separately, and necessitates analysis based on the pooled data over the six prey densities in each situation. Analysis of the preferences for surface or depth perch sites is given in Appendix XVI, and comparisons of proportions of time spent in the two areas between the three predators are given in Appendix XVI(b). (Fig. 59, 60, 61: Appendix XV).

IV. 4.2.2. Results

At rest in the complex environment, N. glauca shows strong preference for perch sites at depth, the greatest proportion of time spent there with Gammarus and Musca, and the least with mosquito larvae. In the simple environment, N. glauca again shows preference for perch sites at depth, equally so with all prey types, but spends a significantly shorter time here than in the complex environment. During handling time, in the complex environment, N. glauca again shows preference for perch sites at depth with Gammarus and mosquito larvae, significantly more time spent here with Gammarus, but no preference is exhibited while feeding on Musca. Significantly more time is spent at depth during rest than during handling, except with mosquito larvae, the most found with Musca. In the simple environment during handling, there is a switch to strong preference for the surface sites with all three prey types, with a marked reduction in time spent at depth from that during rest. Of the three prey more time is spent at depth during handling with mosquito larvae.

N. maculata shows a different allocation of time to surface and depth than N. glauca. In the complex environment, during rest, N. maculata shows weak preference for perch sites at depth with Musca prey ($P = 0.1$), and no preference for either position with mosquito larvae and Gammarus, there being no significant differences in the

LEGENDS TO FIGS 59, 60 and 61

Histograms showing the proportion of Rest time (A) and Handling time (B) spent at different positions in the waterbody, by the three predators feeding on six densities of mosquito larvae (70, 50, 30, 10, 5 and 2) in both simple and complex environments.

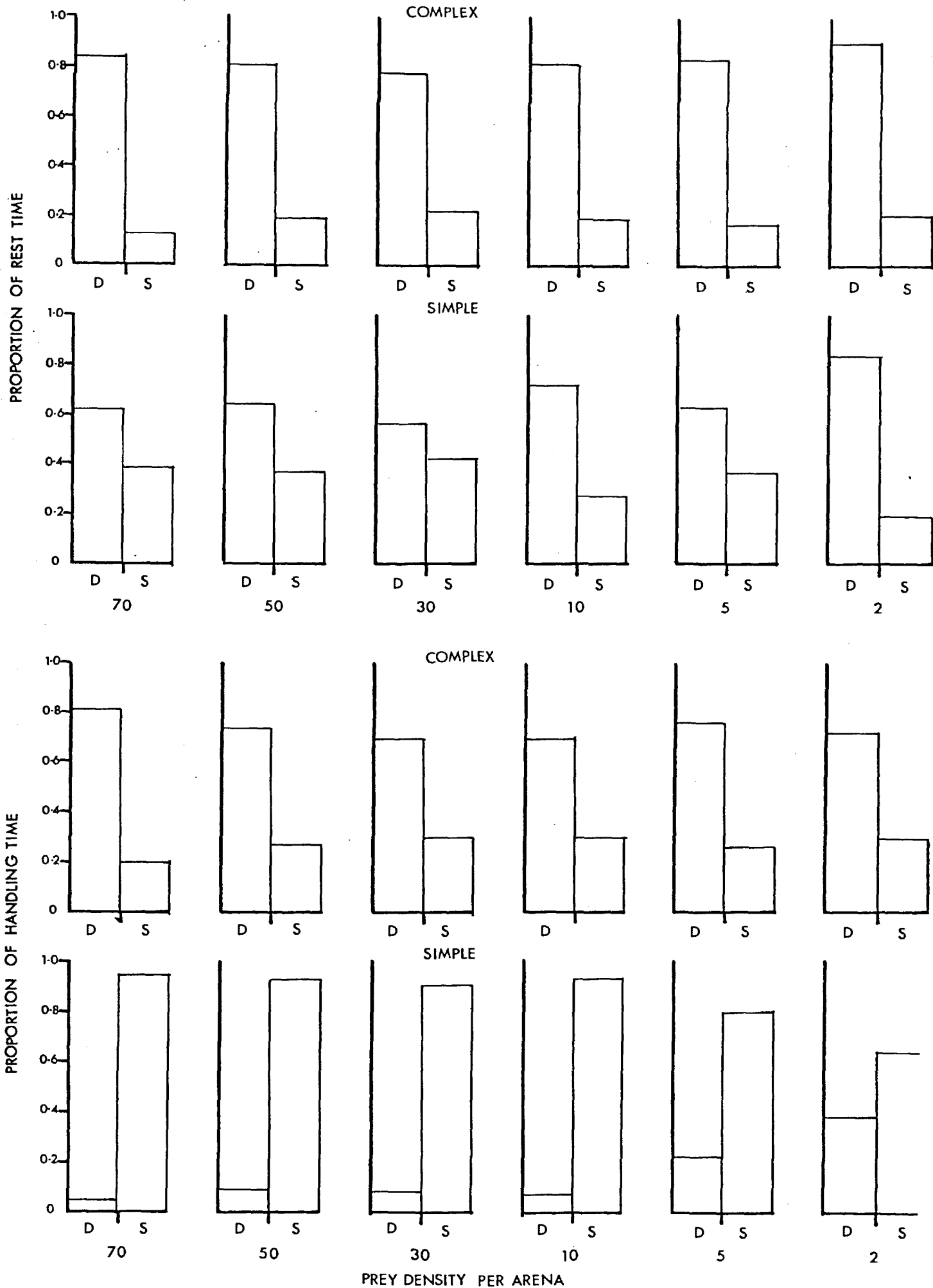
D - positions at depth

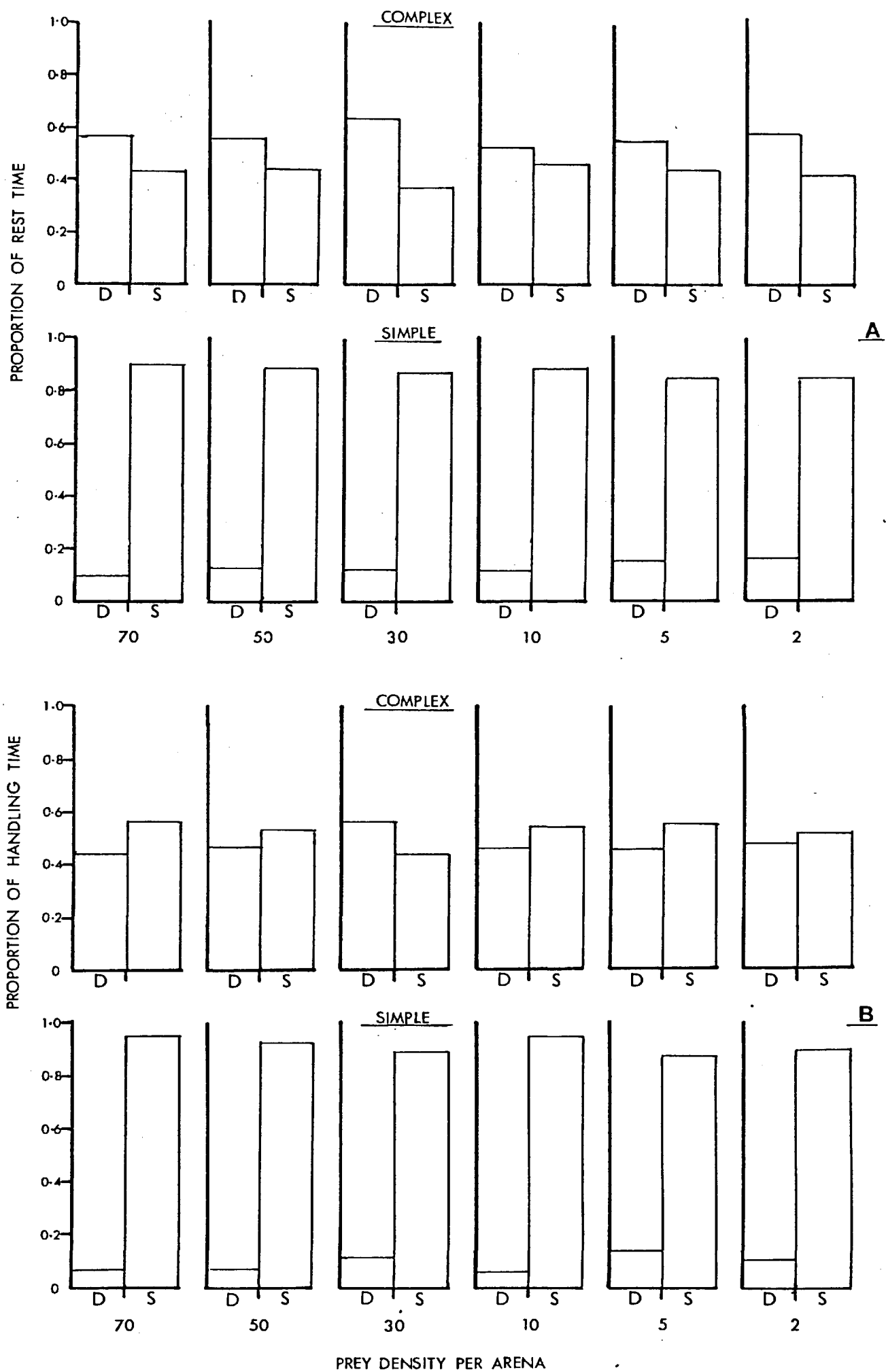
S - positions at surface

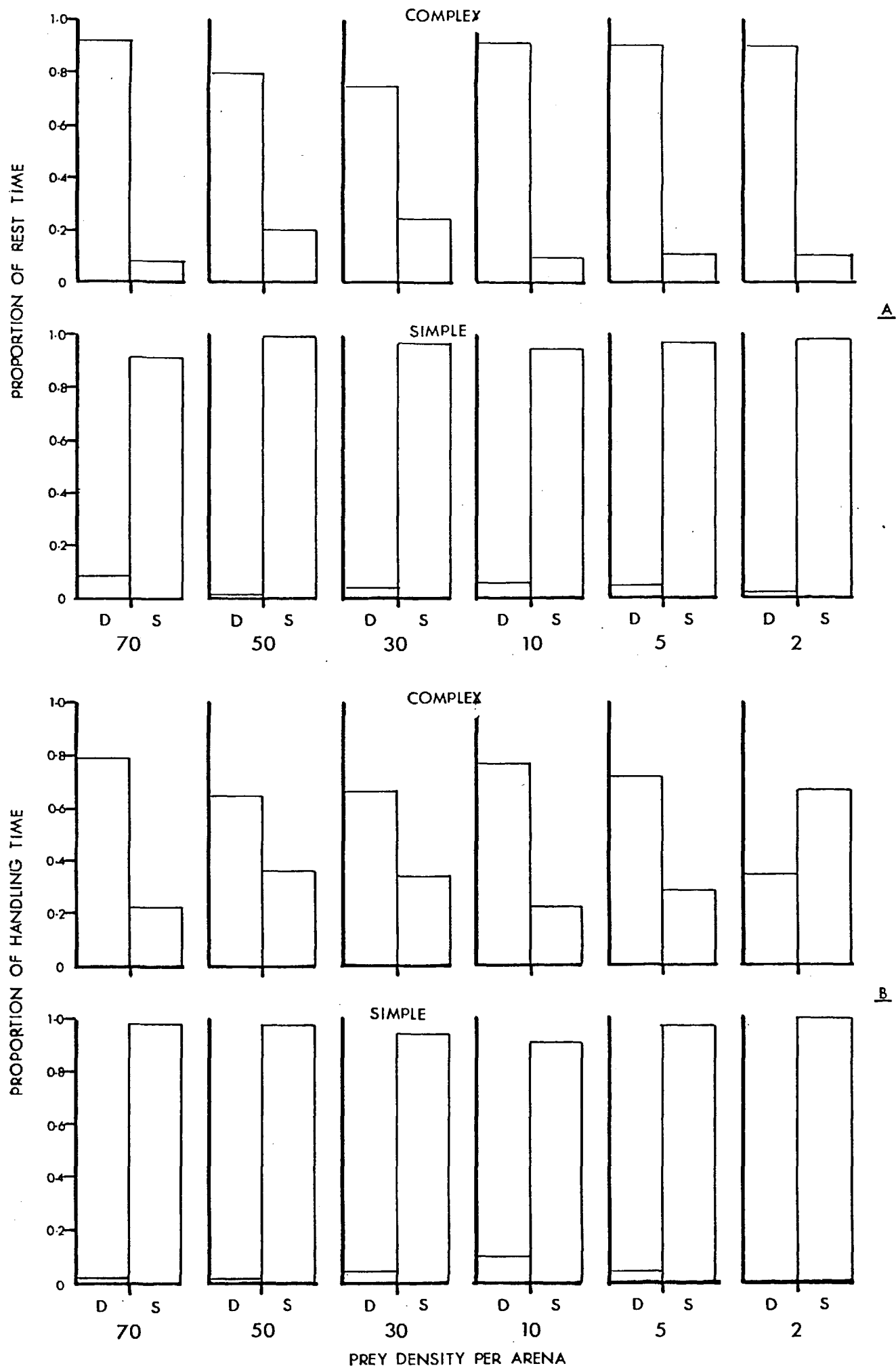
Fig. 59 N. glauca

Fig. 60 N. maculata

Fig. 61 N. obliqua

N. glauca feeding on mosquito larvae





time spent at depth with all three prey. In the simple environment during rest, there is a switch to preference for surface sites with all three prey, the lowest preference found with Musca, but significantly shorter proportions of time spent at depth compared to those in the complex environment with all three prey. During handling time in the complex environment, there is no change from rest with Gammarus and mosquito larvae, where no preference is shown for either site but with Musca, there is a preference for surface sites, a switch from the selection of deeper sites during rest. Proportion of time at depth is also the shortest during handling in the complex environment with Musca. In the simple environment, the preference for surface sites shown during rest is strengthened during handling on all prey types except mosquito larvae, where there is no change. Again, much smaller proportions of time are spent at depth in the simple compared to the complex environment during handling.

N. obliqua shows similar behaviour to N. glauca in the complex environment and N. maculata in the simple one. During rest in the complex environment there is strong preference for perch sites at depth, there being little differences with the three prey types. In the simple environment during rest, there is equally strong preference for surface sites with Gammarus and mosquito prey, and a smaller preference for surface sites with Musca, showing a strong switch from preference in the complex environment. During handling time in the complex environment, there is a reduction in the proportion of time spent at depth from that during rest, such that there is only weak preference for perch sites at depth with Gammarus and mosquito larvae, and no preference with Musca, there being no significant difference in the proportion of time at depth of the three sets of results though. In the simple environment, there is an increase

in preference for surface sites during handling with Musca compared to that during rest, but with mosquito larvae and Gammarus there is no change.

The general difference in results between complex and simple environments, where there is a reduction of time spent at depth during both rest and handling in the simple one, can be simply explained on the basis of lack of available perch sites here, the predator being restricted to irregularities on the bucket sides, which are fairly difficult to locate.

Another general observation is that during handling in the complex environment, less time is spent at depth with Musca than with Gammarus and mosquito larvae, and the trend is for most time to be spent there with Gammarus. There are two possible explanations for this. This first may involve some form of learning, where, during feeding, the predator stays in positions near those where the prey was captured or occurs, either to assess prey availability for the control of handling time (see Chapter VII), or for increasing the likelihood of subsequent captures. The second, and more probable explanation, simply involves predator morphology and how prey items are grasped. In the initial stages of subduing prey, both fore and middle pairs of raptorial limbs are used, thus the predator is unable to hold onto a perch. In these first stages after capture, the predator invariably floats up to the surface (see Chapter I). When the prey has been subdued, the second pair of limbs are usually released from grasping the prey, and the predator would then be able to cling onto a perch. If the prey item is large however, as is the case with Musca, both pairs of limbs may be required for continual handling, and also too much effort may be required in taking such a large and bouyant prey item down to a perch site, so more time is likely to be spent at the surface.

This second explanation would also explain the results in the simple environment, where practically all handling time is spent at the surface. The problems of locating a perch site on the arena sides would be accentuated when handling prey, as only one pair of limbs are free for holding on. The fact that with the three prey types, the largest proportion of time spent at depth during handling is found with the smallest prey (i.e. mosquito larvae) also substantiates this conclusion.

IV. 4.2.3. Conclusions

N. glauca and N. obliqua show equally strong preferences for perch sites at depth in the complex environment during rest with all prey types, but N. maculata spends much shorter periods there, showing only a weak preference for depth with Musca, and no preference with the other two prey. In the simple environment during rest, N. glauca shows a reduced preference for depth than in the complex one, but both N. maculata and N. obliqua show strong preferences for surface sites, N. obliqua generally the greatest, perhaps prohibited from searching for perch sites at depth due to the high energetic costs this would entail.

During handling in the complex environment, both N. glauca and N. obliqua show reduced preference for depth from that during rest with Gammarus and mosquito larvae, N. glauca showing the strongest of the two, and both show no preference with Musca. N. maculata shows the lowest proportions of time at depth showing no preference with Gammarus and mosquito larvae, and preference for surface sites with Musca. In the simple environment during handling, all three predators spend most time at the surface.

IV. 4.3. Selection of perch sites at depth.

IV. 4.3.1. Introduction

In the previous section, the behaviour of the predators was considered

FIG 62

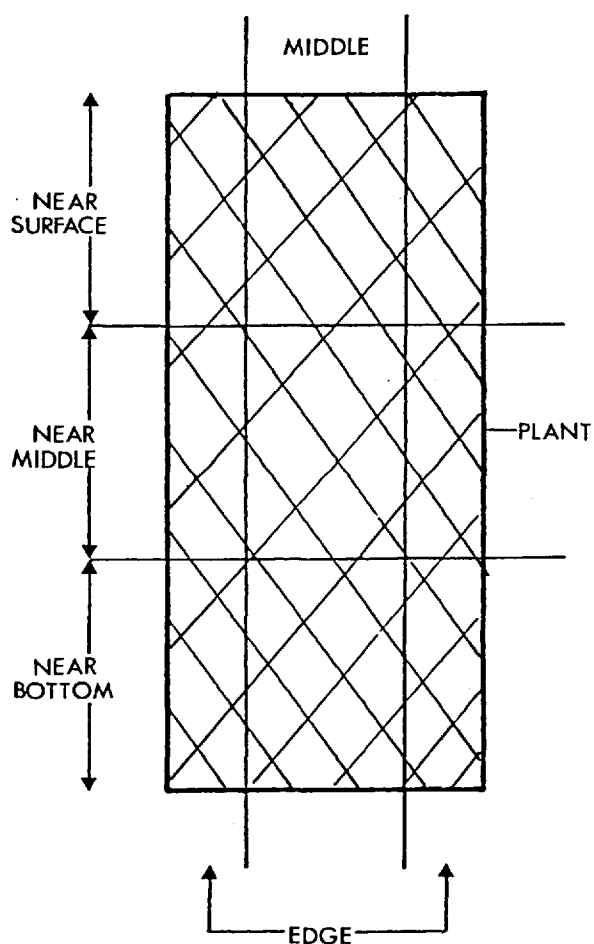
LEGEND TO FIG 62

Diagram showing the arbitrary divisions of the netlon 'plant' for analysis of perch site selection.

in terms of time allocation to the surface or at depth. In this section, the interest lies in how the predators utilise the available perch sites, and only data from the complex environment is considered. Perch utilisation has been examined in two ways. Firstly, in respect of the depth of perch site selected on the plants, where the plant is arbitrarily divided into three sections; the top third designated near surface; the middle third designated near middle; and the bottom third designated near bottom. Secondly, in respect of how the predator actually uses the plant as a perching site, where consideration is given to what parts of the plant the predator uses (i.e. middle or edge of the plant), and whether there is preference for a particular plant or perch site.

The plant can be considered to be divided into nine sections, as shown in Fig 62. Records were kept during experiments of the perch sites visited (results being combined over all prey densities), and the analysis of the results are described in each sub-section.

IV. 4.3.2. Perch selection with respect to depth.

The results represent proportions of total visits with each prey type to each of the three main areas, and are presented in the form of histograms (Figs 63-65). Perch selection is considered during rest (not feeding) and during handling time (feeding). The total number of visits to each area of the plants are compared by χ^2 and the significances of the differences are shown on the figures.

N. glauca in general prefers near middle perch sites, except during rest with Gammarus, where there is no preference between near middle and near bottom sites. Preference for these near middle sites appears to increase during feeding. Near surface sites are the least preferred, except during feeding on Musca, where this is no difference from selection of near bottom sites. This may be partly explained by the greater difficulty in swimming underwater carrying large prey.

LEGEND TO FIGS. 63, 64 and 65

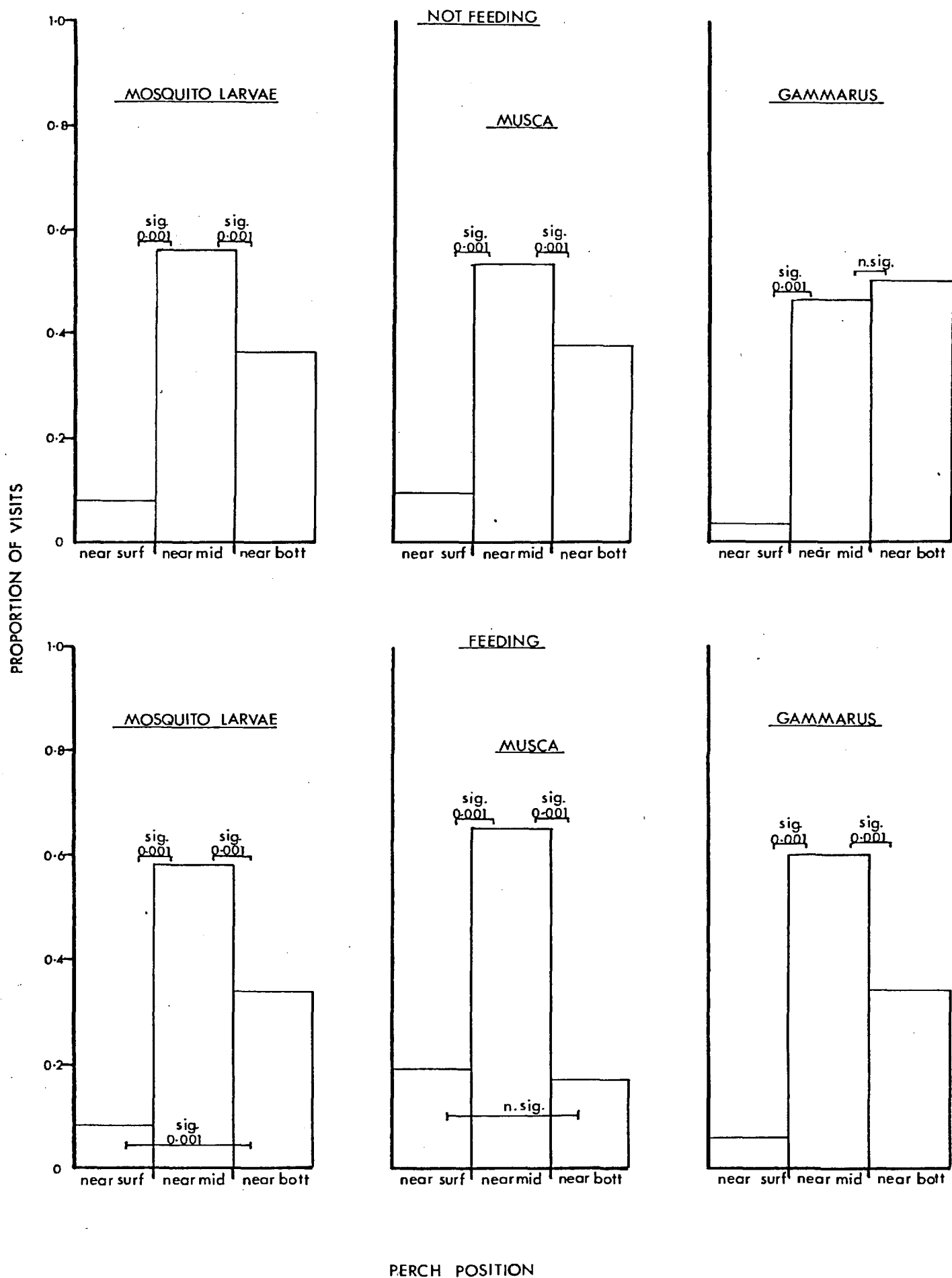
Histograms showing perch selection during periods of feeding and not feeding by the three predators in the presence of each of the three ^{prey} types in the complex environment (results pooled for all prey densities)

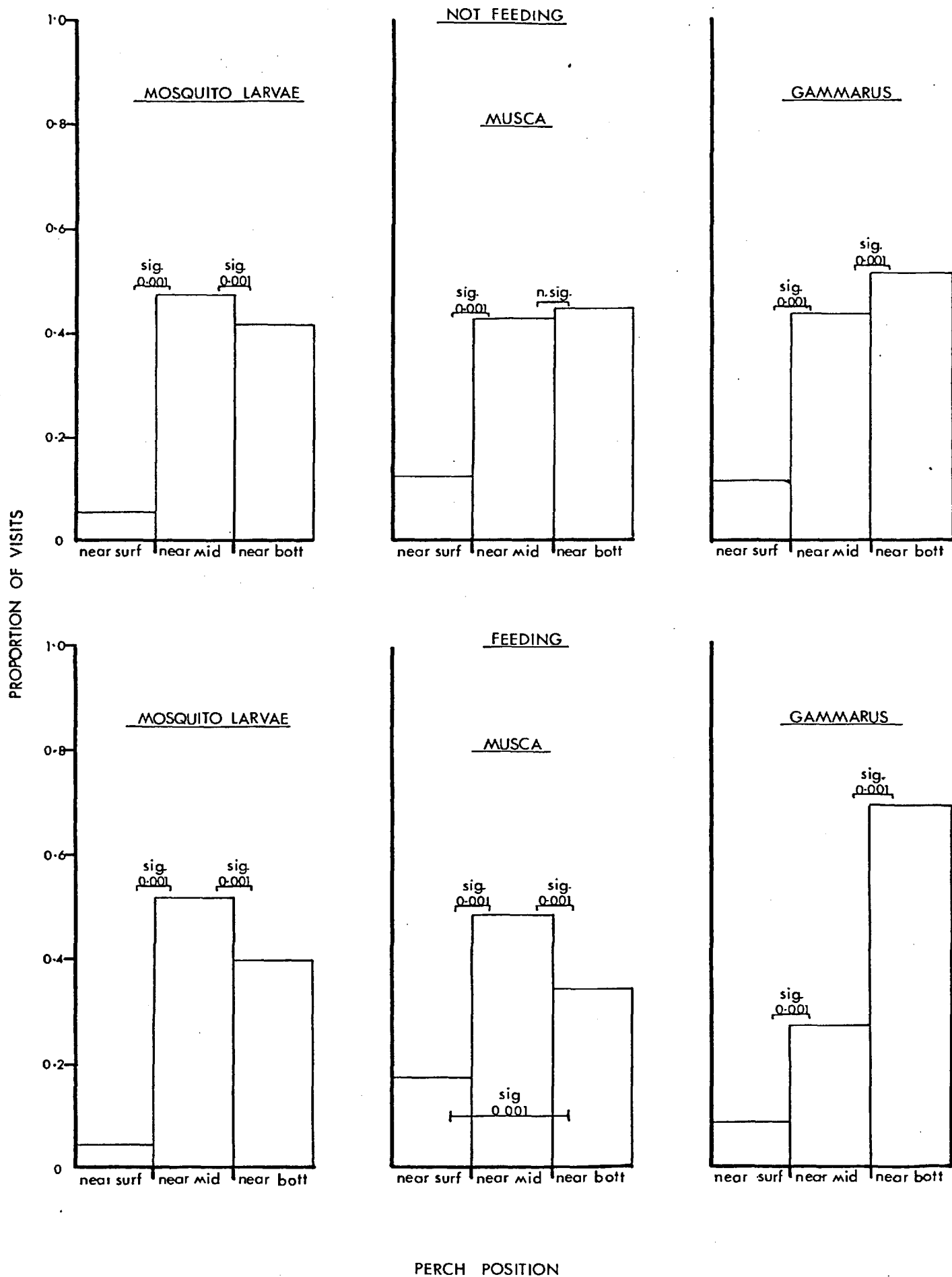
- Near surf. - perch sites on the top third of
the plants
- Near midd. - perch sites on the middle third
of the plants
- Near bott. - perch sites on the bottom third
of the plants

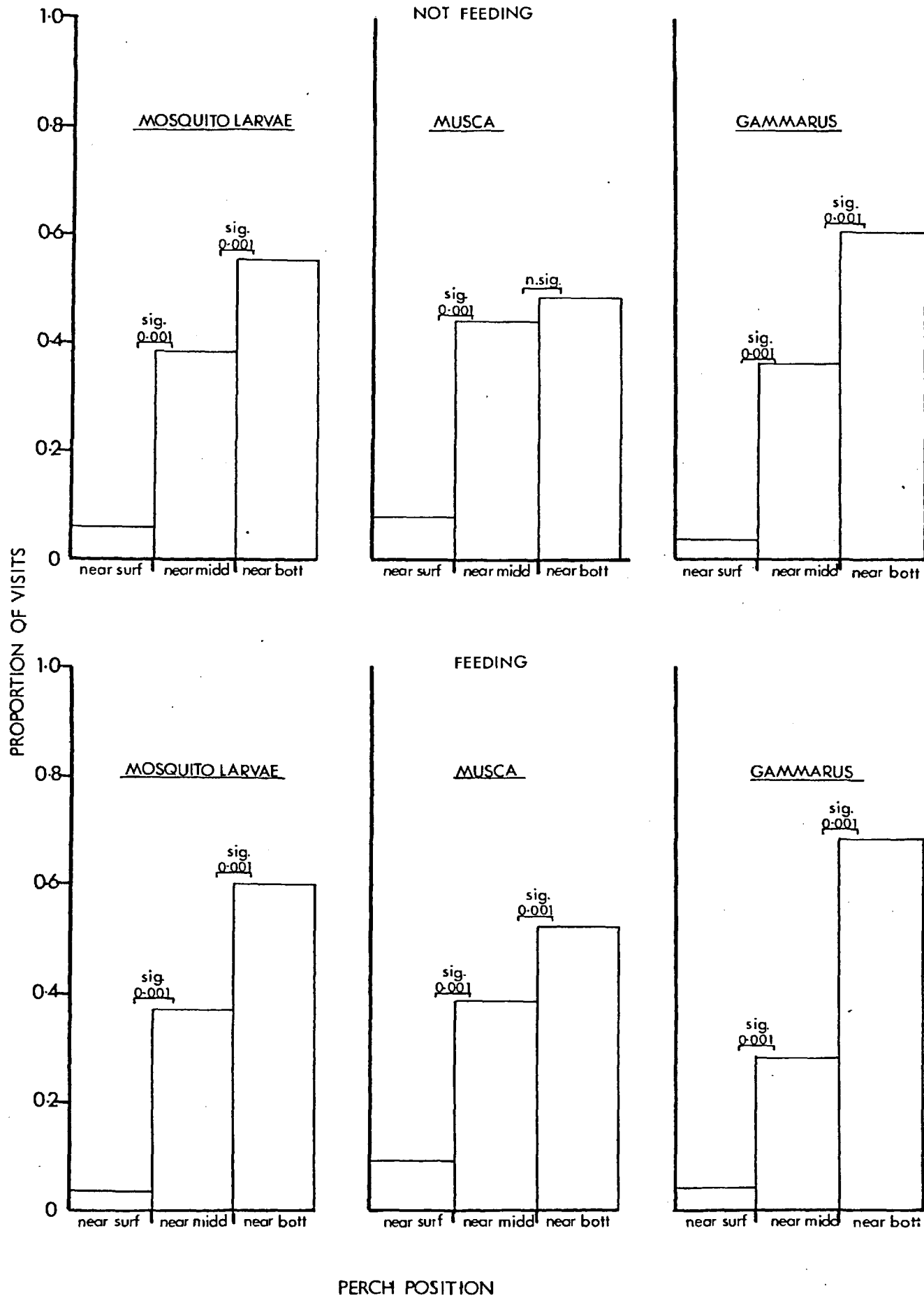
Significance of the differences between values shown
(χ^2 test)

- Fig. 63 N. glauca
- Fig. 64 N. maculata
- Fig. 65 N. obliqua

PERCH SITE SELECTION BY N. glauca



PERCH SITE SELECTION BY *N. maculata*

PERCH SITE SELECTION BY N.obliqua

Selection of sites by N. maculata is slightly different. With mosquito prey, there is a preference for middle sites during both rest and handling. With Musca, there is equal selection for near middle and near bottom sites during rest, but a marked preference for middle sites during handling. With Gammarus, N. maculata shows preference for bottom sites, which apparently increases during feeding. The general trend is for the largest proportion of visits to near surface sites to be found with Musca, to near middle sites to be found with mosquito larvae, and to near bottom sites with Gammarus. It appears that selection of perch sites by N. maculata is strongly affected by prey distribution (see Chapter II), this effect being accentuated during feeding, indicating the possibility of some learning process, as suggested in the previous section.

N. obliqua shows preference for near bottom sites, significantly so in all situations except with Musca at rest. The largest proportion of visits to these areas appears with Gammarus prey, and the lowest with Musca, indicating that the basic preference for near bottom sites may be slightly affected by prey distribution. This preference seems to be increased during handling.

In conclusion, N. glauca shows a general preference for near middle perch sites, N. obliqua for near bottom sites, and both seem to be affected to some extent by the prey distribution, which slightly modifies the preference. N. maculata appears to be most affected by prey type in its selection of perch sites. During feeding, the general preferences of N. glauca and N. obliqua seem to be increased, and the effect of prey type has an increased effect on selection by N. maculata. It should be pointed out, that these results are based on numbers of visits, not time spent at each perch site, so for a more complete picture of perch selection, these results should be considered with those of the previous section.

IV.4.3.3. Use of perch sites

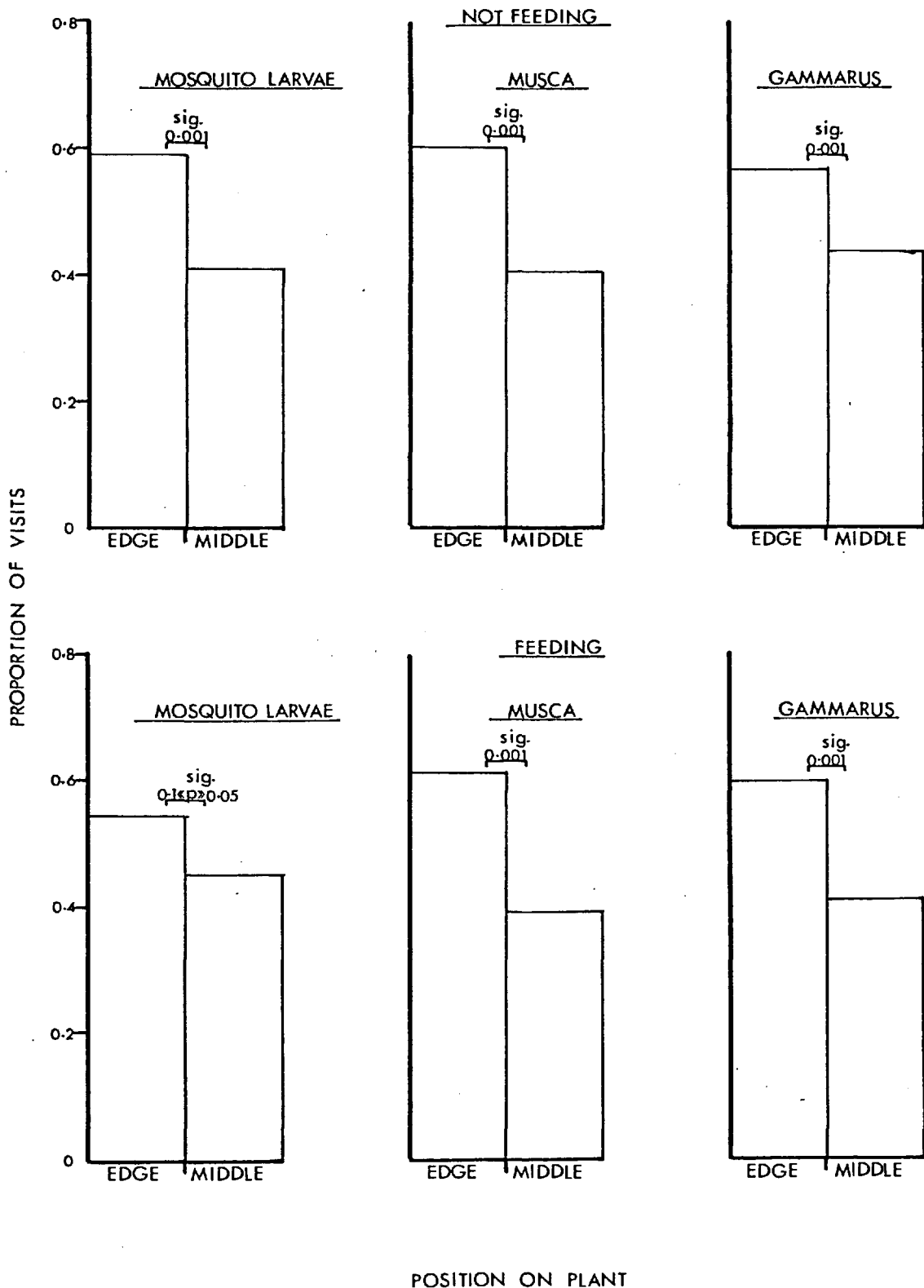
In this section, the problems of interest are a) What part of the plant does the predator prefer?, b) Whether specific plants, and c) specific perch sites are favoured?

a) Each visit to a perch site was scored as either being at the edge or in the middle of the plant (Fig. 62). The total visits to each part were then compared using χ^2 , for periods of rest and handling, and the data is presented as proportions of total visits in the form of histograms (Figs. 66, 67 and 68).

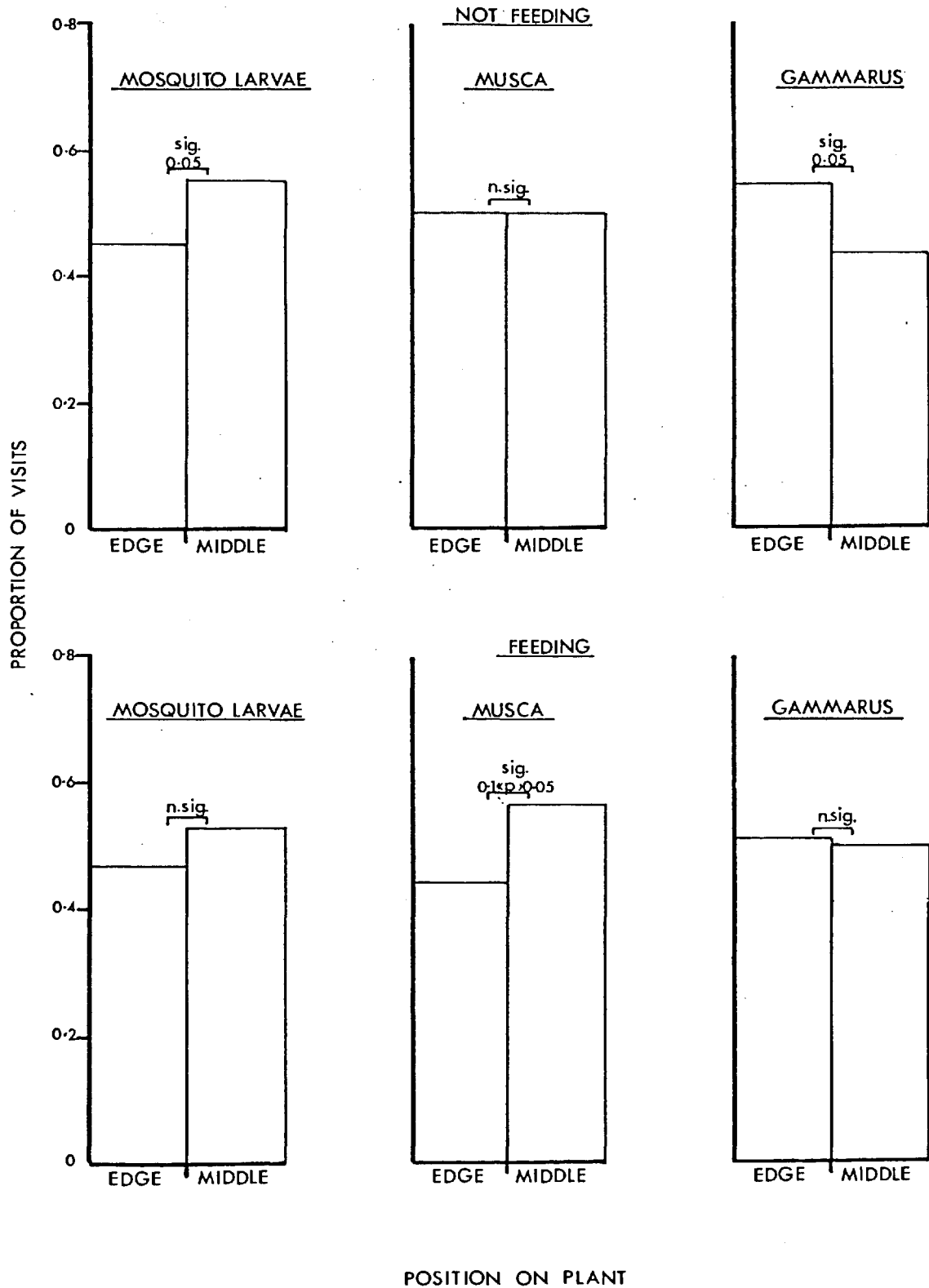
Both N. glauca and N. obliqua show preferences for perch sites at the plant edge, during both rest and handling periods, the preference by N. obliqua tending to be stronger. Prey type does not seem to affect this preference. For N. maculata, there is little preference for either part of the plant, but the trend seems to be for selection of middle areas with mosquito larvae and Musca to a lesser extent, and for the plant edge with Gammarus.

One would imagine that perch sites at the plant edge would offer better vantage points for monitoring the surrounding areas and from which to launch an attack after prey swimming past in the water body, and on this basis, it is considered that N. maculata is showing the least efficient use of the perch sites.

b) For further examination of the use of perch sites, one can investigate whether predators preferentially return to the same plant they have just left, after a swim. Records were kept of the number of times the predators returned to the same and to different plants during rest and handling, and these were compared using χ^2 to a null hypothesis of random selection, where it is expected that there will be a proportion of 1 in 3 returns to the same plant. Table 4.5 presents the numbers of returns to the same and to different plants, the χ^2 value for differences from the expected results, and the significance

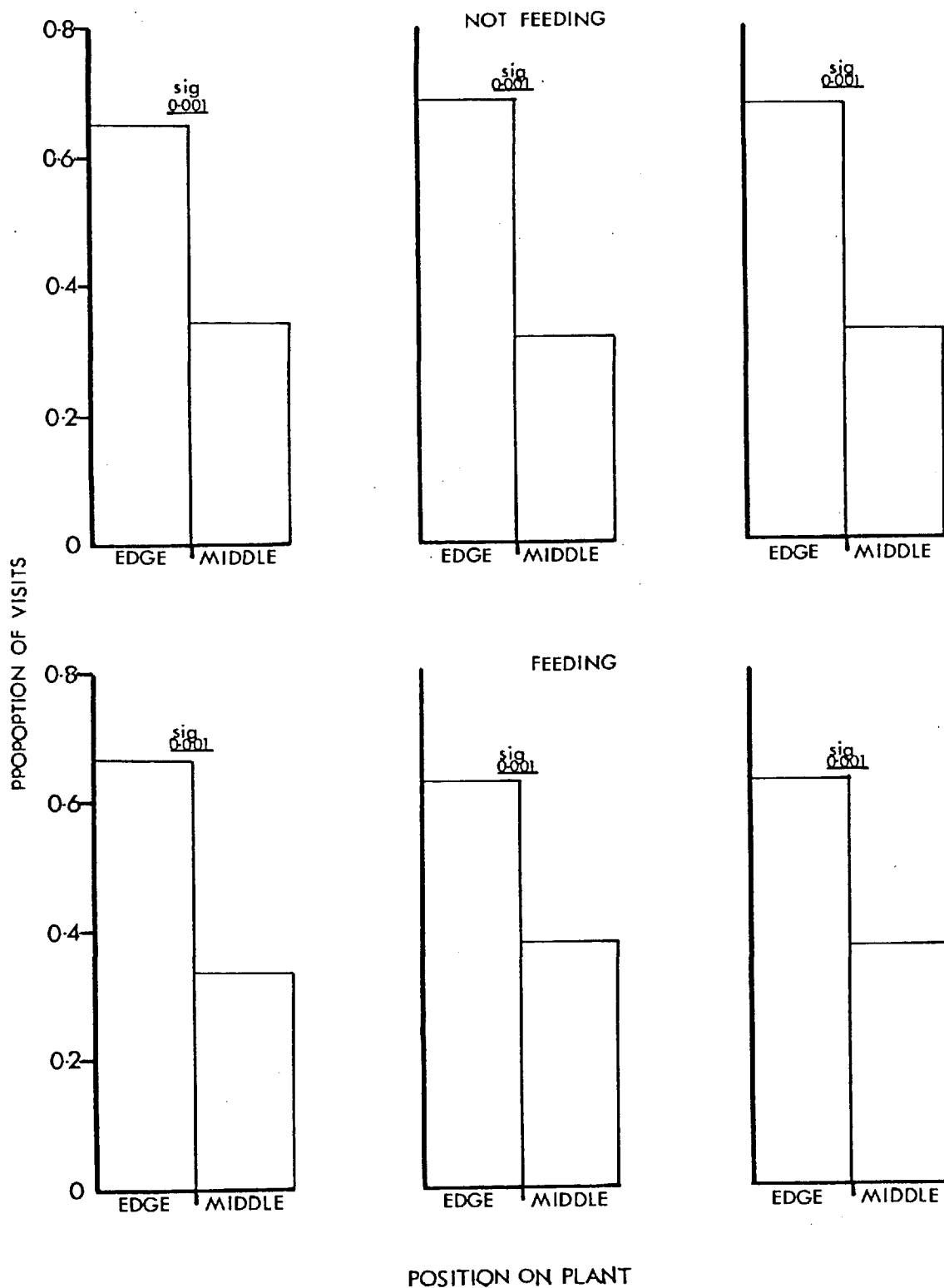
SELECTION OF EDGE OR MIDDLE SITES BY N. glaucaLEGEND TO FIG 66

Histograms showing selection by N. glauca of edge or middle perch sites on the plant for all three prey types not feeding and feeding. Significance of differences between values are shown (χ^2). Data for all densities and near surface, near middle and near bottom perch sites are pooled.

SELECTION OF EDGE OR MIDDLE SITES BY N. maculataLEGEND TO FIG 67

Histograms showing selection by N. maculata of edge or middle perch sites on the plant for all prey types, not feeding and feeding. Significance of differences between values are shown (χ^2). Data for all densities and near surface, near middle and near bottom perch sites are pooled.

SELECTION OF EDGE OR MIDDLE SITES BY

N. obliquaLEGEND TO FIG 68

Histograms showing selection by N. obliqua of edge or middle perch sites on the plant for all prey types, not feeding and feeding. Significance of differences between values are shown (χ^2). Data for all densities and near surface, near middle and near bottom perch sites are pooled.

Table 4.5 Table showing the total number of returns to the same and to different plants during rest (not feed) and handling (feed) periods for the three predators with the three prey types.

Ho = 1:3 random choice. 1 in 3 probability of returning to the same plant.

		Returns to same plant	Returns to different plant	χ^2	Significance to reject Ho	Probability of returning to same plant	Conclusions
<u>N. glauca</u>							
Mosquito	not feed	146	110	64.64	0.001	0.57	Strong pref. for same plant
	feed	138	84	83.03	0.001	0.6216	" " " " "
<u>Musca</u>	not feed	74	52	36.57	0.001	0.587	" " " " "
	feed	65	48	29.75	0.001	0.575	" " " " "
<u>Gammarus</u>	not feed	181	166	52.07	0.001	0.525	" " " " "
	feed	144	75	69.53	0.001	0.657	" " " " "
<u>N. maculata</u>							
Mosquito	not feed	121	193	3.825	0.1<P>0.05	0.385	Weak pref. for same plant
	feed	278	147	196.8	0.001	0.654	Strong " " " "
<u>Musca</u>	not feed	56	81	3.51	0.1<P>0.05	0.408	Weak " " " "
	feed	113	109	30.83	0.001	0.509	Weak " " " "
<u>Gammarus</u>	not feed	259	219	93.52	0.001	0.542	Strong " " " "
	feed	194	115	120.59	0.001	0.628	Strong " " " "
<u>N. obliqua</u>							
Mosquito	not feed	172	128	77.72	0.001	0.573	Strong pref. for same plant
	feed	267	125	213.4	0.001	0.681	" " " " "
<u>Musca</u>	not feed	26	32	3.446	0.1<P>0.05	0.448	" " " " "
	feed	151	117	63.83	0.001	0.563	" " " " "
<u>Gammarus</u>	not feed	188	150	75.55	0.001	0.556	" " " " "
	feed	277	192	139.7	0.001	0.596	" " " " "

with which H_0 can be rejected.

All three predators appear to show some preference for returning to the same plant, which appears to increase during feeding. N. glauca generally shows a marked preference for the same plant with all prey types, N. obliqua shows a similarly marked preference except during rest periods with Musca, and N. maculata only weak selection during rest with Musca and mosquito larvae.

c) When considering the preference for returns to the same perch site after a swim, a slightly more complex null hypothesis is required. Each plant can be considered as comprising of nine sections (Fig. 62), but there is generally little selection of near surface perch sites, so a null hypothesis of random selection of perch sites after a swim is considered to be represented by a 1 in 18 ratio of returns to the same perch site (3 plants each with effectively 6 sub-sections). Table 4.6 presents the numbers of returns to the same and to different perches, the χ^2 value for differences from the expected ratio and the significance with which to reject H_0 . Data is again given for rest and handling periods.

N. glauca shows a significantly greater than random selection of the same perch site, indicating quite strong preferences for such sites, which appears to increase during handling. N. maculata shows only weak preferences for the same perch site with mosquito and Musca prey but a strong preference during feeding on Gammarus. N. obliqua shows strong preference for returning to the same perch with Gammarus, weak preference with mosquito larvae, but with Musca, only during feeding is any preference shown.

Most of the movements from a perch site during rest are likely to be in pursuit of or attack on prey, and in such cases, it would be a sensible strategy for the predator to return to the perch site from

Table 4.6

Table showing the total number of returns to the same and to different perch sites

during rest (not feed) and handling (feed) periods for the three predators with the three prey types.

Ho = 1:18 chance of returning to same perch site.

		Returns to same perch	Returns to different perch	χ^2	Significance to reject . Ho	Probability of returning to same perch.	Conclusion
<u>N. glauca</u>							
<u>Mosquito</u>	not feed	46	220	69.88	0.001	0.173	Strong pref. same perch
	feed	50	172	121.8	0.001	0.225	" " " "
<u>Musca</u>	not feed	18	108	18.3	0.001	0.143	" " " "
	feed	27	86	72.5	0.001	0.24	" " " "
<u>Gammarus</u>	not feed	73	273	159.3	0.001	0.211	" " " "
	feed	67	152	261.78	0.001	0.306	" " " "
<u>N. maculata</u>							
<u>Mosquito</u>	not feed	30	284	9.57	0.001	0.0955	Weak pref. same perch
	feed	49	375	29	0.001	0.1155	" " " "
<u>Musca</u>	not feed	14	123	5.68	0.05	0.102	" " " "
	feed	22	200	8.01	0.01	0.099	" " " "
<u>Gammarus</u>	not feed	57	419	37.38	0.001	0.1197	" " " "
	feed	72	237	222.88	0.001	0.233	Strong pref. same perch
<u>N. obliqua</u>							
<u>Mosquito</u>	not feed	44	300	34.48	0.001	0.146	Pref. for same perch
	feed	76	392	101.81	0.001	0.1938	Strong pref. same perch
<u>Musca</u>	not feed	4	58	0.093	n.sig.	0.0689	No preference.
	feed	34	268	18.74	0.001	0.127	Pref. for same perch.
<u>Gammarus</u>	not feed	60	338	68.75	0.001	0.1775	Strong pref. same perch.
	feed	75	464	70.25	0.001	0.1599	" " " "

which the attack was made, as there is likely to be a greater chance of encountering another prey item. In many studies considering optimal foraging, the predators were found to stay within a patch provided the rate of encounter was high (e.g. Krebs (1974), (1978), Waage (1978)). This use of perch sites has also been reported for Robber flies (Oldroyd (1964), which are, like Notonectids, generally 'sit and wait' predators. Several species have regular beats, and if no prey appear after several minutes, the flies move off to another perch site. If prey did pass by, but the attack was unsuccessful, the fly returned to the same perch site.

It appears that this form of activity may occur in Notonectids, with preference for returns to the same plant and the same perch site. However, there does seem to be a weak preference for the same plant, and a weaker one for the same perch, regardless of the presence of prey, as shown by the preferences with the surface prey Musca. This may be explained on the basis that certain perch sites are more prominent or more easily accessible, hence the increase in preference with this prey for the same plant and same perch during feeding. The general increase in preference for the same plant or perch site during feeding on mosquito larvae and Gammarus may be explained on the basis of the use of more prominent perch sites and the advantage of returning to the same site from which the prey capture was made or to where the prey occur, in order to increase the likelihood of subsequent captures, as discussed earlier. On the basis of this assumption, it again appears that N. maculata shows least efficient use of the perch sites and N. glauca and N. obliqua appear to be the most efficient.

IV. 4.4. Positions from where Responses to prey are made.

IV. 4.4.1. Introduction

The net effect of the use of space by the predators will be shown in the positions from which responses to prey are made. Records were

kept of the predator position when making a response to a prey item, positions being separated into three categories in the simple environment; at the surface; down from the surface; or from a perch site at the arena sides, and into two categories in the complex; from the surface and from perch sites. Unfortunately, the data for perch sites were not broken down into depth categories for N. glauca, so comparisons at this level cannot be made between all species. Only responses with mosquito larvae and Gammarus have been considered, as responses to Musca all took place at the surface. It was also possible to segregate the data for total attempted captures and successful captures.

IV. 4.4.2. Results

Tables 4.7, 4.8 and 4.9 show the proportion of responses made from each area for all predators feeding on different densities of both mosquito larvae and Gammarus in the two environments, the differences tested by χ^2 using the original data. Figs. 69 and 70 show plots of proportion of responses from surface against proportion of responses from perch sites at depth.

In the simple environment, the three predators seem to capture prey from similar positions, whereas in the complex one, quite marked differences occur between the predators. In this environment, N. maculata tends to capture more prey from the surface than from perch sites at depth. Both N. glauca and N. obliqua capture more prey from perch sites at depth, and the positions tend to overlap to quite an extent. At depth though, most captures by N. obliqua were made from the near bottom areas. No data is available to separate out the data for N. glauca into depth categories, but generally captures by N. maculata and N. obliqua seem to be made from favoured perch sites (see Sections IV. 4.2. and IV. 4.3.), so it is likely that most captures by N. glauca will be made from near middle perch sites. For all three predators, captures

Table 4.7 Proportion of responses to prey made by N. glauca from various positions with Gammarus and mosquito larvae in both environments. Significance of differences by T. test. * = 0.05 sig. ** = 0.01 sig. *** = 0.001 sig. n.sig. = not significant. Middle + Bottom = from perch sites at depth.

<u>Complex</u>		<u>Mosquito larvae</u>					
<u>Response</u>	<u>Position from which response made</u>	<u>Density</u>					
		70	50	30	10	5	2
Captures	From surface	0.35	0.47	0.55	0.7	0.72	0.28
	Middle + Bottom	0.65	0.53	0.45	0.3	0.28	0.72
Total Responses	From surface	0.37	0.43	0.6	0.72	0.66	0.3
	Middle + Bottom	0.63	0.57	0.4	0.28	0.34	0.7

<u>Complex</u>		<u>Gammarus</u>					
<u>Response</u>	<u>Position from which response made</u>	<u>Density</u>					
		25	20	15	10	5	2
Captures	From surface	0.09	0.08	0.19	0	0	0
	Middle + Bottom	0.91	0.92	0.81	1.0	1.0	1.0
Total Responses	From surface	0.19	0.19	0.13	0.09	0.02	0.12
	Middle + Bottom	0.81	0.81	0.87	0.91	0.98	0.88

Cont.....

Table 4.7 (Continued)

<u>Simple</u>		<u>Mosquito larvae</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	70	50	30	10	5	2
Captures	At surface	0.813] ***	0.785] ***	0.72] ***	0.66] ***	0.822] ***	0.75] **
	Down from surface	0.12] n.sig.	0.12] n.sig.	0.22] ***	0.207] n.sig.	0.089] n.sig.	0.2] n.sig.
	Middle + Bottom	0.067	0.042	0.058	0.132	0.089	0.05
Total Responses	At surface	0.819] ***	0.75] ***	0.765] ***	0.66] ***	0.802] ***	0.773] ***
	Down from surface	0.133] *	0.143] n.sig.	0.234] ***	0.22] n.sig.	0.144] *	0.22] *
	Middle + Bottom	0.047	0.107	0	0.117	0.053	0.044
<u>Simple</u>		<u>Gammarus</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	25	20	15	10	5	2
Captures	At surface						
	Down from surface						
	Middle + Bottom						
Total Responses	At surface	0.6] *	0.737] *	0.66] n.sig.	0.58] n.sig.	0.857] ***	Insufficient data.
	Down from surface	0.266] n.sig.	0.263] *	0.33] **	0.29] n.sig.	0] n.sig.	
	Middle + Bottom	0.133	0	0	0.117	0.143	

Table 4.8 Proportion of responses to prey made by N. maculata from various positions with Gammarus and mosquito larvae in both environments.

Middle - From mid water sites. D.S.-Down from surface. Bottom - From Bottom sites. M + B - From perch sites at depth. Significance of differences by T test. * = 0.05 sig. ** 0.01 sig. *** 0.001 sig.

N. sig. - not significant.

<u>Complex</u>		<u>Mosquito larvae</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	70	50	30	10	5	2
Captures	From surface	0.73] ***	0.735] ***	0.67] ***	0.84] ***	0.84] ***	0.745] ***
	Middle	0.2] ***	0.133] n.sig.	0.2] *	0.10] n.sig.	0.12] *	0.2] **
	Bottom	0.07]	0.133]	0.13]	0.06]	0.04]	0.055]
Total Responses	From surface	0.76] ***	0.77] ***	0.73] ***	0.85] ***	0.84] ***	0.81] ***
	Middle	0.175] ***	0.115] n.sig.	0.16] n.sig.	0.09] n.sig.	0.09] n.sig.	0.16] **
	Bottom	0.065]	0.115]	0.11]	0.06]	0.07]	0.03]

Cont.....

Table 4.8 (Continued)

<u>Complex</u>		<u>Gammarus</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	25	20	15	10	5	2
Captures	From surface	0.66	0.33	0.27	0.41	0.4	0.5
	Middle	0.28	0.46	0.59	0.31	0.4	0.19
	Bottom	0.06	0.21	0.14	0.28	0.2	0.31
Total Responses	From surface	0.46	0.44	0.38	0.49	0.47	0.29
	Middle	0.34	0.37	0.5	0.31	0.43	0.56
	Bottom	0.2	0.09	0.12	0.2	0.1	0.15
<u>Simple</u>		<u>Mosquito larvae</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	70	50	30	10	5	2
Captures	At surface	0.703	0.708	0.643	0.624	0.674	0.659
	D.S.	0.258	0.27	0.335	0.364	0.316	0.319
	M & B	0.038	0.021	0.022	0.012	0.009	0.02
Total Responses	At surface	0.722	0.699	0.645	0.647	0.717	0.703
	D.S.	0.243	0.281	0.338	0.345	0.283	0.275
	M & B	0.035	0.081	0.016	0.008	0.000	0.021

Table 4,8 (Continued)

<u>Simple</u>		<u>Gammarus</u>					
<u>Response</u>	<u>Position from which response made</u>	<u>Density</u>					
		25	20	15	10	5	2
Captures	At surface	0.46	0.428	0.323	0.348	0.2	0.09
	D.S.	n.sig. 0.405	n.sig. 0.321	n.sig. 0.294	n.sig. 0.26	n.sig. 0.48	** 0.545
	M & B	* 0.135	 0.25	 0.382	 0.39	 0.32	n.sig. 0.363
Total Responses	At surface	0.494	0.449	0.519	0.489	0.273	0.175
	D.S.	n.sig. 0.422	n.sig. 0.415	** 0.235	** 0.265	** 0.547	** 0.508
	M & B	*** 0.084	*** 0.315	n.sig. 0.245	n.sig. 0.244	** 0.179	n.sig. 0.315

Table 4.9 Proportion of responses to prey by N. obliqua from various positions with Gammarus and mosquito larvae in both environments. M + S - Perch sites near middle and near surface. B - Perch sites near bottom. D.S.-Down from surface. M + B - From perch sites at depth. Significance of differences by T. test. * = 0.05 sig. ** = 0.01 sig. ***=0.001 sig. n.sig. = not significant.

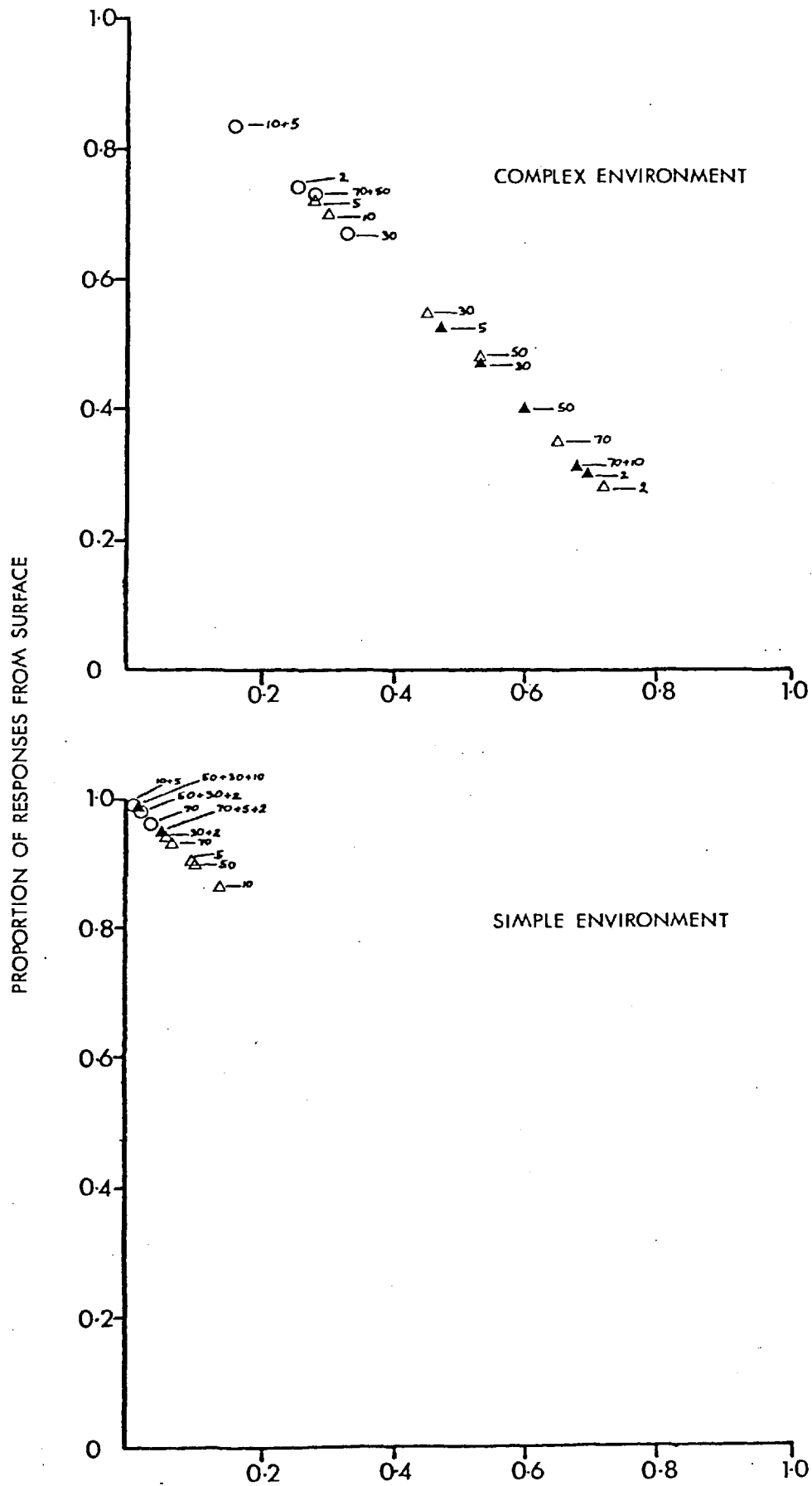
<u>Complex</u>		<u>Mosquito larvae</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	70	50	30	10	5	2
Captures	From surface						
	M + S	n.sig. $\left[\begin{array}{c} 0.313 \\ 0.275 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.397 \\ 0.262 \end{array} \right]$	* $\left[\begin{array}{c} 0.467 \\ 0.289 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.315 \\ 0.298 \end{array} \right]$	* $\left[\begin{array}{c} 0.526 \\ 0.193 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.304 \\ 0.261 \end{array} \right]$
	B	$\left[\begin{array}{c} 0.412 \end{array} \right]$	* $\left[\begin{array}{c} 0.34 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.243 \end{array} \right]$	$\left[\begin{array}{c} 0.386 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.28 \end{array} \right]$	$\left[\begin{array}{c} 0.435 \end{array} \right]$
Total Responses	From surface						
	M + S	* $\left[\begin{array}{c} 0.292 \\ 0.256 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.416 \\ 0.225 \end{array} \right]$	* $\left[\begin{array}{c} 0.472 \\ 0.303 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.269 \\ 0.359 \end{array} \right]$	* $\left[\begin{array}{c} 0.469 \\ 0.247 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.325 \\ 0.162 \end{array} \right]$
	B	$\left[\begin{array}{c} 0.452 \end{array} \right]$	* $\left[\begin{array}{c} 0.358 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.225 \end{array} \right]$	$\left[\begin{array}{c} 0.372 \end{array} \right]$	n.sig. $\left[\begin{array}{c} 0.283 \end{array} \right]$	** $\left[\begin{array}{c} 0.511 \end{array} \right]$

Table 4.9 (Continued)

<u>Complex</u>		<u>Gammarus</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	25	20	15	10	5	2
Captures	From surface	0.192	0.0	0.047	0	0.048	0
	M + S	n.sig.	**	n.sig.	**	*	**
	B	0.269	0.28	0.318	0.33	0.43	0.35
		n.sig.	*	n.sig.	n.sig.	n.sig.	n.sig.
		0.538	0.72	0.636	0.66	0.524	0.65
Total Responses	From surface	0.256	0.024	0.063	0.068	0.079	0
	M + S	n.sig.	**	*	*	**	***
	B	0.307	0.293	0.229	0.273	0.368	0.295
		n.sig.	**	***	**	n.sig.	**
		0.436	0.683	0.708	0.659	0.553	0.705
<u>Simple</u>		<u>Mosquito larvae</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	70	50	30	10	5	2
Captures	At surface	0.73	0.675	0.705	0.742	0.645	0.62
	D.S.	***	***	***	***	***	***
	M + B	0.219	0.31	0.273	0.232	0.307	0.33
		***	***	***	***	***	***
		0.05	0.023	0.022	0.026	0.047	0.05
Total Responses	At surface	0.737	0.678	0.71	0.758	0.692	0.637
	D.S.	***	***	***	***	***	***
	M + B	0.2	0.294	0.264	0.224	0.263	0.33
		***	***	***	***	***	***
		0.056	0.028	0.026	0.017	0.044	0.032

Table 4.9 (Continued)

<u>Simple</u>		<u>Gammarus</u>					
		Density					
<u>Response</u>	<u>Position from which response made</u>	25	20	15	10	5	2
Captures	At surface	0.364	0.055	0.364	0.2	0.286	0.273
	D.S.	0.454	n.sig. 0.78	0.41	n.sig. n.sig. 0.65	0.429	n.sig. 0.454
	M + B	0.182	0.167	0.23	0.15	0.286	0.273
Total Responses	At surface	0.453	0.302	0.472	0.22	0.361	0.286
	D.S.	0.434	n.sig. 0.535	0.305	n.sig. 0.54	0.444	n.sig. 0.571
	M + B	0.113	0.163	0.22	0.24	0.194	0.143

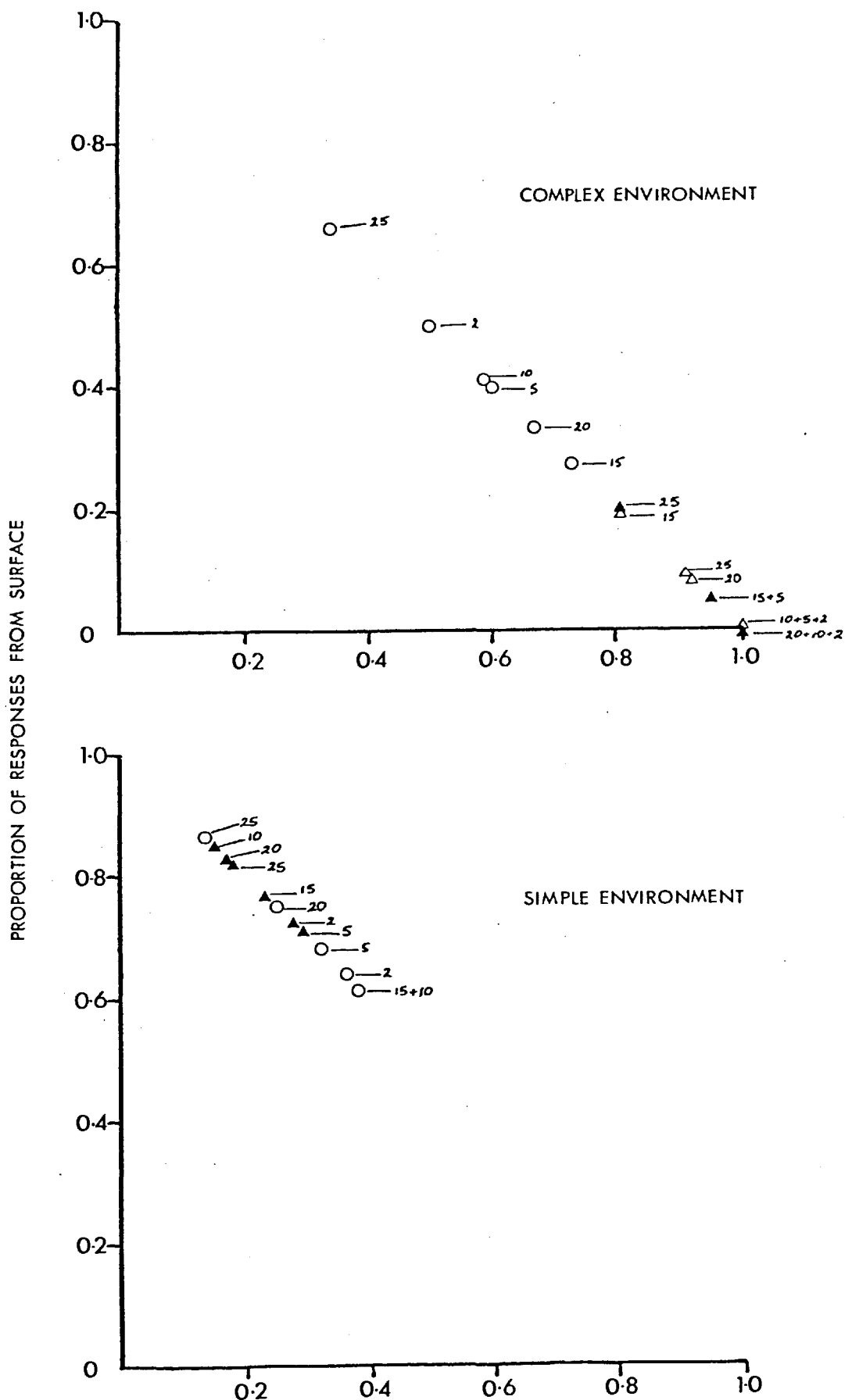
LEGEND TO FIG 69

PROPORTION OF RESPONSES FROM DEPTH

Predator positions from where mosquito larvae are
captured in complex and simple environments.

0 - N. maculata▲ - N. obliqua△ - N. glauca

Numbers indicate prey density.

**LEGEND TO FIG 70**

PROPORTION OF RESPONSES FROM DEPTH

Predator positions from where Gammarus pulex prey are captured in complex and simple environments.

0 - N. maculata▲ - N. obliqua△ - N. glauca

Numbers indicate prey density. Results are not presented for

N. glauca in the simple environment due to insufficient data.

of mosquito larvae tend to be made more from the surface than do captures of Gammarus, which can be explained on the basis of prey distribution.

Overlap in the positions from which captures are made by predators, is likely to cause competition in natural environments, and unless surplus prey are available, coexistence would not be possible for extended periods. This situation might occur in simple environments. Where positions from which captures are made are different, it is possible that available resources could be partitioned, allowing coexistence. This situation may occur in complex environments between N. maculata and the other two predator species. N. obliqua and N. glauca positions tend to overlap here, but differential perch selection may compensate for this, and possibly allow resource partitioning.

IV. 4.5. Effect of Predator Position on Prey Selection.

IV. 4.5.1. Introduction

These simple experiments were designed to test whether the position of the predator in the water body could affect prey selection. N. glauca and N. maculata were tested, as they represent the two types of selection of resting sites amongst the species used in this study, the former spending most time *within* the water body, the latter at the surface. Two strains of Daphnia magna were kindly supplied by Dr. S. Young and Dr. E. Watts; the normal eye strain, which possesses black eye pigments; and the clear eye strain, without these pigments, the other characteristics being similar. (Due to the small size of the eye spot, this difference is unlikely to have any effect on the ability of the predators to detect them.). However, there is a difference in behaviour between the two strains, the normal eye variety being fairly evenly distributed, with a tendency to prefer the top half of the water column, and the clear eye variety showing a marked preference for the bottom half of the water column (Dr. Watts pers. commun.). On this basis, it is expected that

differential selection of prey by the two predators should occur when both types are presented in combination.

IV. 4.5.2. Method

Simple 3h tests were conducted, using different prey densities (5, 15, 30 and 50 per arena) of each prey type, and then different combinations of the two (20:20, 10:30, 30:10). Experiments were carried out in the simple environment for both predators, and also with added complexity in some tests, with N. glauca. Predators were starved for 24hrs prior to each test, and given excess mosquito larvae for a further 21h. after. They were then starved again prior to the next test. Prey were replaced in the density experiments as numbers decreased by 10%, but not in the combination tests. The numbers of prey killed were recorded. The results with prey combinations were analysed by comparing observed numbers killed with predicted numbers killed, on the basis of no selection, by χ^2 , where H_0 for equal proportions of prey is a ratio of 1:1 clear eye to normal eye, and H_0 for a 30/10 combination is 3:1, based on random encounters and no preference.

IV. 4.5.3. Results

The functional response curves for both predators and each prey type are shown in Fig. 71. For N. maculata, the general trend is for more normal eyes to be killed at all densities (signs test $P < 0.05$), whereas for N. glauca the trend was for larger numbers of clear eyes to be killed at each density (signs test $P < 0.05$).

In all combination tests, N. maculata shows strong preference for normal eye Daphnia, as can be seen from Table 4.10. The preference for normal eyes seems to be greater in combinations with larger numbers of prey (preference in 30:30 combination more significant than in 20:20 combinations). This is likely to be caused by exploitation of the preferred normal eye prey before termination of the experiment in

LEGEND TO FIG. 71

Functional responses of N. glauca and N. maculata
feeding on two strains of Daphnia magna;

(Δ) clear eye strain

($\blacktriangle$) normal eye strain

95% confidence limits shown.

Analysis of variance:

N. glauca Clear eye F = 110.6 sig. 0.001

T test 50 30 15 5 sig. 0.05

Normal eye F = 2.699 n.sig

T test 50 30 15 5 sig. 0.1

Difference between clear and normal data

Signs test n = 4 x = 0 P 0.05

N. maculata Clear eye F = 11.597 sig. 0.001

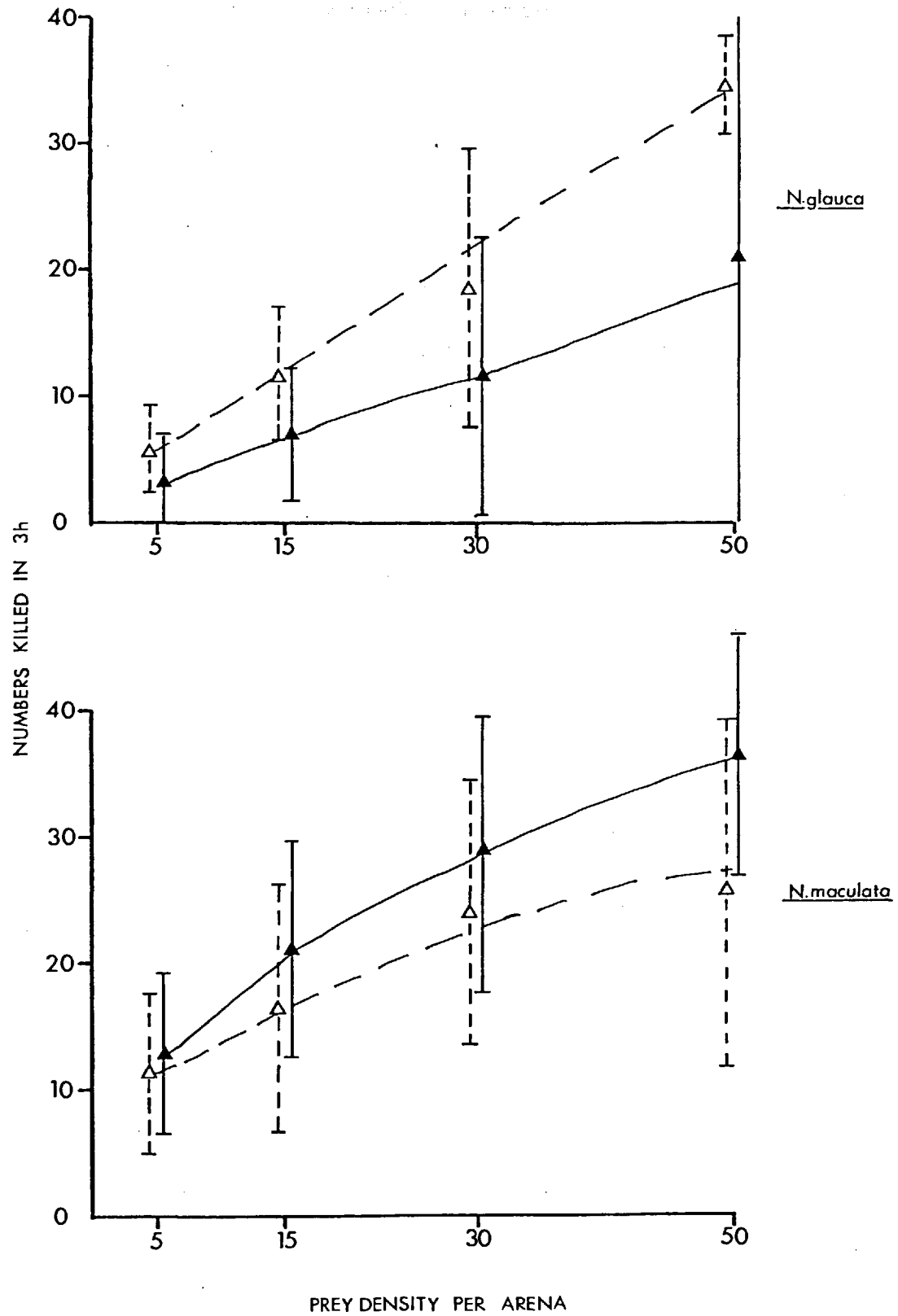
T test 50 30 15 5 sig. 0.001

Normal eye F = 3.007 sig. 0.05

T test 50 30 15 5 sig. 0.02

Difference between clear and normal data

Signs test n = 4 x = 0 P 0.05

FUNCTIONAL RESPONSES ON TWO STRAINS OF DAPHNIA MAGNA

	<u>Clear eye</u>		<u>Normal eye</u>		χ^2	Sig. to reject Ho	Conclusion		
	Combination		Numbers killed.	Proportion				Numbers killed.	Proportion
	<u>Clear</u>	<u>Normal</u>							
Ho 1:1	20	: 20	207	0.45	266	0.561	7.36	0.01	Pref. for normal eye
Ho 3:1	30	: 10	235	0.543	185	0.456	81.27	0.001	Strong pref. normal eye
Ho 1:3	10	: 30	19	0.0766	182	0.923	25.91	0.001	" " " "
Ho 1:1	30	: 30	33	0.148	151	0.851	75.67	0.001	" " " "

Table 4.10 Number of Daphnia killed by N. maculata females (staved for 24h) in 3h. with various combinations of two prey types.

		<u>Clear eye</u>		<u>Normal eye</u>		χ^2	Sig. to reject Ho	Conclusion		
		Numbers killed.Proportion		Numbers killed.Proportion						
Combination										
		<u>Clear</u>	<u>Normal</u>							
Ho	no plant	20 :	20	243	0.547	203	0.453	3.587	0.1<P>0.05	Weak pref. clear eye.
Ho	1:1 + plant	20 :	20	279	0.645	175	0.355	23.82	0.001	Strong pref. clear eye.
Ho	3:1	30 :	10	539	0.772	158	0.228	2.02	n.sig.	No preference.
Ho	1:3	10 :	30	160	0.325	368	0.675	7.919	0.001	Pref. for clear eye.

Table 4.11 Number of Daphnia killed by N. glauca females (starved for 24h) in 3h with various combinations of two prey types.

the lower density combination, resulting in feeding solely on clear eyes, thus biasing the results slightly.

In combination tests with N. glauca, there is generally a weak preference for clear eye Daphnia, as seen in Table 4.11. This preference for clear eyes appears to be accentuated in the presence of 'plants', which offer additional perch sites enabling N. glauca to rest more in its preferred positions, where more contact with clear-eye Daphnia is expected. The lack of significant preference for clear-eye Daphnia in the 30:10 combination (normal:clear ratio) is likely to be due to exploitation of the clear-eye prey before termination of the experiment, as described above.

The preferences shown in these experiments are those expected on the basis of preferred predator resting positions described in previous sections, and do strengthen this apparent difference in perch site selection between these two predators, as well as demonstrating that predator position can affect prey selection.

IV. 5. Light and Dark Experiments

IV. 5.1. Introduction

These simple experiments were designed to investigate differences in the relative importance of the visual and tactile senses within and between predator species. The most straightforward method of assessing the differences in feeding in light and dark conditions, is by a comparison of the numbers of prey killed in the two environments. At the same time as assessing numbers killed, the total weight of food extracted during each test can be compared in the two environments, giving a clearer indication of feeding efficiency (data not available for N. maculata)

IV. 5.2. Method

The experiments were carried out using four densities of mosquito larvae, 5, 20, 60 and 100 per arena. The simple environment was used,

and eight replicates were obtained for each density. The predators were divided into four groups of two, and each group was subjected to the prey densities in a different order. A typical experiment consisted of a 48hr. period of starvation, then the introduction of prey at specific densities to all eight predators, with replacement of dead prey every half hour. Data was obtained for all three predator species for 3h. tests. At the end of this period, predator hunger levels were standardised by adding prey to or removing from each arena such that the sum of prey eaten and prey available equaled the largest number of prey consumed by a predator during the test. At the end of 24h, all predators were presented with a further 30 prey for a further 24h, then starved for 48h, prior to the next test. Lighting conditions were alternated from one test to the next.

Numbers killed were recorded at the end of each hour, and dead prey removed, washed in distilled water, and freeze-dried along with a sample of live prey. A correlation between collar width and dry weight was obtained, and weight of food removed from each prey item was assessed, as described in Chapter III.

Finally, numbers killed and weight of food extracted were compared between light and dark conditions at each density. It has been assumed that lighting regime does not affect predator or prey distributions.

IV. 5.3. Results

Data presented in Table 4.12. indicates mean values of numbers killed and weight extracted from both conditions at each prey density, and the significance of the differences between the two environments.

N. glauca shows a general trend for increased feeding, in terms of both numbers killed and weight of food extracted, in the dark environment. A similar picture is apparent for N. obliqua, where the differences are even more pronounced. The results for N. maculata on the other hand

Table 4.12 Number of mosquito larvae killed and weight extracted by the three predator species (starved for 48 hours) in 3 hours in light and dark conditions in the simple environment.

<u>Predator species</u>	<u>Prey density</u>	<u>Number killed</u>			<u>Weight extracted</u>		
		Light	Dark	Significance	Light	Dark	Significance
<u>N. glauca</u>	5	1.33+1.73	5.50+2.38	sig. 0.05	0.095+0.002	0.61+0.47	sig. 0.05
	20	5.67+6.2	7.60+4.67	n. sig.	0.456+0.39	0.95+0.84	sig. 0.1
	60	4.4 +5.15	6.0 +5.24	n. sig.	0.36 +0.42	0.53+0.33	n.sig.
	100	6.16+5.77	10.875+9.15	n. sig.	0.44 +0.518	1.067+0.73	sig. 0.1
<u>N. obliqua</u>	5	8.33+6.82	8.0 +2.26	n. sig.	0.689 +0.59	0.743+0.26	n. sig.
	20	5.2 +4.8	13.25 +7.9	sig. 0.05	0.19 +0.14	0.717+0.7	sig 0.1
	60	7.28+6.9	17.83 +6.25	sig. 0.05	0.65 +0.563	1.664+0.46	sig. 0.01
	100	10.66	18.0 +7.39	sig. 0.1	0.557 +0.75	1.307+0.51	sig. 0.1
<u>N. maculata</u>	5	16.444+8.13	11.333 +3.22	n. sig.			
	20	23.66+6.66	18.0 +5.252	n. sig.			
	60	20.83+8.79	20.083 +5.49	n. sig.			
	100	25.917+10.78	22.727 +8.7	n. sig.			

do not suggest any significant effect of lighting, although at all prey densities, more prey are killed in light compared to dark conditions (signs test $P < 0.05$), the opposite trend to the other two species.

These results generally support the conclusions of Chapter III, indicating N. glauca and N. obliqua are generally better foragers in a complex environment (i.e. dark) and N. maculata is better in a simple one (i.e. light). They also indicate with N. glauca and N. obliqua, the possibility of confusion effects with prey in the light conditions, which are reduced when visual cues are removed. In N. maculata, it appears that on removal of visual cues, a slight reduction in feeding efficiency ensues, indicating that perhaps in this species, the visual stimuli are the most important, and perhaps the visual sense is more acute than the tactile one. In the other two predators, the tactile sense is good on its own, (as no loss of feeding efficiency occurs in the dark), but in combination with the visual stimuli, the predators efficiency may be reduced in simple environments by confusion effects.

IV. 6.

General Summary

In this section, the differences in behaviour between the three predator species will be summarised for all the components of predation analysed in this study.

a) Handling Time

Generally N. glauca shows the longest handling times, and although there is little difference in handling times between N. maculata and N. obliqua, the general trend is for shorter times with N. maculata. Due to the differential extraction rates and the handling time differences, it was estimated that approximately equal amounts of food are being extracted from each prey type.

b) Time allocation

All predators show low proportions of time spent active, substantiating

their description as 'sit and wait' predators.

Time spent handling - similar times are shown by N. maculata and N. obliqua, but the general trend is for longer times spent by N. obliqua on larger prey, and by N. maculata on small prey. N. glauca generally spends the shortest time feeding.

Activity - little difference in the complex environment, but in the simple one N. glauca is the most active, and N. obliqua tends to be the least active.

c) Response to prey

Pursuit Success - general trends show greatest success by N. obliqua in both simple and complex environment and lowest success by N. maculata in the complex and by N. glauca in the simple environments.

Attack success - general trends show greatest success by N. obliqua and lowest by N. glauca with large prey, but little difference with small prey.

Capture success - general trends again show greatest success by N. obliqua and lowest success by N. glauca.

Limiting components - for N. glauca, success of capture is limited by pursuit success in the simple environment, and with Musca in the complex, but by attack success with Gammarus and mosquito larvae in the complex environment. Success of capture by N. maculata is limited by pursuit success in all conditions except with Gammarus in the complex environment, where the limit is imposed by capture success. N. obliqua is limited by pursuit success with Musca, and by attack success with Gammarus and mosquito larvae in both environments.

Type of attack sequence - in complex environment largest proportion of pursuit attacks tends to be found by N. glauca, and smallest by N. obliqua. In the simple one, N. maculata shows largest proportion with Musca and mosquito larvae, but by N. obliqua with Gammarus, and N. glauca

tending to show the lowest values.

Functional responses - N. glauca shows lowest capture rates with all prey in both environments, N. obliqua generally shows largest rates with large prey, and N. maculata with small prey.

Reaction areas - general trends show N. maculata has the largest reaction areas, N. obliqua the smallest at the surface, and N. glauca the smallest from the surface and from perch sites at depth.

d) Use of space

Time allocation to surface and depth - N. glauca and N. obliqua show equally strong preferences for perch sites at depth in the complex environment during rest, and N. maculata shows a weaker preference. This preference is reduced during handling with N. glauca and N. obliqua. In the simple environment, N. glauca still shows preference for perch sites at depth, but N. maculata and N. obliqua show strong preference for surface sites, as do all three predators during handling in the simple environment.

Selection of perch sites - N. glauca shows preference for near middle perch sites, N. obliqua for near bottom perch sites, both affected to some extent by prey distribution. N. maculata's perch selection modified to great extent by prey distribution. During feeding, perch preferences are all enhanced.

Use of perch site - N. glauca and N. obliqua both show efficient use of perches showing preference for plant edges; N. maculata shows much lower efficiency. All three predators show preference for returning to the same plant and the same perch site, but again N. maculata shows least efficient use of perches in this manner, and N. glauca perhaps the most efficient use.

Positions from which responses to prey are made - preferences for prey were affected by predator position, as seen in the experiments with the

two strains of Daphnia. In the simple environment, there is general overlap in positions from which prey captures are made, but in the complex one, there is some separation based on the differences in preferred perch sites shown by the three predator species.

e) Effect of Lighting on feeding levels

The results of light and dark experiments indicate that in N. maculata vision may be the more important of the two senses, but in the other two predators it may cause confusion with the tactile senses. These effects indicate N. maculata is more efficient in simple environments, N. glauca and N. obliqua more efficient in more complex environments.

CHAPTER V

PREY PREFERENCES

V. 1.

Introduction

Notonectids are reported to feed on a wide variety of foods, which makes the task of assessing general prey preference in natural situations a rather difficult one. Mcpherson (1965) reports that N. hoffmani (a North American species) normally feeds on insects which fall on the surface of water e.g. Hymenoptera, Diptera and other Hemiptera, especially Mirids. N. undulata (another American species) is reported to feed on a variety of terrestrial and aquatic invertebrates, and even some vertebrates (Ellis and Borden (1970)), but may have a preference for larvae and pupae of Aedes aegypti (Toth and Chew (1972)). Southwood and Leston (1959) suggest that N. glauca will feed on any swimming animal up to the size of a large tadpole or fully grown Dytiscid larva, and small fish are readily caught.

Prey preference by Notonectids may well depend on several factors, either singly, or in combination

a) Prey size may be important through the effect of such factors as ease of capture, (Gittleman (1978), Holling (1964)); the predator's reaction area, where prey size affects distance to which they can be detected (Holling (1966), and see Chapter IV); and calorific content, where larger prey generally possess a greater useable calorific value (Schoener (1971), Tullock (1971)).

b) Prey mobility, which includes spatial movements involved in search, feeding etc. by the prey, and prey motility in avoidance of capture by predators (Ellis and Borden (1970)). Very active and rapidly moving prey may be difficult to capture, very slow moving inactive prey may be difficult to detect. (Low motility but high detectability make

prey trapped in the surface film a good choice as food. However, the irregular nature of such food availability, may preclude Notonectids from complete dependence on this prey source (Ellis and Borden (1970)).

c) Ellis and Borden (1970) and Gittleman (1975) suggest that the level of overlap between predator's and prey's preferred microhabitat, both spatially and temporally, may be an important factor in prey selection.

d) Prey posture in the water may affect prey selection by predators, probably by affecting prey detection. This has been demonstrated by differential selection of Culicines, which hang down from the water surface in preference to Anophelens, which lie parallel to the water surface by Enithares bergnathi, a South Pacific Notonectid (Ellis and Borden (1970)).

e) The abundance of prey may also affect selection by the predator. Where there is no preference, prey should be taken in the ratio of their abundances, unless a specialised strategy is required to detect and capture prey. In these cases, and where there is a weak preference, only when the abundance of that prey is high is it a sensible strategy to specialise. This is known as switching (Murdoch et al (1975), Lawton et al (1974)). Where strong preferences for a certain prey type exists, relative abundance of this type is predicted to affect how many other types of prey will be included in the diet (Estabrook and Dunham (1976), Krebs (1978), Pyke et al (1977)).

f) Food palatability probably has the least effect on prey preferences (Ellis and Borden (1970)).

g) Many of the above factors combine to give the net energy return of the prey to the predator, which many authors (e.g. Emlen (1966), Schoener (1971) etc.,) believe to be the main factor controlling prey

preferences, where prey are ranked according to this value, and taken in the ranking order (see Chapter I).

One of the most common methods for analysing food preferences by polyphagous predators involves a comparison of the feeding behaviour on each food type separately with the feeding behaviour on various combinations of the prey (Cock (1978), Lawton et al (1974), Murdoch (1973)). The method has been reviewed by Hassell and Southwood (1978). Firstly, searching efficiency and handling times for each prey type are estimated from functional response experiments. Preference resulting from differences in the functional response parameters can be expressed as ratios of prey types eaten plotted against the ratio of their availabilities, and any innate preference can be detected by a deviation from a slope of unity passing through the origin. Secondly, various ratios of the two (or more) prey types are presented together, ideally for the range of total prey densities used in the functional response experiments. Any differences between the predicted preference arising from the rates of search and consumption in the first experiments, and that observed from the mixtures will be due to either an active rejection of one of the food types or some change in the parameters of the functional response when the forager is experiencing two or more food types together.

Again, there is the problem that different prey may exist in somewhat different habitats, so that preferences may be the result of differential patch or habitat selection by the predator (i.e. switching). Hassell and Southwood (1978) finally point out that preference and switching studies conducted in the laboratory often bear little relation to the natural situation.

An alternative method of presenting preferences is through the use of electivity indices, a review of which is given by Cock (1978), and

is not considered here.

In this study, prey preferences were examined in the light of current literature to determine, if possible, the major factors governing prey choice in these insects.

V. 2.

Method

Assessment of the predatory efficiency on each prey type separately were obtained during the continuous observation experiments described in Chapters III and IV. At the end of these experimental units, tests were carried out to examine prey preference with various combinations of the three prey types. The experimental procedure and design are basically similar to the main experiments, the differences being discussed in Chapter II (section II.6.). Combinations of high and low densities of each prey type were used, providing eight treatments. Densities of 5 and 20 per arena were selected for Musca and Gammarus, and of 10 and 50 for mosquito larvae. The treatments tested were; 5, 5, 10; 5, 20, 10; 5, 20, 50; 5, 5, 50; 20, 5, 10; 20, 5, 50; 20, 20, 10; and 20, 20, 50, for Musca, Gammarus and mosquito larvae respectively, and each of the nine predators was presented with the above treatments in a different order.

During each test, records were kept of the prey captured and the order they were captured in, handling times spent on each item so that energy gains could be ascertained (see Chapter III), activity time so that energy losses could be calculated (see Chapter III), and of the use of space (see Chapter IV). Thus for each predator species, data was available for prey preferences, net energy gains and use of space when presented with all eight of the prey combinations in both simple and complex environments.

V. 3.

Net Energy Gains.

Table 5.1 shows the mean net energy gain in each of the treatments

Table 5.1 Net energy gains in preference experiments (Joules)

Difference between environments tested by signs test due to large variance in data.

Combination.

Predator and environment		5510	52010	52050	5550	20510	20550	202010	202050
<u>N. glauca</u>	Simple	29.084	22.199	18.584	26.9	30.376	24.25	39.071	31.00
		+13.88	+18.06	+9.04	+15.2	+14.37	+12.35	+13.8	+14.79
	Complex	<u>35.26</u>	<u>35.59</u>	<u>32.365</u>	<u>26.97</u>	<u>41.39</u>	<u>35.59</u>	<u>38.04</u>	<u>33.04</u>
	Sign test	+30.4	+16.15	+17.26	+12.05	+16.67	+23.06	+12.65	+29.65
		n = 8 x = 1 P = 0.035							
<u>N. maculata</u>	Simple	65.99	69.5	70.59	75.265	77.3	77.965	77.957	75.83
		+29.3	+22.39	+15.55	+15.96	+9.36	+8.126	+12.55	+9.643
	Complex	<u>60.07</u>	<u>56.177</u>	<u>54.66</u>	<u>43.898</u>	<u>61.027</u>	<u>63.44</u>	<u>61.69</u>	<u>50.69</u>
	Sign test	+20.808	+18.24	+16.6	+21.12	+11.47	+34.81	+16.42	+23.07
		n = 8 x = 0 P = 0.004							
<u>N. obliqua</u>	Simple	39.26	56.59	48.03	48.4	41.704	42.04	47.608	42.69
		+22.74	+17.51	+14.196	+13.2	+17.47	+17.48	+13.602	+10.03
	Complex	<u>35.4</u>	<u>34.11</u>	<u>31.09</u>	<u>30.43</u>	<u>39.84</u>	<u>35.16</u>	<u>41.9</u>	<u>39.65</u>
	Sign test	+10.5	+23.14	+17.36	+17.15	+13.28	+18.37	+13.78	+21.675
		n = 8 x = 0 P = 0.004							

Table 5.2. Differences in net energy gains between prey combination treatments within each environment. Treatments joined by lines do not show differences at 0.1 level (T test)

	Simple									Complex								
<u>N. glauca</u>	20	20	20	5	5	20	5	5		20	20	20	5	5	20	5	5	
	20	20	5	5	5	5	20	20		5	20	5	20	5	20	20	5	
	10	50	10	10	50	50	10	50		10	10	50	10	10	50	50	50	
<u>N. maculata</u>	20	20	20	20	5	5	5	5		20	20	20	5	5	5	20	5	
	5	20	5	20	5	20	20	5		5	20	5	5	20	20	20	5	
	50	10	10	50	50	50	10	10		50	10	10	10	10	50	50	50	
<u>N. obliqua</u>	5	5	5	20	20	20	20	5		20	20	20	5	20	5	5	5	
	20	5	20	20	20	5	5	5		20	5	20	5	5	20	20	5	
	10	50	50	10	50	50	10	10		10	10	50	10	50	10	50	50	

for all three predator species, and shows the significance of the differences between values in the two environments. Table 5.2 shows the difference in net energy gains between treatments in both environments, and the proportion of time spent handling is shown in Table 5.3

N. maculata shows significantly the greatest net energy gains of the predator species in all treatments (Appendix XVII). In the simple environment, the trend is for larger gains by N. obliqua than by N. glauca (signs test $P = 0.004$), but in the complex one, there is no difference (signs test $P = 0.687$). (See Appendix XVII).

N. glauca, as predicted from the net energy gains on each prey type separately, generally shows greater gains in the complex than in the simple environment ($P = 0.035$ signs test). The proportion of time spent handling, however, is similar in both environments (Appendix XVIII). indicating that N. glauca makes larger net energy gains in the complex environment than in the simple one in the same feeding time. These proportions are comparable with the largest values from the single prey experiments in the complex environment, but in the simple one, the proportion of time spent feeding in prey combination experiments is generally larger than in single prey experiments. In both environments, the general trend shows the largest net energy gains are made in the presence of high Musca densities, and the lowest ones with low Musca density combinations, or high mosquito larvae density combinations (few differences are significant though).

N. maculata, again as predicted from Chapter III, shows largest net energy gains in the simple environment ($P = 0.004$ signs test), which is reflected in larger proportions of time spent feeding here than in the complex environment (Appendix XVIII). As with N. glauca, a larger proportion of time is spent feeding with prey combinations in the

simple environment than during single prey experiments. The largest gains tend to be made in the presence of high Musca densities and the lowest gains generally with low Musca densities, or in the simple, also with high mosquito/high Gammarus combinations.

The results for N. obliqua are not quite as expected on the basis of those reported in Chapter III. In these latter results, there was no effect of environmental complexity with Musca prey, slightly larger gains in the complex environment with Gammarus, and significantly larger gains in the simple environment with mosquito larvae. The data from Table 5.1., shows a general trend for larger gains in the simple environment ($P = 0.004$ signs test). This is reflected in larger proportions of time spent feeding in the simple than in the complex environment in these combination experiments (Appendix XVIII). These values are also lower than the higher values during single prey experiments in both environments. In the simple environment, the trend is for largest gains to be made with low Musca/high Gammarus combinations, and the lowest gains with low Gammarus/high Musca combinations. In the complex environment, the opposite trends are observed.

It might be expected that greater net energy gains will be made when a variety of prey occupying a variety of positions in the environment are available, than when just one prey type is presented. This has not been found to be the case with the prey densities used here. Both N. glauca and N. maculata show similar energy gains with prey combinations to those made with the largest prey types in both environments in the single prey experiments (i.e. with Musca and Gammarus, gains on the small mosquito larvae are substantially lower). This may indicate that these predators have achieved a maximum energy gain in the period of the experiments, the level controlled either through satiation or

some internal physiological balance being achieved. This value is analogous to Schoeners M value (1971), where an optimal strategy for a given predator is one which minimises the time spent feeding to gather this given energy requirement, i.e. a time minimising strategy.

N. obliqua, however, does not achieve the net energy gains made in the single prey experiments during the prey combination tests. Either this predator is less efficient when presented with a variety of prey, or there is some physiological difference in the state of this predator during these experiments compared to the single prey ones, which has come about as the predators have aged.

V. 4. Use of space.

During the preference experiments, records were kept of the allocation of time between surface and depth during rest and handling in both environments, and of perch selection in the complex one, in the same way as described in Chapter IV.

V. 4.1. Allocation of time between surface and depth (Table 5.3 Appendix XIX).

In the complex environment, N. glauca shows a marked preference for depth during rest, dropping during feeding, which was the pattern found during single prey experiments. In the simple environment, there is generally a weak preference for the surface during rest, which is in contrast to the weak preference for depth during single prey experiments, but during handling practically all time is spent at the surface in both combination and single prey experiments.

N. maculata shows a very weak preference for depth during rest in the complex environment, but switches to a preference for the surface during handling here. These preferences are almost identical to those with Musca in the single prey experiments (see Appendix XV/a) In the simple environment, there is no significant preference for either position during rest, although the trend is for weak preference for

Table 5.3 Time allocation between surface and depth during preference experiments, and proportion of time spent handling. (D = Depth. S = Surface)

		5		5		5		5		20		20		20		20	
		5		20		20		5		5		5		20		20	
		10		10		50		50		10		50		10		50	
		D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
<u>N. glauca</u> Complex	Rest	0.83	0.17	0.953	0.065	0.93	0.07	0.89	0.11	0.84	0.16	0.88	0.12	0.98	0.02	0.88	0.12
	Feeding	0.69	0.31	0.89	0.11	0.67	0.33	0.82	0.18	0.69	0.31	0.65	0.35	0.78	0.22	0.755	2.245
	Prop. time handling	0.58		0.51		0.55		0.555		0.67		0.625		0.495		0.6	
<u>N. glauca</u> Simple	Rest	0.41	0.59	0.4	0.6	0.35	0.65	0.5	0.5	0.49	0.51	0.39	0.61	0.21	0.79	0.32	0.68
	Feeding	1.0		1.0		1.0		1.0		1.0		1.0		1.0		1.0	
	Prop. time handling	0.56		0.51		0.41		0.54		0.6		0.5		0.78		0.61	
<u>N. maculata</u> Complex	Rest	0.7	0.3	0.7	0.3	0.61	0.39	0.58	0.42	0.65	0.35	0.53	0.47	0.68	0.32	0.36	0.64
	Feeding	0.3	0.7	0.32	0.68	0.27	0.73	0.47	0.53	0.29	0.71	0.14	0.86	0.29	0.71	0.47	0.53
	Prop. time handling	0.73		0.7		0.64		0.6		0.73		0.77		0.71		0.65	
<u>N. maculata</u> Simple	Rest	0.5	0.5	0.27	0.73	0.44	0.56	0.49	0.51	0.36	0.64	0.48	0.52	0.5	0.5	0.2	0.8
	Feeding	1.0		1.0		1.0		1.0		1.0		1.0		1.0		1.0	
	Prop. time handling	0.68		0.82		0.8		0.865		0.865		0.897		0.86		0.858	
<u>N. obliqua</u> Complex	Rest	0.83	0.17	0.79	0.21	0.88	0.12	0.86	0.14	0.95	0.05	0.935	0.065	0.774	0.226	0.84	0.16
	Feeding	0.19	0.81	0.28	0.72	0.51	0.49	0.23	0.77	0.63	0.37	0.55	0.45	0.39	0.61	0.125	0.875
	Prop. time handling	0.435		0.373		0.283		0.356		0.463		0.446		0.419		0.469	
<u>N. obliqua</u> Simple	Rest	0.01	0.99	0.01	0.99	0.0	1.0	0.08	0.92	0.01	0.99	0.037	0.963	0.01	0.99	0.0	1.0
	Feeding	1.0		1.0		1.0		1.0		1.0		1.0		1.0		1.0	
	Prop. time handling	0.507		0.659		0.653		0.643		0.577		0.526		0.614		0.608	

the surface, but during handling, all time is spent at the surface. Again, this preference is very similar to that with Musca in single prey experiments.

N. obliqua shows a marked preference for depth during rest in the complex environment, as it did during single prey experiments, but during feeding, the preference switches to the surface in prey combination tests, but was still for depth during single prey experiments. During both rest and feeding in the simple environment, N. obliqua spends practically all its time at the surface, as was generally found during single prey experiments.

In conclusion, the allocation of time between surface and depth is, on the whole, similar to that in single prey experiments for N. glauca and N. obliqua, and specifically similar to that with Musca in single prey experiments for N. maculata.

V. 4.2. Perch selection.

The results for perch selection in the complex environment for each prey combination during feeding and rest are shown in Figs. 72, 73 and 74, for combined edge and middle sites.

a) N. glauca

During rest, although the general trend for N. glauca appears to be selection of near middle perch sites, in only one prey combination (5, 20, 10) is this difference significant from the selection of near bottom sites. In this respect, perch selection seems to be most similar to that with Gammarus in single prey experiments (Chapter IV section 4.4.3.). Also with high Musca/low Gammarus combinations, there is no difference between selection of near surface and near bottom sites, indicating that the most abundant large prey may also affect perch choice.

During feeding, there is still a preference trend for near middle perch sites, which is generally greater than during rest (greater than

LEGEND TO FIGS. 72, 73 and 74

Histograms showing perch selection at Rest (not feeding) and while feeding by the three predators in the presence of eight combinations of the three prey types.

Significance of differences shown (χ^2)

*** 0.001

** 0.01

* 0.05

n.sig not significant

S - Perch sites near surface

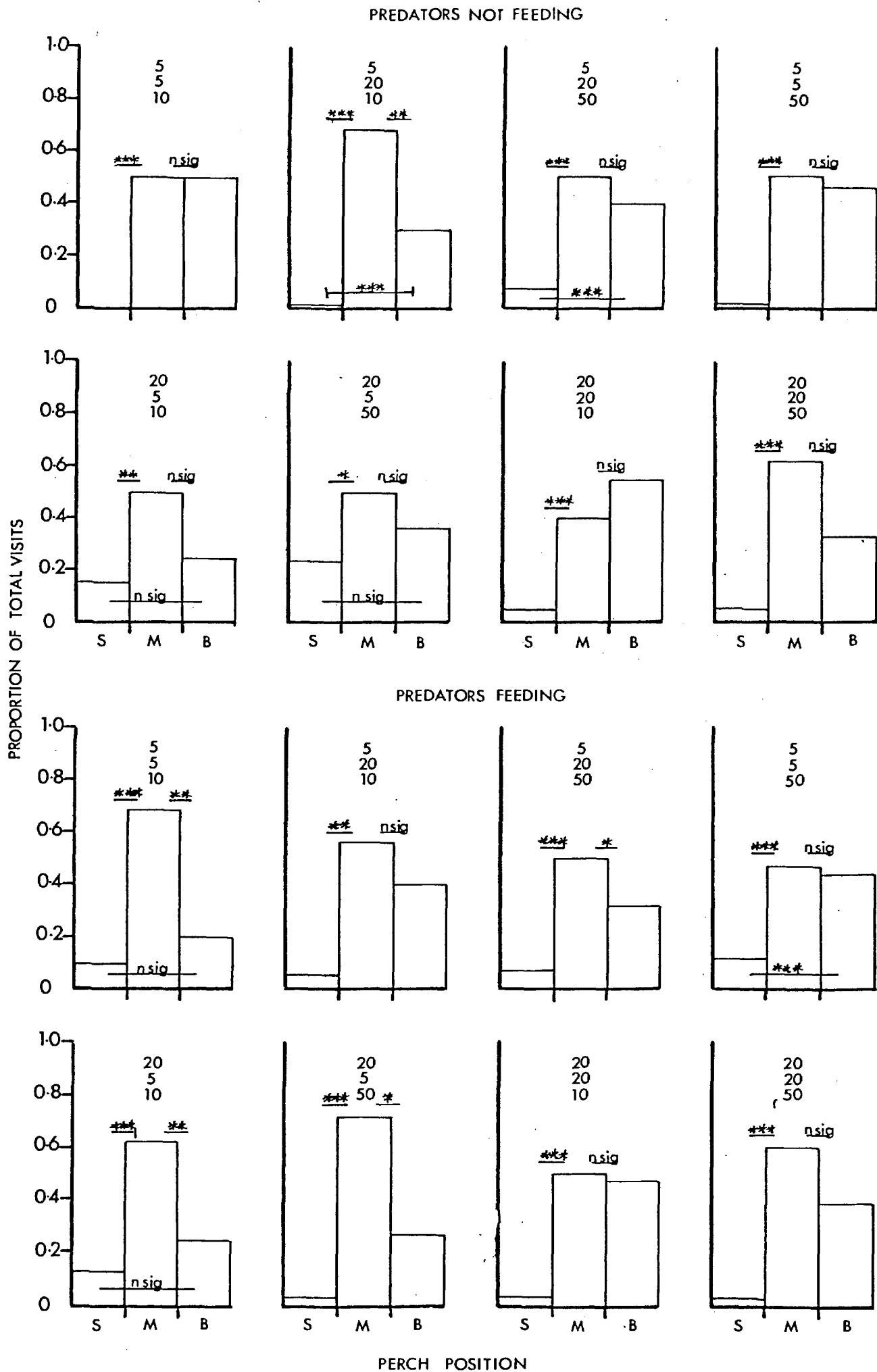
M - Perch sites near middle

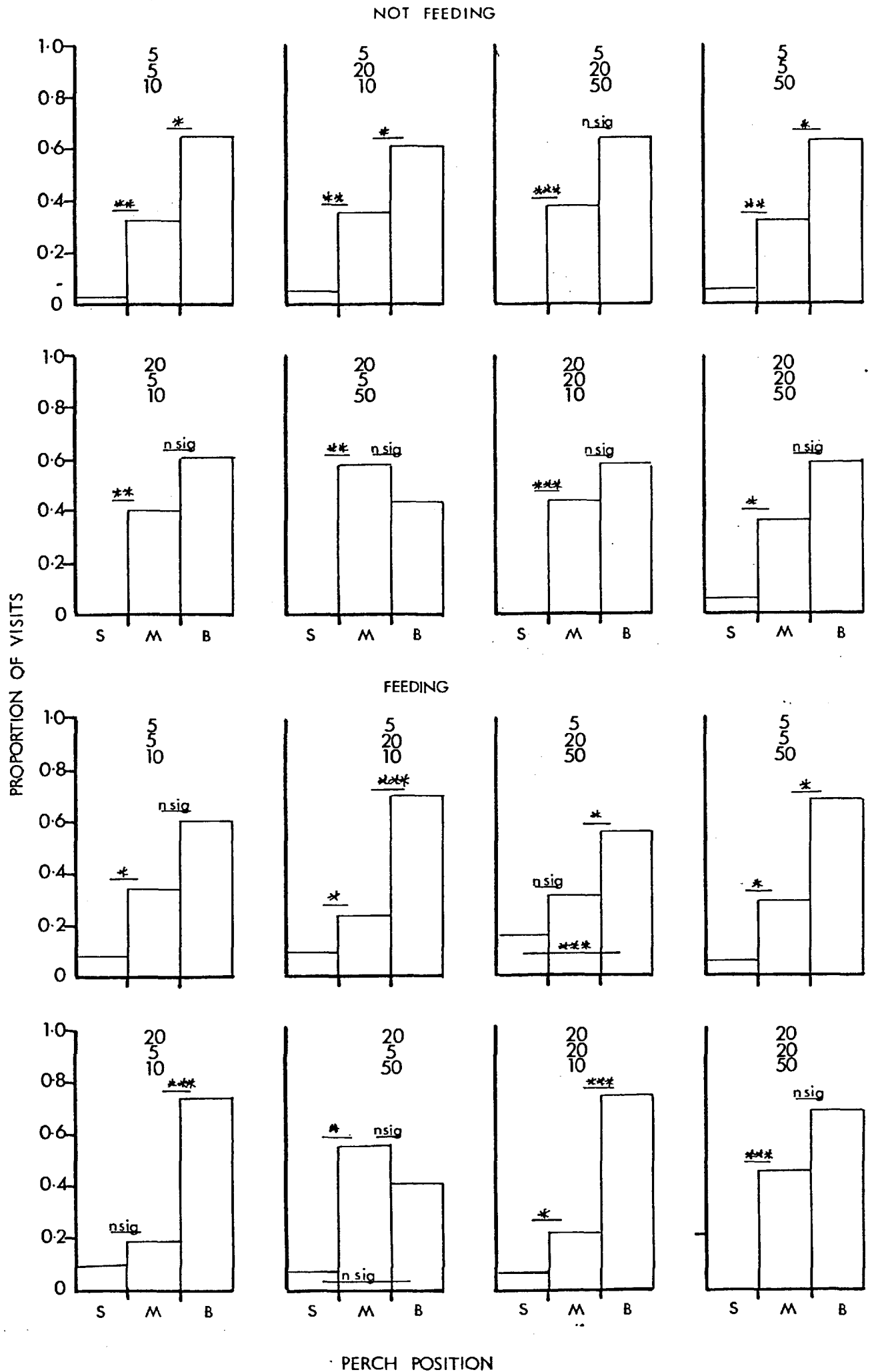
B - Perch sites near bottom

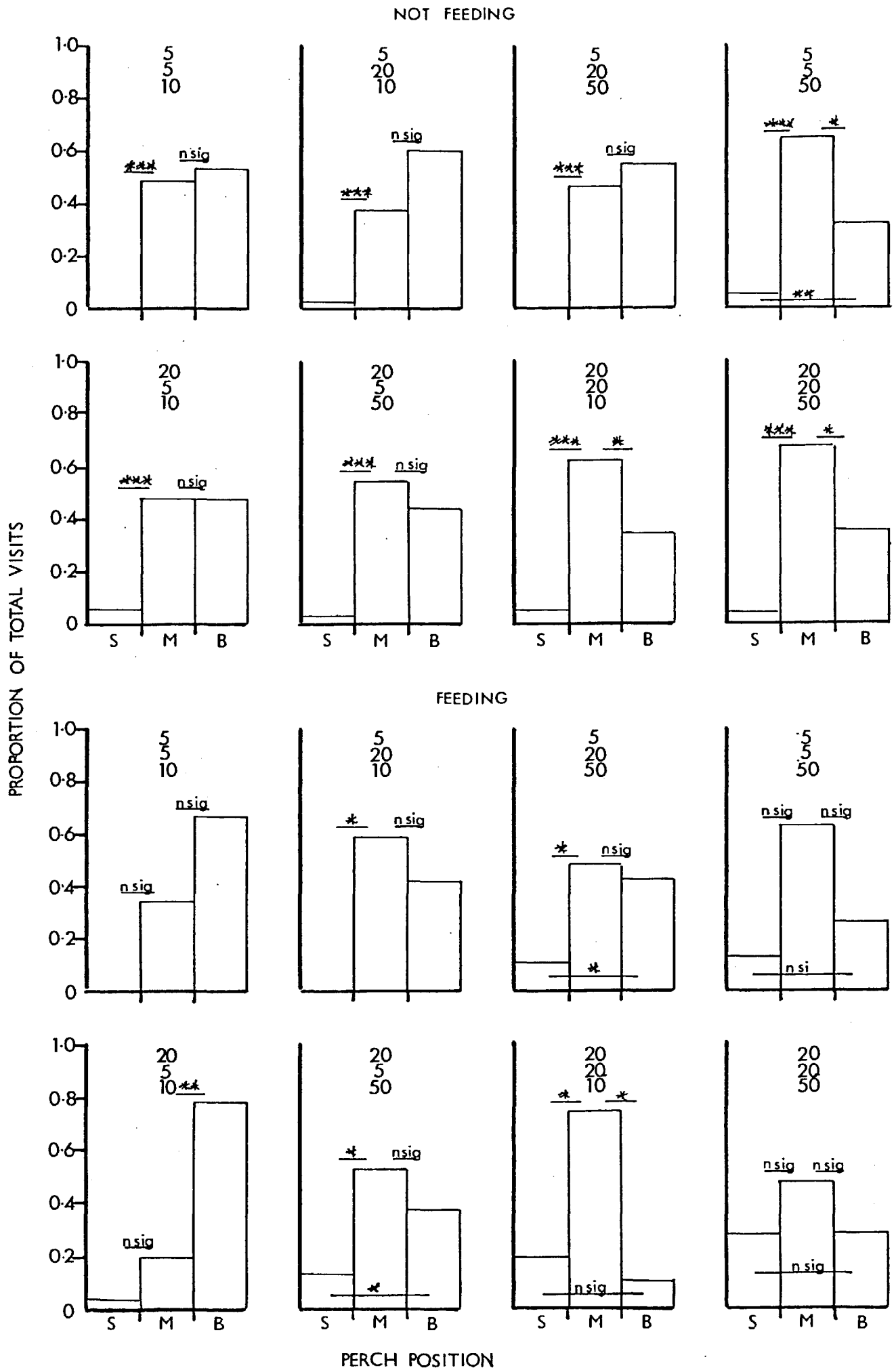
Fig. 72 N. glauca

Fig. 73 N. maculata

Fig. 74 N. obliqua







selection of bottom sites in 4 out of the 8 combinations), the trend found in single prey experiments. Notably, of the four combinations showing no significant difference in selection between near middle and near bottom sites, three include high Gammarus density.

It appears that perch selection by N. glauca is most affected by Gammarus, the most active of the prey types, but this selection can be altered when there is low Gammarus and high Musca combinations.

b) N. maculata

N. maculata on the other hand, shows a general trend for near bottom perch sites during rest, but the difference from near middle sites is significant in only three combinations. During feeding, this preference appears to increase (significant in five combinations). Such perch selection is very similar to that with Gammarus in the single prey experiments. During rest four of the five combinations which showed no significant difference between selection of near middle and near bottom perch sites, contained high Musca densities, indicating that although perch preference is most affected by Gammarus, high densities of an alternate large prey can also affect perch selection.

c) N. obliqua.

Perch selection by N. obliqua seems most changed in the presence of prey combinations from selection with single prey. The general trend during rest is for selection of near middle perch sites with high Musca combinations (only significantly greater than near bottom sites in two of the four combinations though), and for selection of near bottom perch sites (with the exception of low Gammarus/high mosquito combinations) with low Musca combinations (although no significant differences from near middle selection). These results are not close to any of the single prey results.

During feeding, due to the small number of visits made, there are

very few significant differences. The trend is for selection of near middle sites (six combinations). In the single prey experiments, the trend was for selection of near bottom sites during rest, which was increased during feeding. This difference in perch selection in the prey combination experiments may be one of the reasons for lowered predatory efficiency compared to single prey conditions, and can probably be most easily explained by a change in the predator's physiological state.

V. 5. Prey preference

V. 5.1. Introduction

The prey captured and the order they were captured in were recorded for all prey combinations in both environments for nine replicates. The results were grouped into six broad groups of prey combinations to give sufficiently large numbers for analysis. Data from combinations with high and low densities of each prey type were pooled so that prey selection results were available for combinations with densities of 5 and 20 Musca, 5 and 20 Gammarus, and 10 and 50 mosquito larvae. For example, the data from the following prey combinations (order Musca, Gammarus, Mosquito); 5, 5, 10; 5, 20, 10; 5, 5, 50; and 5, 20, 50 were pooled to give prey selection with low Musca density. (There is some justification in this, for there is very little difference in predatory efficiency on the two densities of Musca and Gammarus in the single prey experiments.).

Differences in the numbers of each prey type captured at each stage in the catch sequence were tested using χ^2 , and where numbers caught at one stage in the catch sequence fall below 12, the results are pooled over these and subsequent captures.

The observed prey selection was then compared to predicted selection based on models constructed for the various hypotheses concerning prey selection (see section V. 1.). These models can be roughly assigned

to five groups, prey selection on the basis of; a) energy gains; b) ease of capture; c) relative predator and prey positions and micro-habitat overlap; d) prey abundances and relative proportions; and finally e), combinations of the above four types. There are different values of the above factors with each prey type in the eight different prey combinations, and when pooling the data into broader categories (i.e. combinations with 5 Musca etc), the average value of the four combinations making up this category is used. The models predicted proportions of each prey type to be captured at each stage in the catch sequence, and these can be compared to the observed values.

The predictions of the following models were examined:-

- 1) Selection based on predator rest position, assuming no prey preference. In the complex environment, proportion of time spent between surface and depth, and perch preferences are taken into account, assuming Musca captured at surface, mosquito larvae at near surface and near middle perch sites and Gammarus at near bottom sites, in the simple environment assuming Musca and mosquito larvae taken from surface, Gammarus from depth.
- 2) Selection based on net energy gain on basis of single prey experiments, where either the prey type offering greatest net energy gain at the density in the prey combination, or the prey offering largest $\frac{E}{T}$ values should be selected.
- 3) Selection based on prey offering largest energy gain per individual prey item.
- 4) Selection of first capture based on predator rest position as in model 1, second and subsequent captures based on predator position during handling (worked out as in 1).
- 5) Selection based on relative prey abundance, assuming random encounters for all types and no preference.

- 6) Selection of first capture as in model 1, after this capture, predator rises to surface so that all prey types have been encountered, second and subsequent captures are then based on energy gains.
- 7) Selection based on probability of successful capture on random encounters, worked out by multiplying proportions of successful pursuit, attack and captures for each prey density used.
- 8) Selection based on predator position as in Model 1 modified by success of capture as in Model 7.
- 9) Selection based on combination of predator position (Model 1) and relative prey abundance (Model 5), assuming no preference.
- 10) Selection based on combination of success of capture (Model 7) and relative prey abundance (Model 5).
- 11) Selection based on a combination of Models 8 and 5.
- 12) Selection based on a combination of Models 4 and 5.
- 13) Selection based on a combination of Models 10 and 4.

The predicted proportions of each prey captured given by these Models, are presented in Appendix XX.

V. 5.2. Results

The proportions of each prey type captured at each capture of the catch sequence are shown in Tables 5.4, 5.5 and 5.6. The differences between numbers of each prey type captured have been tested by χ^2 , and the significance is shown in the Tables. It should be noted that with N. obliqua and later captures in the catch sequence of the other two predators, lack of significant differences between proportions of prey types selected, is due to the low numbers of captures made.

a) N. glauca (Table 5.4.)

In the complex environment, selection of prey by N. glauca does not show any strong constant preference for one prey type, but the preference seems to change with relative prey densities. This indicates, in these

Table 5.4 Proportion of each prey type captured by N. glauca with different prey combinations in both environments.

Differences tested by χ^2 on raw data, and significance shown. M = Musca, G = Gammarus, Q = mosquito larvae

Complex		CAPTURE													
Combination.		1		2		3		4		5-9					
5 <u>Musca</u>	Q	0.636	] 0.05] 0.1	n=23	0.739	] 0.01] n.sig	n=18	0.722	] 0.05] n.sig.	n=15	0.667	] 0.05] n.sig.	n=17	0.53	] n. sig.
	G n=33	0.273			0.13			0.166			0.2			0.294	
	M	0.091			0.13			0.11			0.133			0.176	
20 <u>Musca</u>	M	0.148	] 0.1] n.sig.	n=21	0.428	] n.sig.	n=10	0.5	] sig.] 0.5	n=60	0.16	] n. sig.	n=8	0.25	] n. sig.
	Q n=27	0.44			0.33			0.5			0.83			0.75	
	G	0.407			0.238			0			0			0	
5 <u>Gammarus</u>	Q	0.643	] 0.05] n.sig.	n=24	0.542	] n.sig.] 0.05	0.01 n=17	0.647	] n.sig.] 0.058	n=11	0.454	] n. sig.	0.05 n=13	0.69	] n. sig.
	M n=28	0.107			0.375			0.294			0.454			0.31	
	G	0.25			0.083			0.058			0.09			0.0	
20 <u>Gammarus</u>	Q	0.468	] n.sig.] 0.05	0.05 n=20	0.55	] n.sig.	n=12	0.58	] 0.1] n.sig.	n=10	0.6	] n. sig.	n=12	0.50	] n. sig.
	G n=32	0.406			0.3			0.167			0.2			0.25	
	M	0.125			0.15			0.166			0.2			0.25	
10 Mosquito	Q	0.375	] 0.05] 0.05	n=20	0.45	] n.sig.	n=14	0.643	] n.sig.] 0.05	n=12	0.33	] sig.			
	M n=32	0.156			0.3			0.35			0.44				
	G n.sig	0.468			0.25			0.0			0.22				
50 Mosquito	Q	0.75	] 0.001] n.sig.	n=24	0.625	] 0.05] n.sig.	n=14	0.643	] 0.05] n.sig.	0.05 n=12	0.66	] n.sig.] n.sig.	n=22	0.73	] 0.01] n. sig.
	M n=28	0.07			0.25			0.143			0.25			0.18	
	G	0.178			0.125			0.214			0.083			0.09	

Table 5.4 (Continued)

<u>Simple</u>		<u>CAPTURE</u>		
<u>Combination.</u>		1	2	3-4
5 <u>Musca</u>	M	0.848	0.682	0.5
	Q n=33	0.152	0.273	0.5
	G	0	0.045	0
		0.001 0.05	0.05 0.05	n.sig.
20 <u>Musca</u>	M	0.906	0.88	1.0
	Q n=32	0.094	0.12	0
	G	0.0	0	0
		0.001 n.sig.	0.001 n.sig.	0.01
5 <u>Gammarus</u>	M	0.848	0.826	0.625
	Q n=33	0.152	0.130	0.375
	G	0	0.043	0
		0.001 0.05	0.001 n.sig.	n.sig.
20 <u>Gammarus</u>	M	0.906	0.75	0.89
	Q n=32	0.094	0.25	0.11
	G	0	0	0
		0.001 n.sig.	0.05 0.05	0.05 n.sig.
10 <u>Mosquito</u>	M	0.935	0.815	0.75
	Q n=31	0.065	0.148	0.25
	G	0.0	0.037	0
		0.001 n.sig.	0.01 n.sig.	n.sig. n.sig.
50 <u>Mosquito</u>	M	0.844	0.75	0.77
	Q n=32	0.156	0.25	0.23
	G	0.0	0	0
		0.001 0.05	0.05 0.05	n.sig. n.sig.

experiments at least, that prey selection is not being based on net energy gains, calorific value of prey or $\frac{E}{T}$ values, so the models incorporating these factors need not be examined.

On the whole, a larger proportion of mosquito larvae are captured than of the other two prey, which is most apparent with high mosquito combinations, and least with low mosquito combinations. The proportion of the other two prey captured seems to increase in combinations of high densities of these prey. The most likely explanation of such selection is on the basis of relative abundance of the three prey, and there is a significant fit with the observed data and the predicted proportions of Model 5 over the first few captures (Appendix XXI). The fact that Gammarus is generally taken in greater proportions than Musca at the first capture and vice versa for subsequent captures suggests selection may be based on predator and prey overlap in microhabitats, and Model 12 provides as good a fit as Model 5 to the observed data. This model also predicts the switch in preference between Gammarus and Musca from the first to subsequent captures, which Model 5 does not. Prey selection may also be influenced by success of capture, as Model 10 (combination of prey abundance and success of capture) provides quite a good prediction of prey selection for the second and subsequent captures though not for the first. No other models provide a good fit to the data.

In the simple environment, prey selection is very straightforward, with strong selection of Musca, a small proportion of mosquito larvae taken, and practically no Gammarus captured. This selection can be most easily explained on the basis of selection for greatest net energy gain, largest $\frac{E}{T}$ values or greatest calorific gain from an individual item, i.e. Models 2 and 3. As no such selection was shown in the complex environment, alternative explanations should be considered for the results in the simple environment. On the basis of optimal diets,

prey should either be totally included or totally excluded from the diet (Pyke et al (1977)), but the results indicate there is partial inclusion of mosquito larvae. All of the models other than 2, 3 and 6 are constructed on the basis of no preference for any prey type, and prey are attacked as encountered. If there is a weak preference for Musca over mosquitos, then any model including predator position (e.g. Models 1 and 4) could predict the observed results when proportions of Musca captured are increased at the expense of mosquito proportions. The proportions of Gammarus taken in the first captures are most closely predicted by a combination of predator position at rest and success of capture (Model 8), and for subsequent captures by any model incorporating predator position during handling (i.e. Models 4, 12 and 13). It thus appears that a combination of predator/prey overlap in microhabitats and weak preference for larger prey control prey selection in the simple environment.

b) N. maculata (Table 5.5).

In the complex environment, there is again no clear preference for any one prey type, indicating energetic gains etc., are not very important in controlling prey selection, as on this basis, in no combinations should mosquito larvae be selected. The lowest level of prey captures in all prey combinations is of Gammarus, and the levels between Musca and mosquito larvae vary depending on relative prey abundances, although there are no significant differences between the proportions of captures. These results as a whole can only be predicted on the basis of combinations between predator position, success of capture and relative prey abundances. (Models 1, 7, 8, 10 and 11 for first captures). Of these Models 7 and 10 provide the best fit (based on success of capture and prey abundance), but Models 8 and 11 also fit the observed proportions (Appendix XXI). The model based solely on

Table 5.5 Proportion of each prey type captured by N. maculata with different prey combinations in both environments.

Differences tested by χ^2 on raw data, and significance shown. M = Musca. G = Gammarus. Q = Mosquito larvae.

Complex

Combination		Capture														
		1		2		3		4		5+						
5 <u>Musca</u>	Q	n=39	0.41	n.sig.	n=30	0.533	n.sig.	n=19	0.647	n.sig.	n=10	0.7	n.sig.	n=18	0.777	0.01
	M		0.384			0.4			0.294			0.2			0.166	
	G		0.205			0.066			0.059			0.1			0.055	
20 <u>Musca</u>	M	n=32	0.562	n.sig.	n=20	0.55	n.sig.	n=11	0.545	n.sig.	n=15	0.4	n.sig.	n=15	0.4	0.05
	Q		0.375			0.25			0.272			0.6			0.6	
	G		0.062			0.2			0.182			0			0	
5 <u>Gammarus</u>	Q	n=35	0.514	n.sig.	n=27	0.407	n.sig.	n=15	0.6	n.sig.	n=12	0.58	n.sig.	n=19	0.736	0.05
	M		0.428			0.48			0.33			0.33			0.21	
	G		0.057			0.11			0.066			0.083			0.05	
20 <u>Gammarus</u>	M	n=36	0.5	n.sig.	n=23	0.435	n.sig.	n=13	0.46	n.sig.	n=12	0.25	0.05	n=12	0.25	0.05
	Q		0.278			0.435			0.384			0.75			0.75	
	G		0.222			0.13			0.154			0			0	
10 Mosquito	M	n=39	0.564	0.05	n=25	0.48	n.sig.	n=12	0.58	n.sig.	n=9	0.56	n.sig.	n=9	0.56	n.sig.
	Q		0.33			0.32			0.33			0.33			0.33	
	G		0.102			0.2			0.083			0.11			0.11	
50 Mosquito	Q	n=32	0.468	n.sig.	n=25	0.52	n.sig.	n=16	0.625	n.sig.	n=10	0.9	0.05	n=14	0.768	0.05
	M		0.344			0.44			0.25			0.1			0.208	
	G		0.187			0.04			0.125			0			0.683	

Table 5.5 (Continued)

<u>Simple</u>			<u>Capture</u>							
<u>Combination</u>			1		2		3			
5 <u>Musca</u>	M	n=35	0.514	n.sig. 0.05	n=28	0.893	0.001 n.sig.	n=18	0.875	0.05 n.sig.
	Q		0.371			0.071			0.125	
	G		0.114			0.036			0	
20 <u>Musca</u>	M	n=36	0.5	n.sig. n.sig.	n=34	0.91	0.001 n.sig.	n=22	0.944	0.01 n.sig.
	Q		0.33			0.059			0.055	
	G		0.05			0.166			0.0629	
5 <u>Gammarus</u>	M	n=35	0.486	n.sig. 0.05	n=31	0.903	0.001 n.sig.	n=21	0.944	0.01 n.sig.
	Q		0.4			0.096			0.052	
	G		0.114			0			0	
20 <u>Gammarus</u>	M	n=36	0.527	n.sig. n.sig.	n=31	0.903	0.001 n.sig.	n=19	0.875	0.01 n.sig.
	Q		0.305			0.032			0.125	
	G		0.05			0.166			0.064	
10 Mosquito	M	n=35	0.628	0.01 n.sig.	n=31	0.903	0.001 n.sig.	n=12	1.0	0.001
	Q		0.143			0.096			0	
	G		0.228			0			0	
50 Mosquito	M	n=36	0.389	n.sig. 0.01	n=31	0.903	0.001 n.sig.	n=28	0.864	0.01 n.sig.
	Q		0.555			0.032			0.136	
	G		0.055			0.064			0	

predator position at rest does not fit the data (i.e. Model 1). Similarly for subsequent captures, the best fit to the observed data is predicted by Model 10 and when predator position at rest or during handling is considered, poorer fits are apparent. It thus appears that the main factors affecting prey selection by N. maculata in the complex environment are success of capture and prey abundance, with a smaller effect of predator position.

In the simple environment for the first capture, generally more Musca are taken than mosquito larvae, except in high mosquito density combinations, where the reverse is true. Very few Gammarus are captured. Models based on predator position, success of capture and relative abundance all predict similar proportions of prey captured to the observed data (i.e. Models 7, 8, 10 and 11) but of these, Models 7 (based on success of capture) and 8 (based on success of capture and predator position) offer the best fits, models based solely on predator position do not fit well with the data. The increase in proportions of mosquito larvae captured in high mosquito combinations does indicate some effect of prey abundance. In second captures, there is very marked selection of Musca and very few mosquito larvae or Gammarus are captured, and in subsequent captures, there is still strong selection of Musca, but no Gammarus are taken. This appears to be selection on the basis of calorific value per individual (Model 3), but as with N. glauca these results can also be explained on the basis of predator position during handling and a preference for Musca over mosquito larvae. Thus, it appears that selection is based mainly on a combination of predator position and success of capture, with a preference for larger prey.

c) N. obliqua (Table 5,7)

Due to the small number of results, little can be deduced of prey

selection by N. obliqua in the complex environment, however, the general trends can be observed. As described for N. glauca and N. maculata, selection is not being based on energetic gains etc., as described in the optimal diet theory. There does appear to be an effect of relative prey abundance for the first captures, where at low density combinations, the particular prey is caught in the smallest proportions, but at high density combinations, it is caught in the greatest proportions. Although the predictions of Model 5 fit the data, the fit is not particularly good (Appendix XXI). None of the other models appear to give an accurate description of the general trends shown by N. obliqua. The relationship between Musca and Gammarus proportions in the different combinations is however demonstrated by Model 11 (based on predator position at rest, success of capture and relative prey abundance), but this model, based on no preference for any prey, predicts high proportions of captures of mosquito larvae, which does not occur in the results. It may be possible that there is weak preference for large prey i.e. for Gammarus at depth and for Musca at the surface at the expense of the small mosquito larvae.

The increase in proportions of Musca captured for the second captures also reflects the predator position during handling, with increased time spent at the surface. Very few captures were made in subsequent stages of the catch sequence, so no conclusions have been drawn.

Of the first prey captured by N. obliqua in the simple environment, the largest proportion are Musca, the lowest Gammarus, with evidence of increased proportions of abundant prey taken. In subsequent captures, Gammarus are effectively dropped from the diet, Musca still being taken in the greatest proportions. This selection can be most easily explained by a combination of predator position, where most of the rest time and all of the handling time is spent at the surface (Model 4), and a weak

preference for Musca over mosquito larvae, as described in the previous paragraph, which may be affected by the relative abundance of the two prey.

V. 5.3. Conclusion

In the complex environment, the most important factors affecting prey selection by N. glauca appear to be overlap in predator and prey positions and relative prey abundance. For N. obliqua the additional factor of success of capture appears to affect prey selection as well, but for N. maculata, success of capture and relative prey abundance appear to be the most important factors, predator position of secondary importance. In the simple environment, overlap in predator and prey positions and success of capture seem to be the most important factors affecting prey selection by N. glauca and N. maculata, with a weak preference for larger prey being superimposed on these factors. N. obliqua seems most affected by predator position and prey abundance in its selection in the simple environment, and appears to show a preference for large prey in both environments.

The apparent preference for larger prey by the three predators in the simple environment, and by N. obliqua in the complex one as well, could be due to a number of factors e.g. larger prey creating a greater disturbance; giving a greater contrast to the environment, or providing a greater calorific gain to the predator per individual, than smaller prey. These preferences may also occur in the complex environment with N. glauca and N. maculata, but are being obscured by the accuracy of other factors in predicting prey selection.

The fact that the predators do not seem to select prey by the optimal diet rules for maximising energy gains in time, tends to suggest that these predators do not appear to optimise their diet on this basis. Similar findings are reported by Gittleman (1978), where Notonectids

did not select for prey size as would be expected for an optimal diet. Instead, he suggested that Notonecta species select prey of the most familiar size. This is similar to Charnov's risk hypothesis for mantid prey selection (Charnov (1976)). Charnov suggested that rather than optimising energy/time, the mantids were minimising risks associated with stalking prey, such as detection by predators, displacement from hunting perch, and attack of unsuitable prey. It may be that Notonectids are subject to the same risks, and select prey on this basis, but also, within these constraints, some preference based on energy reward may be shown when several types of prey are available within the predators microhabitat at the same time.

Prey selection shown here basically supports the conclusions of Ellis and Borden (1970) for N. undulata and Gittleman (1975) for Bueno antigone and Martarega hondurensis (family Notonectidae). In both studies, the authors concluded that prey selection was based on maximum overlap of predator and prey microhabitat, and also on the ease of prey capture in the former case, and greatest contrast in the latter case. Gittleman (1975) also predicted that the differential prey selection based on differences in predator position could allow coexistence between the two genera of Notonectidae used in his study. In the present study, different prey selection between the three predators is apparent in the complex environment, where there is differential use of space, but not in the simple one, where there is similar use of space. Other studies also suggest, as does the present one, that relative prey abundance (Murdoch (1975)), and success of prey capture (Gittleman (1978)) are also important.

One can conclude that differences in predator behaviour (including use of space, success of capture and response to prey density, which seem to control prey selection) between the three predators, appear to

be large enough in complex environments to allow differential prey selection and on this basis, coexistence, while in simple environments, competition might be expected, where the most efficient predator is likely to dominate.

Chapter VI

Morphometric constraints on the Predation StrategyVI.1. Introduction

As was mentioned in Chapter I (Section 1.1.3), for many measurements of animals, the optimum with respect to survival is usually near the measured mean value (Holling (1964)). It is thus likely that differences in habitat and prey selection between similar species may be expressed in different sizes and forms of body parts utilised. As we are interested, in this study, in foraging behaviour, the study of morphometrics in this case will naturally be confined to organs and limbs used in this behaviour. This will include a comparison of measurements made of body parts associated with locomotion, prey capture, and to some extent prey recognition.

VI.2.

LocomotionVI.2.1. Introduction

When a body moves through a fluid, a force known as drag, acts backwards on it, resisting its motion. Drag on a body is given by the following equation:-

$$D = \frac{1}{2} \rho u^2 A C_D$$

Where D is the drag, ρ is the fluid density, U is the velocity of the fluid relative to the body (or in other words, the velocity of the body in a stationary fluid), A is the frontal area of the body in the direction of flow and C_D is the drag coefficient, which depends on the body shape and the Reynolds number (Alexander (1971)). The larger this value of D, the lower the swimming efficiency. The value ρ for water equals 1.00. As all Notonectids are of a streamlined form (more or less rounded at the front, and tapering gradually to a point at the back) the drag coefficients are low. The Reynolds number itself, is derived from the relation-

ship:-

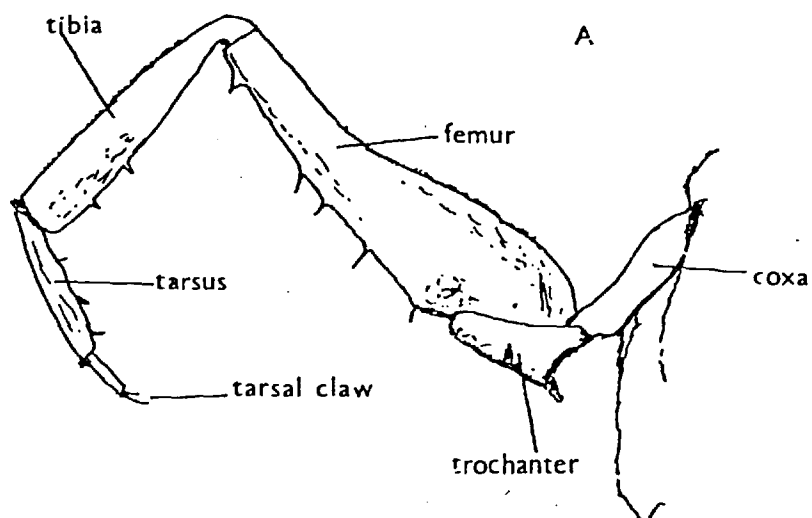
$\frac{\rho u a}{\eta}$, where ρ and η are the density and viscosity of the fluid, u the mean velocity of the body, and a , the body length in the direction of the flow. For water, $\rho = 1.00$, $\eta = 0.01$ (at 20°C Alexander (1971)). Unfortunately, no data is available on the mean velocities of the different species of Notonecta. However, if one assumes similar velocities are possible, then a comparison of the general magnitude of the drag forces and efficiency of locomotion can be derived by considering the values of A and a , i.e. the frontal area and the body length. As A increases, so D increases, and likewise as a gets larger, so C_D will increase, and this, in turn, increases the size of D . However, as Alexander (1971) points out, for the water beetles Aciluis and Dytiscus (a similar size to Notonectids, and a similar rowing form of locomotion), the Reynolds numbers at which both beetles swim are in the range where drag coefficient is more or less independent of the Reynolds number for streamlined bodies. Thus the largest effect on drag will be caused by the size of A , the frontal area.

Another method of examining the efficiency of locomotion has been discussed by Gittleman (1974). He considered the metathoracic swimming leg of several genera of Notonectids as a simple lever system, with the fulcrum at the articulation between the trochanter and the coxa (Fig 75B). Muscle insertions on the proximal end of the trochanter supply the force for swimming. The resultant force applied to the water (Fr), can be derived from the following equation:-

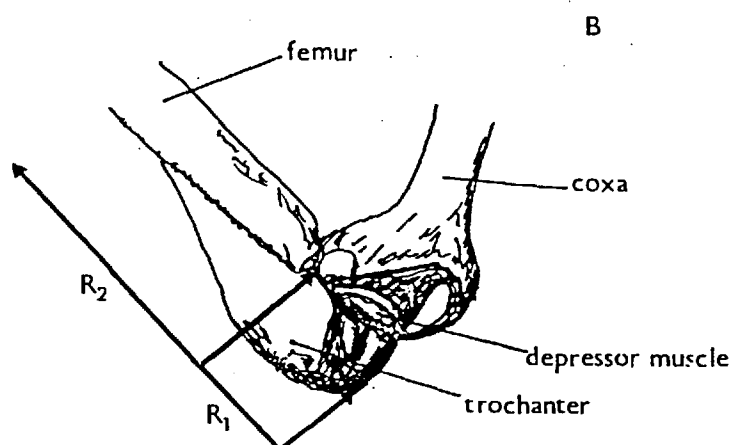
$$Fr = \frac{R_1}{R_2} F_m$$

, where F_m is the muscle force, R_1 is the length of the lever arm (the distance from the fulcrum to where the force is applied) and R_2 is the total distance from the fulcrum to the area where the resultant force is applied. The ratio $\frac{R_1}{R_2}$ is termed the mechanical advantage. In the Not-

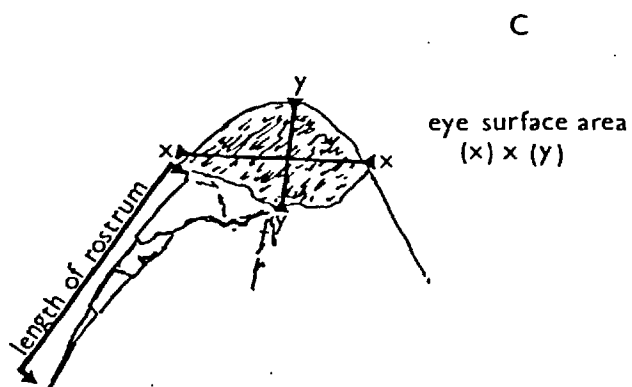
Morphology of the Notonectid leg and head.



A) Segments of the mid-leg.



B) Measurements R_1 and R_2 on the hind leg.



C) Length of rostrum and approximate measurement of eye surface area.

onectid leg, R_1 is the distance from the trochanter-coxa articulation to the proximal end of the trochanter, and R_2 is the total length of the hind leg from the trochanter-coxa articulation to the distal tip of the tarsi (not including the tarsal claw).

A low mechanical advantage is considered as an adaptation for increasing mobility, with sustained rapid but weak leg movements, whereas an increased mechanical advantage allows stronger action in the form of short bursts of rapid acceleration, which is unlikely to be sustained (Alexander (1971), Gittleman (1974)).

An examination of the ratio of leg length and body length can also give a hint as to the locomotory efficiency, where a large value (greater than unity) would be expected with weak but sustained movement, and a lower value (less than unity) would allow strong actions from the leg (Gittleman (1974)).

VI. 2. 2 Results

Table 6.1 shows the results of the analysis of the above parameters for the three species of Notonecta used in this study.

From the results, it is clear that N. obliqua is likely to experience the greatest drag force when swimming, as both frontal area and body length are significantly greater than the other two species. There is no difference between the frontal areas of N. glauca and N. maculata, but N. glauca has a significantly longer body, thus may experience slightly greater drag than N. maculata.

In his measurements of the mechanical advantage of several different genera of Notonectidae, Gittleman (1974) reported values ranging from 0.026 to 0.051. The two species of the genus Martarega studied, showed values of 0.028 and 0.026. These species are found in flowing water, feeding on insects trapped in the surface film, and the low mechanical advantage is described as being an adaptation for maintaining position in the water with small, rapid locomotory movements. At the other extreme,

Table 6.1 Table comparing relative measurements of body parts associated with locomotary efficiency between the three Notonecta species. (Significance of differences tested by T test, *** = 0.001, ** = 0.01, * = 0.05 species underlined show no significant differences.)

MEASURE	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. maculata</u>	Significance
FRONTAL AREA	n-31 0.2027 $\pm$ 0.009 sq.cms.	n-27 0.264 $\pm$ 0.0071 sq. cms	n-18 0.2058 $\pm$ 0.006 sq. cms.	*** ob-mac. gl.
BODY LENGTH	n-31 1.543 $\pm$ 0.031 cms.	n-27 1.729 $\pm$ 0.028 cms.	n-21 1.469 $\pm$ 0.028 cms.	*** *** ob-gl-mac.
BODY WIDTH	n-25 0.499 $\pm$ 0.028 cms.	n-27 0.527 $\pm$ 0.011 cms.	n-21 0.5038 $\pm$ 0.0119 cms.	** ob-mac. gl
BODY DEPTH	n-26 0.410 $\pm$ 0.007 cms.	n-27 0.447 $\pm$ 0.006 cms.	n-21 0.425 $\pm$ 0.01 cms.	*** * ob-mac-gl.
R ₂ (leg length)	n-39 1.559 $\pm$ 0.018 cms.	n-30 1.7116 $\pm$ 0.0177 cms.	n-23 1.5756 $\pm$ 0.016 cms.	*** *** ob - mac - gl
R ₁ (lever arm)	n-39 0.0665 $\pm$ 0.001 cms.	n-29 0.0754 $\pm$ 0.0014 cms.	n-23 0.0663 $\pm$ 0.001 cms.	*** ob - gl mac
<u>Leg Length</u> Body Length	n-31 1.0161 $\pm$ 0.0165	n-27 0.993 $\pm$ 0.0162	n-21 1.076 $\pm$ 0.0179	*** *** mac - gl - ob
<u>R₁</u> <u>R₂</u>	n-39 0.0427 $\pm$ 0.0005	n-29 0.0441 $\pm$ 0.0005	n-23 0.0421 $\pm$ 0.0004	*** ob - gl mac

the four species of the genus Bueno studied, showed values ranging from 0.036 to 0.051. These species live in static water, and feed preferentially on free swimming prey, utilising a 'sit and wait' strategy, thus the higher mechanical advantage is described as an adaptation for rapid acceleration in pursuit of these prey items. The four species of the genus Notonecta studied, showed values intermediate between the other two genera, ranging from 0.031 to 0.036. This genus is described as spending more time at the surface than Bueno, and taking more terrestrial prey trapped at the surface, and so is described as representing an ecological compromise between the other two genera.

The values shown in Table 6.1 for the three British species of Notonecta all fall in the range of values for Bueno in Gittleman's study. Thus, on the basis of Gittleman's conclusions, these three species of Notonecta are more adapted to rapid acceleration with strong leg movements than to a more active but weaker locomotory form. Of the three British species, N. obliqua has significantly the largest mechanical advantage, there being no difference in values between the other two species.

The reverse is true when considering the leg length/body length ratio, where N. maculata has significantly the largest value, and N. obliqua the smallest. In Gittleman's study, the largest value was found in Martarega (1.2 and 1.33), there being little difference between Notonecta and Bueno, although there is a tendency for the value to fall as mechanical advantage increases.

In summary, N. obliqua is likely to experience the most drag, possesses the largest mechanical advantage, and the smallest leg length/body length ratio. These three factors all suggest that N. obliqua is likely to be the least active, with the lowest locomotory efficiency but the strongest action over short periods of rapid acceleration. In contrast, N. maculata probably experiences the smallest drag, the lowest mechanical advantage

(although not significantly different to that of N. glauca) and the highest leg length/body length ratio. These three factors again reinforce each other and suggest that N. maculata is likely to be the most active of the three species, with the greatest efficiency of locomotion, but perhaps the weakest activity over short periods of rapid acceleration. N. glauca seems to fall inbetween the above two strategies, and although it has the smallest frontal area (although not significantly different from N. maculata), it has the second largest body length, the second largest mechanical advantage (again not significantly different from N. maculata), and the second largest leg length/body length ratio. These findings fit in well with the respiration data, where the highest respiratory values are found in N. obliqua after a percentage of time for activity of 3%, and this species also shows the steepest respiration rate/activity curve indicating the largest increase in rate with activity of the three species i.e. lowest locomotory efficiency. N. maculata, although having a higher rate of oxygen consumption up to 20% time active than N. glauca, it has a shallower slope to the curve, and a lower overall respiratory rate over longer periods of activity, indicating the lowest effect of activity on the respiratory rate i.e. highest locomotory efficiency.

These morphological and physiological differences may explain the differences in success of the various components of the attack sequence between the three predators (Chapter IV, Section IV.3.1.). The fact that N. obliqua appears to be the strongest swimmer over short distances, has greatest costs from prolonged activity, and generally has a relatively small reaction area, may explain the high pursuit success (Section IV. 3.1. 3.), where N. obliqua has possibly adapted a strategy where short, rapid and successful pursuits are made, reducing energy loss. On the other hand, N. maculata has the largest reaction area, most efficient, but weakest locomotory potential, and lowest active metabolism, so can afford longer pursuits and stalks, and suffer the lower pursuit success found, without

incurring too large an energy loss. N. glauca appears to fall in-between.

Likewise, a successful attack requires a rapid strike, and on the basis of the morphology of the locomotory systems of the three species, one would expect N. obliqua to show the greatest success, and N. maculata the lowest. The results in Section IV.3.1.3. indicate that the first prediction is generally correct, but N. maculata generally has a greater attack success than N. glauca, except with small prey.

VI. 3. Morphometrics of the prey capturing limbs.

VI. 3.1. Introduction

As was discussed in Chapter I, Notonectids capture prey with the first two pairs of legs. A comparison of the relative sizes of these legs amongst the three Notonectid species in this study may give further evidence for morphological adaptations to reduce competition, in the actual size of prey each species can handle, (as suggested by Streams (1974)).

In a classic study, Holling (1964) considered the grasping foreleg of the mantid Hierodula crassa. It is a simple grasping mechanism, a fundamental feature of which is the locking device formed by the femur, the tibia and the tibial hook. Holling predicted the optimum size of prey from the geometry of this locking device, compared this to actual prey sizes selected, and showed an extremely close fit between predicted and observed size selection. In Notonecta, the grasping mechanism is more complex. The prey is locked between the ventral side of the body, the femur, the tibia, the tarsus and the tarsal claw (Fig. 75A). The two pairs of legs also act together to form a four cornered grasping mechanism.

Gittleman (1977) considered the raptorial legs of Notonectids and Pleids as simple levers, where the main force will be applied from the femur to the tibia and tarsus, and acts at the tarsal claw. He suggests that long

raptoral appendages (R_2 large - see Section VI.2.), lacking a proportionate increase in the lever arm (R_1) length, have lower mechanical advantages and so, are capable of weaker, but faster movements than appendages with higher mechanical advantages. It is suggested this is an adaptation to the capture of small, mobile prey as in the Bueno genus. Conversely, it is suggested that short raptoral appendages with a large mechanical advantage are more suited to handling relatively large prey, capable of some defensive struggle, as in the genus Martarega, feeding on terrestrial insects falling on the water surface. In the former case, the femur length is less than half the length of tibia and tarsus combined, each of these two segments as long or longer than the femur. With high mechanical advantages, the femur tends to be larger than each of the tibia and tarsus, as in Pleids which can handle larger prey than similar sized Bueno individuals. In both cases, the femur of the second pair of legs is proportionally longer than that of the first, indicating a larger mechanical advantage, but slower speed of movement. However, given equal mechanical advantages, the longer the raptural limbs, the larger the prey item that can be handled.

VI. 3.2. Results

Table 6.2 shows the measurements of the first two pairs of legs for all three species of Notonecta used in this study.

The values of the ratio of femur length/total leg length indicate for all three species a relatively large mechanical advantage, as the femur clearly contributes the largest proportion to the total leg length and is longer than either tibia or tarsus (c.f. Pleids). This seems to indicate that all three species in the adult stage are adapted to handling relatively large prey which are perhaps capable of some defensive struggle.

There is no significant difference in the ratio of femur length/total length between the three species, indicating the likelihood of

Table 6.2 Table showing relative lengths of prey catching appendages. (Significance of differences tested by T test, *** = 0.001, ** = 0.01, * = 0.05, species underlined are not significantly different)

SPECIES	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. maculata</u>	Significance
TOTAL LENGTH OF LEGS	n-27 0.8822+0.0132 cms.	n-28 1.0143+0.0114 cms.	n-19 0.8336+0.0118 cms.	*** *** ob - gl - mac
2nd pair	n-26 1.0646+0.0149 cms.	n-28 1.2096+0.018 cms.	n-20 1.014 +0.0086 cms.	*** *** ob - gl - mac
LENGTH OF FEMUR	n-30 0.3566+0.0054 cms.	n-27 0.4053+0.0042 cms.	n-19 0.3347+0.0047 cms.	*** *** ob - gl - mac
2nd pair	n-30 0.449 +0.0071 cms.	n-27 0.5114+0.0073 cms.	n-21 0.429 +0.0069 cms.	*** *** ob - gl - mac
LENGTH OF TARSAL CLAW	n-30 0.0533+0.0023 cms.	n-29 0.0541+0.00179 cms.	n-19 0.0428+0.0023 cms.	*** ob - gl - mac
2nd pair	n-29 0.055 +0.0028 cms.	n-29 0.0525+0.00276 cms.	n-21 0.0455+0.00258 cms.	*** gl - ob - mac
RATIO FEMUR TOTAL LENGTH	1st pair 0.404	0.3996	0.4015	n.sig.
2nd pair	0.4217	0.4228	0.423	n.sig.
ROSTRUM LENGTH	0.3004 +0.008	0.3122 +0.008	0.2422 +0.0054	* *** ob - gl - mac

similar mechanical advantages. Also the ratio is larger for the second pair of legs than the first, indicating as suggested by Gittleman (1977), a stronger, but slower grasping movement in the second pair. This fits with observations on the actual capture of a prey item, where an initial rapid grasp is made with the fore limbs, and the prey item is then held secure with the aid of the second pair of legs (strength rather than speed of movement being more important).

As the mechanical advantages of the three species appear to be similar, it can be assumed the longer raptural limbs can optimally handle larger prey items. On this premise, further reduction in competition may occur in choice of prey size, as N. obliqua has significantly the largest legs and would be expected to capture larger prey than both the other two species, and N. maculata has the shortest legs and would be expected to capture relatively smaller prey. N. glauca again falls between these two. The length of the rostrum also supports this idea, with N. obliqua having the longest, N. maculata the shortest and N. glauca falling between the two again (Fig. 75C).

Gittleman (1978) also found, as expected, that an increase in prey size decreased success of capture by Neoplea and Notonecta. One would expect, on this basis, that the larger the prey catching appendages, the greater the success of capture would be on a certain sized prey. This prediction is verified to some extent by the results of Section IV. 3.1.4, where N. obliqua, with the largest prey catching appendages, generally shows the greatest capture success of the three predators. On this basis, one would expect N. glauca to have a greater success than N. maculata but this is not generally so. The difference in size of the prey catching appendages of these two predators may not be large enough to affect capture success, or other factors may operate.

The relative size of these appendages, and the physiological differences, may well explain the differences in proportion of time spent at depth

during handling in the complex environment by the three predators (Section IV. 4.2.2.). N. maculata shows the smallest proportion of time at depth during handling, which could be due to the small raptorial appendages not allowing grasping of perch sites as easily as in the other predators during feeding. Although N. obliqua has larger appendages than N. glauca, it also has a high active metabolic rate, which may handicap it in carrying large prey down to perch sites. This may explain why the proportion of handling time at depth in the complex environment is generally shorter than that for N. glauca, and why this species shows such a low proportion of time at depth during rest in the simple environment.

Gittleman (1974) points out that smaller fore and mid legs probably present less resistance to water, as they can be tucked more easily out of the way, thus streamlining the body to a greater degree, which increases the efficiency of swimming. This adaptation was found in Martarega, which also had the lowest mechanical advantage. A similar finding is apparent in this study, where N. maculata, apparently the more active and efficient swimmer, also possesses the smallest fore and mid legs.

VI. 4. Prey Recognition

In Chapter I, two types of organs involved in prey detection were described, namely tactile organs for detection of water disturbances, and eyes for visual recognition of prey. No differences in the external morphology of the tactile organs were found, and one can only assume that if differences do exist between species, they will be found in the sensitivity of these organs. The size of the eye, however, is often a good indicator of the visual ability of the animal and its importance. Large eyes are usually attributed to better visual powers, and indicate that these organs are likely to be the main sense organs (Chapman (1969)).

The size of the eyes of the three species of Notonecta studied, in terms of surface area (length x height, Fig. 75C) were examined, and the results shown in Table 6.3.

SPECIES	<u>N. glauca</u>	<u>N. obliqua</u>	<u>N. maculata</u>	Significance (T-test)
AREA OF EYES	n-27 0.0355cm ² +0.002	n-27 0.0423cm ² +0.0011	n-18 0.0385cm ² +0.0011	ob.*** mac.** gl.
Ratio of AREA OF EYES FRONTAL AREA	0.175	0.16	0.187	

TABLE 6.3 Table comparing the relative sizes of eyes amongst the three Notonectid species (Significance *** 0.001, ** 0.01)

N. obliqua has significantly the largest eyes, and N. glauca the smallest. However, when size of the eyes is taken in relation to the frontal area of the body, the order of size changes, with N. maculata having the largest value, and N. obliqua the smallest. This relative value is likely to be more pertinent to the problem than simply the size of the eyes. This ^{is} supported to some extent by the results of light and dark experiments in Chapter IV, where N. maculata feed more efficiently in the light than in the dark, whereas the other two species showed the reverse.

It thus appears possible that a certain amount of reduction in competition can occur on the basis of morphological differences, which when added to other differences in the predation strategies, can help explain habitat selection and coexistence in this genus.

CHAPTER VII

THE CONTROL OF HANDLING TIME AND ITS EFFECT ON THE FORAGING STRATEGYOF NOTONECTA

VII. 1.

Introduction

There has been much recent discussion of the factors controlling how long a foraging predator should spend in a patch of a certain profitability. Two types of model have received a lot of attention. One type suggests that the predator can monitor the relative resource qualities of patches in the environment : the selection of and time spent on patches is based on this knowledge (e.g. Charnov (1976(a)) Krebs et al (1974), Krebs (1978)). Other models predict that the time spent in patches is dependent on some innate responses the predator makes to each patch on its own, and do not require the predator to have a knowledge of the overall environmental profitability (e.g. Hassell and May (1974), Waage (1978)).

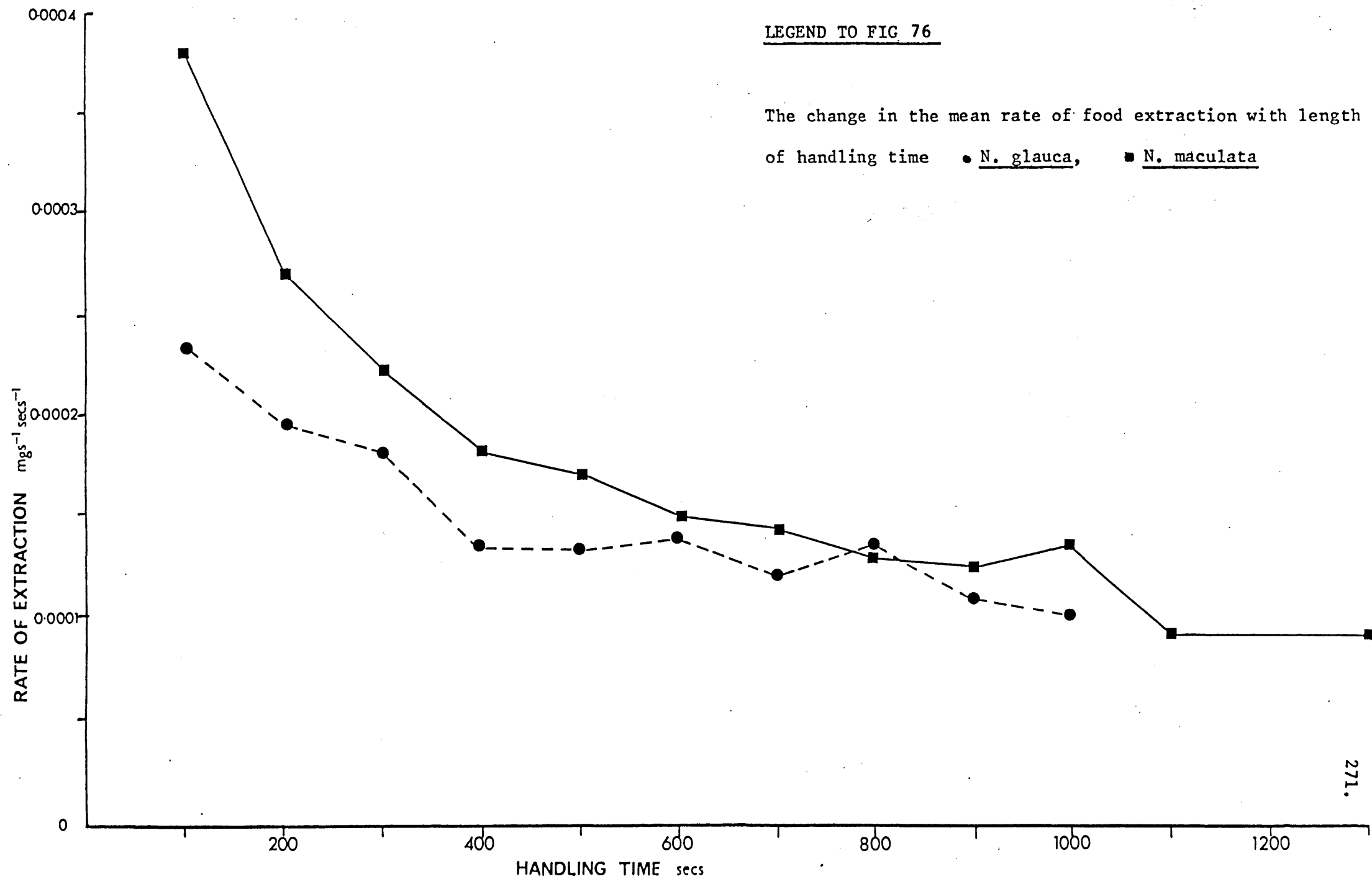
The construction of these models and description of the controlling mechanisms have generally been based on predators or parasitoids utilising patches of resource consisting of different densities of prey in discrete units. However, the way in which predators such as heteropterans utilise single prey items can be considered in a similar way. Each prey item can be thought of as a patch in its own right, from which the insect removes food over fairly long periods of time. As food is removed, so the quality of the patch of resource being utilised decreases, because the amount of food left in the prey carcass, and its ease of extraction, decreases. After some period of time, the predator will leave the patch (by dropping the carcass) and go in search of another prey item.

One of the models in the literature which attempts to describe how

the handling time (time spent feeding on an item) of Notonecta is controlled, does so on the basis of optimal feeding ideas (Cook and Cockrell (1978)). One way in which a predator can be said to feed optimally, is by the maximisation of its rate of food intake (Krebs (1978), Pyke et al (1977), Schoener (1971)). In the case of a predator which engulfs the whole prey, this strategy would imply maximising the number of prey eaten per unit ^{feeding} time, given prey of equal size. In the case of a predator which removes only part of each prey item caught (such as the sucking predators), optimal feeding behaviour would maximise the rate of food extraction from each prey item and so maximise the total food extracted per feeding time.

The total amount of food extracted from a single prey item can be shown to increase in a decelerating manner with time for Notonecta (see Chapter III Fig. 20 and Cook and Cockrell (1978)). This form of patch depletion is similar to the generalised curve of diminishing returns reported by Charnov (1976(b)), Krebs (1978), Parker and Stuart (1976) and Schoener (1971). In other words, the rate of food extraction from an individual prey item gradually decreases as the resources are consumed (Fig. 76).

After some time, the rate of food extraction from the prey falls to near zero, and so the prey item should be discarded. In this situation, it is a sensible and an optimal strategy to release the prey item before complete utilisation, and capture another. As the probability of finding the next prey increases, so the feeding time on each item should become shorter, resulting in an increase in the overall rate of food intake, i.e. a larger total weight of food is extracted in a given time period than if each item was fully exploited. However, the same effect might be noted at high prey density simply through the disturbance of the feeding predator by active prey in-



dividuals. Thus, decreased handling time per. se might not be conclusive proof of optimisation.

The mechanism suggested by Cook and Cockrell (1978) which would allow optimisation through the assessment^{of} this probability involves the measurement of the mean intercatch interval (mean time from dropping a prey item to catching the next), the handling time for each prey item being determined by this value, such that each prey item should be abandoned when the ingestion rate reaches that of the average rate of energy harvest (i.e. similar to the marginal value theory (Charnov 1976(a))). The longer this interval, the lower the probability of prey capture and the lower the average rate of energy harvest, so the predator should use a relatively long handling time. Overall, the weight of food extracted per unit time should be at, or near, a maximum possible value, given the prey density and the time available for feeding.

The other model, also proposed by Cook and Cockrell, involves a process of gut-filling. Such a system would necessitate at least a two compartment gut, where the first compartment fills at a faster rate than it empties into the second compartment. (Similar models have been proposed by Johnson et al (1975) Fig. 1(d) Chapter I, and Gelperin (1971) for damselfly larvae and horse flies respectively). It is assumed that each meal from each prey item fills the first compartment of the gut, and the prey item is discarded when this compartment is filled. During the intercatch interval, food leaves the first compartment and enters the second. The length of the intercatch interval determines how empty the first compartment will be at the start of the next feed. This will control how much food can be taken in and hence the handling time.

It is expected that mean intercatch interval should fall as prey

density increases. It is therefore predicted from both models, that mean handling time should decrease with increased prey density. The two models, however, will predict different relationships between individual intercatch intervals and the ensuing individual handling time. No correlation between these two parameters is expected in the optimal feeding model, as the handling time for all prey items caught at each density is set at a value determined by the average intercatch interval. The gut-filling model, however, predicts a positive correlation, as handling time on each item is related to the time since the last meal.

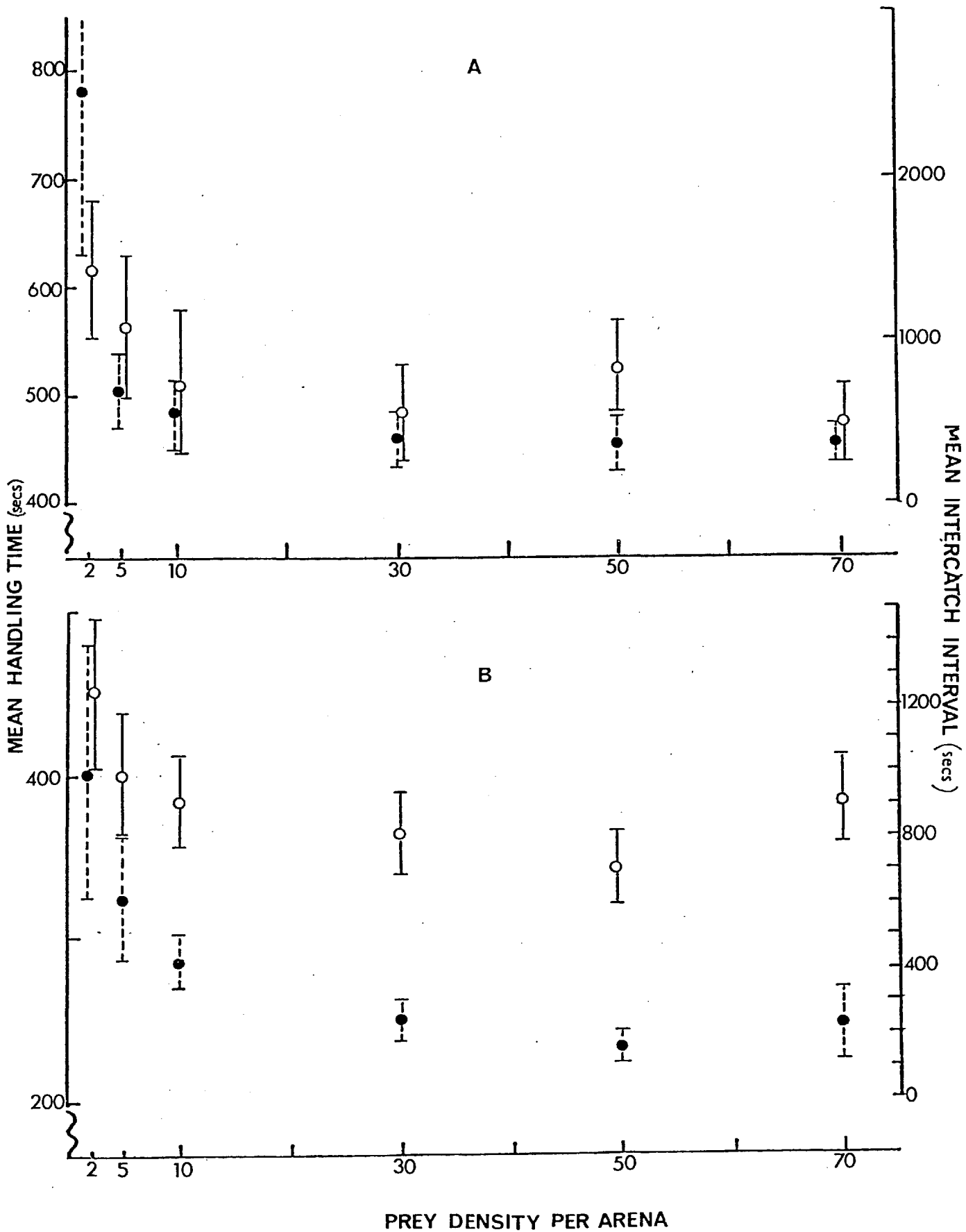
This chapter examines the predictions of these two models in the light of data from the present study, and introduces evidence for additional mechanisms operating in the control of handling time in Notonecta.

VII. 2.

Methods

For the consideration of the controlling factors of handling time in Notonectids, the single prey experiments on mosquito larvae in the complex environment offered the most suitable data, as sufficient numbers of prey were captured (which was not true of experiments with the larger prey). The experimental details have been discussed in Chapter II. The parameters of interest here were; the handling time on each item (time from capture to release of prey item); weight of food extracted from each item (described in Chapter III); and the time between release of one item after feeding and capture of the next, measured during the continuous observation experiments. Data from all six prey density tests were used, with nine replicates at each density.

Only the results from experiments with N. glauca (with the lowest attack rate) and N. maculata (with the highest attack rate) have been



LEGEND TO FIG 77

The effect of prey density on mean handling time per prey item (O) and mean intercatch interval (●) A) *N. glauca*, B) *N. maculata*.

95% confidence limits shown.

considered in the main, but data showing several aspects of the feeding behaviour of N. obliqua has been cited to show that conclusions reached with the other two predators can also be applied to N. obliqua.

VII. 3.

Results and Discussion

Fig. 77 shows the predicted relationships between mean handling time, mean intercatch interval and prey density, for both species of Notonecta, where mean intercatch interval and mean handling time increase as prey density decreases, which supports the similar findings of Cook and Cockrell (1978). Their data, however, showed no relationship between individual intercatch interval and individual handling time (using Kendal rank correlation coefficient), which supported the prediction of their optimal feeding model, but the data presented here show a positive correlation, which supports the gut-filling model (Table 71.)

Table 7.1

CORRELATION BETWEEN INDIVIDUAL INTERCATCH INTERVAL
AND INDIVIDUAL HANDLING TIME.

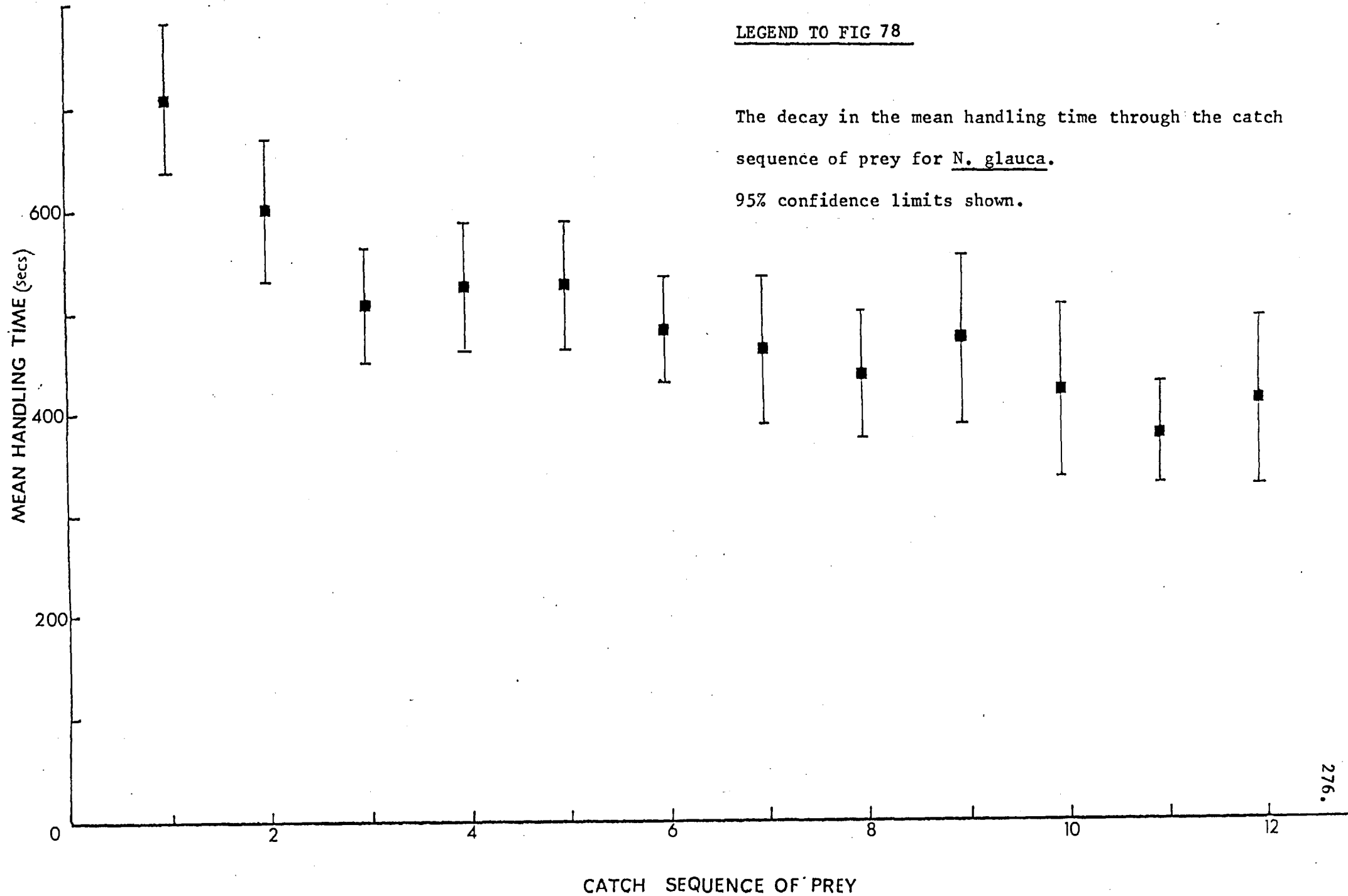
Prey Density	N. glauca	N. maculata
70	0.0013	0.00003
50	0.003	
30	0.00003	
10	0.0007	
5	0.0071	
2	0.2	

Kendal rank correlation analysis between individual intercatch interval and individual handling time. The table shows the significance of positive correlation.

LEGEND TO FIG 78

The decay in the mean handling time through the catch sequence of prey for N. glauca.

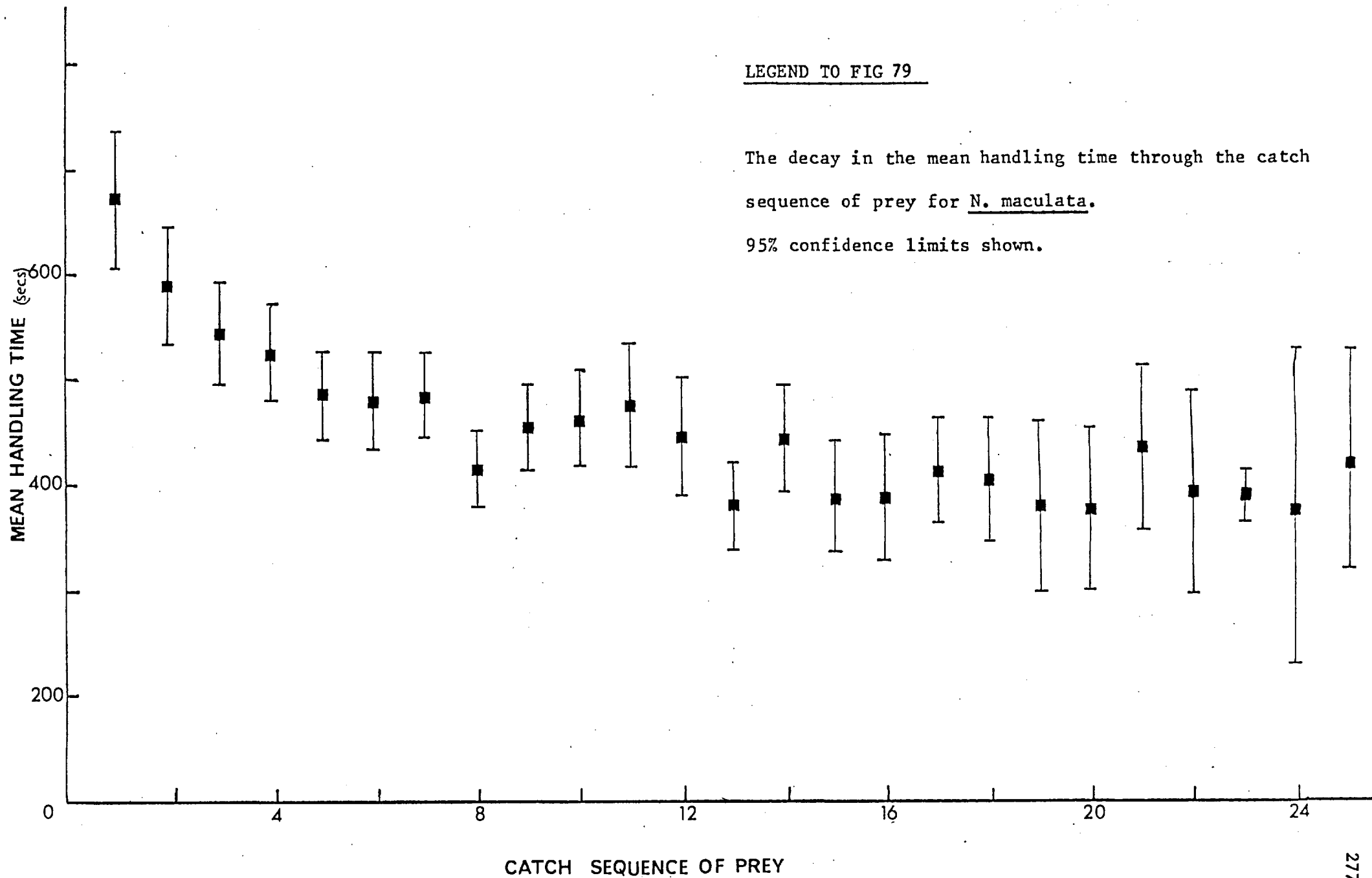
95% confidence limits shown.

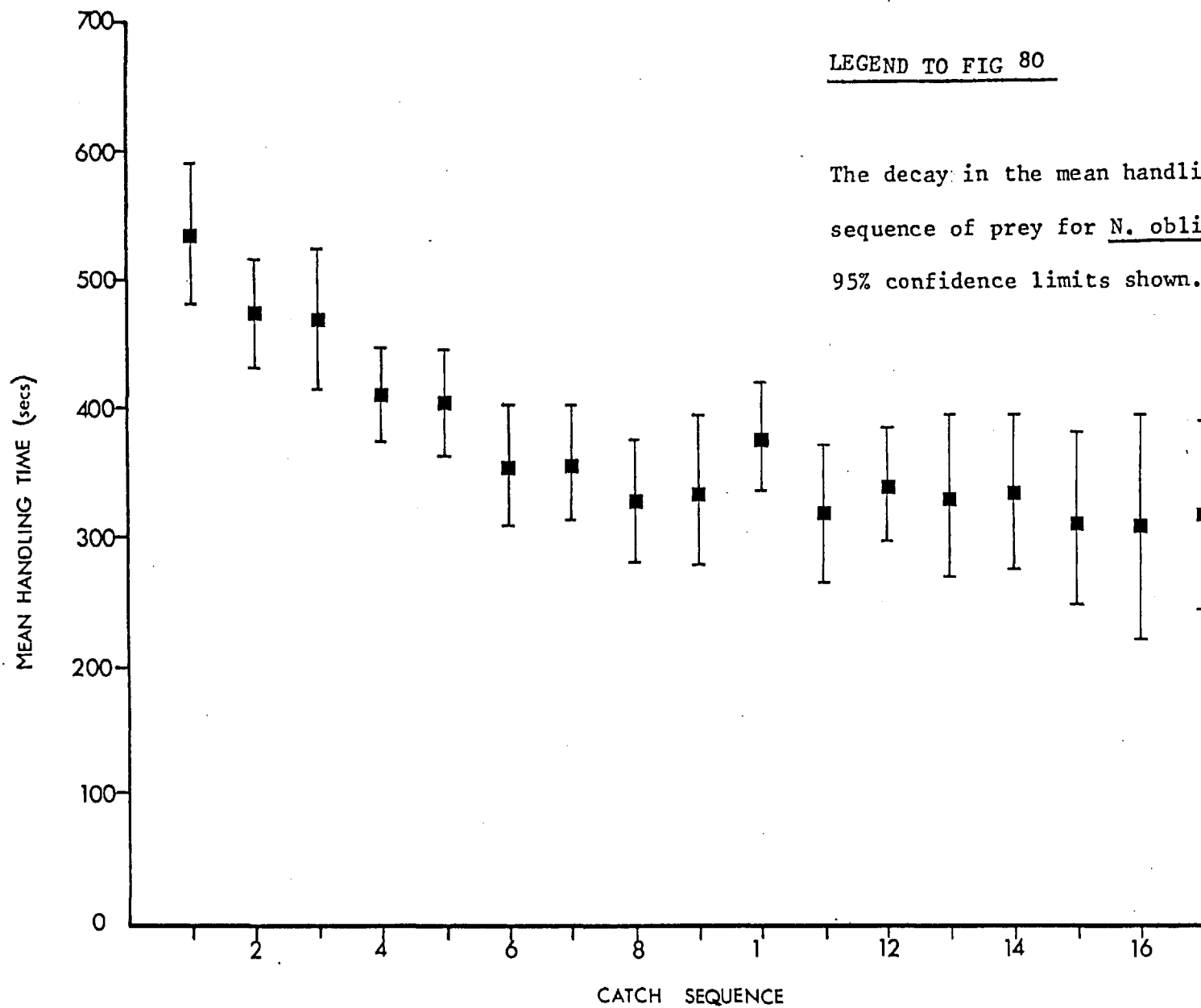


LEGEND TO FIG 79

The decay in the mean handling time through the catch sequence of prey for N. maculata.

95% confidence limits shown.





By examining the mean handling times of each capture in the catch sequence for each density (i.e. mean handling time of the first captures, second captures, etc.), a positive decay in the handling time through the catch sequence is apparent for all three predator species. This decay is not constant but appears gradually to level off. Furthermore, analysis of variance indicated that the values of mean handling times for each catch in the sequence do not differ significantly between prey densities. (This was spot checked by T test comparisons between density pairs, and only a very few comparisons, showing no trends, were found significant.) The handling times for each catch in sequence were therefore pooled to produce a single decay curve for each predator. (Figs. 78- 80).

The relationship between mean handling time and prey density (Fig. 77), can be adequately predicted by a combination of the declining handling time for each sequential capture (Fig. 78- 80) and the number of prey killed at each density (functional response data from Chapter IV, Figs 51-53). At low densities, only the first few prey in sequence are captured, resulting in a high mean handling time for that density. At higher densities, where larger numbers of prey are caught, correspondingly lower mean handling times result. Similar declines in handling time through a sequence of captures have been found by Ellis and Borden (1970) and Fox and Murdoch (1978) for Notonectids.

If it is assumed that the handling time will be gradually changed in accordance with new and revised values of the mean intercatch interval, then a handling time decay (and some level of correlation between individual intercatch interval and ensuing handling time) may occur if there is a corresponding decline in the intercatch interval through the catch sequence. The handling time decay could also be predicted by the gut filling model if there is a similar decline in the intercatch interval.

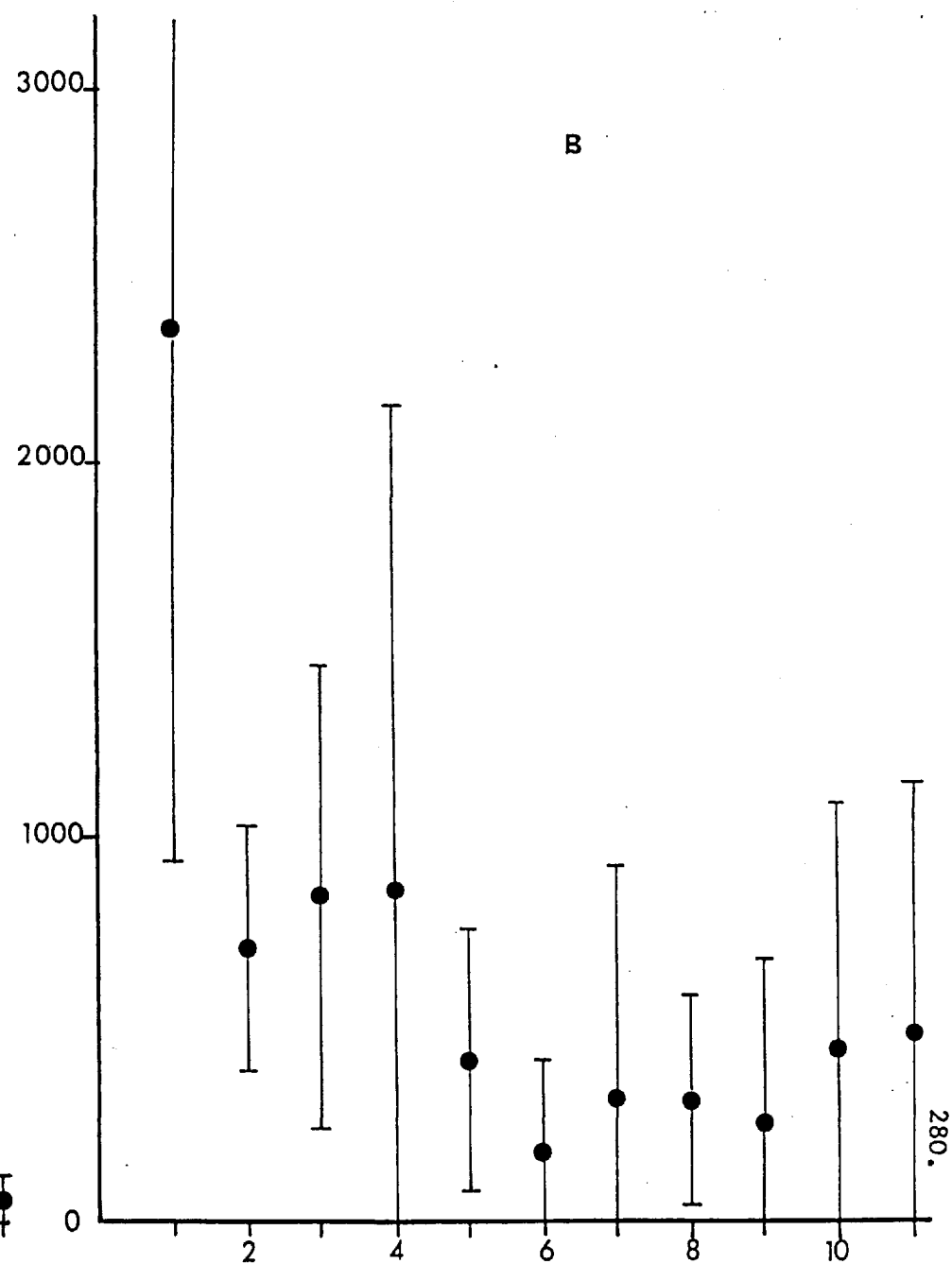
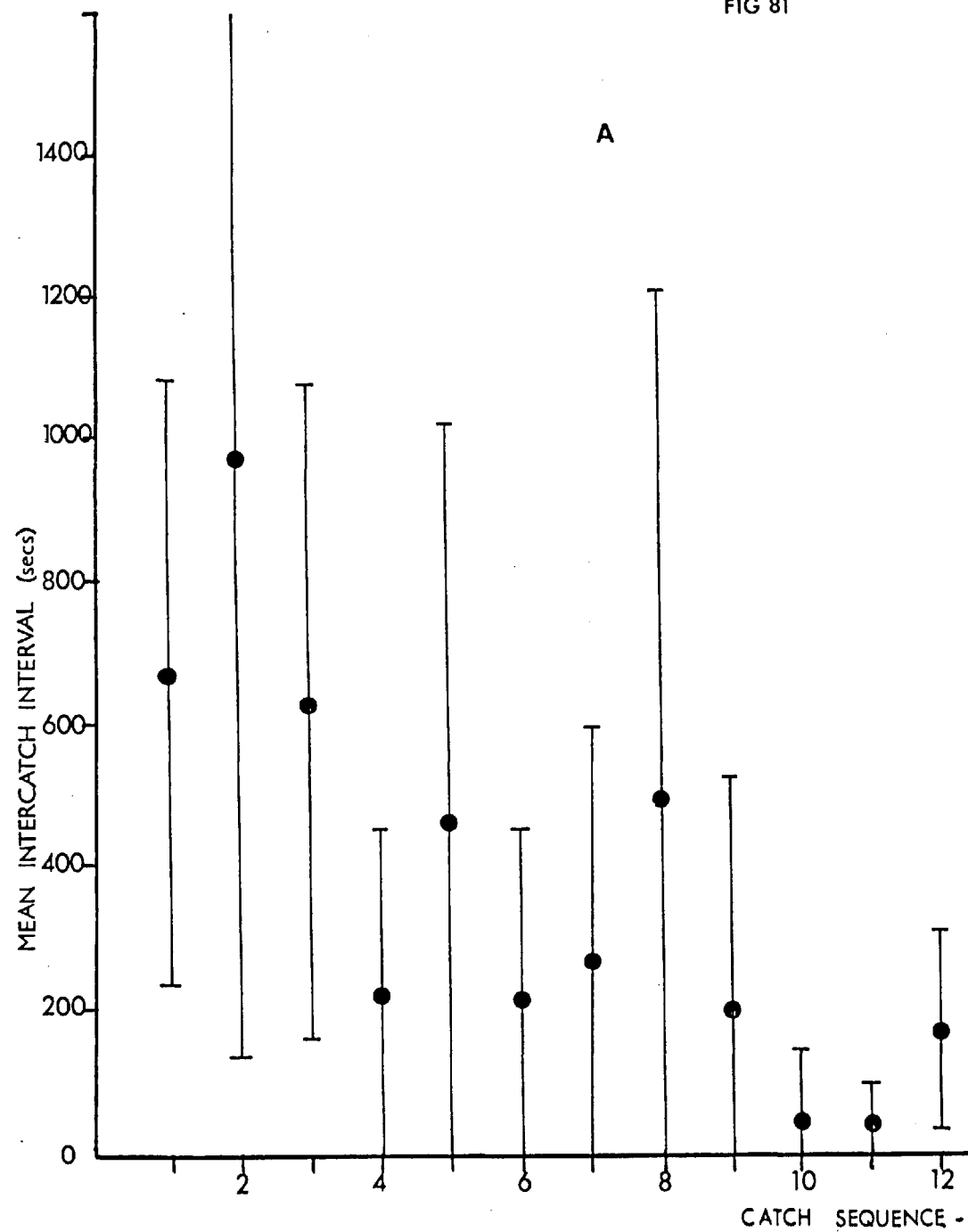
LEGEND TO FIG. 81

The change in mean intercatch interval through
the catch sequence for

- A) N.glauca at prey density 30
- B) N. maculata at prey density 5.

95% confidence limits shown.

FIG 81

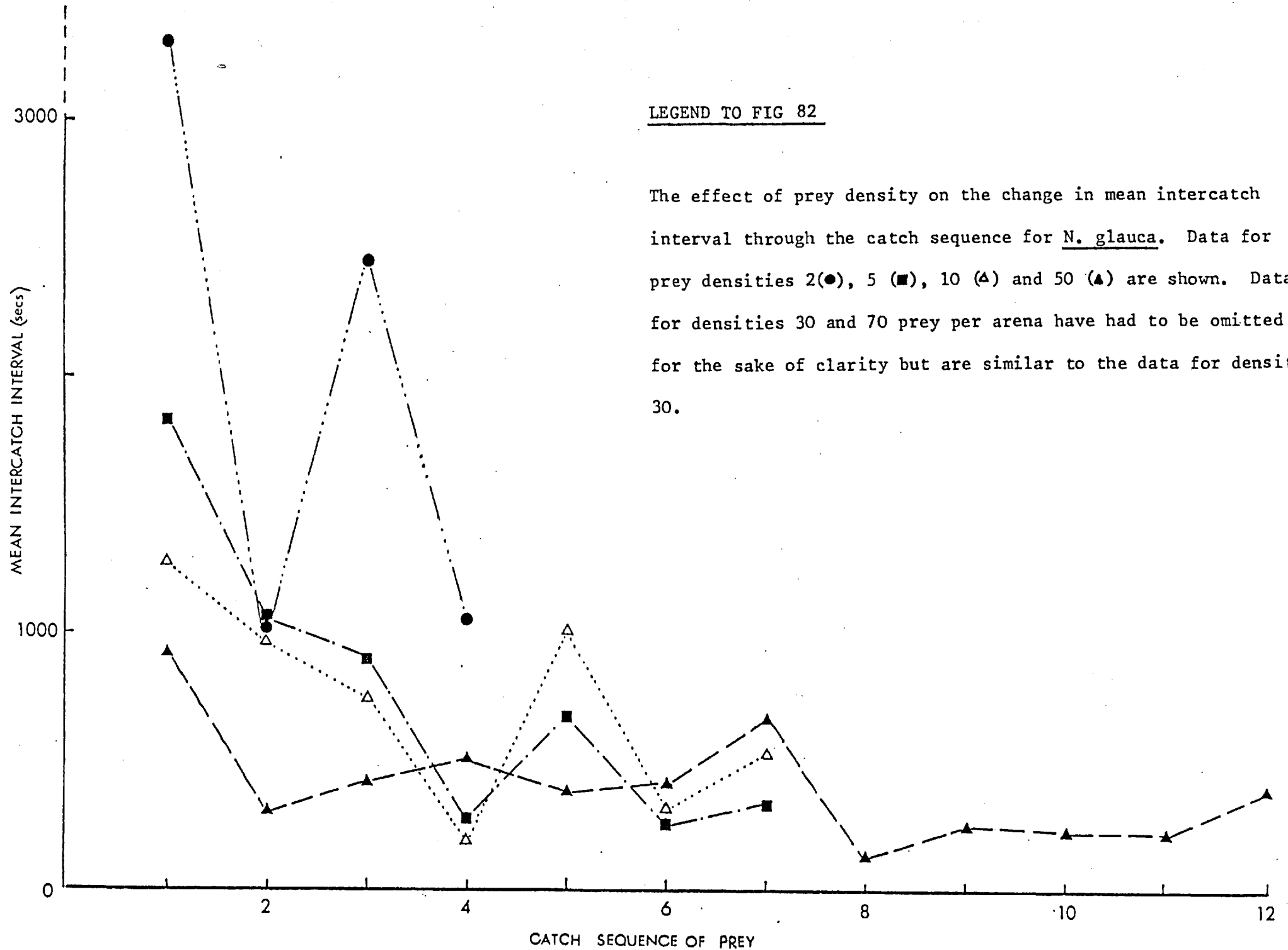


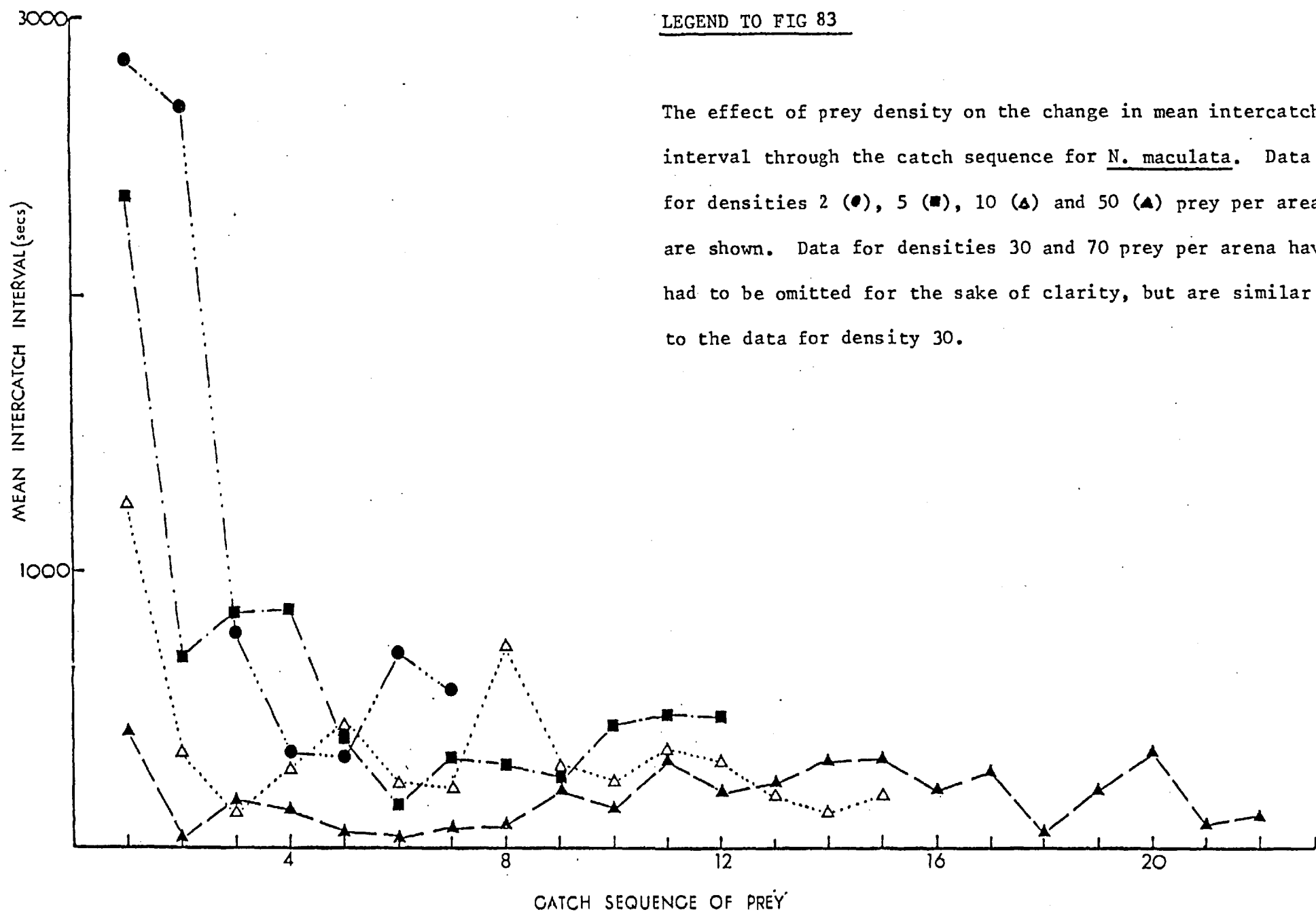
The evidence from Fig. 81 does suggest a certain amount of decay of the mean intercatch interval through the catch sequence, which then appears to level off. Such decay in the intercatch interval indicates an increase in searching efficiency, and can possibly be explained on the basis of the formation of a search image, which becomes progressively more marked with experience gained from successive captures. One would expect a full search image to be formed, and thus a stable level of intercatch interval to be reached, sooner and at a faster rate at high prey densities than at low, simply on the basis of random encounters (as suggested by Gibb (1961)). As Fig. 82-84 show, this appears to be the case. It is interesting to note that the formation of the search image seems to be most rapid in N. maculata and generally slowest in N. obliqua.

It is rather difficult in the present circumstances to ascertain which of the two models gives the best explanation of the decline in handling time. Current optimal foraging theory suggests a principle of moving averages (e.g. Krebs (1974)) i.e. predators assess their performance over the last few minutes or hours, and so it becomes rather important to know the size of this memory window (if it exists). The present experimental design is such that the predator has been kept for 24h. without prey, and depending on the size of the memory window, so all, part, or none of this period may affect the predators assessment of the environmental profitability during the experiment. If the memory window is long, differences would not be expected between mean handling times at different densities or at different captures. If it is short, one would expect such differences, as there will be large differences in the average intercatch interval between densities, and between successive captures in the sequence. The fact that there is both a decline in mean handling time through the catch sequence, and no differences in

LEGEND TO FIG 82

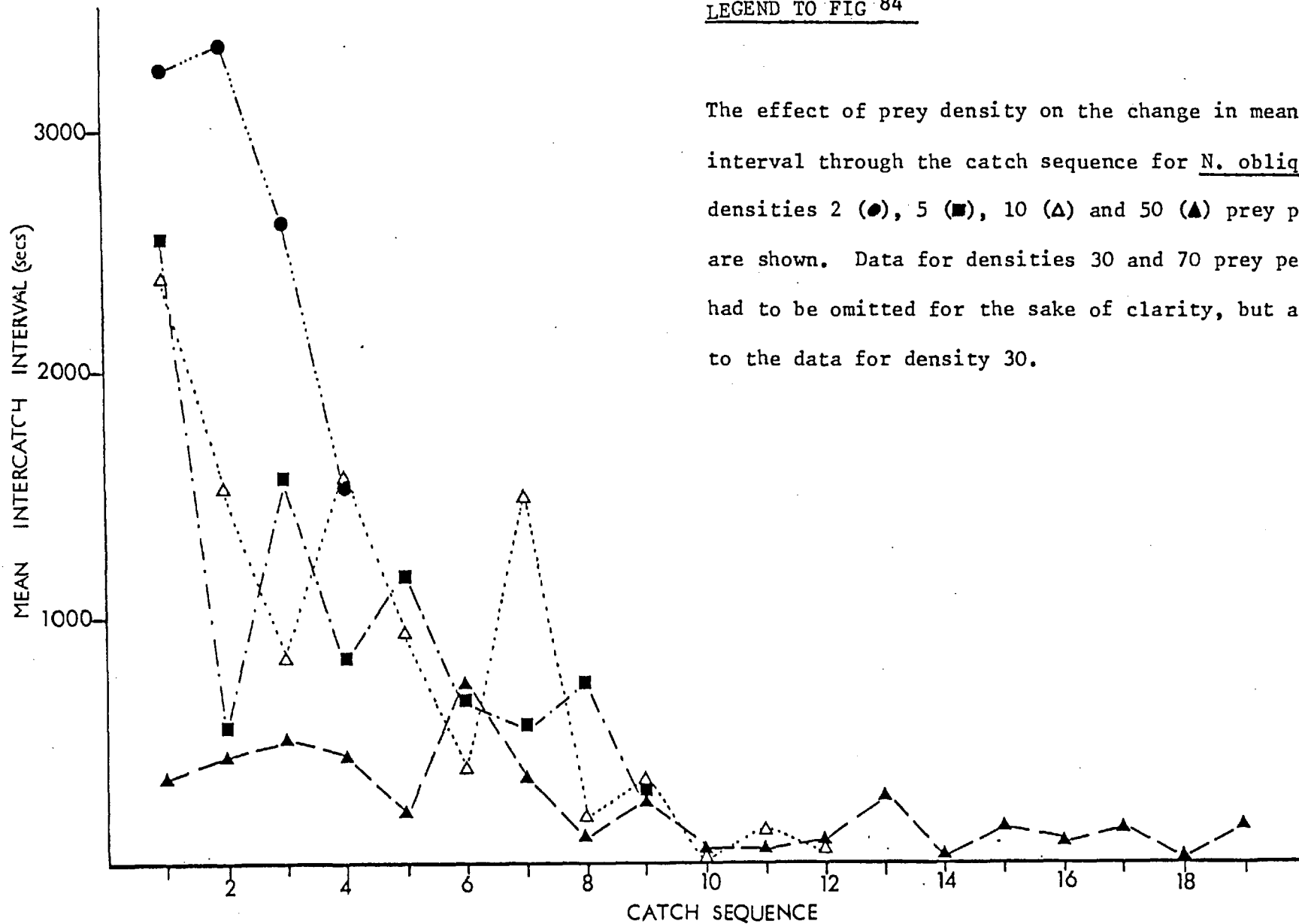
The effect of prey density on the change in mean intercatch interval through the catch sequence for N. glauca. Data for prey densities 2 (●), 5 (■), 10 (△) and 50 (▲) are shown. Data for densities 30 and 70 prey per arena have had to be omitted for the sake of clarity but are similar to the data for density 30.



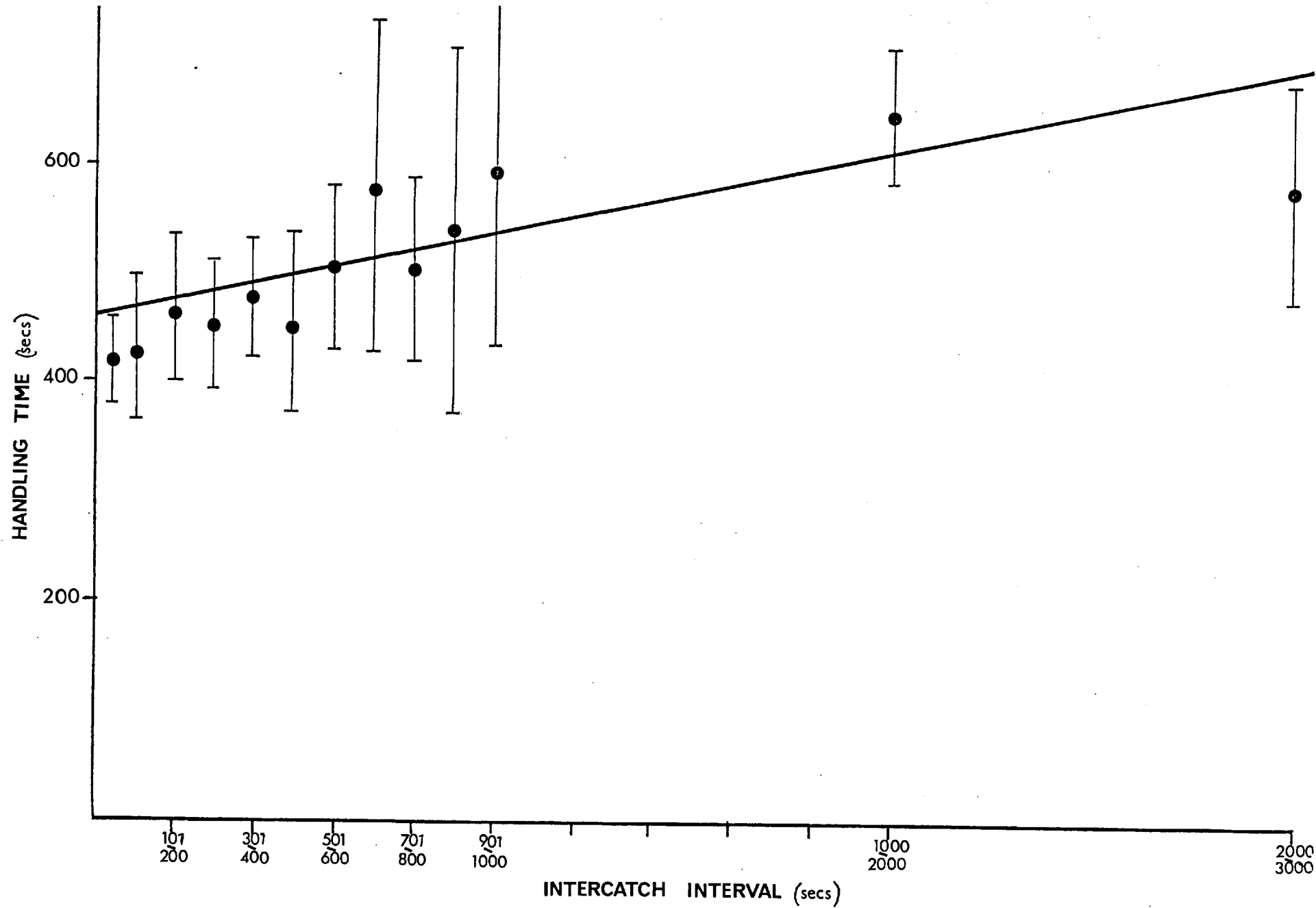


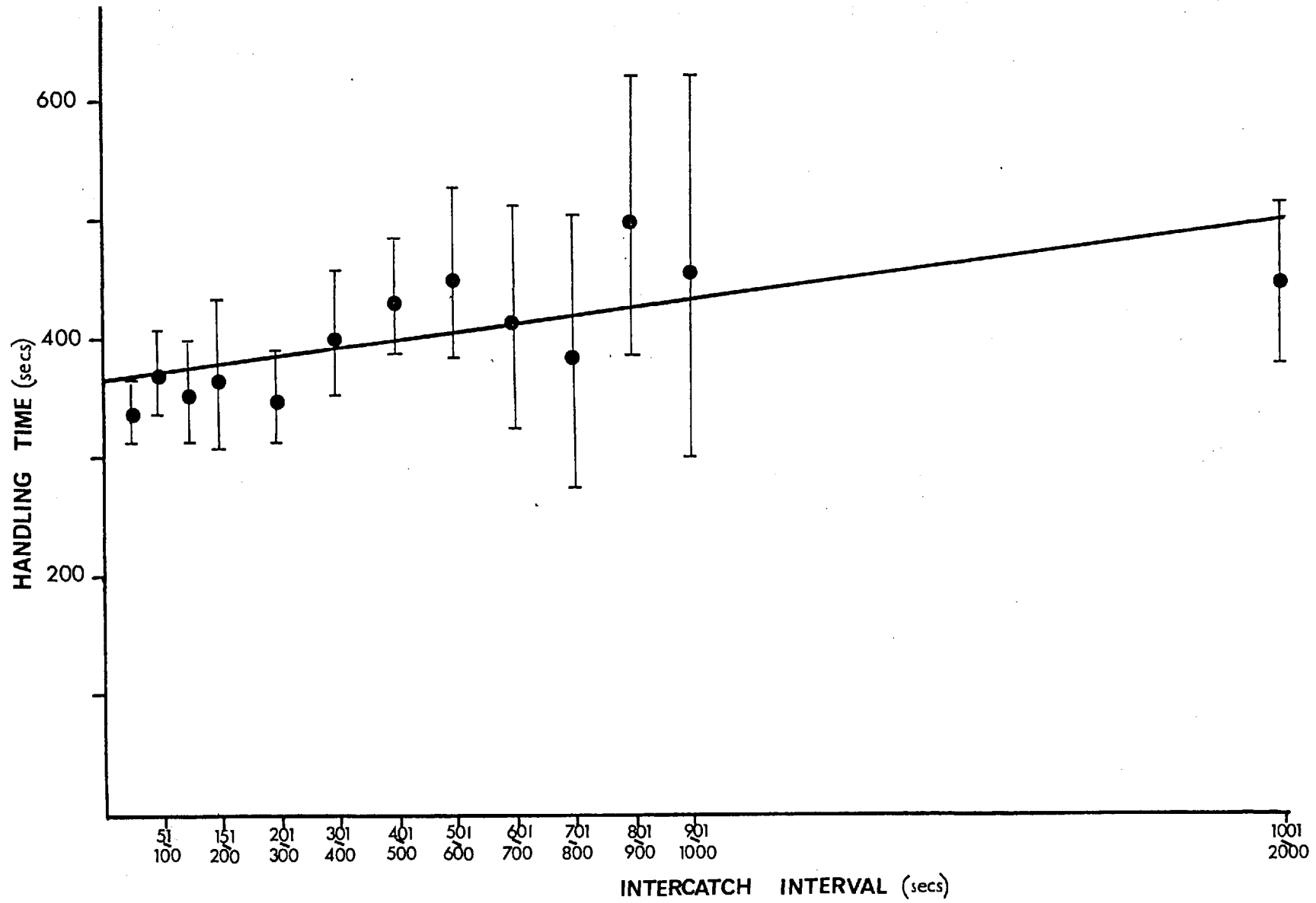
LEGEND TO FIG 84

The effect of prey density on the change in mean intercatch interval through the catch sequence for N. obliqua. Data for densities 2 (●), 5 (■), 10 (△) and 50 (▲) prey per arena are shown. Data for densities 30 and 70 prey per arena have had to be omitted for the sake of clarity, but are similar to the data for density 30.



LEGEND TO FIGS. 85 and 86





these values between prey densities suggests that neither of the above two cases can adequately describe the present data. A memory window of some intermediate length might however.

The gut filling model does gain some support. Assuming no satiation over the catch sequence, all individual correlations (over all densities and captures) between intercatch interval and handling time, can be pooled, and give a general positive relationship (Figs 85,86). This creates an apparent contradiction in the data, where there is a positive correlation between individual intercatch interval and handling time (Fig 87 and Table 7.1), differences in intercatch intervals through the catch sequence between prey densities (Fig. 82- 84) but no such differences in handling times between densities. This can be explained by the shallow slope of the intercatch interval/handling time relationship, and the quite large variation in data of handling times between individual predators, so that the differences in intercatch interval between densities at each capture are not sufficient to significantly affect the handling time values. This does indicate that there is some gut-filling effect, but it is obviously not large enough to adequately explain the handling time decline by itself.

An examination of the rate of intake for each capture in the sequence for N. glauca appears to show that there is a gradual increase (Fig 88). This suggests that this predator is gradually approaching a maximum feeding rate as it captures more prey. This could come about passively, where an increase in searching efficiency during feeding (through the production of a search image) could act on handling time through some gut-filling mechanism, and due to the shape of the extraction curve, could thus affect extraction rate. Alternatively, if the predator assesses profitability through a memory window, then increase in searching efficiency through the catch sequence would effectively increase profitability

LEGEND TO FIGS. 88 and 89

The rate of food intake for each sequential capture
by N. glauca and N. maculata with prey densities

2 (●)

5 (■)

10 (Δ)

30 (O)

50 (▲)

and 70 (□)

per arena.

Trend lines fitted by linear regression.

Fig. 88 N. glauca $Y = 0.0000479 - 0.0000049 X$
 $r = 0.56$ sig 0.001

Fig. 89 N. maculata Y = 0.0000216 + 0.0000068 X
r = 0.56 sig 0.01

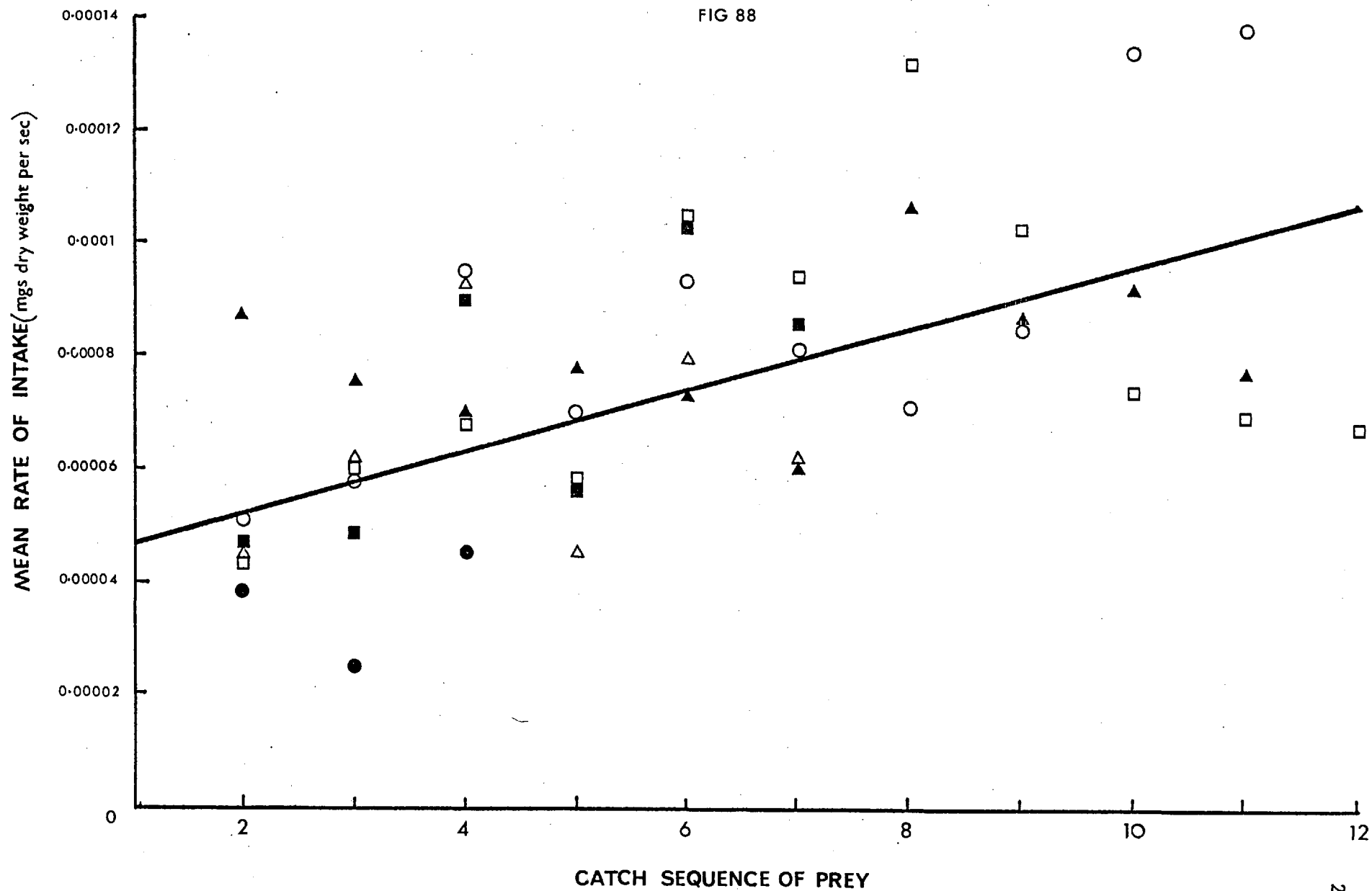
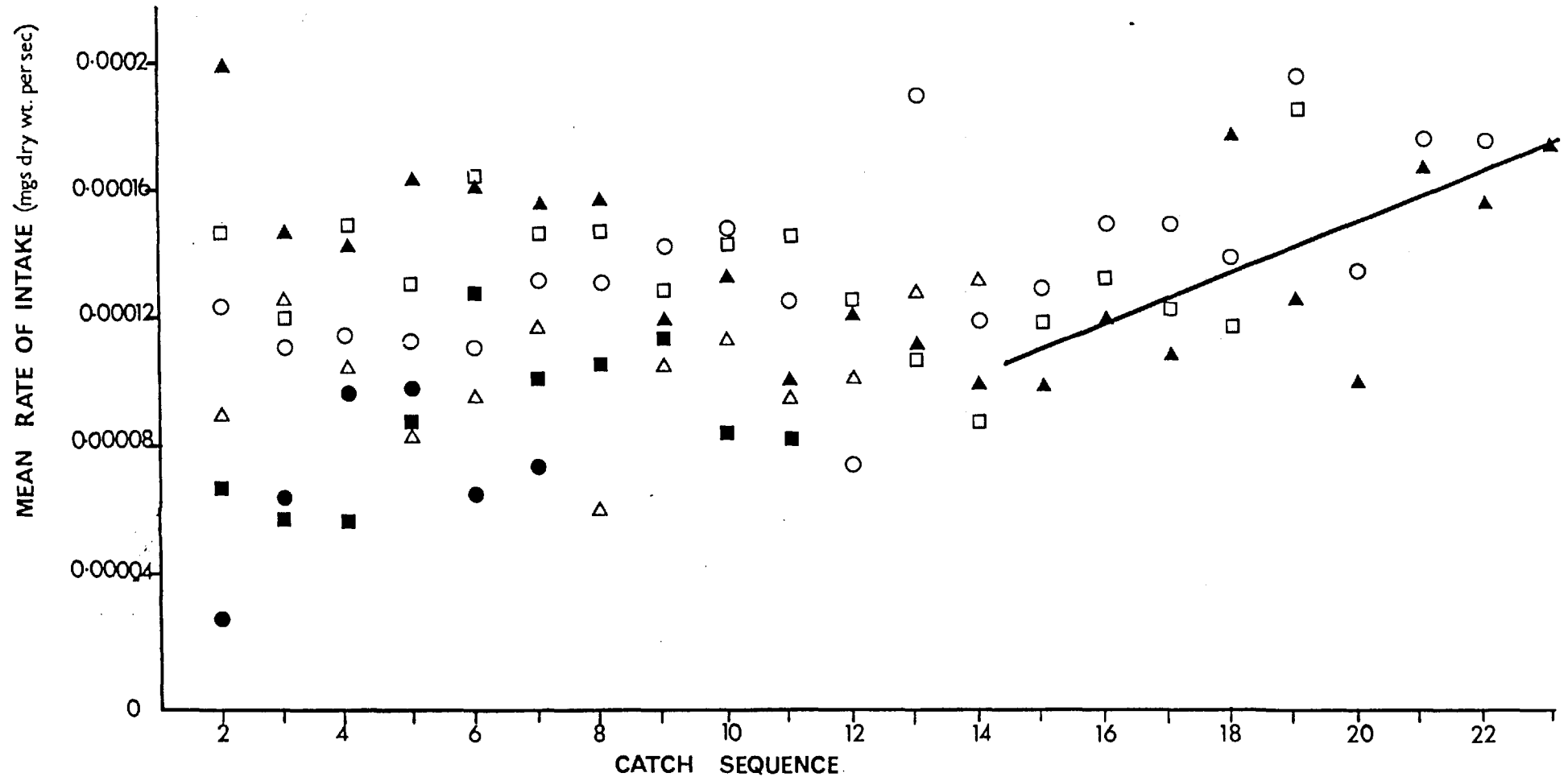


FIG 89



and so handling time is decreased to allow maximisation of the rate of intake under current circumstances.

The widely fluctuating rates of intake for N. maculata over the catch sequence (Fig. 89) show regions of stable rate, declining rate, then increasing rate. These changes would not be indicative of the present optimal feeding model, which would require the maintenance of a near maximum rate of intake, or a gradually increasing one.

VII. 4.

Conclusion

The process of feeding in this insect is not as simple as described by the optimal feeding hypothesis as it stands. Such models generally are much too simple minded to apply to such a variable predator as Notonecta (showing changing searching efficiency and extraction efficiency with position of the prey in the catch sequence), and would need to incorporate such variability before they could adequately describe the behaviour of such predators. Processes such as increasing searching efficiency through search image formation and gut-filling, though also not completely explaining the results, may play a more important part than the measurement of environmental parameters.

The present experimental design does not readily allow discrimination between the two models. A much more critical test would be to establish a 'steady state' predation over a long period of time at various constant densities of prey, and then the true nature of the intercatch interval/handling time correlation could be ascertained. Then, by transferring the predator from one density treatment to another, the presence of a memory window could be tested, and if verified, it's size measured.

That the predator is making better use of resources on the whole, by discarding prey items before their complete exploitation, cannot be disputed. In Table 72, the right hand column shows actual weight extracted, the left hand column shows predicted weight extracted with

Table 7.2.

		Net Intake Total Exploitation	Net Intake Observed Exploitation
<u>N. maculata</u>	Prey Density		
	70	1.08 mgs	1.291 mgs
	50	1.172 mgs	1.613 mgs
	30	1.055 mgs	1.354 mgs
	10	0.84 mgs	1.031 mgs
	5	0.67 mgs	0.828 mgs
	2	0.48 mgs	0.549 mgs
<u>N. glauca</u>	70	0.66 mgs	0.809 mgs
	50	0.66 mgs	0.896 mgs
	30	0.66 mgs	0.809 mgs
	10	0.55 mgs	0.511 mgs
	5	0.66 mgs	0.511 mgs
	2	0.266 mgs	0.17 mgs

Legend A comparison between the observed net intake of food and the net intake predicted on the basis of total exploitation of each item caught.

total exploitation of all items caught, on the basis of time for total exploitation, intercatch intervals through the sequence, total time available for feeding, and the amount of food extracted from a fully exploited prey item. Although neither the optimal foraging nor gut-filling models adequately describe the present results, it is possible that physiological processes, such as search image formation and gut-filling either on their own, or through some modified optimal feeding mechanism are providing the innate mechanisms which allow the predator to forage in what appears to be a near optimal fashion.

This type of study shows the importance, when assessing whether or not predators forage optimally, of examining in the first instance, the processes involved in foraging in detail (which includes an examination of the physiology associated with the feeding processes), and then determining how close this foraging is to optimal. Often, the reverse procedure is undertaken. A model is described where the only variable factor is the set of behavioural strategies, and such factors as the predator's structure, locomotary or perceptual skills are treated as constants (Maynard-Smith (1978)). The variability in these and other skills between individuals may play a fundamental role in predator/prey population processes (Chesson (1978)). Large variation, as found in all data with Notonecta, would not be predicted in most current optimal foraging models, due to the deterministic nature of the models and the implicit assumption that there should, by definition, be only one optimal solution under any given conditions. There has been a tendency indeed, to regard such variability as noise obscuring the deterministic strategy, as well as being a destabilising influence (Chesson (1978)). As Maynard-Smith (1978) points out, in testing a model we are not testing the 'general proposition that nature optimises', but testing whether we have 'correctly identified the selective forces responsible for the trait in question'

on the basis of the assumptions about constraints and optimisation criteria made in the formation of the model.

Such models must attempt to incorporate the physiological processes behind predator foraging and the variation inherent in such processes, before they can adequately start to describe predator behaviour in nature.

Chapter VIII

Habitat SelectionVIII. 1. Introduction

The main goal of this chapter is to predict, on the basis of the findings of the previous chapters, the type of habitat one would expect to find each of the three predator species, and to compare these predictions with the habitat selection observed during field sampling and with that described in the literature.

Table 8.1 gives a summary of the differences found between the three predator species under a variety of conditions and for a variety of activities which have been examined during this study. From this, one can predict the sort of habitat which the predator might prefer or survive and reproduce best in.

VIII. 2. Predictions of habitat typeVIII. 2.1. N. glauca

On the basis of feeding efficiency, the most suitable habitat type appears to be a complex one. Net energy gains are higher and $\frac{E}{T}$ values larger in the complex environment, and feeding rate is higher in dark than in light conditions. The reduction in feeding efficiency in simple environments may be partly due to a reduced pursuit success here compared to that in the complex environment. When perch sites are available, N. glauca also makes efficient use of them, by showing strong selection for the plant edges, and for returning to the same plant and perch site. Most rest time is spent at depth in such conditions and most captures are made from here. Perch sites in the middle areas are preferred, and as prey selection and capture seems to be largely dependent on predator/prey overlap in space, one would expect habitats with sufficient numbers and types of prey which inhabit or pass through these areas, to be selected by this species.

Table 8.1

Summary of differences between predators.

	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>
<u>Oviposition</u>	In plants	On solid objects	In plants or on supports
<u>Food extraction rate</u>	Slowest	Highest rate for large prey	Highest rate for small prey
<u>Handling time per item</u>	Longest	Shortest on large prey Same as <u>Obliqua</u> on small.	Intermediate in large prey Same as <u>Maculata</u> on small
<u>Success of attack Components</u>	Lowest pursuit Success in simple for large prey	Lowest pursuit success in complex and lowest pursuit success in simple for small prey.	Highest pursuit success
	Lowest attack success except small prey in simple	Intermediate attack success except lowest in simple with small prey	Highest attack success
	Lowest capture success except for <u>Gammarus</u> in simple.	Intermediate capture success except lowest with <u>Gammarus</u> in complex.	Highest capture success.
<u>Prey-capture Appendages</u>	Intermediate length of prey-catching appendages, most similar to <u>N. maculata</u> Intermediate rostrum length.	Shortest prey catching appendages (perhaps catches smallest prey) Shortest rostrum length	Longest prey catching appendages (perhaps catches largest prey) Longest rostrum length.
<u>Type of Attack</u>	Generally greatest proportion of pursuit attacks in complex Affected by predator/prey positions.	Shows greatest proportion of pursuit attacks in simple.	Shows lowest proportion of pursuit attacks in complex. Affected by prey abundance.
<u>Attack Rate</u>	Generally shows lowest rate	Greatest rate with small prey or with active prey in simple.	Greatest rate with large prey or active prey in complex

Cont.

Table 8.1 (Continued)

	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>
<u>Reaction Area</u>	Smallest reaction area from perch or from surface.	Largest reaction area from all positions.	Smallest reaction area at surface.
<u>Size of eyes</u>	Intermediate	Largest relative eye size	Smallest relative eye size.
<u>Light/dark effects</u>	Increase in feeding in dark	No. sig. difference, but trend for increase feeding in light.	Large increase in feeding in dark.
<u>Development of search images</u>	Intermediate development	Fastest development	Slowest development.
<u>Net Energy Gains</u>	Increased feeding efficiency in complex both for N.E.G. and E values, most marked for $\bar{T}$ active prey.	Increased feeding efficiency in Simple, most marked for active prey.	Increased efficiency at low densities of large prey in simple, no effect at high densities of large prey. Trend for larger $\bar{E}$ in simple. $\bar{T}$
	Lowest N.E.G.	Largest N.E.G. in simple.	Largest N.E.G. in complex.
<u>Allocation of Time</u>	Least time spent feeding on large prey, and on small prey in simple. Most active in simple.	Most time spent feeding on small prey and on <u>Gammarus</u> in simple. Most active in complex.	Most time spent feeding on <u>Musca</u> and on <u>Gammarus</u> in simple. Least active.
<u>Respiration</u>	Lowest basal metabolic rate.	Highest basal metabolic rate Lowest effect of activity on rate.	Intermediate basal rate, Greatest effect of activity on rate.
<u>Locomotion</u>	Intermediate efficiency	Likely to be most active, experiences least drag, shows greatest efficiency of locomotion but weakest swimmer.	Likely to be least active, experiences most drag, lowest locomotary efficiency, but strongest swimmer over short distances.

Cont....

Table 8.1 (Continued)

	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>
<u>Use of Space</u>	Complex-nearly all rest at depth simple-preference for depth at rest. During feeding-reduced time at depth in complex strong pre- ference for surface in simple. Prefers near middle perch sites Affected by prey position some- what. Preference increase during feeding. Prefers plant edge. Strong selection of same plant, increased during feeding. Strong selection for return to same perch increased during feeding.	Complex-lowest preference for depth at rest. Simple-strong preference for surface at rest. Dung handling strong preference for surface. Selection of perch sites greatly affected by prey position. During feeding middle sites for top prey, bottom sites for bottom prey. No preference for edge or middle. Weak selection for same plant, increased with active prey, and with feeding. Weak selection for same perch, in- creased with active prey and with feeding.	Complex-strong preference for depth at rest. Simple- strong preference for surface at rest. During handling, preference for depth in complex, for surface in simple. Preference for near bottom sites, slightly affected by prey position. Similar preference during feeding. Prefers plant edge Strong selection for same plant except with surface prey. Selection increased during feeding. No selection for same perch site with <u>Musca</u>, selection with mosquito prey and strong selection with <u>Gammarus</u>. Increased with feeding.
<u>Position from which response to prey made</u>	Complex-most captures from depth, affected by prey type. Simple-most captures from surface.	Complex-more prey captured from surface. Simple-most captures from surface.	Complex-most captures from depth, affected by prey type. Simple-most prey captured from surface.

Cont.....

Table 8.1 (Continued)

	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>
<u>Prey Preference</u>	Complex-1st capture. Main selection for mosquito larvae except high <u>Musca</u> densities. Subsequent selection for <u>Gammarus</u> ; least for <u>Musca</u> except at high <u>Musca</u> density. Strong effect of predator position.	Complex-early selection for <u>Musca</u> later captures for mosquito, very low selection of <u>Gammarus</u>	Complex-1st capture. Selection dominated by prey abundance and predator position. Subsequent captures, low selection of mosquito larvae, little difference for <u>Gammarus</u> and <u>Musca</u>
	Simple-strong preference for <u>Musca</u> No feeding on <u>Gammarus</u>	Simple-1st capture preference for <u>Musca</u> , low preference for <u>Gammarus</u> Subsequent captures strong preference for <u>Musca</u>	Simple-preference for <u>Musca</u> , very low preference for <u>Gammarus</u>
	Preference control mainly by predator position and prey abundance.	Preference control mainly by prey abundance and success of capture	Preference control mainly by predator position, prey abundance and success of capture.

The low attack rate, long handling times and slow extraction rate of this species suggests that it might only survive (and obtain sufficient food for reproduction) in habitats with high prey density (i.e. prey rich habitats), and would not be able to exploit habitats with low levels of food, or of unstable prey availability as would be found in temporary ponds etc. The relatively large number of captures required to maximise prey capture efficiency (perhaps through search image formation) on one prey type also indicates that this species may not be adapted to exploit environments with low prey diversity.

The preference for depth and the increased use of the same plant and perch site during handling indicates that the predator may be reducing the risk of capture by other predators while being increasingly conspicuous during feeding. The small reaction area from perch sites may be a similar adaptation. Such predators (e.g. fish) would be expected in stable, complex habitats.

In summary, this predator species would be expected to select complex, stable, habitat types, with a large prey diversity and a high and stable prey abundance, a large proportion of which will overlap in microhabitat with the predator.

VIII. 2.2. N. maculata

On the basis of feeding efficiency, it appears that the most suitable habitat is the simple environment. There is both increased net energy gains and $\frac{E}{T}$ values, and a trend for increased feeding rate in light compared to dark conditions. This difference may be partly due to reduced attack and capture success in the complex environment, especially with the most active prey.

When perch sites are available, N. maculata spends the lowest proportion of rest time at depth of the three species and shows the least efficient use of plants and specific sites. Perch selection during rest changes with the distribution of the prey, and with several different

prey, is based on the distribution of the most active. Prey selection seems most affected by prey abundance and success of capture. During handling, practically all time is spent at the surface, partly due to the small size of prey catching appendages (making it harder to hang onto perch sites while feeding). This increase in conspicuousness, due to the long time spent at the surface, would be a relative disadvantage in complex stable habitats due to the presence of other predators.

N. maculata generally shows the highest capture rate, shortest handling times and fastest extraction rates of the three species of predator. This could allow exploitation of habitats with low prey availability, or temporary habitats, where sufficient food must be gathered in a short time period before the pond dries out. (The ability of N. maculata's eggs to undergo dessication and the rapid development rate (see Chapter II) may be further adaptations to 'temporary ponds').

This bug shows the largest reaction area (in part due to high visual acuity), the greatest locomotory efficiency and the lowest active metabolic rate, which would allow this predator to exploit prey widely distributed in the environment. The rapid maximisation of searching efficiency (search image formation) may also be an adaptation to simple environments, where few prey types are likely to be available. The prey types that are available, will normally be either ones with a short development time, but occurring in fairly large numbers, or terrestrial prey which become trapped in the surface film e.g. from swarms of Dipterans etc., where several prey are likely to be trapped at once.

In summary, this predator appears to be an opportunistic one, and is apparently adapted to exploit simple and/or temporary habitats, which have low prey availability and diversity. The increased conspicuousness during feeding may also preclude this species from habitats with large

predators.

VIII. 2.3. N. obliqua

There is generally no clear indication of which habitat should be selected on the basis of feeding efficiency, as there is no effect of environmental complexity on net energy gains with high prey densities, a tendency for increased gains at low densities in the complex, but for larger $\frac{E}{T}$ values in the simple environment. The predator was more efficient in dark conditions though. In prey combination experiments, there was also a trend for increased gains in the simple environment. In the complex environment there is a strong preference for resting at depth from where most captures are made. Perch sites in bottom areas are selected in single prey treatments but this preference is affected with combinations of prey, and N. obliqua shows efficient use of the 'plants'. In the simple environment most rest time is spent at the surface, and all handling is spent there.

N. obliqua shows high rates of extraction for small prey, and relatively high rates for large, relatively short handling times and high attack rates, which could allow it to exploit habitats with relatively low prey abundance. However, this species also shows a high active metabolism, a small reaction area at the surface and has slow increase in searching efficiency which suggests that this bug may not be as well adapted for such simple conditions as N. maculata.

Selection of prey is largely dominated by relative predator/prey positions and prey abundance, but there is evidence for preference of larger prey within these constraints.

In summary, this predator seems to be equally suited to simple and complex environments as far as feeding efficiency is concerned, though fairly simple ones, with at least some perch sites but with rather greater prey availability and diversity than normal would probably be the most suitable.

It appears as though the three predators under study include two specialists and one generalist, in respect of predicted habitat selection, N. glauca being best adapted to complex environments, N. maculata to simple environments and N. obliqua seemingly able to utilise both. On this basis, one might expect some competition between the specialist and generalist in the two environments. In the complex one, although N. obliqua seems the better competitor in terms of foraging efficiency, in the present study, the differences in morphology, physiology and behaviour seem sufficient to allow coexistence in the more complex natural habitats, with high food availability and diversity. In the simple environment, there is much less scope for such resource division, and if foraging efficiency were the only criterion, it is likely that N. maculata could outcompete N. obliqua, and so one would not expect coexistence between these two, even though there are such large differences in morphology and physiology. It is also possible that coexistence between all three predators might occur given a sufficiently heterogeneous habitat in terms of complexity, prey diversity and distribution in some situations.

VIII. 3.

Field Sampling

VIII. 3.1. Introduction

In the program of field sampling, it was intended to try and correlate habitat type, predator species and prey diversity and abundance. To this end, eleven different ponds were chosen ranging from very simple to very complex, and these were sampled at monthly intervals over a year. Unfortunately, laboratory experimental timetables did not allow sufficient time for a detailed analysis of the abundances of predators and prey, and so only general patterns could be discerned.

VIII. 3.2. Method

The parameters investigated in each pond were; a) environmental complexity, including type and extent of emergent and submerged vegetation; b) type and relative abundance of predator species; c) diversity of probable

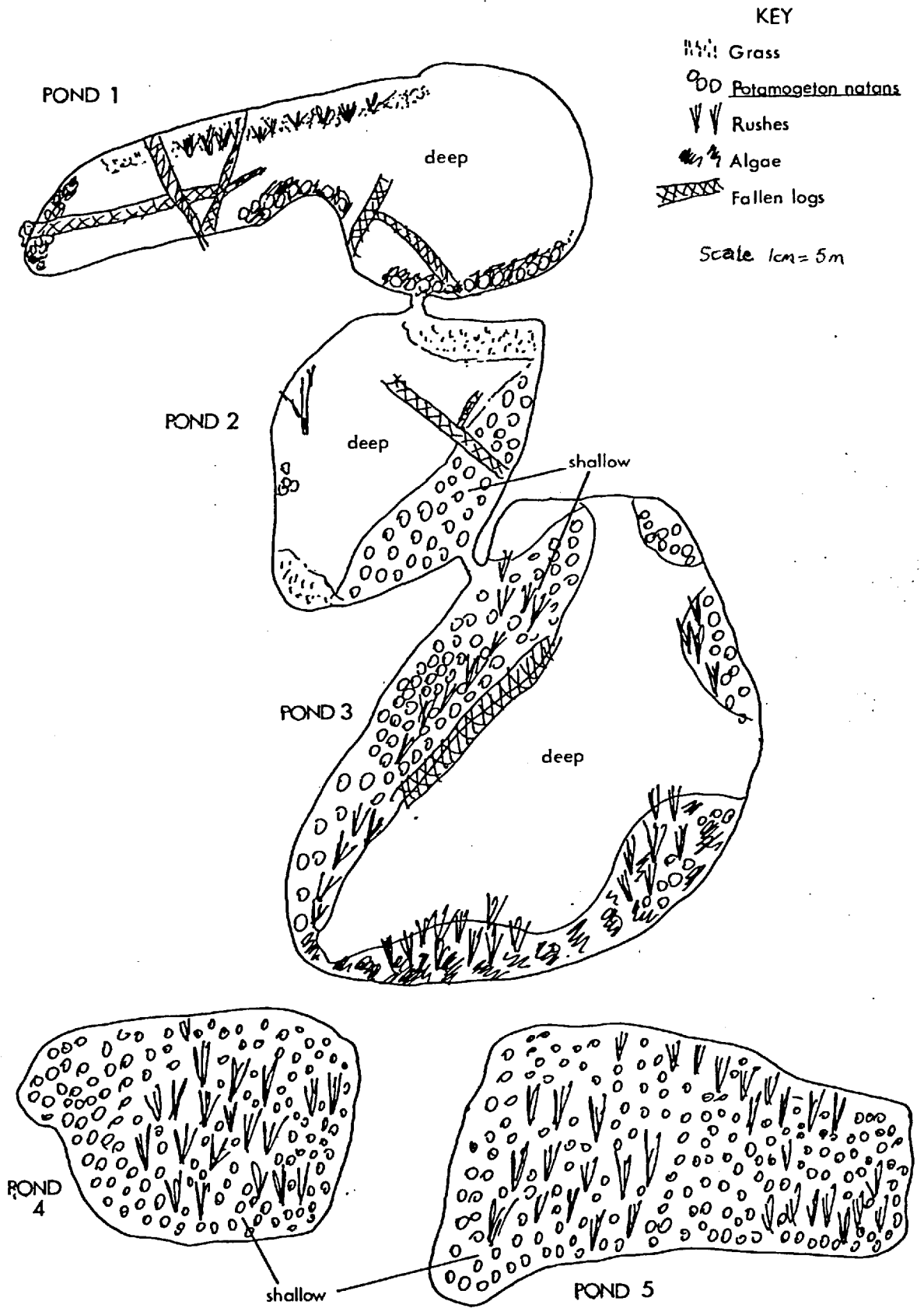
prey species in different depths of the pond; and d) relative abundance of prey types.

Parameters b), c) and d) were estimated on the basis of a fixed sampling time at each pond. Samples were taken from each pond within about 20cms of the surface and where possible, from middle and bottom areas, for a total of 20 seconds. This time interval was determined by the size of the smallest pond, where no more than a quarter of the volume was sampled at one time. Sampling was restricted to within 5m of the edge, where most Notonectids are usually found (Macan (1965), Walton (1943) etc).

The predators were counted and returned to the ponds (except some late instars), and the rest of the sample was taken to the laboratory for analysis. The first predator instars could be quite easily identified (see Chapter I, Fig. 2), but examples of the latter instars were brought back to the laboratory and reared to adult for identification. The abundance of predators was scaled into three relative abundance categories, - F (few) where only 1 or 2 predators per sample were captured, - S (several), where between 3 and 10 per sample were captured, and - M (many) where over 10 were captured during one sampling period.

To analyse prey diversity, the prey samples were identified into several main groups:- i) Gerrids, ii) corixids, iii) chaeoborinae (Diptera), iv) chironomidae (Diptera), v) mosquito larvae and pupae (Diptera) vi) ephemeroptera, vii) coleoptera (Beetle adults and larvae), viii) Anisoptera, ix) Daphnids, x) Other Crustacea (other cladocerans, ostracods etc), xi) Animals of terrestrial origin, xii) cast stars indicating relative abundance of emerging insects. Prey abundance was estimated in a similar way to predator abundance, where F indicated less than 5 individuals per sample, S indicated between 5 and 15 individuals per sample, M indicated between 15 and 30 individuals per sample, VM indicated between 30 and 100 individuals per sample, and VVM indicated over 100 per sample.

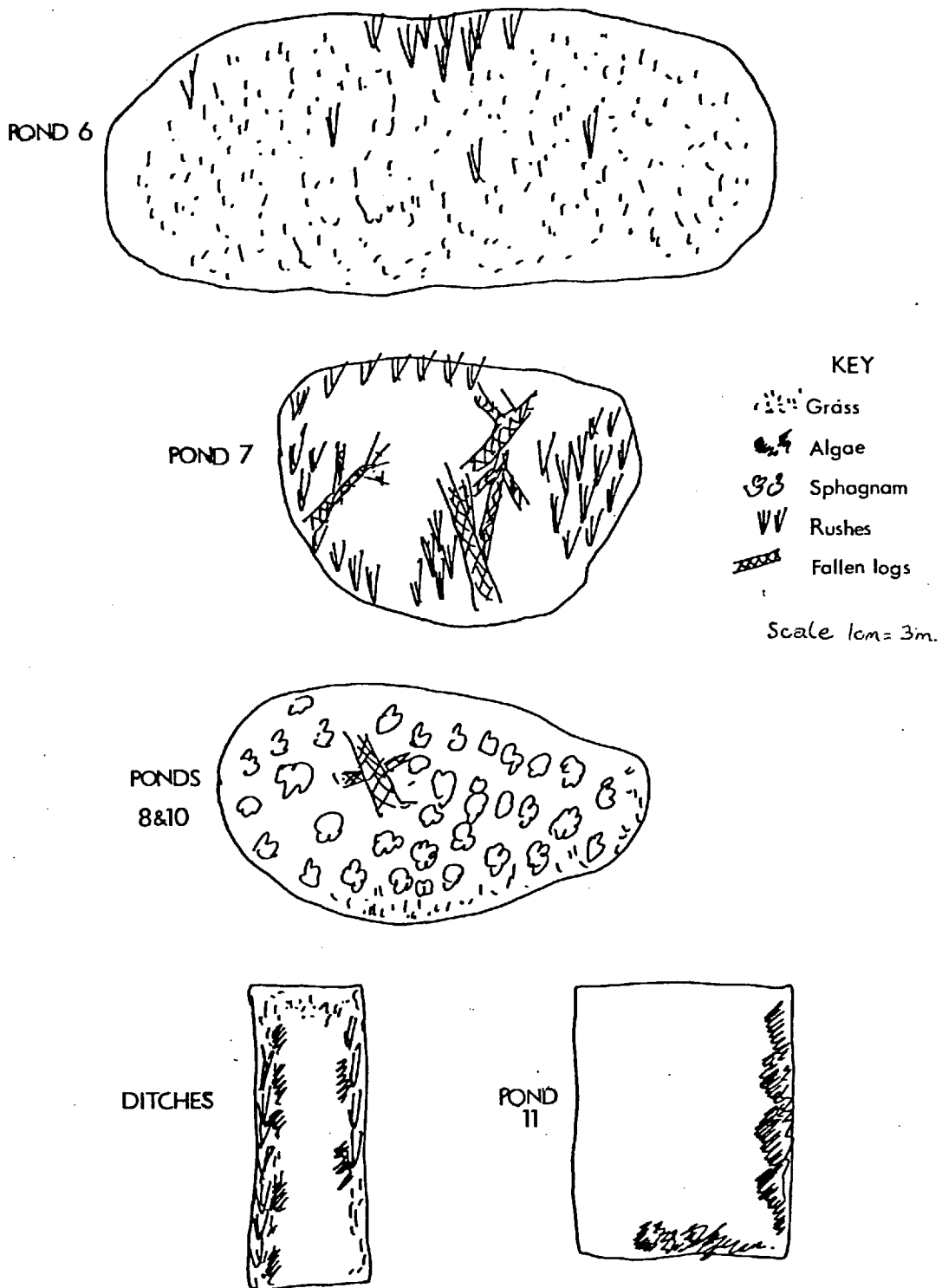
SAMPLING PONDS



LEGEND TO FIG 90

Diagrams of the sampling ponds showing relative sizes and vegetation present.

SAMPLING PONDS



LEGEND TO FIG 91

Diagrams of the sampling ponds showing relative sizes and vegetation present.

VIII. 3.3. Results

Maps showing the type and approximate extent of vegetation are given in Figs 90, 91. The description was found to change very little through the year. The results of the sampling program are shown in Tables 8.2 and 8.3. Predators are only considered to efficiently utilise a habitat if they successfully reproduced in it. Occasionally, a few of one species will be found in a habitat in which it has not bred, and these individuals have obviously migrated in as adults e.g. N. maculata being found in ponds 3, 8 and 10 from August or September, N. glauca being found in ponds 5 and 10 from September or October, and N. viridis being found in ponds 8 and 10 from September or October.

The type of habitats where reproduction has occurred, seems to fit well with those predicted from the laboratory studies.

N. glauca was found to breed in ponds 1, 2, 3 and in the ditches. The main characteristics of the first three ponds are the presence of many submerged plants and quite cloudy water producing a generally complex environment, a broad diversity of possible prey types and a high prey abundance. No N. glauca populations were found in ponds 4 and 5, which were the most complex of the lot. These ponds however, showed relatively low prey abundance, and as there was so much vegetation, both emergent and submerged, such ponds may be difficult to locate by a migratory bug. The ditches sampled did not have much submerged plant life, but the water was extremely cloudy. There was however, low species diversity and abundance of possible prey types, which presents this particular selection by N. glauca as somewhat of an anomaly.

N. maculata was found in breeding populations in ponds 1, 7, 11 and in the ditches. Although pond 1 has submerged vegetation, it is confined to the pond sides, leaving much of the rest of the pond free from any vegetation. Pond 7 has no submerged vegetation, but some emergent vegetation, pond 11 has no vegetation of any type except for some filamentous

Table 8.2 Table showing predator species captured in sample ponds over the sampling period. G = N. glauca,
M = N. maculata, O. = N. obliqua, V = N. viridis; N = nymph, A = adult, (F) = Few, (S) = Several,
(M) = Many, (VM) = Very Many. Nymph instars shown.

		DATE													
POND		5/78	6/78	7/78	8/78	9/78	10/78	11/78	12/78	1/79	2/79	3/79	4/79	5/79	6/79
1.	SURFACE MIDDLE & BOTTOM	/	GN ON MW 1-41-3 1	/	/	/	/	—	/	← FROZEN →			/	GN ON(S) 1st	
				GN ON 4th & 5th	AG-(VM) GN 5th AO-(F) AM-(F)	AG(M) AO(S)	AO(M) AG(S)		AG(M) AO(M) AM(F)				AO(S) AG(S)		
2.	SURFACE MIDDLE & PLANT BOTTOM SANDY	/	/	/	/	/	/	—	← FROZEN →				/	ON	ON
			GN ON 3rd 4th & 5th /	GN ON 5th AO(M) AG(S) GN ON 5th	AO(S) AO(M) AG(S)	AO(M) AO(S)	AO(M) AO(M)						AO(S) (MATING)		
3.	SURFACE MIDDLE & BOTTOM	/	GN ON 3-5 4-5 /	/	/	AO(F)	AO(F)	—	← FROZEN →				GN(M) 1st AG(S)	GN ON (VM) 1st, 2nd /	
				AO AG GN ON 5th	AO(M) AG(S)	AG(M) AO(M) AM(F)	AO(M) AG(M) AM(F)		AO(M) AG(S) AM(F)						
4.	SURFACE, MIDDLE & BOTTOM	/	/	/	AO(F)	AO(S)	AO(F)	—	← FROZEN →				ON(F)	ON(F)	
5.	SURFACE, MIDDLE & BOTTOM	/	ON(F) 4th	ON(F) 5th	AM(VF)	AO(S) AG(F)	AO(S)	—	AG(VF) ← FROZEN →				/	/	
6.		/	ON(4th & 5th) DRIED INTO SEVERAL	←	DRIED UP	—	—	—	—	→ /	/	/	/	ON(M) 1st, 2nd 3rd	309.

Table 8.2 (Continued)

		DATE														
POND		5/78	6/78	7/78	8/78	9/78	10/78	11/78	12/78	1/79	2/79	3/79	4/79	5/79	6/79	
7.		/	MN(M) 3rd,4th	MN 5th	AM(S)	← M eggs	DRIED UP						→	/	/	
8.	SURFACE MIDDLE	/	/ ON(M) 4th	ON(S) 5th /	AO(S) AO(M) AM(F)	AO(S) AO(M) AV(F)	/ AO(M)	/	/ AO(S)	← FROZEN			→	/	ON 1st, 2nd /	ON
9.	DITCHES	/	GN ON MN 4th,5th	AM(F) AO(F) MN ON (5th)	AG(S) AM(S) AO(F)	←	DRIED UP						→	/	/	
10.		—	—	AO ON(M) 5th	AO (M) AM(S)	AO (S)	AO(M) AV(S) AG(F)	—	AO (S) AV(F) AG(F)	← FROZEN			→	/	ON or 2nd	
11.		—	—	AM(M)	AM(M) +eggs	/	← DRIED UP									

Table 8.3 Table showing prey type and relative abundance sampled from ponds during sampling period

(F) = Few, (S) = Several, (M) = Many, (VM) = Very many.

POND	5/78	6/78	7/78	8/78	DATE 9/78	10/78	12/78	4/79	5/79	
1. SURFACE	-	Gerrids (S) Corixids(F) Chaeob (F) Terres (F) Castskins(F)	Corixids (S) Chaeob (S) Chiron (F) Mosq (F) Ephem (F) Daph. (F) Castskins(S) Terres (F)	Corixids (S) Chaeob (F) Beetle (S) Daph. (VM) Crust (VM) Terre (S)	Chaeob (M) Chiron (F) Mosq. (F) Ephems (S) Beetle (M) Daph. (VVM) Crust (S) Terre (F)	Corixids (F) Chaeob (M) Ephem (M) Daph. (VVM) Terres (M)	Chaeob (M) Mosq (F) Ephem (M) Beetle (F) Daph. (VM) Terre (S)	Corixid (F) Chaeob (M) Ephem (M) Daph (S)	Corixids (S) Chaeob (S) Ephem (M) Beetle (S) Anis (M) Daph (S) Crust (VM)	
MIDDLE AND BOTTOM	Corixids (S) Chaeob (S) Mosq (M) Ephem (F) Beetle (M)	Corixids (M) Chaeob (S) Chiron (M) Mosq (F) Beetle (S)	Corixids (M) Chaeob (S) Chiron (M) Mosq (F) Beetle (S) Ephem (VM) Daph (VM)	Corixids (M) Chaeob (S) Chiron (M) Mosq (F) Ephem (M) Beetle (F) Daph (VVM)	Corixid (VM) Chaeob (M) Chiron (F) Mosq (F) Ephem (VVM) Beetle (M) Daph (VVM)	Corixids (M) Chaeob (S) Chiron (S) Ephem (VVM) Beetle (S) Daph (M)	Corixids(F) Chaeob (VM) Ephem (VM) Beetle (F) Daph (VVM)	Corixids (M) Chaeob (VM) Chiron (M) Ephem (VM) Beetle (F) Daph (VVM)		
2. SURFACE	Corixids (S) Chaeob (M) Chiron (F) Ephem (F) Beetle (S) Terre (S)	Corixids (S) Chaeob (M) Chiron (M) Beetle (S) Daph (S) Castskin (M) Terre (F)	Gerrids (F) Corixids (M) Chaeob (VM) Chiron (M) Ephem (F) Beetle (M) Daph (M) Terre (F)	Gerrids (S) Chaeob (F) Chiron (F) Ephem (S) Beetle (F) Anis (M) Daph (VM) Crust (VVM) Terre (F)	Gerrids (M) Corixid (S) Chaeob (M) Chiron (S) Ephem (S) Mosq (F) Ephem (F) Beetle (F) Anis (VM) Daph (S) Crust (VVM)	Corixid (M) Chaeob (M) Chiron (S) Ephem (M) Anis (F) Daph (S) Crust (S) Terre (F)		Corixid (F) Chaeob (M) Chiron (S) Ephem (S)	Corixid (S) Chaeob (M) Ephem (S) Beetle (S) Crust (VVM)	
MIDDLE AND BOTTOM Plant side	Corixid (M) Chaeob (M) Beetle (S)	Corixid (S) Chaeob (VM) Chiron (M) Beetle (M)	Corixid (M) Chaeob (M) Chiron (M) Mosq (F)	Corixid (M) Chaeob (S) Chiron (S) Beetle (S)	Corixid (S) Chaeob (F) Chiron (F) Ephem (S)	Corixid (S) Chaeob (M) Chiron (S) Beetle (F)	Corixid (F) Chaeob (M) Chiron (F) Ephem (S)	Corixid (F) Chaeob (M) Ephem (S)		

Table 8.3 (Continued)

POND	DATE								
	5/78	6/78	7/78	8/78	9/78	10/78	12/78	4/79	5/79
MIDDLE Plant AND side BOTTOM (Cont.)		Anis (S) Daph (S)	Beetle (M) Anis (S) Daph (M)	Anis (VM) Daph (M) Crust (S)	Beetle (M) Anis (VM) Crust (M)	Anis (VM)	Beetle (F) Anis (S) Crust (M)		-
Sandy side			Corixid (M) Chaeob (M)	Corixid (M) Chaeob (M) Mosq (S) Beet (M) Anis (S) Daph (VM)	Chaeob (M) Beet (S) Anis (S) Daph (S) Crust (M)	Corixid (S) Chaeob (M) Beet (S) Anis (M) Daph (S) Crust (S)	Corixid (F) Chaeob (M) Ephem (F) Crust (M)	Corixid (F) Chaeob (VM) Chiron (F) Ephem (F)	-
3. SURFACE	Gerrid (M) Chaeob (F) Chiron (F) Beet (F) Anis (F) Crust (S) Terr (M)	Corixid (M) Chaeob (F) Mosq (F) Beet (S) Anis (F) Daph (M)	Gerrid (S) Chiron (M) Mosq (F) Ephem (M) Beet (F) Anis (M) Daph (S) Crust (VM)	Gerrid (M) Chaeob (F) Chiron (S) Ephem (S) Beet (S) Anis (M) Daph (S) Crust (VM)	Gerrid (S) Chaeob (M) Chiron (S) Mosq (S) Ephem (M) Beet (S) Anis (VM) Daph (S) Crust (VVM)	Chaeob (M) Chiron (S) Ephem (S) Beet (S) Anis (M) Daph (M) Crust (VM) Terr (S)	Chaeob (M) Chiron (F) Ephem (S) Crust (M) Terr (F)	Chaeob (M) Ephem (S) Beet (S)	Corixid (S) Chaeob (S) Mosq (F) Ephem (M) Beet (M) Anis (S) Crust (VVM)
MIDDLE	Corixid (S) Chaeob (S) Chiron (S) Beet (S) Anis (S) Crust (S)	Corixid (M) Chaeob (S) Chiron (M) Mosq (M) Beet (M) Anis (M) Daph (M)	Chiron (M) Ephem (M) Beet (S) Anis (M) Daph (M)	Corixid (F) Chaeob (M) Chiron (M) Mosq (M) Ephem (M) Beet (S) Anis (VM) Daph (M) Crust (VM)	Chaeob (VM) Chiron (VM) Ephem (M) Beet (S) Anis (VM) Daph (M) Crust (M)	Corixid (M) Chaeob (VM) Chiron (M) Ephem (M) Beet (S) Anis (VVM) Daph (M) Crust (M)	Corixid (F) Chaeob (M) Chiron (M) Ephem (M) Anis (S)	Corixid (F) Chaeob (M) Chiron (M) Anis (S)	

Table 8.3 (Continued)

POND	DATE								
	5/78	6/78	7/78	8/78	9/78	10/78	12/78	4/79	5/79
4.	Corixid (S) Chiron (S) Ephem (S) Anis (S) Crust (M)	Corixid (VM) Chaeob (F) Chiron (F) Beet (F) Anis (S) Daph (VM)	Corixid (VM) Ephem (S) Anis (M) Daph (F)	Gerrid (S) Corixid (M) Chaeob (F) Chiron (S) Ephem (S) Beet (F) Anis (M) Daph (S)	Corixid (M) Chiron (S) Beet (F) Anis (VM) Daph (F)	Corixid (M) Chiron (S) Anis (M) Daph (F)	Corixid (F) Chaeob (S) Chiron (S) Ephem (S) Anis (M) Crust (M)	Corixid (VM) Chaeob (M) Chiron (M) Ephem (S) Anis (M) Crust (M)	-
5.	Corixid (M) Chaeob (M) Chiron (M) Ephem (S) Anis (F) Crust (M)	Corixid (M) Chiron (F) Beet (S) Anis (S) Crust (S)	Corixid (M) Chiron (S) Beet (S) Anis (S) Daph (M) Crust (VM)	Corixid (S) Chiron (S) Ephem (S) Beet (F) Anis (M) Daph (S) Crust (VM)	Corixid (F) Chaeob (F) Chiron (S) Mosq (F) Ephem (M) Anis (VM) Daph (S) Crust (S)	Corixid (S) Chaeob (S) Chiron (M) Ephem (S) Beet (F) Anis (M) Daph (F)	Corixid (F) Chaeob (S) Ephem (M) Anis (M) Crust (M)	Chaeob (M) Chiron (S) Ephem (VM) Anis (F)	-
6.	Corixid (M) Chiron (M) Mosq (S) Beet (S) Anis (F)	Gerrid (S) Corixid (M) Chaeob (F) Chiron (M) Mosq (F) Beet (M) Anis (S) Crust (M)	-	-	-	-	-	Chiron (S) Mosq (M) Beet (F) Crust (VM)	Corixid (S) Mosq (S) Beet (M) Crust (M)
7.	Corixid (S) Chaeob (M) Chiron (M) Mosq (M) Beet (S)	Corixid (M) Chaeob (S) Chiron (M) Mosq (F) Beet (S)	Gerrid (M) Corixid (VM) Chaeob (VM) Chiron (S) Mosq (S) Beet (S)	Corixid (M) Chaeob (M) Chiron (M) Mosq (F) Anis (F) Crust (M)	-	-	Mosq (VM) Beet (S)	-	Mosq (VM) Beet (S) Terr (F)

Table 8.3 (Continued)

POND	DATE								
	5/78	6/78	7/78	8/78	9/78	10/78	12/78	4/79	5/79
7 (Cont.)			Anis (S) Daph (F) Terres (M)	Terres (S)					
8. SURFACE	-	-	Gerrid (F) Corixid (S) Chiron (S) Anis (S) Terres (S)	Gerrid (M) Corixid (M) Anis (S) Terres (S)	Gerrid (S) Chiron (S) Mosq (F) Anis (S) Crust (M) Terr (M)	Gerrid (F) Chaeob (S) Chiron (S) Terres (S)	Corixid (S) Chiron (M) Mosq (F) Anis (S) Terres (S)	Corixid (F) Chiron (M) Mosq (M) Beet (S) Anis (S)	Crust (S) Terres (F)
MIDDLE	Corixid (S) Chiron (S) Mosq (F) Beet (F) Anis (F)	Corixid (M) Chiron (S) Anis (M)	Corixid (S) Chiron (S) Anis (M)	Corixid (M) Chiron (M) Anis (S)	Corixid (S) Chiron (M) Beet (S) Anis (F) Crust (M)	Corixid (S) Chiron (M) Mosq (S) Beet (S)	Corixid (M) Chaeob (F) Chiron (VM) Mosq (S) Beet (F) Anis (F)	-	Chiron (F) Anis (S)
DITCHES	Corixid (S) Chiron (F) Beet (S) Anis (F) Terres (F)	Gerrid (M) Corixid (M) Chiron (S) Mosq (F) Beet (S) Anis (M) Terres (F)	Gerrid (M) Corixid (M) Chiron (S) Beet (S) Anis (M) Terres (F)	Gerrid (M) Corixid (M) Chiron (F) Mosq (M) Beet (S) Anis (M) Castskins (M)	Corixid (M) Mosq (F) Beet (M) Anis (VM) Terres (S)	-	Corixid (F) Chiron (S) Beet (S) Terres (F)	Mosq (VM) Beet (S)	Mosq (S) Beet (F) Terres (S)

Table 8.3 (Continued)

POND	DATE									
	5/78	6/78	7/78	8/78	9/78	10/78	12/78	4/79	5/79	
10.	-	-	-	Corixid (S) Anis (S) Terres (S)	Corixid (F) Anis (S) Terres (F)	Corixid (F) Chaeob (S) Chiron (M) Beet (S) Anis (M)	Corixid (F) Chiron (M) Anis (S)	-	-	
11.	-	-	Gerrid (M) Corixid (VM) Chiron (VM) Ephem (M) Beet (S) Castskin (M) Terres (VM)	Gerrid (M) Corixid (M) Chiron (M) Ephem (VM) Anis (F) Crust (M) Castskin (S) Terres (M)	Gerrid (S) Ephem (VM) Beet (S) Anis (S) Crust (M)	-	-	-	-	

KEY

Chaeub	-	Chaeoborinae
Chiron	-	Chironomidae
Mosq	-	Mosquito larvae+Pupae
Ephem	-	Ephemoptera
Beet	-	Beetles (Adult + Larvae)
Anis	-	Anisoptera
Daph	-	Daphnids
Crust	-	Crustaceans (Ostracods, Cladocerans etc)
Terr	-	Terrestrial organisms.

algae, and the ditches, as described earlier, have little submerged or emergent vegetation. The substrate in pond 11 is stone and concrete, in ponds 1 and 7 firm mud and sand, but with fallen trees on top (providing solid supports for imposition). Ponds 7, 11 and the ditches are all subject to drying out, restricting time available for successful reproduction, and they also show a relatively low species diversity of possible prey. There is also a trend for low prey abundance in these ponds except over short periods. Ponds 7 and 11 also have clear water. N. maculata does not appear to have been very successful in pond 1, and did not reproduce for the second year. Again, the selection of the ditches with the cloudy water presents an anomaly. The lack of selection for the relatively simple ponds 8 and 10 may be due to the lack of solid supports for oviposition.

N. obliqua was found in reproducing populations in ponds 1, 2, 3, 4, 5, 6, 8, 10 and in the ditches. Although such selection covers a wide range of environmental complexity, all the ponds have at least some submerged vegetation. The selection also covers a wide range of diversity and abundance of possible prey, from the most prey rich ponds, such as ponds 2 and 3, to the rather poor ponds 8 and 10.

To date, the most detailed surveys of habitat selection by Notonectids in Britain have been reported by Brown (1948), Pearce and Walton (1939), Southwood and Leston (1959) and Walton (1943). It is not clear however, whether the bugs found were in reproducing populations or simply transient ones. However, from such surveys, one can draw up several characteristics of the habitat which appear to attract the predator species. Table 8.4. shows the preferences of the three predator species for a number of habitat variables, as predicted from the laboratory results, as found during field sampling, and as concluded from the various surveys in the literature.

It is encouraging to note that the predictions of habitat selection based on the predation strategies of the three species fit in quite closely

Table 8.4 The preferences for various habitat variables as predicted from laboratory results, as found during Field sampling, and as concluded from surveys in the literature.

Habitat variables	Predator species	Preferences		
		Predicted	Field sampling	Literature
<u>Type of Habitat.</u>	<u>N. glauca</u>	Complex stable habitats	Brick pit ponds and ditches.	Favours ponds, ditches, canals and lakes. Also meadow ponds, quarry ponds, stagnant pools brick pools.
	<u>N. maculata</u>	Simple and temporary habitats	Concrete pond, ditches simple temporary pools.	Stone ponds or artificial ponds, but is found in slow flowing rivers with stony substrata.
	<u>N. obliqua</u>	Wide range	Brick pit ponds, ditches, temporary pools, acidic pools.	Favours ponds, lakes, bog pools, also found in stone ponds, detritus ponds, lowland waters.
<u>Presence of Vegetation</u>	<u>N. glauca</u>	Complex with many perch sites.	Many submerged plants in the main	Prefer water bodies with lot of vegetation. Are found with little but infrequently with no macroscopic veg.
	<u>N. maculata</u>	Simple with few perch sites	Little or no vegetation in most of habitat	Prefers little or no macroscopic vegetation
	<u>N. obliqua</u>	At least some perch sites	Always at least some vegetation	Prefers ponds with lot of vegetation, but found in ponds with no emergent vegetation.
<u>Type of Vegetation</u>	<u>N. glauca</u>	/	<u>Potamogeton natans</u> , rushes, submerged grass	<u>Potamogeton natans</u> , <u>Ranunculus aqualitis</u> , <u>Alisma</u> , <u>Callitriche</u> , <u>Juncus</u> , <u>Sparganium</u> , <u>Scirpus</u> , grasses
	<u>N. maculata</u>	/	/	/
	<u>N. obliqua</u>	/	<u>Potamogeton</u> , rushes, submerged grass, <u>Sphagnum</u>	<u>Juncus</u> , <u>Potamogeton</u> , <u>Callitriche</u> , <u>Sphagnum</u> , <u>Ranunculus</u> . Also <u>Scirpus</u> , <u>Alisma</u> , <u>Glyceria</u>

Table 8.4 (Continued)

Habitat variables	Predator species	Predicted	Preferences Field sampling	Literature
Opacity of water	<u>N. glauca</u>	Cloudy	Quite cloudy water	/
	<u>N. maculata</u>	Clear	Generally clear water	Prefers clear water
	<u>N. obliqua</u>	Range of both	Clear and cloudy	Prefers clearer water
Ph. of water	<u>N. glauca</u>		Not acidic	Range 6.5-7.5 but favours low acid or alkaline.
	<u>N. maculata</u>		Not acidic	Range 6.5-7.5
	<u>N. obliqua</u>		Both acidic and alkaline	Range 6-7.8 but prefers acid waters
Prey Abundance	<u>N. glauca</u>	High prey abundance	High prey abundance	
	<u>N. maculata</u>	Low prey abundance	Low prey abundance	
	<u>N. obliqua</u>	Wide range	Both high and low abundance	
Prey Diversity	<u>N. glauca</u>	High prey diversity	Wide prey diversity	
	<u>N. maculata</u>	Low prey diversity	Low prey diversity	
	<u>N. obliqua</u>	Wide range	Both high and low diversity	
Habitat Bottom	<u>N. glauca</u>		Black mud, detritus and clay	Commonly black mud and detritus-also clay and peat.
	<u>N. maculata</u>		Stone, firm mud and sand.	Stony with little mud or detritus.
	<u>N. obliqua</u>		Detritus, mud, sand, <u>Sphagnum</u>	Muddy or peaty

Table 8.4 (Continued)

Habitat variables	Predator species	Predicted	Preferences Field sampling	Literature
Water depth	<u>N. glauca</u>		Generally shallow areas	Shallow water and shallow sides of water body.
	<u>N. maculata</u>		Generally shallow	Not especially important
	<u>N. obliqua</u>		Wide range	Not especially important
Altitudes	<u>N. glauca</u>			Sea level to 700ft - mostly 150-400 ft.
	<u>N. maculata</u>			Restricted to south mainly below 400 ft.
	<u>N. obliqua</u>			Found from sea level to 1300 ft, large range and wide distribution.

to the actual selection in nature. Likewise, where coexistence does occur, the habitat is heterogeneous enough, and has a rich enough prey source, to allow resource partitioning through the many morphological, physiological and behavioural differences shown by the three species.

However, there are anomalies in the habitat selection, which cannot be explained on the basis of predation strategies. For example, the coexistence of reproducing populations of all three predator species in the ditches, which did not seem complex enough, or to possess a sufficiently prey rich environment, to allow such coexistence. It is possible that the relatively small number of predators there, due to low immigration rates, could explain this. (These ditches are only temporary water bodies, so no perennially resident population of Notonectids are found). The fact that N. maculata was not found in ponds 8, and 10, relatively simple ponds one would have expected this species to be able to exploit, may be due to other factors. The lack of N. glauca in ponds 4 and 5 is surprising, although the relatively homogenous nature of these habitats might not allow coexistence between N. glauca and N. obliqua. The generally low level of prey abundance and high level of competing predators (such as Anisopterans) may also explain the very low numbers of N. obliqua in these ponds.

A major problem in making such comparisons between laboratory results and field data, is the inherent danger of getting unnatural results from the laboratory. Unrealistic environments, imposed feeding regimes, narrow prey choice, external disturbances etc., may all contribute to produce unnatural behaviour in the predator. It is therefore extremely unwise to assume that the laboratory results give anything other than pointers to what is happening in natural conditions. The observations of field populations and habitat selection, demonstrate the net effect of the combination of several different factors operating under natural conditions. If predictions made on the basis of laboratory experiments assessing a

likely factor affecting habitat selection happen to fit quite closely with the natural distribution, then one has perhaps identified this as a contributing factor in the real world selection. This is what, I hope, this study has achieved, by showing that differences in predation strategies and components of predation between superficially similar species, in simple and complex environments, can possibly be adaptations to feeding in certain types of habitat, and so in some way help to explain speciation and habitat selection in this genus of water bug.

A direct continuation of this present study, would be an examination of what the predators are actually feeding on in the field, through the analysis of gut contents (by electrophoretic or immunological techniques), and to compare what is eaten by the different species in relation to what is available in the different types of habitat. The basis of such selection could well be found in the behaviour shown by the different species in the present study. Such further work would indicate more precisely, what effect the morphological, physiological and behavioural differences have on the predation strategy and habitat selection of the different species, and whether these are sufficiently large to allow resource partitioning where several species inhabit the same pond, or whether there is direct competition and perhaps evolution 'in action'.

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Appendix I Number of mosquito larvae killed by unstandardised
N. glauca adults on seven different occasions.

Analysis of variance $F = 0.625$ (n.sig.)

<u>Date</u>	16/8	19/8	28/8	1/9	3/9	7/9	17/9
No. eaten.	13	19	25	10	14	19	19
	21	22	24	24	19	15	21
	30	30	25	12	19	2	3
	5	14	18	8	9	13	13
	15	13	29	18	10	9	21
	20	23	26	19	13	15	13
	5	19	13	19	9	24	16
	20	27	24	16	15	6	23
	23	21	8	8	3	16	8
	9	26	14	11	16	7	15
	19	14	16	9	8	8	18
	17	25	18	5	11	8	16
	11	27	7	17	9	13	14
	6	26	23	11	7	6	21
	4	23	22	5	8	16	14
	29	30	30	12	13	9	24
	7	22	10		10	14	29
	8	23	19		6	13	27
	21	26	17		14		8
$\bar{x}$	14.89	22.63	19.37	12.75		11.38	
s^2	66.54	25.04	46.47	30.33		25.21	
$s/\bar{x}$	4.47	1.13	2.40	2.38		2.47	

Appendix II Number of mosquito larvae killed by unstandardised male
and female N. glauca on seven occasions.

<u>Date</u>	16/8	19/8	28/8	1/9	3/9	7/9	17/9
No. eaten.	13	19	25	10	14	11	19
	21	22	24	24	19	19	21
	20	23	26	18	13	9	13
	20	27	24	19	15	24	23
	9	26	14	16	16	16	15
	17	25	18	8	11	8	16
	6	26	23	9	7	13	21
	4	23	22	5	8	6	14
	29	30	30	17	13	16	24

Analysis of variance $F = 10.3$ sig 0.001

Continued.....

Appendix II (Continued)

Date	16/8	19/8	28/8	1/9	3/9	7/9	17/9
	30	30	25	8	19	15	3
	5	14	18	19	9	2	13
	15	13	29	11	10	13	21
	5	19	13	11	9	15	16
No. eaten	23	21	8	5	3	5	8
	19	14	16	12	8	7	18
	11	27	7		9	8	14
	7	22	10		10	9	29
	8	23	19		6	14	27
	21	26	17		14	13	8

Q
+Analysis of variance $F = 3.655$ sig. 0.05

Appendix III

Prey biomasses presented in single prey experiments.

Mosquito larvae - mean dry weight 0.25mg. per individual

	Prey Density					
	2	5	10	30	50	70
Biomass presented mgs. dry wt.	0.5	1.25	2.5	7.5	12.5	17.5

Gammarus pulex - mean dry weight 3.328mgs per individual

	Prey Density					
	2	5	10	15	20	25
Biomass presented mgs.	6.65	16.64	33.28	49.9	66.56	83.2

Musca domestica - mean dry weight 4.78mgs per individual

	Prey Density					
	2	5	10	15	20	25
Biomass presented mgs.	9.56	23.9	47.8	71.2	95.6	119.5

Appendix IV : Mean energy gains, energy losses and net energy gains from single prey experiments (Chapter III) (in cal)

E.L. = energy loss, E.G. = energy gain, N.E.G. = net energy gain

		<u>Musca domestica</u> prey											
		<u>Complex environment</u>						<u>Simple environment</u>					
		2	5	10	15	20	25	2	5	10	15	20	25
<u>N. glauca</u>	E.G.	7.47 ± 4.068	9.171 ± 3.433	10.33 ± 3.286	8.559 ± 2.769	10.189 ± 2.303	8.1195 ± 3.308	5.066 ± 3.148	6.094 ± 3.847	6.981 ± 3.93	6.085 ± 3.726	6.012 ± 4.76	6.233 ± 3.257
	E.L.	0.366 ± 0.0119	0.361 ± 0.009	0.373 ± 0.0126	0.363 ± 0.009	0.378 ± 0.017	0.374 ± 0.0132	0.599 ± 0.181	0.536 ± 0.088	0.493 ± 0.094	0.5315 ± 0.124	0.505 ± 0.13	0.463 ± 0.087
	N.E.G.	7.1055 ± 4.08	8.809 ± 3.443	9.961 ± 3.3	8.196 ± 2.78	9.811 ± 2.306	7.745 ± 3.319	4.478 ± 3.29	5.558 ± 3.4	6.488 ± 4.02	5.504 ± 3.816	5.507 ± 4.25	5.769 ± 3.3
<u>N. maculata</u>	E.G.	14.99 ± 2.061	14.479 ± 2.93	14.22 ± 3.56	15.856 ± 3.22	16.258 ± 3.35	15.62 ± 4.196	19.004 ± 2.329	14.77 ± 4.327	16.65 ± 3.086	16.594 ± 3.918	15.137 ± 4.263	15.838 ± 3.466
	E.L.	0.662 ± 0.004	0.66 ± 0.008	0.674 ± 0.02	0.673 ± 0.012	0.668 ± 0.0136	0.67 ± 0.0102	0.707 ± 0.067	0.694 ± 0.027	0.728 ± 0.039	0.7067 ± 0.0368	0.7117 ± 0.037	0.691 ± 0.0036
	N.E.G.	13.772 ± 1.93	13.812 ± 2.937	13.54 ± 3.57	15.133 ± 3.23	15.587 ± 3.36	14.95 ± 4.2	18.297 ± 2.36	14.082 ± 4.337	15.896 ± 3.123	15.883 ± 3.437	14.426 ± 4.25	15.18 ± 3.496
<u>N. obliqua</u>	E.G.	9.832 ± 6.099	16.44 ± 2.79	15.77 ± 2	17.048 ± 1.86	15.31 ± 1.718	15.836 ± 2.435	15.436 ± 1.92	16.279 ± 2.385	16.178 ± 2.387	14.709 ± 2.367	15.298 ± 2.599	16.33 ± 1.517
	E.L.	0.517 ± 0.022	0.531 ± 0.021	0.537 ± 0.026	0.532 ± 0.026	0.542 ± 0.029	0.54 ± 0.019	0.596 ± 0.188	0.59 ± 0.05	0.58 ± 0.079	0.607 ± 0.045	0.568 ± 0.047	0.588 ± 0.052
	N.E.G.	9.3459 ± 6.109	15.969 ± 2.805	15.296 ± 2.036	16.449 ± 1.929	14.769 ± 1.702	15.296 ± 2.437	14.839 ± 1.922	15.688 ± 2.416	15.598 ± 2.432	14.101 ± 2.389	14.736 ± 2.64	15.744 ± 1.547

Appendix IV : Continued

		Gammarus pulex prey											
		Complex environment						Simple environment					
		2	5	10	15	20	25	2	5	10	15	20	25
<u>N. glauca</u>	E.G.	4.25 ± 3.7	9.411 ± 3.42	7.21 ± 3.79	10.053 ± 2.933	8.917 ± 2.9	8.74 ± 2.07	0 ± 0.223	0.6166 ± 1.5	1.48 ± 2.9	2.059 ± 2.9	1.498 ± 2.5	1.657 ± 1.68
	E.L.	0.382 ± 0.026	0.401 ± 0.033	0.402 ± 0.029	0.421 ± 0.033	0.41 ± 0.023	0.432 ± 0.035	0.896 ± 0.223	0.842 ± 0.195	0.951 ± 0.265	1.041 ± 0.22	0.994 ± 0.28	0.857 ± 0.194
	N.E.G.	3.872 ± 3.431	9.005 ± 3.218	6.833 ± 3.985	9.632 ± 2.754	8.506 ± 2.74	8.308 ± 2.08	- 0.866 ± 0.223	- 0.225 ± 1.488	0.533 ± 3.05	1.017 ± 3.05	0.5 ± 2.66	0.8 ± 1.836
<u>N. maculata</u>	E.G.	7.258 ± 6.3	12.71 ± 6.9	15.255 ± 4.94	13.46 ± 5	15.758 ± 4.7	13.04 ± 4.88	15.99 ± 6.5	18.88 ± 5.48	19.756 ± 6.56	24.39 ± 6.8	19.825 ± 5.235	22.08 ± 7.404
	E.L.	0.693 ± 0.02	0.693 ± 0.026	0.7013 ± 0.02	0.704 ± 0.02	0.704 ± 0.028	0.707 ± 0.038	0.869 ± 0.126	0.822 ± 0.09	0.798 ± 0.077	0.873 ± 0.136	0.826 ± 0.172	0.794 ± 0.049
	N.E.G.	6.575 ± 6.32	12.016 ± 6.896	14.55 ± 4.936	12.76 ± 4.99	15.054 ± 4.74	12.33 ± 4.86	15.126 ± 6.46	18.062 ± 5.48	18.962 ± 6.598	23.404 ± 6.817	19 ± 5.51	21.388 ± 7.41
<u>N. obliqua</u>	E.G.	15.2 ± 4.25	15.647 ± 4.178	18.5 ± 3.46	18.979 ± 3.97	17.74 ± 2.72	18.545 ± 3.137	11.473 ± 3.31	12.763 ± 2.95	14.43 ± 3.937	18.966 ± 2.769	16.57 ± 5.03	18.75 ± 4.7
	E.L.	0.587 ± 0.04	0.596 ± 0.04	0.606 ± 0.04	0.643 ± 0.02	0.628 ± 0.05	0.627 ± 0.02	0.732 ± 0.25	0.746 ± 0.17	0.774 ± 0.32	0.668 ± 0.07	0.613 ± 0.02	0.713 ± 0.2
	N.E.G.	14.623 ± 4.22	15.05 ± 4.14	17.899 ± 3.45	18.336 ± 3.97	17.112 ± 2.69	17.98 ± 3.13	10.741 ± 3.3	12.017 ± 2.96	13.66 ± 3.8	18.298 ± 2.79	15.96 ± 5.03	18.04 ± 4.65

Appendix IV : Continued

		Mosquito prey											
		<u>Complex environment</u>						<u>Simple environment</u>					
		2	5	10	30	50	70	2	5	10	30	50	70
<u>N.</u> <u>glauca</u>	E.G.	0.78 ± 0.42	2.0 ± 0.96	1.947 ± 0.98	2.948 ± 0.79	2.849 ± 1.45	3.33 ± 0.46	0.576 ± 0.736	1.45 ± 0.68	1.363 ± 0.87	1.816 ± 1.27	1.679 ± 1.21	1.698 ± 1.12
	E.L.	0.383 ± 0.02	0.381 ± 0.019	0.382 ± 0.012	0.391 ± 0.017	0.388 ± 0.012	0.03 ± 0.016	0.67 ± 0.19	0.765 ± 0.172	0.749 ± 0.12	0.667 ± 0.12	0.82 ± 0.224	0.855 ± 0.22
	N.E.G.	0.335 ± 0.397	1.625 ± 0.896	1.564 ± 0.92	2.557 ± 0.743	2.46 ± 0.59	2.71 ± 0.634	- 0.093 ± 0.81	0.685 ± 0.74	0.614 ± 0.85	1.149 ± 0.92	0.859 ± 1.19	0.842 ± 1.06
<u>N.</u> <u>maculata</u>	E.G.	2.198 ± 0.88	3.16 ± 0.99	4.223 ± 0.943	5.386 ± 1.086	6.11 ± 1.33	5.218 ± 0.875	4.283 ± 1.18	5.97 ± 1.48	6.994 ± 1.692	7.149 ± 1.31	8.306 ± 1.708	8.675 ± 2.6
	E.L.	0.702 ± 0.03	0.693 ± 0.019	0.708 ± 0.025	0.72 ± 0.026	0.722 ± 0.027	0.709 ± 0.02	0.883 ± 0.139	0.765 ± 0.08	0.807 ± 0.109	0.849 ± 0.097	0.823 ± 0.148	0.822 ± 0.106
	N.E.G.	1.496 ± 0.85	2.47 ± 0.989	3.516 ± 0.924	4.665 ± 1.06	5.39 ± 1.32	4.52 ± 0.87	3.4 ± 1.19	5.205 ± 1.5	6.187 ± 1.675	6.3 ± 1.3	7.483 ± 1.66	7.857 ± 2.65
<u>N.</u> <u>obliqua</u>	E.G.	0.842 ± 0.388	2.369 ± 0.96	2.61 ± 1.01	4.79 ± 1.28	5.22 ± 1.41	4.79 ± 1.22	2.945 ± 1.019	4.57 ± 1.28	5.36 ± 1.15	6.79 ± 1.16	6.79 ± 0.96	7.081 ± 0.71
	E.L.	0.547 ± 0.03	0.564 ± 0.02	0.597 ± 0.04	0.65 ± 0.04	0.645 ± 0.067	0.637 ± 0.034	0.609 ± 0.05	0.66 ± 0.05	0.62 ± 0.06	0.65 ± 0.08	0.677 ± 0.05	0.794 ± 0.07
	N.E.G.	0.295 ± 0.369	1.8 ± 0.939	2.017 ± 0.991	4.14 ± 1.25	4.58 ± 1.35	4.154 ± 1.19	2.34 ± 1.03	3.97 ± 1.28	4.74 ± 1.11	6.13 ± 1.17	6.11 ± 0.94	6.287 ± 0.738

Appendix v

Test of differences in proportions of captures in each handling time period between the three predator species feeding on all prey types (after Parker 1973).

Tables shows numbers of items in each handling time period and significance of the difference

(From T tables) - Arrows indicate direction of difference. GN = Total number of samples in distribution.

<u>Mosquito prey</u>			<u>Handling time period</u>					
	100 - 200	201 - 300	301 - 400	401 - 500	501 - 600	601 - 700		
<u>N. glauca</u>	$\begin{bmatrix} 15 \\ \uparrow 0.01 \end{bmatrix}$	$\begin{bmatrix} 25 \\ \uparrow 0.01 \end{bmatrix}$	$\begin{bmatrix} 52 \\ \uparrow 0.01 \end{bmatrix}$	$\begin{bmatrix} 84 \\ \uparrow 0.01 \end{bmatrix}$	$\begin{bmatrix} 69 \\ \uparrow 0.001 \end{bmatrix}$	$\begin{bmatrix} 43 \\ \uparrow 0.001 \end{bmatrix}$	(GN = 347)	
<u>N. maculata</u>	$\begin{bmatrix} 71 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 141 \\ \uparrow 0.1 \end{bmatrix}$	$\begin{bmatrix} 174 \\ \uparrow 0.01 \end{bmatrix}$	$\begin{bmatrix} 126 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 58 \\ \uparrow 0.05 \end{bmatrix}$	$\begin{bmatrix} 40 \\ \text{n.sig.} \end{bmatrix}$	(GN = 678)	
<u>N. obliqua</u>	$\begin{bmatrix} 36 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 71 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 141 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 83 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 52 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 22 \\ \text{n.sig.} \end{bmatrix}$	(GN = 427)	
<u>Gammarus prey</u>			<u>Handling time period</u>					
	1000 - 1500	1501 - 2000	2001 - 2500	2501 - 3000	3001 - 3500	3501 - 4000	4001 →	
<u>N. glauca</u>	$\begin{bmatrix} 3 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 4 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 4 \\ \uparrow 0.02 \end{bmatrix}$	$\begin{bmatrix} 13 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 13 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 7 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 20 \\ \uparrow 0.02 \end{bmatrix}$	(GN=61)
<u>N. maculata</u>	$\begin{bmatrix} 5 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 15 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 22 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 14 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 19 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 11 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 13 \\ \text{n.sig.} \end{bmatrix}$	(GN=10)
<u>N. obliqua</u>	$\begin{bmatrix} 6 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 17 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 15 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 24 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 12 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 7 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 20 \\ \text{n.sig.} \end{bmatrix}$	(GN=110)
<u>Musca prey</u>			<u>Handling time period</u>					
	3001 - 4000	4001 - 5000	5001 - 6000	6001 - 7000	7001 - 8000	8001 - 9001		
<u>N. glauca</u>	$\begin{bmatrix} 4 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 3 \\ \uparrow 0.1 \end{bmatrix}$	$\begin{bmatrix} 9 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 5 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 11 \\ \uparrow 0.05 \end{bmatrix}$	$\begin{bmatrix} 9 \\ \text{n.sig.} \end{bmatrix}$	(GN = 67)	
<u>N. maculata</u>	$\begin{bmatrix} 7 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 10 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 14 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 7 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 5 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 5 \\ \text{n.sig.} \end{bmatrix}$	(GN = 79)	
<u>N. obliqua</u>	$\begin{bmatrix} 15 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 9 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 18 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 19 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 12 \\ \text{n.sig.} \end{bmatrix}$	$\begin{bmatrix} 5 \\ \text{n.sig.} \end{bmatrix}$	(GN = 117)	

Appendix VI

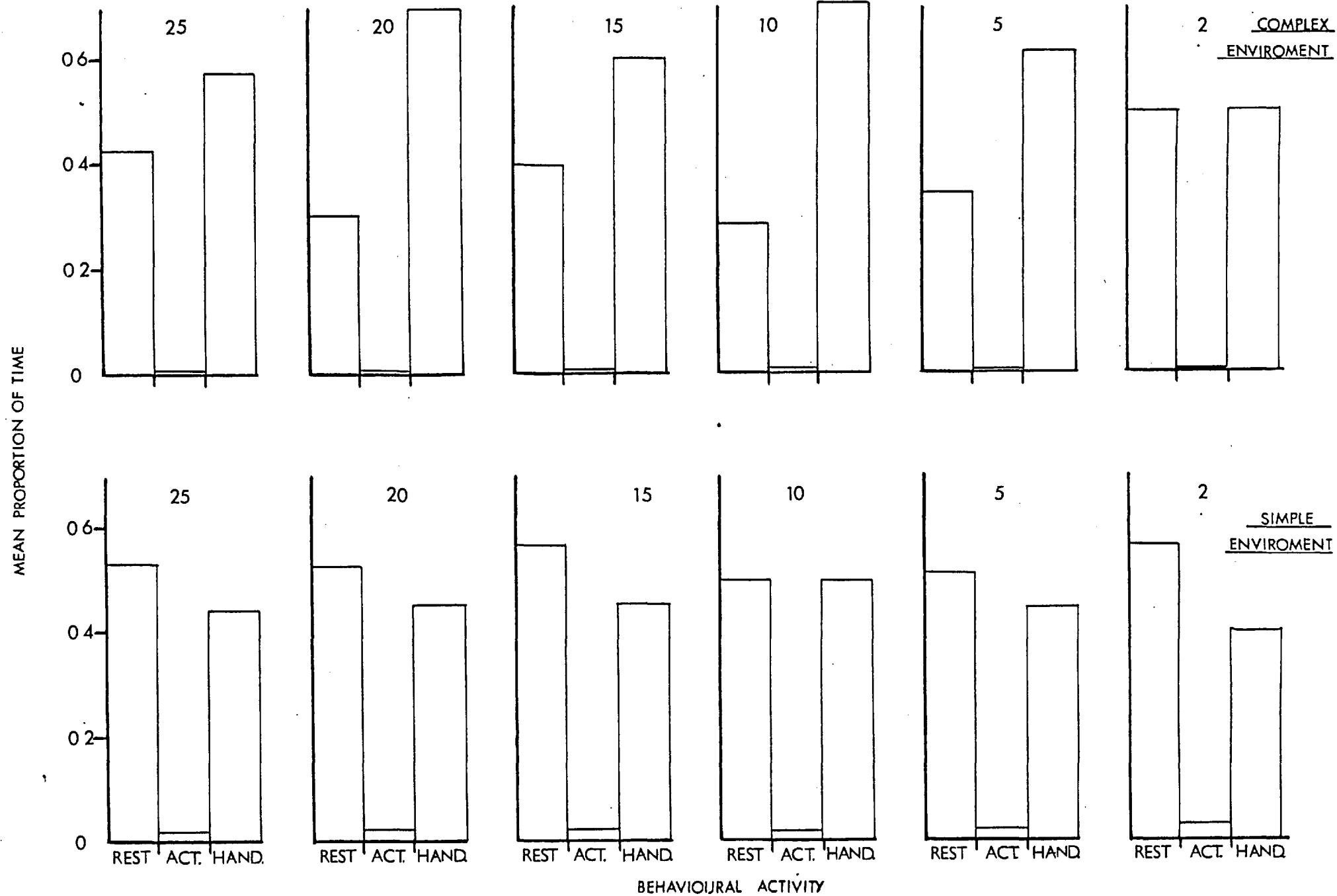
Time allocation of the three main behavioural activities in the presence of six densities of Musca domestica and Gammarus pulex (25, 20, 15, 10, 5 and 2) by N. glauca, N. maculata and N. obliqua in both simple and complex environments during 3h experiments.

REST - Total rest time

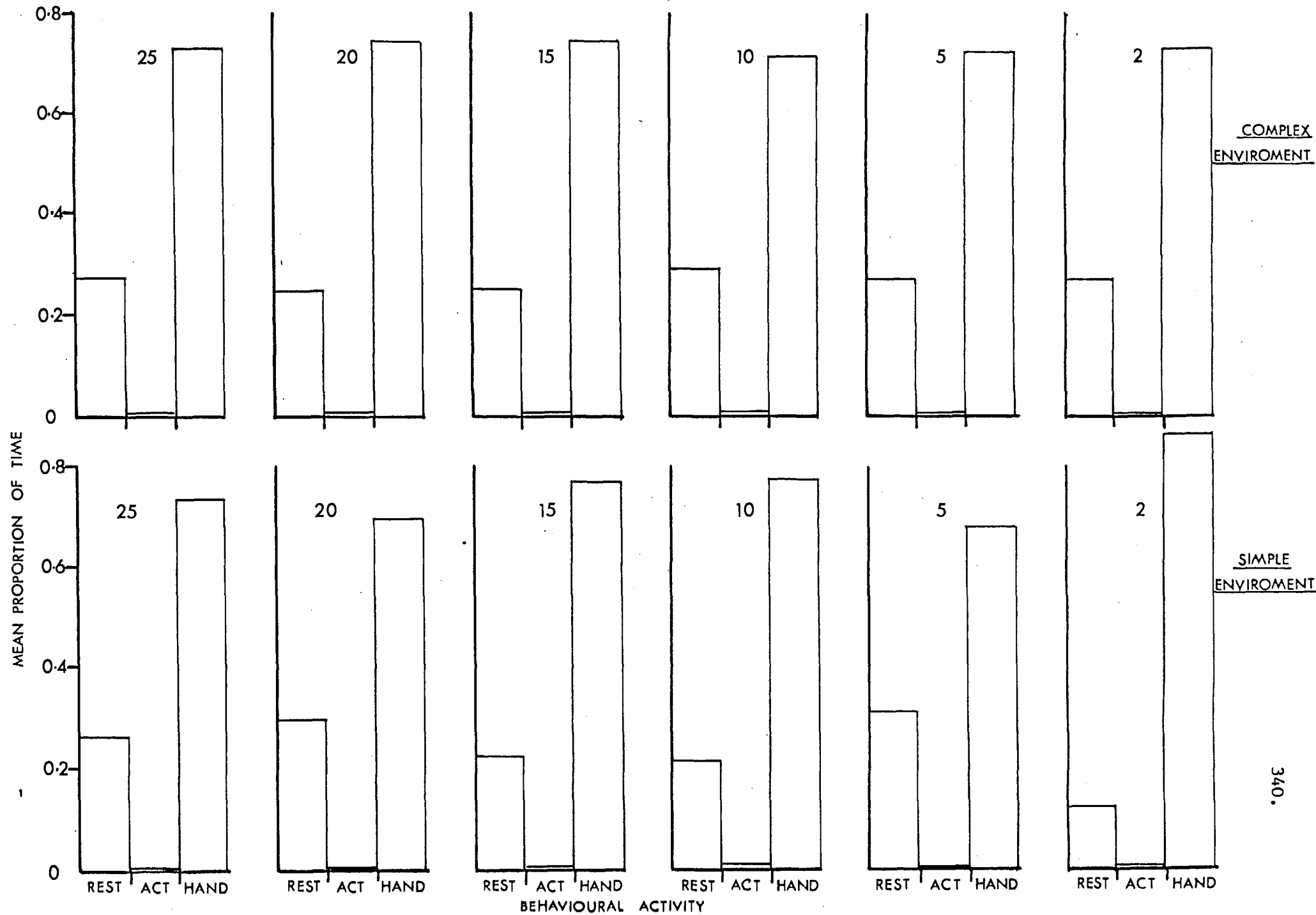
ACT - Total time active including activity associated with and without feeding.

HAND - Total handling time on prey.

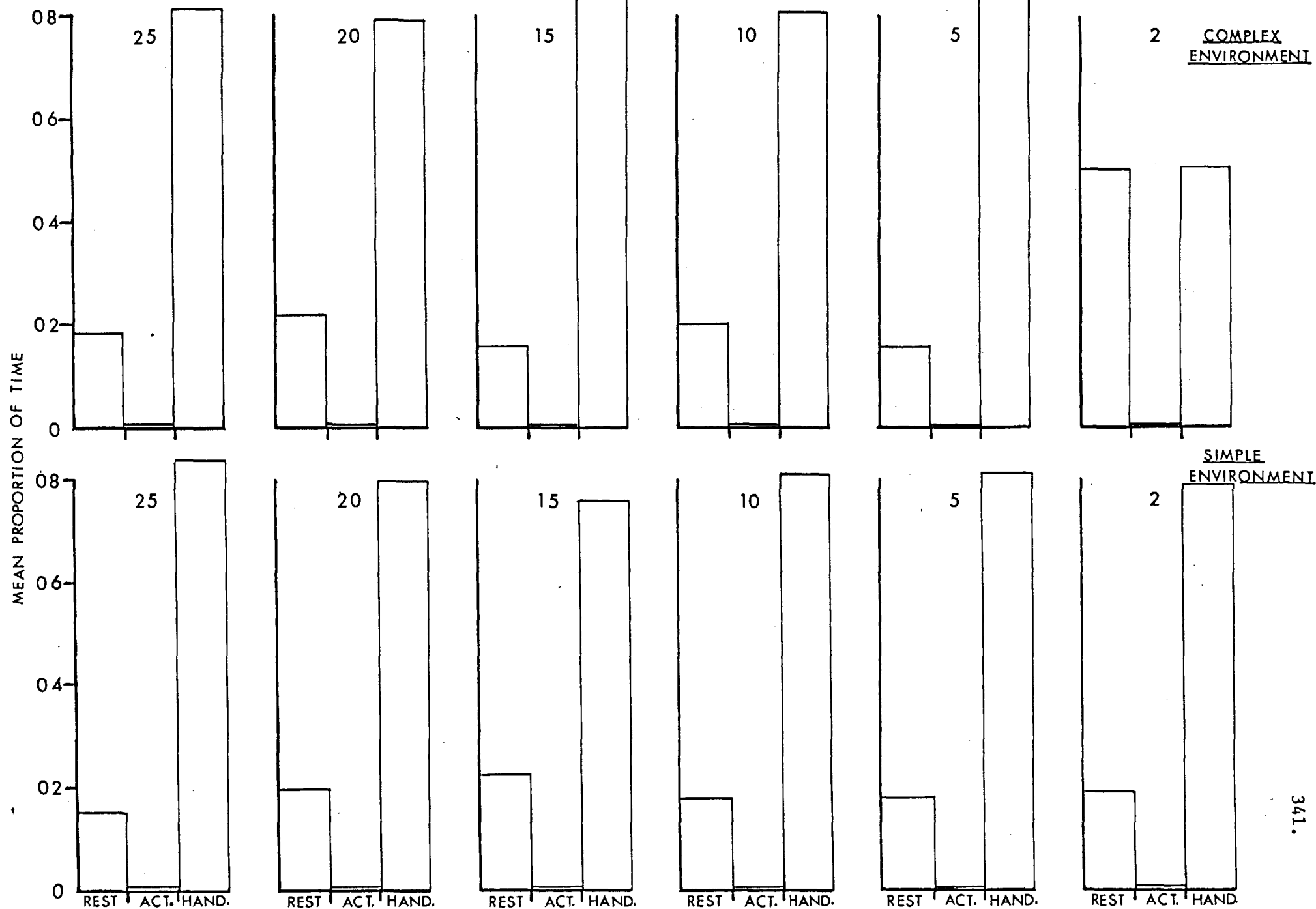
N. glauca feeding on Musca domestica



N. maculata feeding on Musca domestica

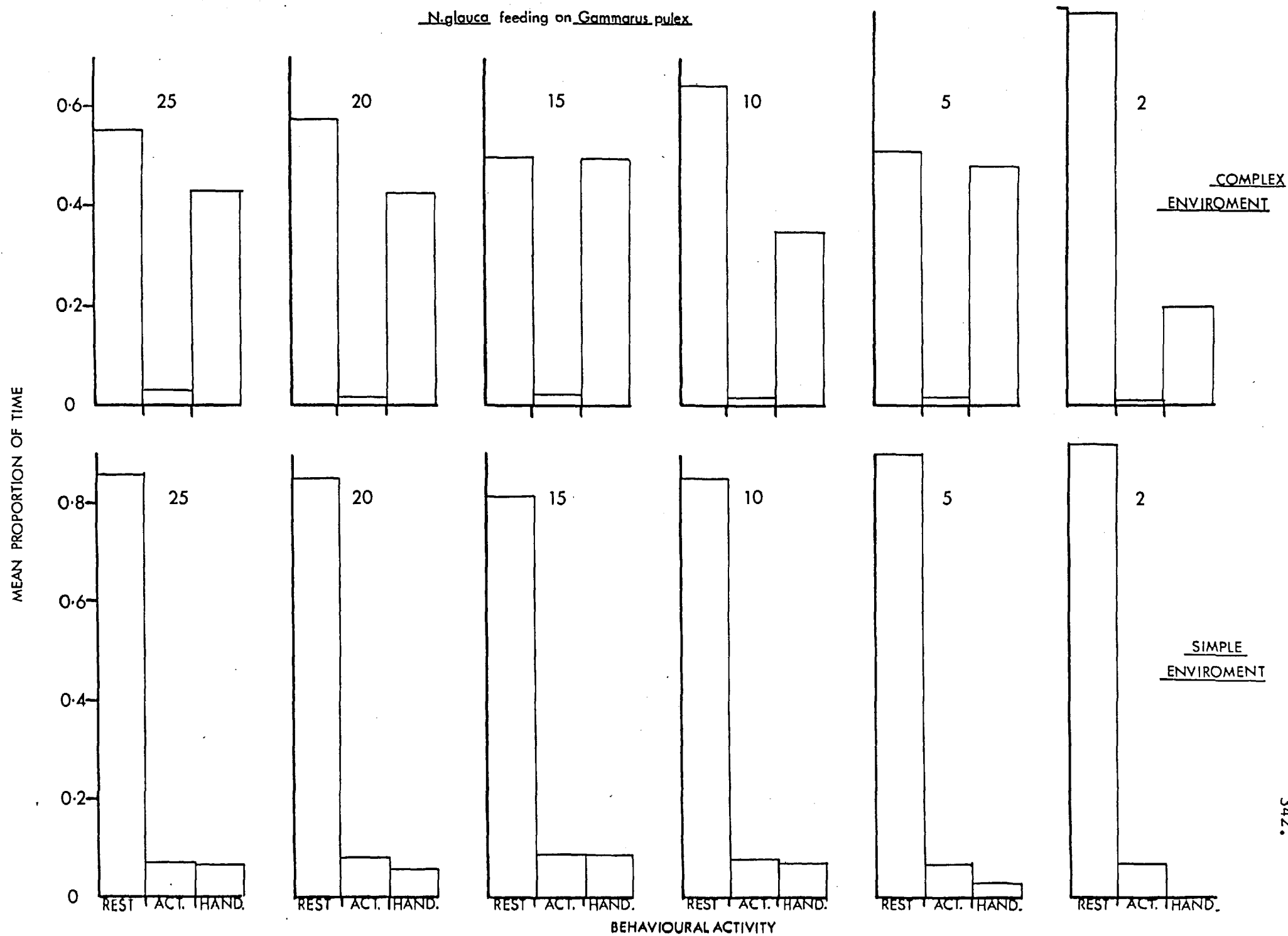


N. obliqua feeding on Musca domestica

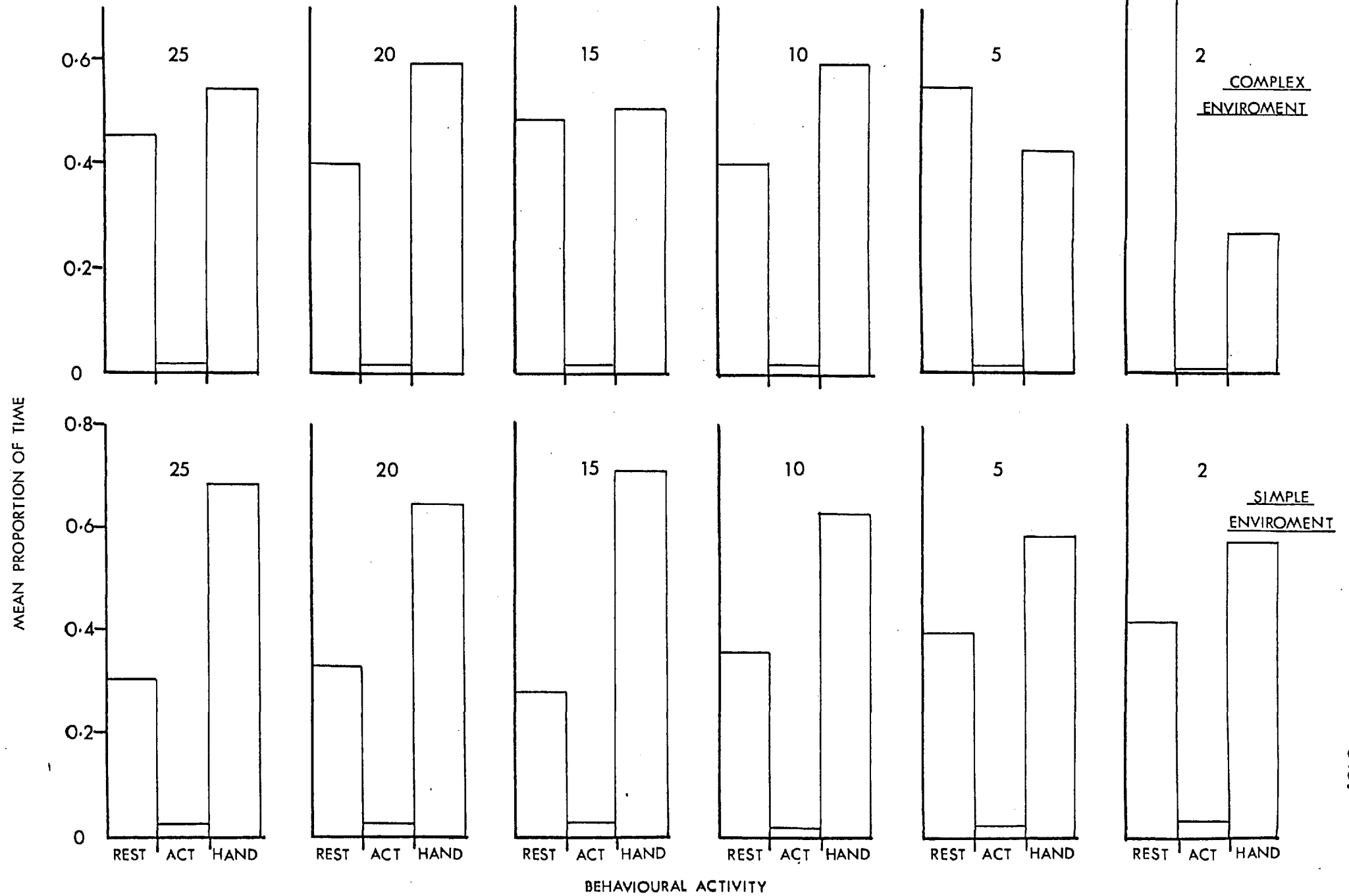


-A JOURNAL ACTIVITY

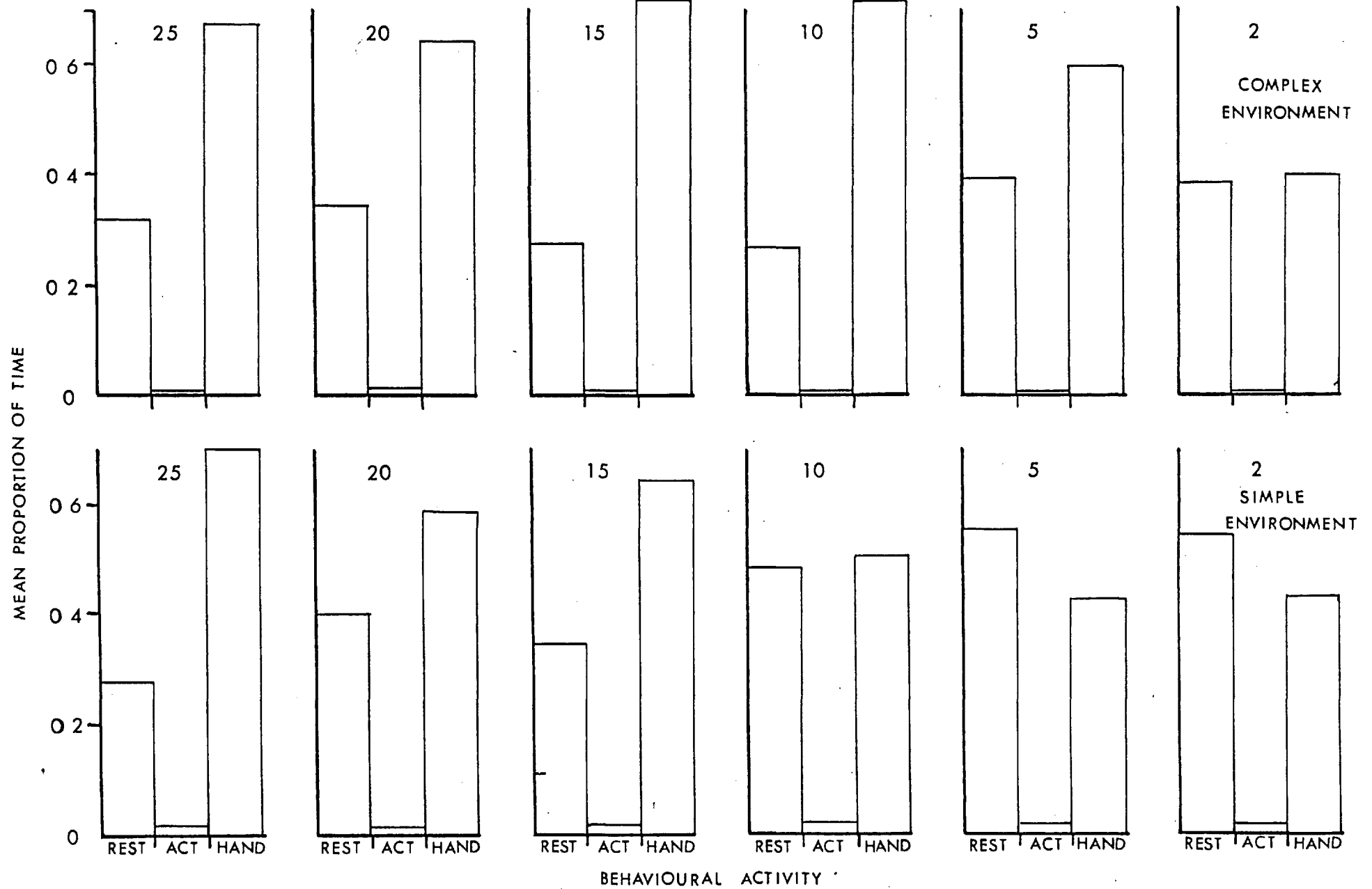
N. glauca feeding on Gammarus pulex



N. maculata feeding on Gammarus pulex.



N. obliqua feeding on Gammarus pulex



Appendix VII(a)

Comparison of the proportions of time spent feeding on each of the three prey types, and between environments for each predator species.

Tables show mean proportions of time feeding and significance between values (T test on original data).

Q = Mosquito larvae; M = Musca; G = Gammarus; S = Simple; C = Complex.

Prey Density (mosquito density in brackets)

<u>N. glauca</u>		2	5	10	15(30)	20(50)	25(70)
Complex	Q						
	M	n.sig.	n.sig.	n.sig.	n.sig.	n.sig.	n.sig.
	G						
Simple	Q						
	M	0.1	0.002	0.1	0.1	0.05	0.02
	G						
Difference		S C	S C	S C	S + C	S + C	S + C
Between		S C	S C	S C	S C	S + C	S C
Environments		S + C	S + C	S + C	S + C	S + C	S + C

Cont.....

Appendix VII(a) (Continued)

Prey Density (mosquito density in brackets)

N. maculata		2	5	10	15(30)	20(50)	25(70)
Complex	Q			0.54		0.67	
	M	n.sig [0.29] 0.001	n.sig [0.4] 0.01	0.71	n.sig. n.sig [0.63] n.sig.	0.75	n.sig. n.sig [0.65] n.sig.
	G	[0.73] 0.002	[0.72] 0.05	0.59	[0.74] 0.05	0.61	[0.73] 0.1
Simple	Q		0.607	0.748	0.727	0.775	0.782
	M	n.sig [0.494] 0.001	0.68 n.sig.	0.777 n.sig.	0.772 n.sig.	0.695 n.sig.	0.735 n.sig.
	G	[0.869] 0.005	0.585	0.628	0.71	0.647	0.681
Difference	Q	S + C	S + C	S + C	S + C	S C	S C
		0.01	0.02	0.01	0.1		
Between	M	S + C	S C	S C	S C	S C	S C
		0.1					
Environments	G	S + C	S C	S C	S + C	S C	S C
		0.1			0.1		

Prey Density (mosquito density in brackets)

N. obliqua		2	5	10	15(30)	20(50)	25(70)
Complex	Q						
	M	0.001 [0.116] 0.02	0.001 [0.274] 0.002	0.001 [0.301] 0.001	0.05 [0.544] 0.001	n.sig [0.596] 0.05	0.1 [0.531] 0.02
	G	[0.501] n.sig.	[0.839] n.sig	[0.801] n.sig	[0.843] n.sig.	[0.784] 0.05	[0.811] 0.05
Simple	Q						
	M	n.sig [0.333] 0.001	n.sig [0.531] 0.002	n.sig [0.58] 0.002	0.734 n.sig	0.01 [0.723] n.sig	n.sig [0.745] 0.02
	G	[0.791] 0.001	[0.814] 0.001	[0.812] 0.001	0.759	[0.799] n.sig	[0.839] 0.1
Difference	Q	S + C	S + C	S + C	S + C	S + C	S + C
		0.001	0.01	0.001	0.02	0.1	0.01
Between	M	S + C	S C	S C	S C	S C	S C
		0.1					
Environments	G	S + C	S + C	S + C	S C	S C	S C
		0.05	0.01	0.02			

Appendix VII(b) Comparison of feeding times between the three predators with all three prey types in both environments.

Tables show mean proportions of time feeding and significance between values (T test on original data).

Complex		Prey density (mosquito density in brackets)														
		2		5		10		15(30)		20(50)		25(70)				
<u>Musca</u>	G															
	M	n.sig	$\begin{bmatrix} 0.5 \\ 0.73 \end{bmatrix}$	0.1	$\begin{bmatrix} 0.62 \\ 0.72 \end{bmatrix}$	n.sig.	0.71	n.sig.	0.01	$\begin{bmatrix} 0.6 \\ 0.74 \end{bmatrix}$	n.sig	0.69	n.sig.			
	O		$\begin{bmatrix} 0.501 \\ 0.501 \end{bmatrix}$	n.sig.	0.1	$\begin{bmatrix} 0.839 \\ 0.839 \end{bmatrix}$	n.sig.	0.71	n.sig.	0.01	$\begin{bmatrix} 0.843 \\ 0.843 \end{bmatrix}$	n.sig	0.75	n.sig		
<u>Gammarus</u>	G															
	M	0.01	$\begin{bmatrix} 0.2 \\ 0.27 \end{bmatrix}$	n.sig.	0.49	$\begin{bmatrix} 0.43 \\ 0.43 \end{bmatrix}$	n.sig.	0.02	$\begin{bmatrix} 0.35 \\ 0.59 \end{bmatrix}$	0.05	0.05	$\begin{bmatrix} 0.49 \\ 0.51 \end{bmatrix}$	n.sig.	0.01	$\begin{bmatrix} 0.43 \\ 0.61 \end{bmatrix}$	0.1
	O		$\begin{bmatrix} 0.606 \\ 0.606 \end{bmatrix}$		0.6	$\begin{bmatrix} 0.6 \\ 0.6 \end{bmatrix}$		0.05	$\begin{bmatrix} 0.72 \\ 0.72 \end{bmatrix}$	n.sig.	0.05	$\begin{bmatrix} 0.722 \\ 0.722 \end{bmatrix}$	0.05	0.01	$\begin{bmatrix} 0.644 \\ 0.644 \end{bmatrix}$	n.sig.
Mosquito larvae	G															
	M	n.sig	$\begin{bmatrix} 0.112 \\ 0.29 \end{bmatrix}$	0.01	n.sig	$\begin{bmatrix} 0.34 \\ 0.4 \end{bmatrix}$	n.sig.	n.sig	$\begin{bmatrix} 0.33 \\ 0.54 \end{bmatrix}$	0.02	n.sig	$\begin{bmatrix} 0.51 \\ 0.63 \end{bmatrix}$	0.05	n.sig	$\begin{bmatrix} 0.49 \\ 0.67 \end{bmatrix}$	0.05
	O		$\begin{bmatrix} 0.116 \\ 0.116 \end{bmatrix}$	0.01		$\begin{bmatrix} 0.274 \\ 0.274 \end{bmatrix}$	0.1	n.sig	$\begin{bmatrix} 0.301 \\ 0.301 \end{bmatrix}$	0.01	n.sig	$\begin{bmatrix} 0.544 \\ 0.544 \end{bmatrix}$	n.sig	n.sig	$\begin{bmatrix} 0.596 \\ 0.596 \end{bmatrix}$	n.sig

Simple		Prey density (mosquito density in brackets)																	
		2		5		10		15(30)		20(50)		25(70)							
<u>Musca</u>	G																		
	M	0.01	$\begin{bmatrix} 0.4 \\ 0.869 \end{bmatrix}$	0.001	0.01	$\begin{bmatrix} 0.453 \\ 0.68 \end{bmatrix}$	n.sig	0.02	$\begin{bmatrix} 0.49 \\ 0.77 \end{bmatrix}$	0.05	0.05	$\begin{bmatrix} 0.427 \\ 0.772 \end{bmatrix}$	0.05	0.02	$\begin{bmatrix} 0.453 \\ 0.695 \end{bmatrix}$	0.1	0.44		
	O		$\begin{bmatrix} 0.791 \\ 0.791 \end{bmatrix}$	n.sig		$\begin{bmatrix} 0.814 \\ 0.814 \end{bmatrix}$	n.sig.		$\begin{bmatrix} 0.812 \\ 0.812 \end{bmatrix}$	n.sig.		$\begin{bmatrix} 0.759 \\ 0.759 \end{bmatrix}$	n.sig		$\begin{bmatrix} 0.799 \\ 0.799 \end{bmatrix}$	n.sig	0.735	0.839	
<u>Gammarus</u>	G																		
	M	0.001	$\begin{bmatrix} 0 \\ 0.57 \end{bmatrix}$	0.001	0.01	$\begin{bmatrix} 0.028 \\ 0.585 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.065 \\ 0.678 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.088 \\ 0.71 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.063 \\ 0.647 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.0708 \\ 0.681 \end{bmatrix}$	0.001
	O		$\begin{bmatrix} 0.428 \\ 0.428 \end{bmatrix}$			$\begin{bmatrix} 0.414 \\ 0.414 \end{bmatrix}$	0.1	0.001	$\begin{bmatrix} 0.507 \\ 0.507 \end{bmatrix}$	n.sig.	0.001	$\begin{bmatrix} 0.64 \\ 0.64 \end{bmatrix}$	n.sig	0.001	$\begin{bmatrix} 0.586 \\ 0.586 \end{bmatrix}$	n.sig	0.001	$\begin{bmatrix} 0.705 \\ 0.705 \end{bmatrix}$	n.sig
Mosquito larvae	G																		
	M	0.01	$\begin{bmatrix} 0.098 \\ 0.498 \end{bmatrix}$	0.001	0.002	$\begin{bmatrix} 0.249 \\ 0.607 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.229 \\ 0.748 \end{bmatrix}$	0.001	0.002	$\begin{bmatrix} 0.309 \\ 0.723 \end{bmatrix}$	0.002	0.001	$\begin{bmatrix} 0.29 \\ 0.775 \end{bmatrix}$	0.001	0.001	$\begin{bmatrix} 0.279 \\ 0.782 \end{bmatrix}$	0.001
	O		$\begin{bmatrix} 0.333 \\ 0.333 \end{bmatrix}$	0.05		$\begin{bmatrix} 0.531 \\ 0.531 \end{bmatrix}$	n.sig	0.001	$\begin{bmatrix} 0.58 \\ 0.58 \end{bmatrix}$	0.02	0.002	$\begin{bmatrix} 0.734 \\ 0.734 \end{bmatrix}$	n.sig	0.001	$\begin{bmatrix} 0.723 \\ 0.723 \end{bmatrix}$	n.sig	0.001	$\begin{bmatrix} 0.745 \\ 0.745 \end{bmatrix}$	n.sig

G = N. glauca
M = N. maculata
O = N. obliqua

Appendix VIII(a)

Comparison of the proportions of activity time with each of the three prey types in both environments, and between environments for each predator species.

Tables show proportions of time active and significance between values (T test on original data)

Q = Mosquito larvae; M = Musca; G = Gammarus. S=Simple, C=Complex.

		Prey Density (mosquito density in brackets)															
<u>N. glauca</u>		2	5	10	15(30)	20(50)	25(70)										
Complex	Q	0.0037]	0.0028]	0.0041]	0.003]	0.0042]	0.0045]										
	M	0.005 n.sig.	0.0076] 0.05	0.007] 0.1	0.01] 0.01	0.0088] 0.02	0.0113] 0.001										
	G	0.0053]	0.00516] n.sig	0.006] n.sig	0.0063] 0.1	0.006] 0.1	0.0082] n.sig										
Simple	Q	0.032]	0.024]	0.019]	0.024]	0.0203]	0.0154]										
	M	n.sig 0.068] 0.05	0.02 0.0627] 0.01	0.002 0.076] 0.001	0.1 0.0908] 0.001	0.001 0.081] 0.002	0.001 0.0636] 0.001										
	G	0.041] 0.1	0.053] n.sig	0.0508] n.sig	0.041] 0.002	0.0606] n.sig	0.0636] n.sig										
Difference	Q	S → C	S → C	S → C	S → C	S → C	S → C										
		0.01	0.01	0.01	0.01	0.02	0.05										
	Between	M	S → C	S → C	S → C	S → C	S → C	S → C									
Environments	G	S → C	S → C	S → C	S → C	S → C	S → C										
		0.01	0.001	0.001	0.001	0.001	0.001										

Cont.....

Appendix VIII(a) (Continued)

		Prey Density (mosquito density in brackets)												
<u>N. maculata</u>		2		5		10		15(30)		20(50)		25(70)		
Complex	Q													
	M	0.01	$\begin{bmatrix} 0.0027 \\ 0.0055 \end{bmatrix}$	0.02	$\begin{bmatrix} 0.0033 \\ 0.0071 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.0045 \\ 0.0082 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.0042 \\ 0.0085 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.0035 \\ 0.0085 \end{bmatrix}$	0.02	$\begin{bmatrix} 0.00386 \\ 0.0086 \end{bmatrix}$	0.05
	G		n.sig	0.05	n.sig	0.01	n.sig	0.01	n.sig	0.01	n.sig	0.01	n.sig.	
Simple	Q													
	M	0.02	$\begin{bmatrix} 0.0092 \\ 0.0317 \end{bmatrix}$	0.02	$\begin{bmatrix} 0.0045 \\ 0.024 \end{bmatrix}$	0.01	$\begin{bmatrix} 0.0123 \\ 0.0212 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.0091 \\ 0.031 \end{bmatrix}$	0.02	$\begin{bmatrix} 0.0098 \\ 0.0258 \end{bmatrix}$	n.sig	$\begin{bmatrix} 0.0065 \\ 0.0202 \end{bmatrix}$	0.001
	G		n.sig	0.02	n.sig	n.sig	n.sig	0.01	n.sig	0.01	n.sig	0.02	n.sig	
Difference	Q	<u>S</u>	<u>C</u>	<u>S</u>	<u>C</u>	S + C	S + C	S + C	S + C	S + C	S + C	<u>S</u>	<u>C</u>	
Between	M	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	
Environments	G	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	
		0.01	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.05	
		Prey Density (mosquito density in brackets)												
<u>N. obliqua</u>		2		5		10		15(30)		20(50)		25(70)		
Complex	Q													
	M	0.1	$\begin{bmatrix} 0.002 \\ 0.0075 \end{bmatrix}$	0.002	$\begin{bmatrix} 0.0036 \\ 0.0084 \end{bmatrix}$	0.01	$\begin{bmatrix} 0.0034 \\ 0.0093 \end{bmatrix}$	0.001	$\begin{bmatrix} 0.0026 \\ 0.012 \end{bmatrix}$	0.001	$\begin{bmatrix} 0.004 \\ 0.0107 \end{bmatrix}$	0.001	$\begin{bmatrix} 0.004 \\ 0.0108 \end{bmatrix}$	0.001
	G		0.05	0.05	n.sig	0.01	n.sig	0.01	n.sig	0.001	n.sig	0.001	n.sig	
Simple	Q													
	M		$\begin{bmatrix} 0.0083 \\ 0.0186 \end{bmatrix}$	n.sig	$\begin{bmatrix} 0.0079 \\ 0.0195 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.0075 \\ 0.021 \end{bmatrix}$	n.sig	$\begin{bmatrix} 0.0093 \\ 0.0133 \end{bmatrix}$	n.sig	$\begin{bmatrix} 0.0058 \\ 0.0096 \end{bmatrix}$	0.05	$\begin{bmatrix} 0.008 \\ 0.0172 \end{bmatrix}$	n.sig
	G		0.0093	0.05	n.sig	n.sig	n.sig	n.sig	n.sig	0.002	0.02	0.05	n.sig	
Difference	Q	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	
Between	M	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	
Environments	G	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	S + C	
		0.05	0.05	0.05	0.05	0.1	0.01	0.01	0.01	0.01	0.01	0.01	0.05	

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Appendix VIII(b)

Comparison of activity times between the three predators with all three prey types in both environments.

Tables show mean proportions of time active and significance between values (T test on original data).

		Prey Density (mosquito density in brackets)												
<u>Complex</u>		2		5		10		15(30)		20(50)		25(70)		
<u>Musca</u>	G													
	M	0.05	[0.0037]	n.sig		0.0028	n.sig	0.0041	n.sig	0.003	n.sig	0.0042	n.sig	
	O		[0.0027]	n.sig		0.0033	n.sig	0.0045	n.sig	0.00419	n.sig	0.0034	n.sig	
			[0.002]			0.0036		0.0034		0.0036		0.004		
Gammarus	G		0.005			0.0076		0.0075		[0.0101]	n.sig	0.0088		
	M		0.0055	n.sig		0.0071	n.sig	0.0081	n.sig	0.0085	n.sig	0.0085	n.sig	
	O		0.0075			0.0084		0.0093		[0.012]	0.05	0.0107		
Mosquito larvae	G		[0.0053]	n.sig		0.00516		0.006		[0.0063]	0.05	[0.006]	0.01	
	M	n.sig	[0.0082]	n.sig		0.0071	n.sig	0.009	n.sig	0.020.0109	0.05	0.0020.011	0.01	
	O		[0.004]	0.05		0.0062		0.0078		[0.0125]	n.sig	[0.0121]	n.sig	
												0.1	[0.0082]	n.sig
													[0.009]	n.sig
													[0.0115]	n.sig

		Prey Density (mosquito density in brackets)											
<u>Simple</u>		2		5		10		15(30)		20(50)		25(70)	
<u>Musca</u>	G												
	M	0.002	[0.0324]	0.05	0.01	[0.024]	0.001	[0.019]	n.sig	[0.024]	0.05	[0.0203]	n.sig
	O		[0.0092]	n.sig		[0.0045]	0.1	[0.0123]	n.sig	[0.0091]	0.05	[0.0098]	n.sig
			[0.0083]			[0.0079]		[0.0075]		[0.0093]		[0.0058]	
												n.sig	[0.0154]
													0.1
													n.sig
<u>Gammarus</u>	G		[0.068]	0.02	0.002	[0.062]	0.01	[0.076]	0.002	[0.0908]	0.001	[0.081]	0.001
	M	0.001	[0.0317]	n.sig		[0.024]	n.sig	0.002	[0.0212]	0.001	0.002	[0.0258]	0.001
	O		[0.0186]			[0.0195]		[0.021]	n.sig	[0.0133]	0.05	[0.0096]	n.sig
													0.001
													[0.0636]
													0.002
													n.sig
<u>Mosquito larvae</u>	G		[0.0409]	n.sig	0.001	[0.0531]	0.002	[0.0508]	0.01	[0.041]	n.sig	[0.0606]	0.02
	M	0.002	[0.0316]	0.01		[0.0172]	n.sig	[0.0229]	0.01	[0.0286]	n.sig	0.002	[0.025]
	O		[0.0093]			[0.013]		[0.031]	n.sig	[0.0126]	0.01	[0.0145]	0.05
													0.01
													[0.0636]
													0.01
													n.sig

G = N. glauca

M = N. maculata

O = N. obliqua

Appendix IX

Histograms showing the mean proportion of

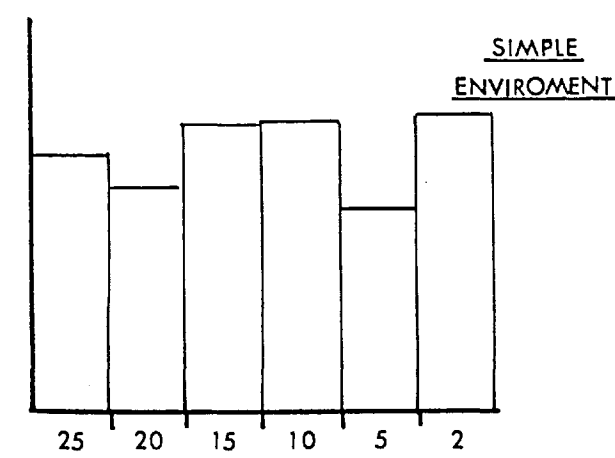
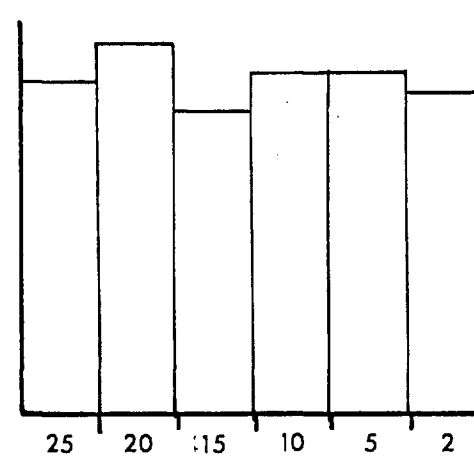
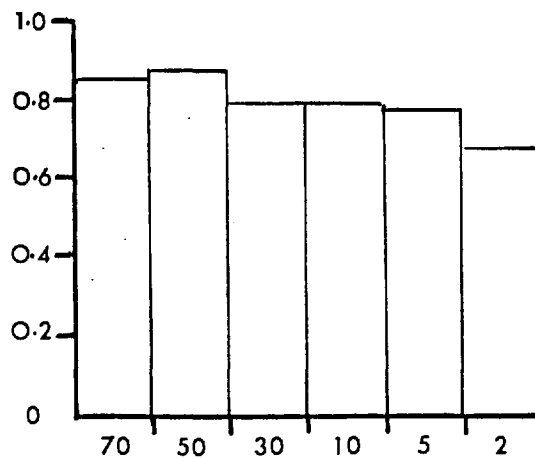
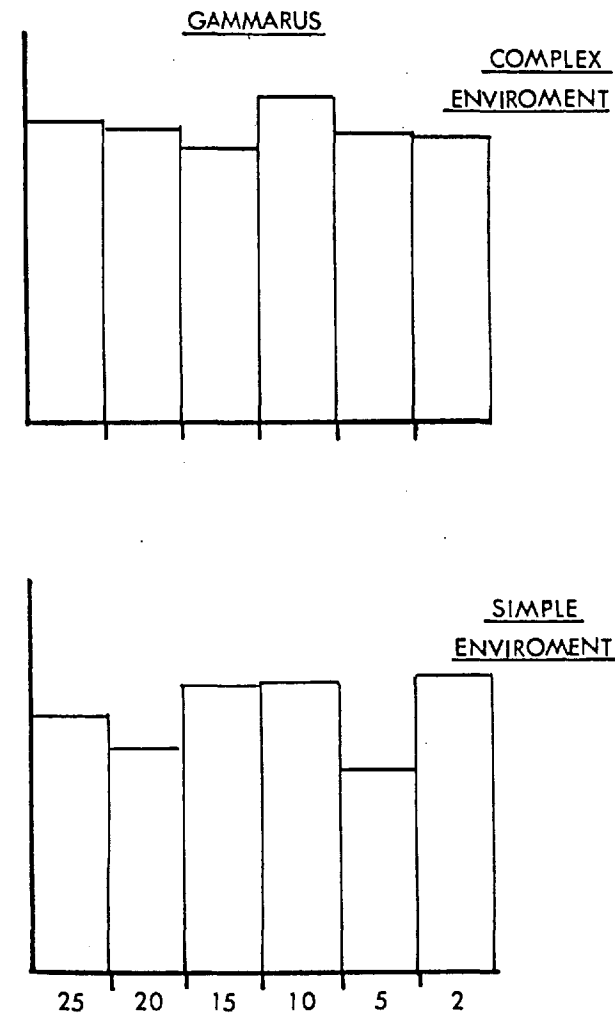
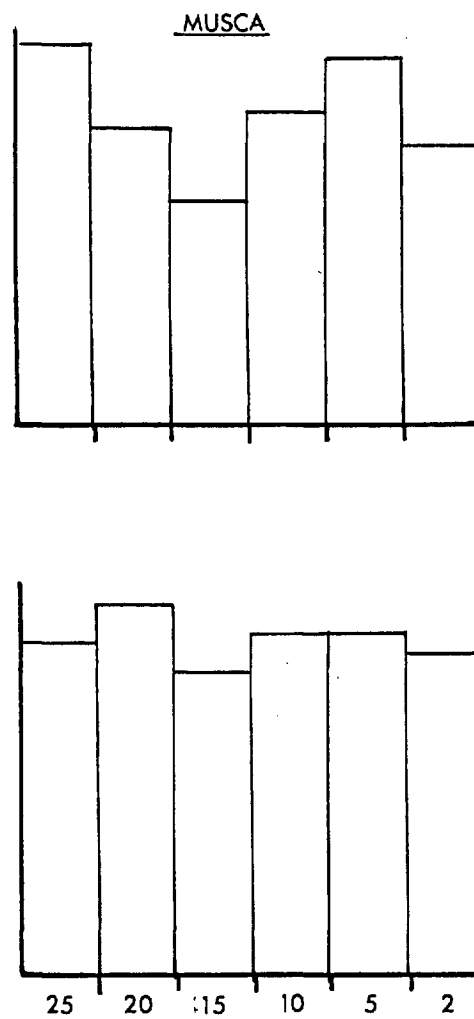
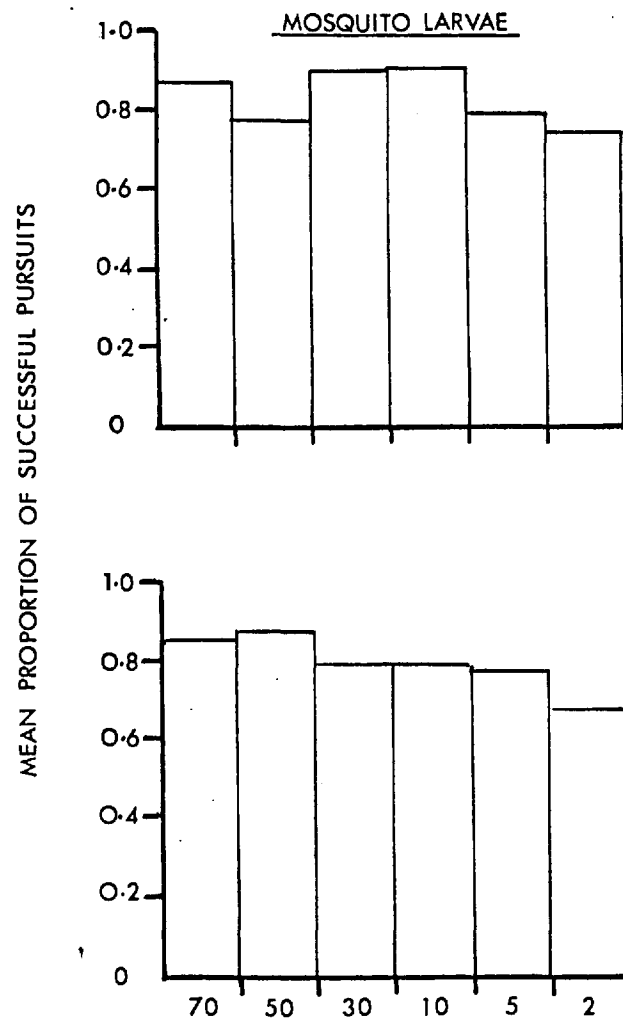
successful pursuits ($\frac{\text{successful pursuits}}{\text{Total pursuits}}$),

successful attacks ($\frac{\text{successful attacks}}{\text{Total attacks}}$),

and successful captures ($\frac{\text{successful captures}}{\text{Total strikes}}$)

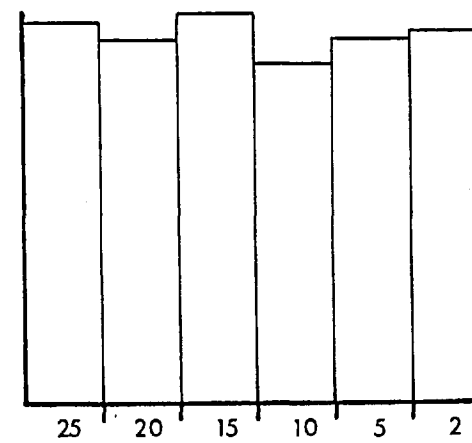
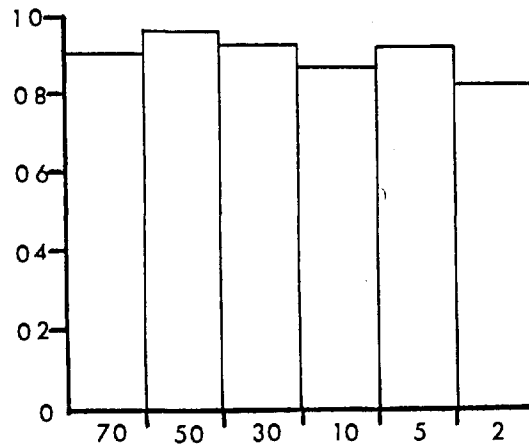
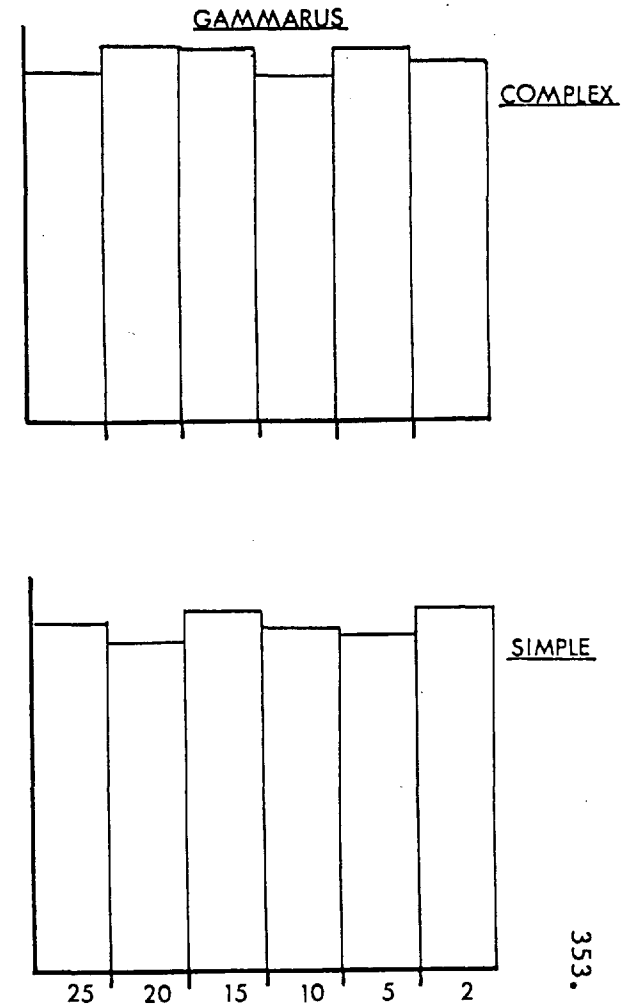
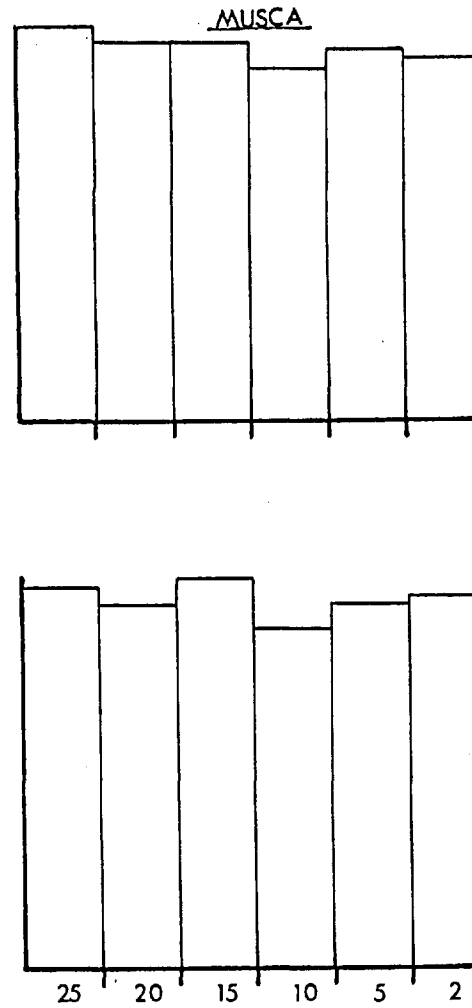
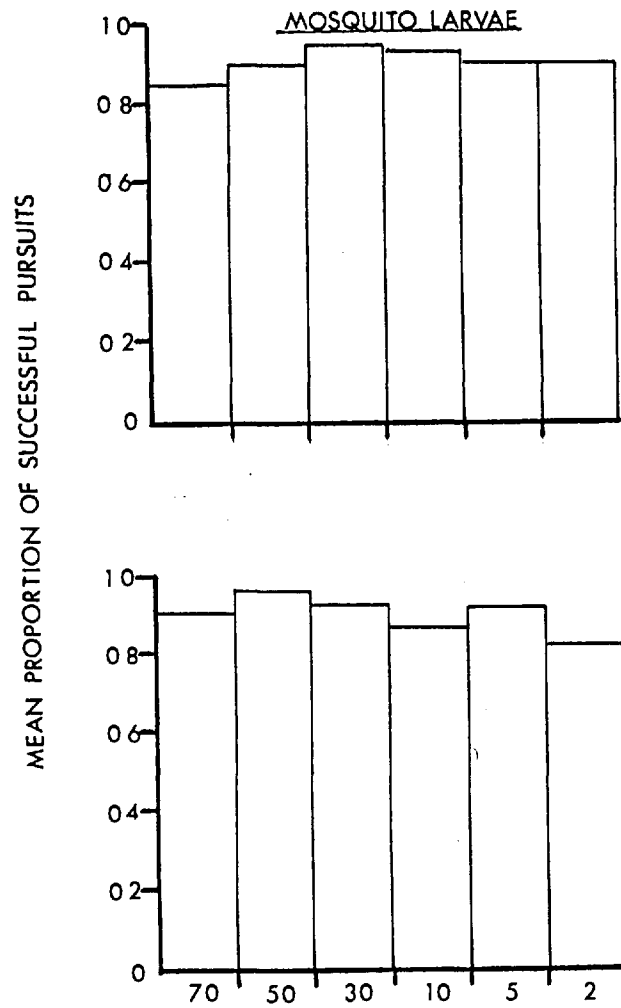
for N. maculata and N. obliqua feeding on six densities of each of the three prey types in both simple and complex environments.

N. maculata pursuit success



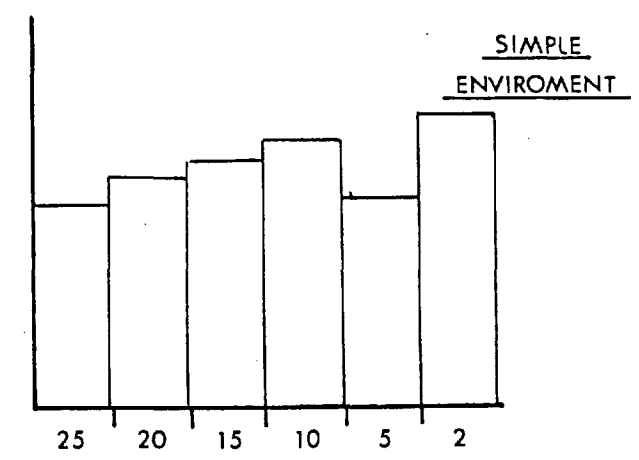
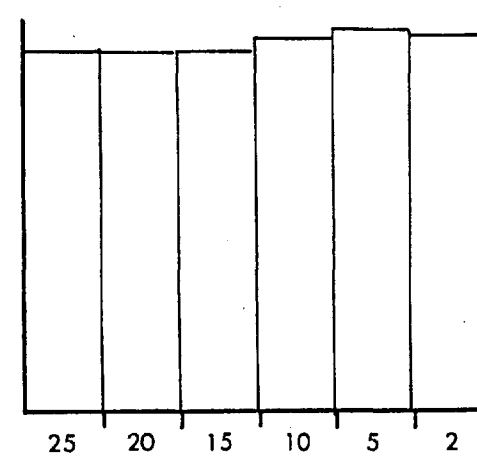
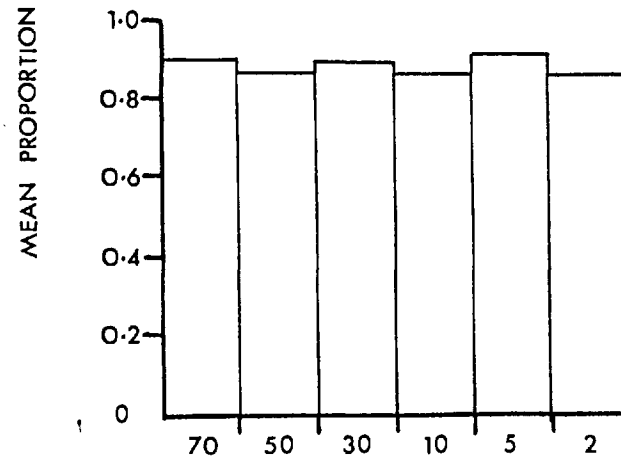
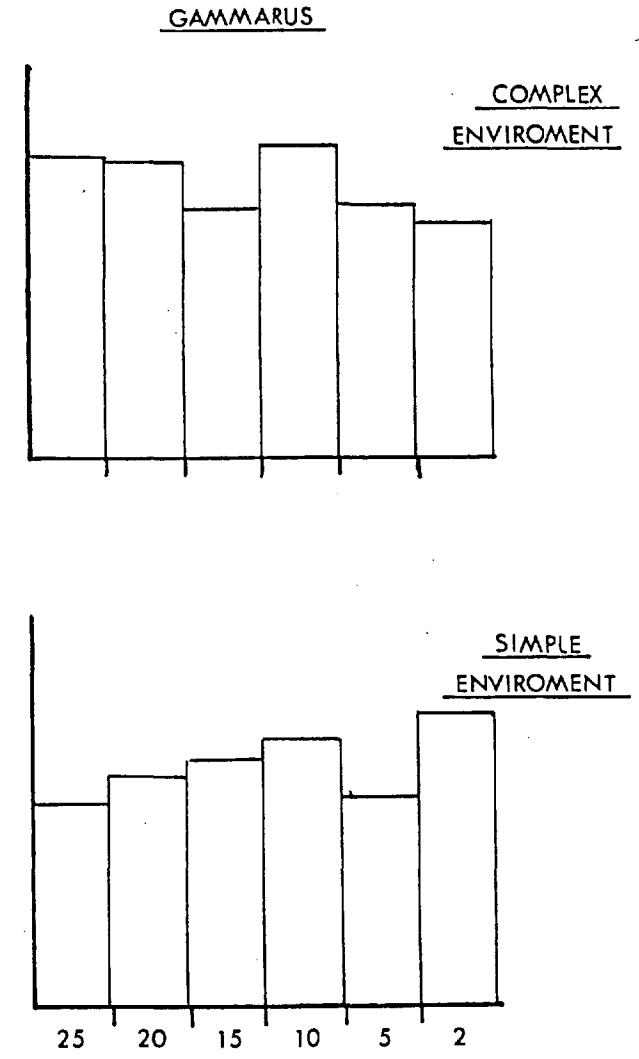
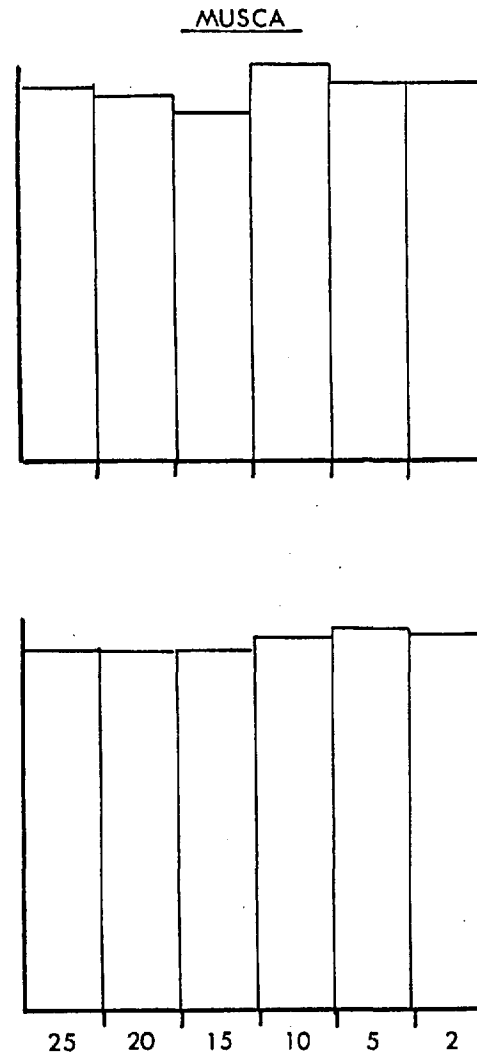
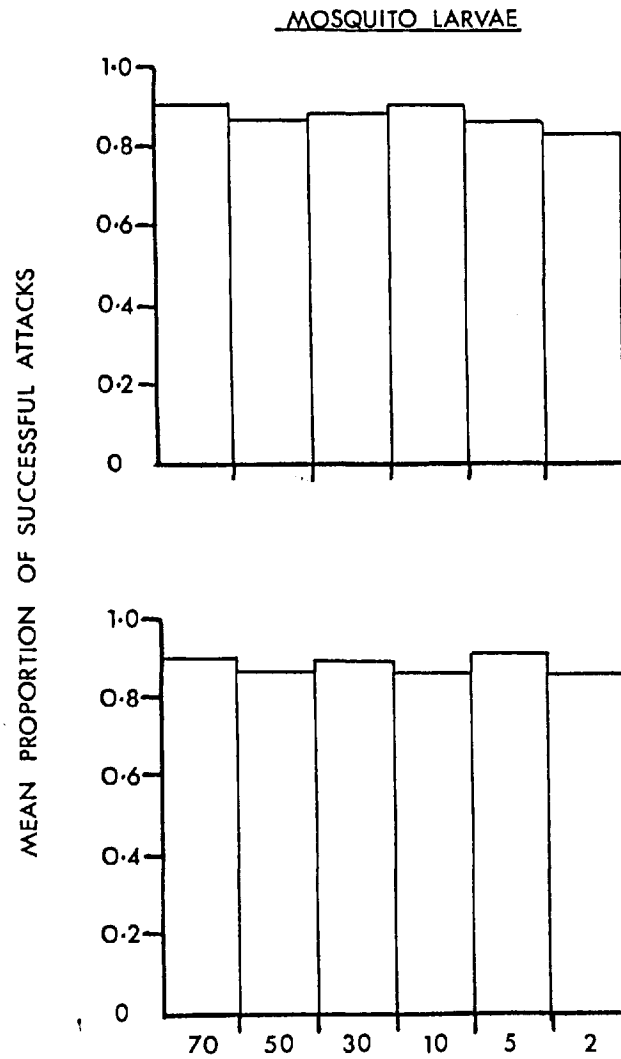
PREY DENSITY PER ARENA

N. obliqua pursuit success



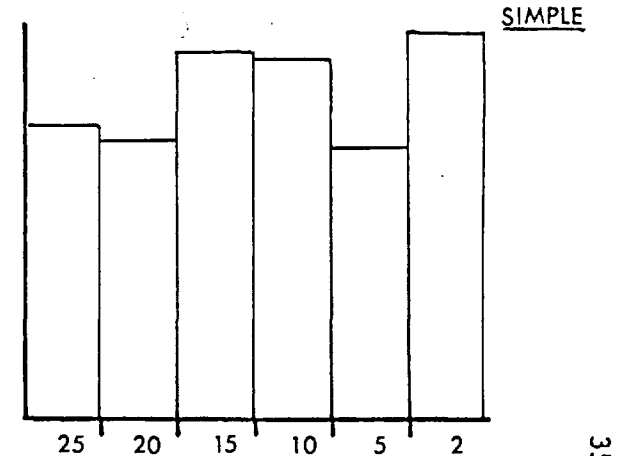
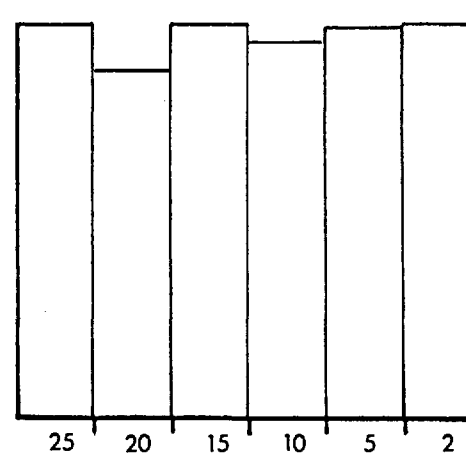
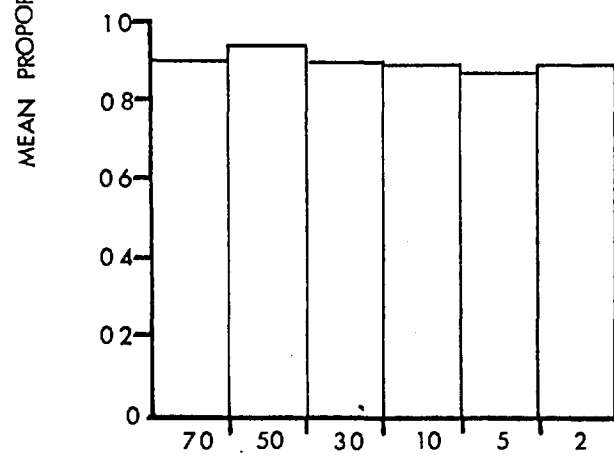
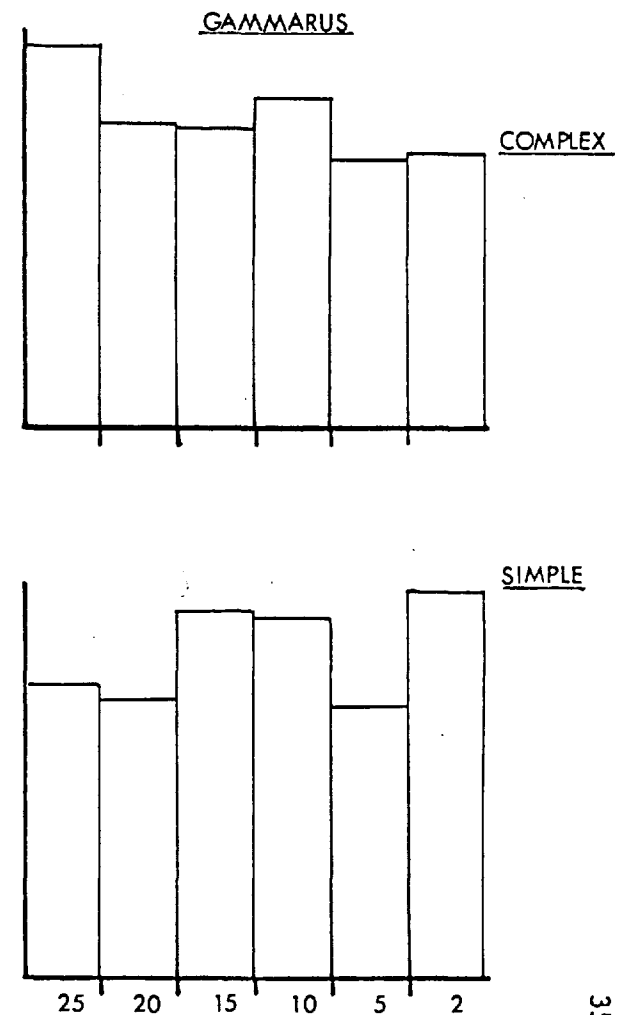
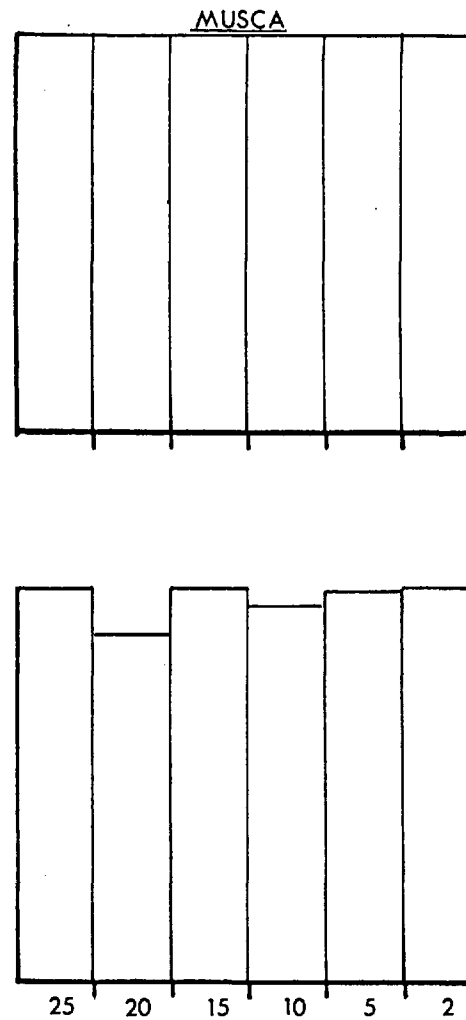
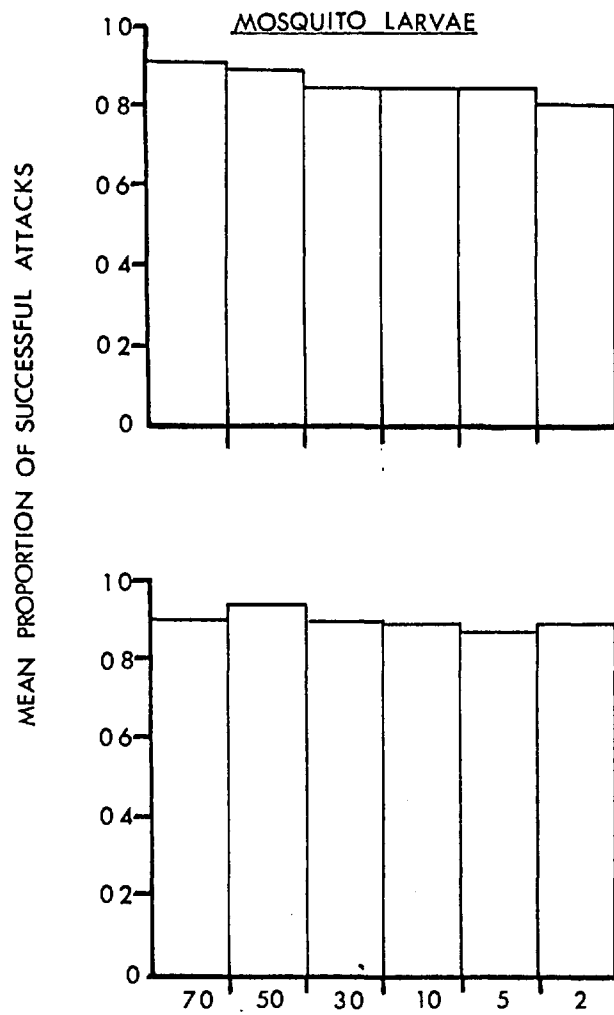
PREY DENSITY PER ARENA

N. maculata attack success

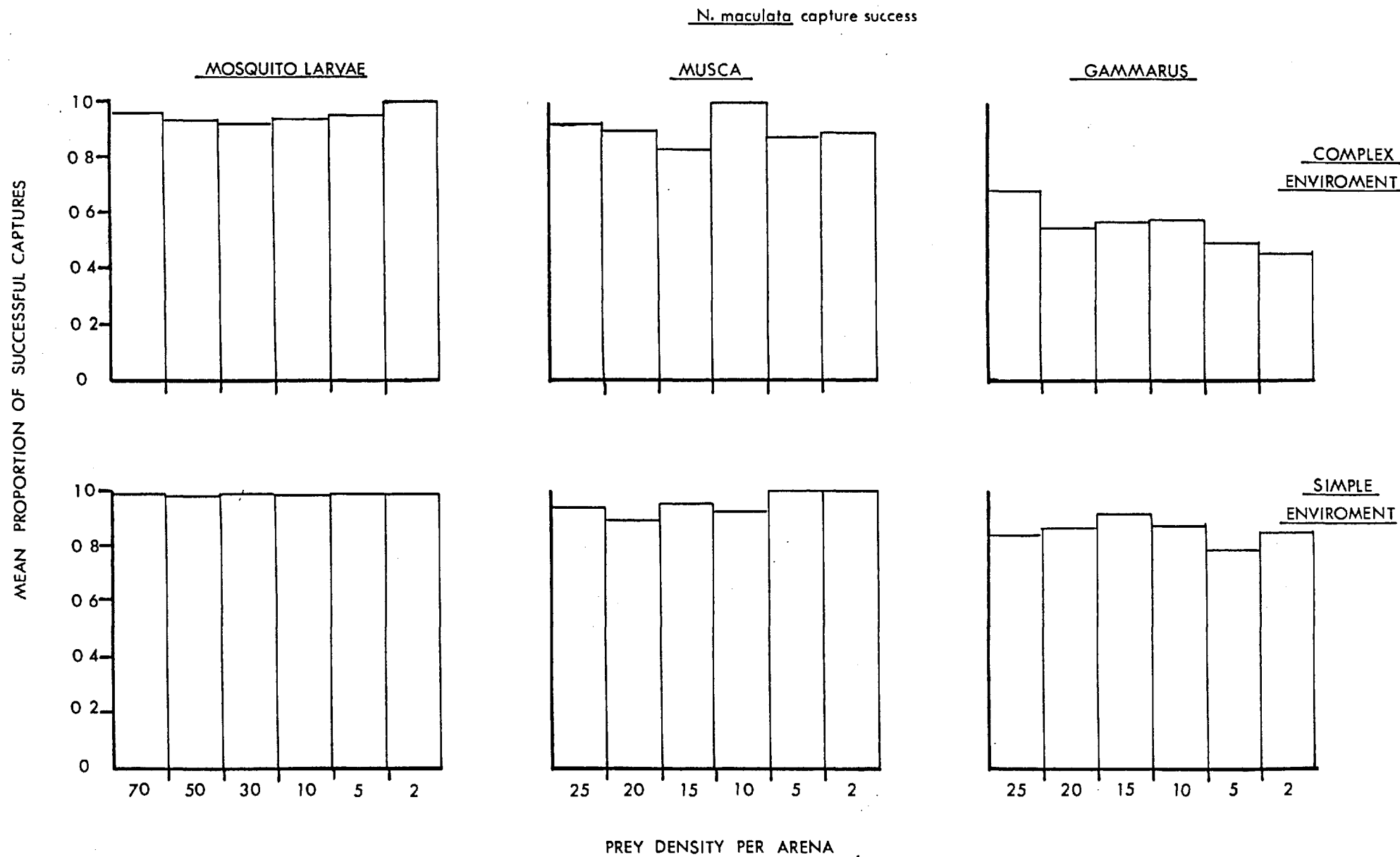


PREY DENSITY PER ARENA

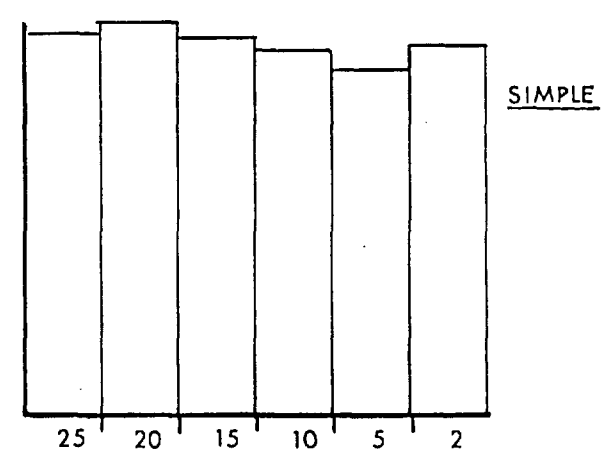
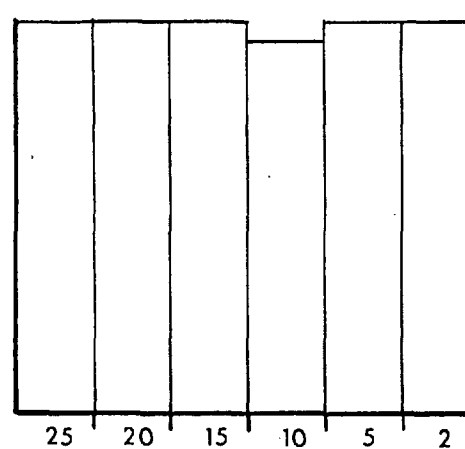
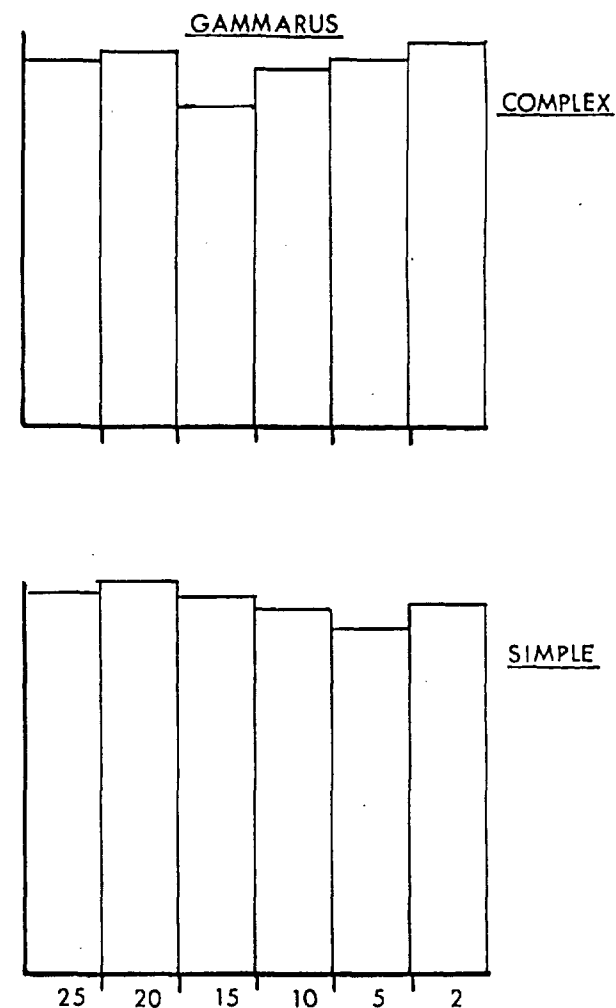
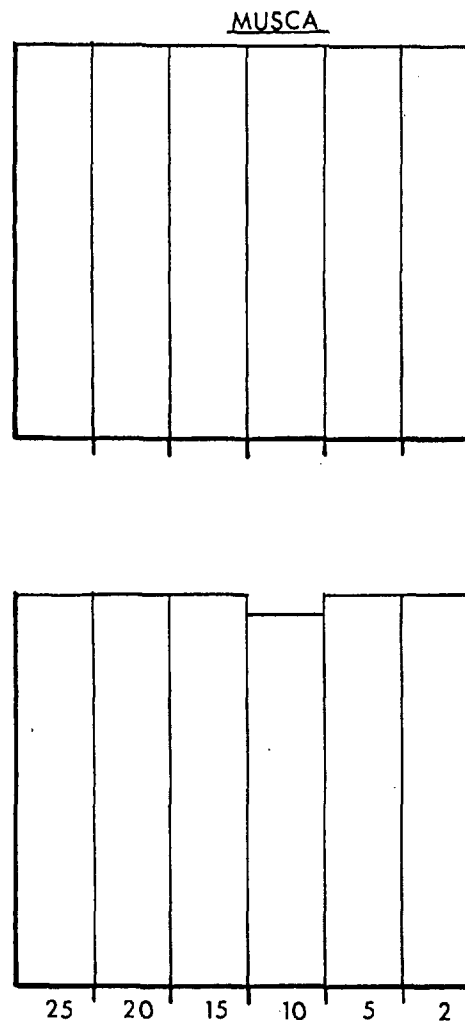
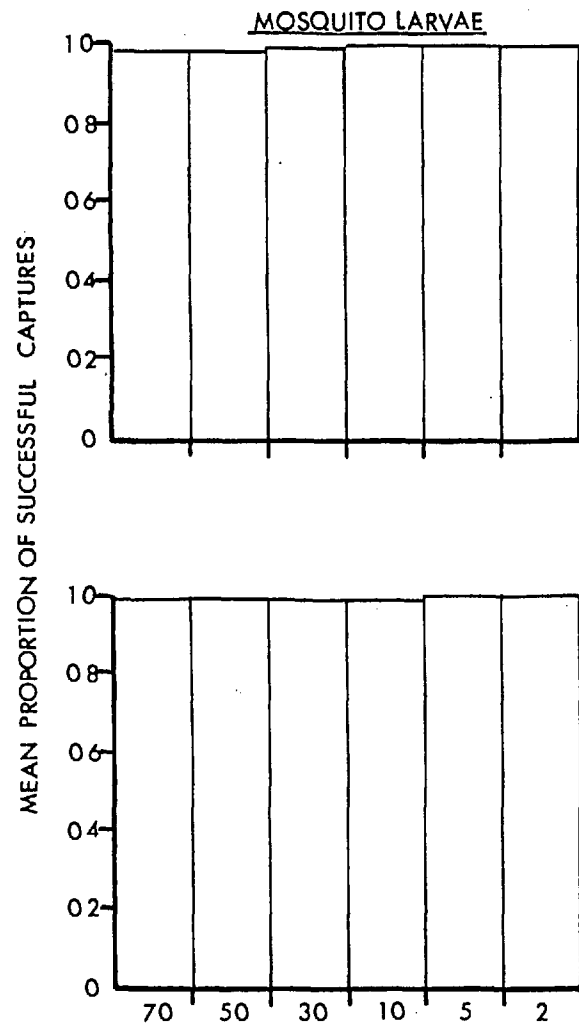
N. obliqua attack success



PREY DENSITY PER ARENA



N. obliqua capture success



PREY DENSITY PER ARENA

Appendix X(a)

Comparison of attack sequence components for each prey type.

Test used $d = \frac{r_1 - r_2}{\sqrt{r(1-r)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$ (Parker 1973)

where r_1, r_2 - different proportions, r = average of two proportions

n = number of samples

Due to size of sample necessary in such analysis, data is pooled over all densities in each situation, giving maximum total sample size of 54, so the binomial distribution approximates to a normal one. Significance of differences shown in tables.

N. glauca comparison between prey types

		Pursuit success	Attack success	Capture success
<u>Complex</u>	<u>Musca</u>			
	<u>Gammarus</u>	n.sig. [0.835] n.sig.	n.sig. [0.897] 0.001	n.sig. [0.877] 0.002
	<u>Mosquito</u>	0.1 [0.748] 0.884	0.01 [0.592] 0.807	0.001 [0.648] 0.918
<u>Simple</u>	<u>Musca</u>			
	<u>Gammarus</u>	0.001 [0.492] n.sig.	n.sig. [0.873] 0.001	n.sig. [0.836] 0.05
	<u>Mosquito</u>	0.001 [0.45] 0.859	0.001 [0.549] 0.93	0.001 [0.654] 0.941

Comparison between attack sequence components with each prey.

	<u>Complex</u>	<u>Simple</u>	
<u>Musca</u>	A] C] n.sig. P]	0.001 [A C] 0.001 P]	P = Pursuit A = Attack C = Capture
<u>Gammarus</u>	0.1 [P] C] n.sig. A] n.sig.	0.05 [C] A] n.sig. P] n.sig.	
<u>Mosquito</u>	0.1 [C] P] n.sig. A] n.sig.	C] A] n.sig. P]	

Comparison of attack sequence components between environments.

	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	
Pursuit	S ← C 0.001	S ← C 0.002	S C	Arrows indicate direction of significance.
Attack	S C	S C	S → C 0.1	
Capture	S C	S C	S C	
				S = Simple C = Complex

Initials underlined denotes no significant difference

Appendix X(a) (Continued)

N. maculata comparison between prey types

		Pursuit success	Attack success	Capture success
<u>Complex</u>	<u>Musca</u>	0.797		
	<u>Gammarus</u>	0.749	n.sig. [0.941] 0.001	n.sig. [0.901] 0.001
	<u>Mosquito</u>	0.829	n.sig. [0.69] 0.05	n.sig. [0.557] 0.001
<u>Simple</u>	<u>Musca</u>	n.sig. [0.85] 0.02	n.sig. [0.936] 0.001	n.sig. [0.95] 0.1
	<u>Gammarus</u>	n.sig. [0.655] 0.1	n.sig. [0.615] 0.002	n.sig. [0.855] 0.01
	<u>Mosquito</u>	n.sig. [0.795]	n.sig. [0.88]	n.sig. [0.99]

Comparison between attack components with each prey.

	<u>Complex</u>	<u>Simple</u>	
<u>Musca</u>	0.02 [A] n.sig. [C] n.sig. [P]	0.1 [C] n.sig. [A] n.sig. [P]	P = Pursuit A = Attack C = Capture
<u>Gammarus</u>	0.05 [P] n.sig. [A] n.sig. [C]	0.01 [C] 0.02 [P] n.sig. [A]	
<u>Mosquito</u>	0.05 [C] n.sig. [A] n.sig. [P]	0.001 [C] 0.02 [A] n.sig. [P]	

Comparison of attack sequence components between environments.

	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	
Pursuit	<u>S C</u>	<u>S C</u>	<u>S C</u>	
Attack	<u>S C</u>	<u>S C</u>	S ← C 0.001	S = Simple C = Complex
Capture	<u>S C</u>	<u>S C</u>	<u>S C</u>	

N. obliqua comparison between prey types.

		Pursuit success	Attack success	Capture success
<u>Complex</u>	<u>Musca</u>	0.944		
	<u>Gammarus</u>	0.918	0.01 [1.0] 0.001	n.sig. [1.0] 0.05
	<u>Mosquito</u>	0.901	n.sig. [0.778] 0.001	n.sig. [0.912] 0.05
<u>Simple</u>	<u>Musca</u>	0.943	n.sig. [0.969] 0.02	0.991
	<u>Gammarus</u>	0.88	n.sig. [0.825] n.sig.	0.947 n.sig.
	<u>Mosquito</u>	0.903	n.sig. [0.896]	0.99

Appendix X(a) (Continued)

Comparison between attack sequence components with each prey.

		<u>Complex</u>		<u>Simple</u>
<u>Musca</u>	0.1	$\begin{bmatrix} C \\ A \\ P \end{bmatrix}$	n.sig. 0.1	$\begin{bmatrix} C \\ A \\ P \end{bmatrix}$ n.sig.
<u>Gammarus</u>	0.05	$\begin{bmatrix} P \\ C \\ A \end{bmatrix}$	n.sig. 0.05	0.05 $\begin{bmatrix} C \\ P \\ A \end{bmatrix}$ n.sig. n.sig.
<u>Mosquito</u>	0.01	$\begin{bmatrix} C \\ P \\ A \end{bmatrix}$	0.05 n.sig.	0.05 $\begin{bmatrix} C \\ P \\ A \end{bmatrix}$ 0.05 n.sig.

Comparison of attack sequence components between environments.

	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	
Pursuit	<u>S C</u>	<u>S C</u>	<u>S C</u>	
Attack	<u>S C</u>	<u>S C</u>	<u>S C</u>	S = Simple
Capture	<u>S C</u>	<u>S C</u>	<u>S C</u>	C = Complex

Appendix X(b) Comparison of attack sequence components between predators.

Significance of differences shown.

		complex	simple
<u>Pursuit</u>	<u>Musca</u>	0.05 $\begin{bmatrix} O \\ G \\ M \end{bmatrix}$ n. sig	0.001 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig 0.001
	<u>Gammarus</u>	0.02 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ 0.02 n. sig	0.001 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ 0.01 0.05
	mosquito	$\begin{bmatrix} O \\ G \\ M \end{bmatrix}$ n. sig	$\begin{bmatrix} O \\ G \\ M \end{bmatrix}$ n. sig
<u>Attack</u>	<u>Musca</u>	0.02 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ 0.1 n. sig	0.1 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig n. sig
	<u>Gammarus</u>	0.05 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig n. sig	0.02 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ 0.1 n. sig
	mosquito	$\begin{bmatrix} M \\ O \\ G \end{bmatrix}$ n. sig	$\begin{bmatrix} G \\ O \\ M \end{bmatrix}$ n. sig
<u>Capture</u>	<u>Musca</u>	0.01 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ 0.05 n. sig	0.01 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig 0.1
	<u>Gammarus</u>	0.01 $\begin{bmatrix} O \\ G \\ M \end{bmatrix}$ 0.001 n. sig	0.001 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig 0.05
	mosquito	0.05 $\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig n. sig	$\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n. sig

O = N. obliquaG = N. glaucaM = N. maculata

Appendix XI Comparison of pursuit attacks between prey, predators and environments.

The small sample numbers requires pooling of data over the prey densities. This will, however obscure any effect of density on the proportion of pursuit attacks. However, such analysis will indicate the general differences in the data for different prey and predators.

Tests used as in Appendix X

Comparison of pursuit attacks between prey.

	<u>N. glauca</u>		<u>N. maculata</u>		<u>N. obliqua</u>
<u>Complex</u>					
<u>Musca</u>	0.1	$\begin{bmatrix} 0.843 \\ 0.816 \\ 0.703 \end{bmatrix}$	n.sig.	0.1	$\begin{bmatrix} 0.742 \\ 0.68 \\ 0.574 \end{bmatrix}$
<u>Gammarus</u>			n.sig.		
<u>Mosquito</u>					
<u>Simple</u>					
<u>Musca</u>	n.sig	$\begin{bmatrix} 0.68 \\ 0.886 \\ 0.588 \end{bmatrix}$	0.05 0.002	n.sig	$\begin{bmatrix} 0.74 \\ 0.93 \\ 0.678 \end{bmatrix}$
<u>Gammarus</u>					
<u>Mosquito</u>					

Comparison of pursuit attacks between environments.

	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>	
<u>Musca</u>	S ← C 0.05	S C	S C	Arrow indicates direction of difference.
<u>Gammarus</u>	S C	S C	S → C 0.001	S = Simple C = Complex
<u>Mosquito</u>	S C	S C	S C	

Comparison of pursuit attacks between predators.

	<u>Complex</u>		<u>Simple</u>	
<u>Musca</u>	0.1	$\begin{bmatrix} G \\ O \\ M \end{bmatrix}$	n.sig.	$\begin{bmatrix} O \\ M \\ G \end{bmatrix}$ n.sig.
<u>Gammarus</u>		$\begin{bmatrix} G \\ M \\ O \end{bmatrix}$	n.sig.	$\begin{bmatrix} O \\ G \\ M \end{bmatrix}$ n.sig.
<u>Mosquito</u>		$\begin{bmatrix} G \\ M \\ O \end{bmatrix}$	n.sig.	$\begin{bmatrix} M \\ O \\ G \end{bmatrix}$ 0.1 n.sig.

O = N. obliqua
G = N. glauca
M = N. maculata

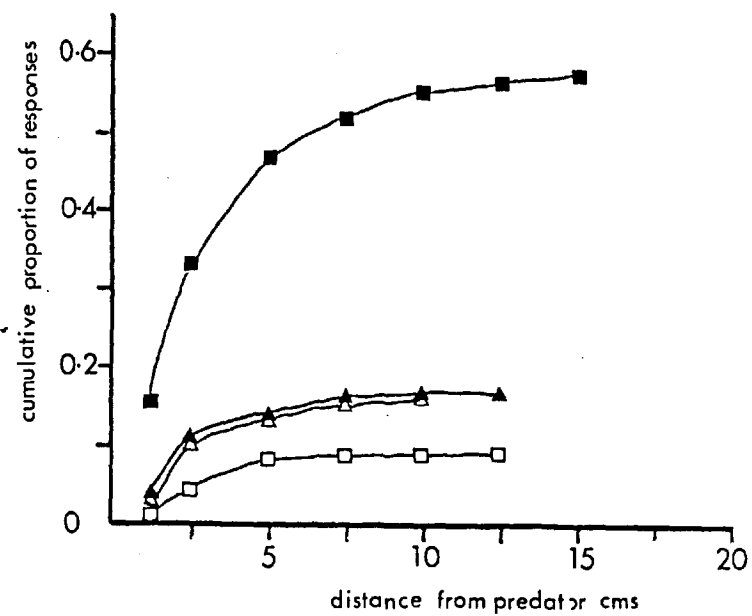
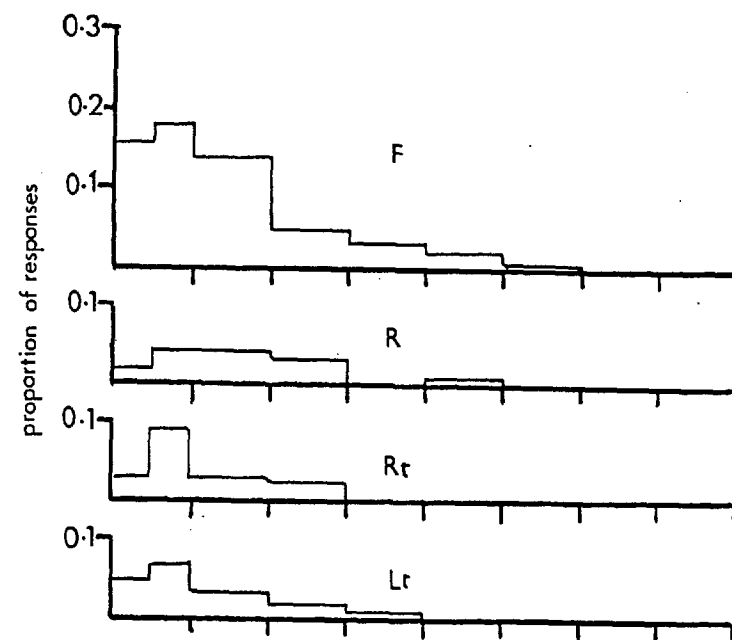
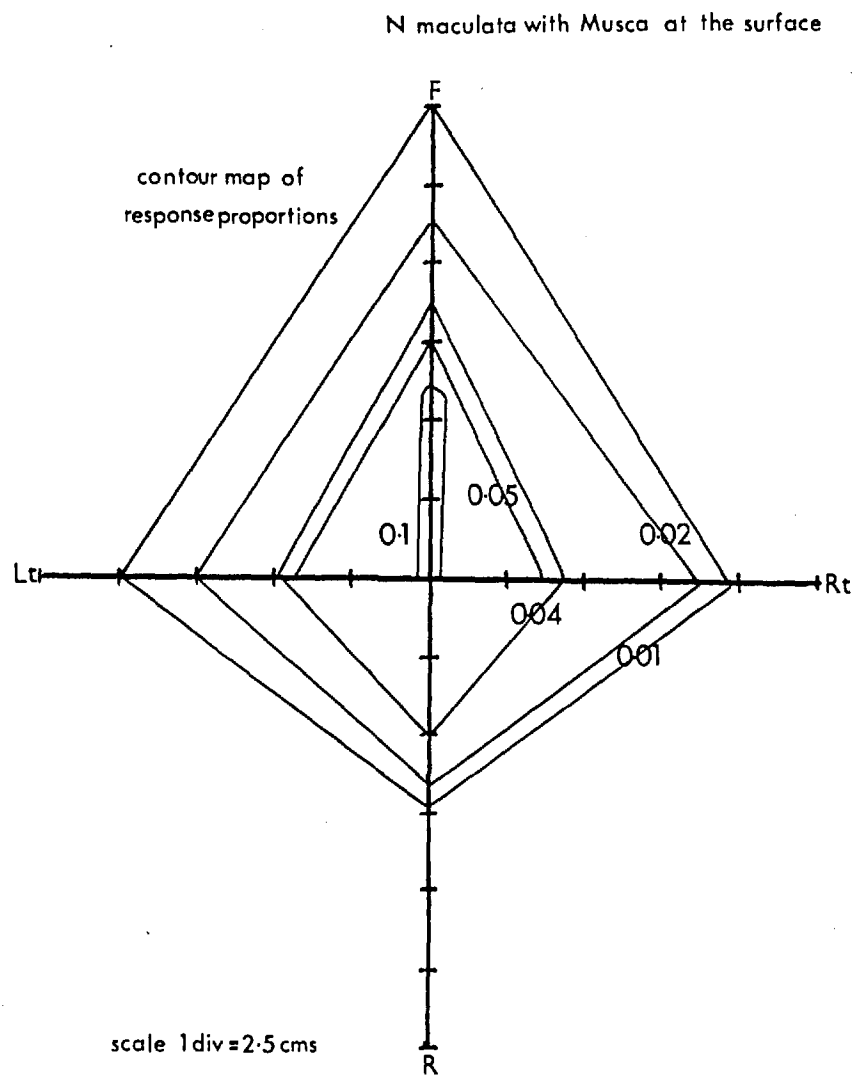
Appendix XII

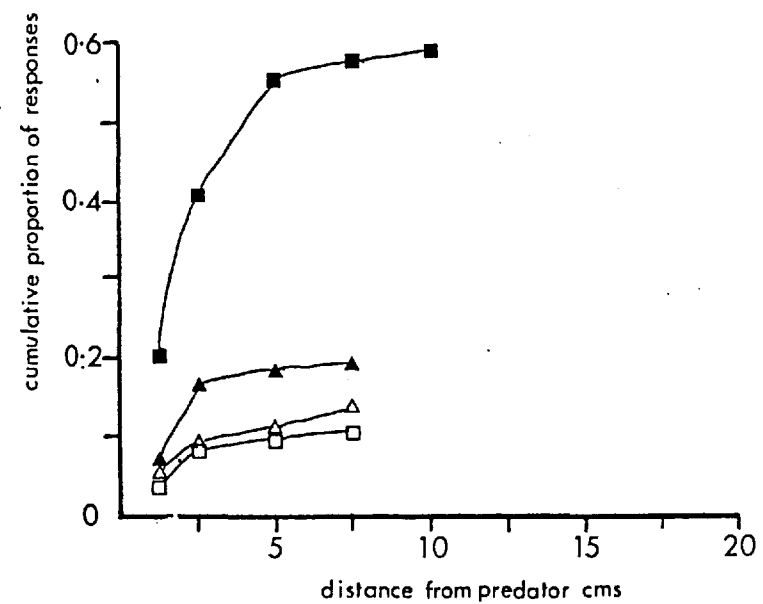
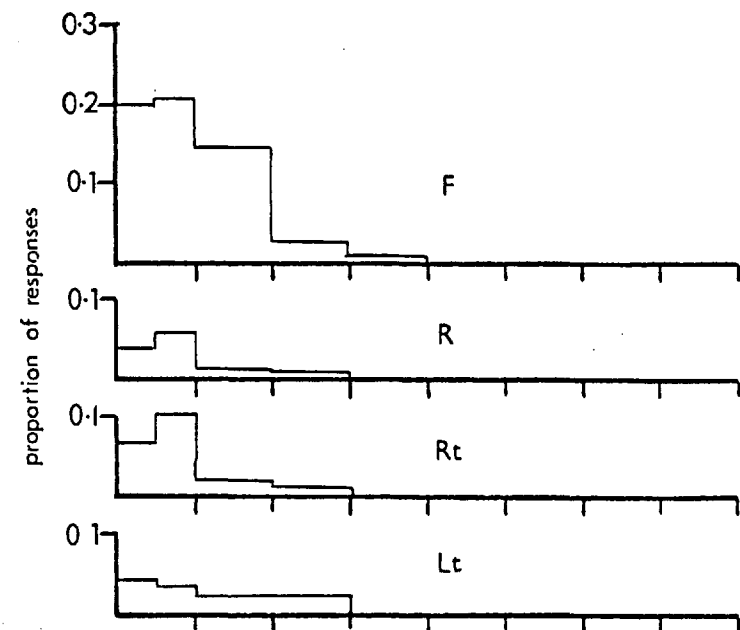
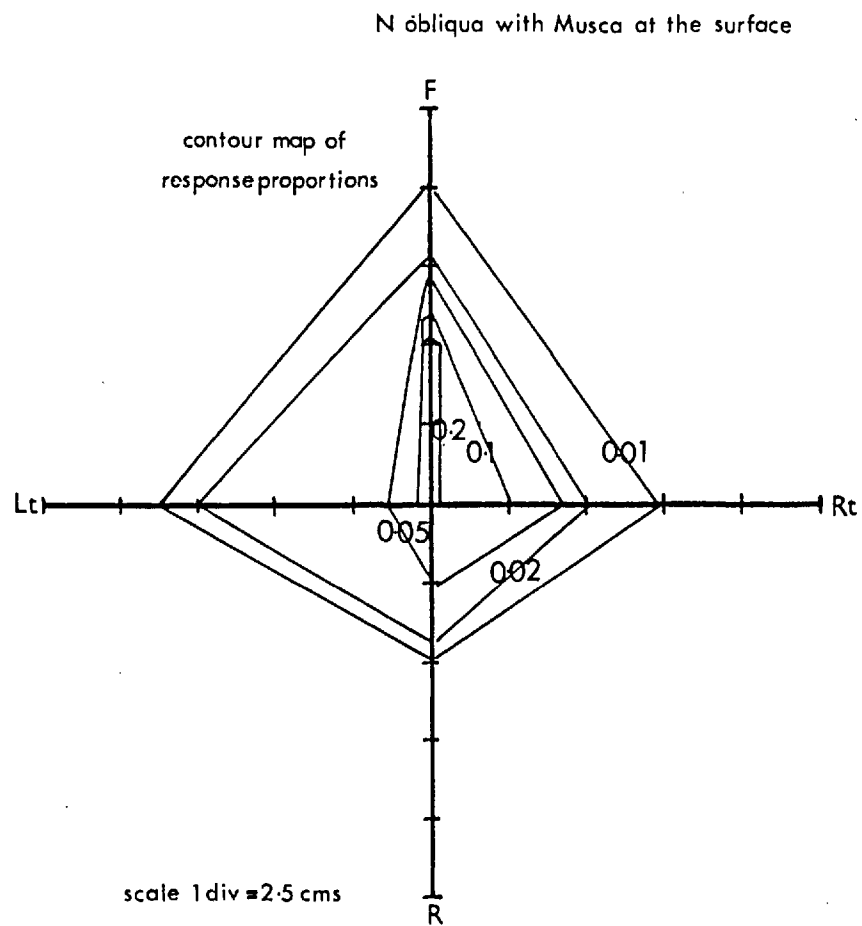
Reaction areas of N. maculata and N. obliqua with the three prey types at the surface.

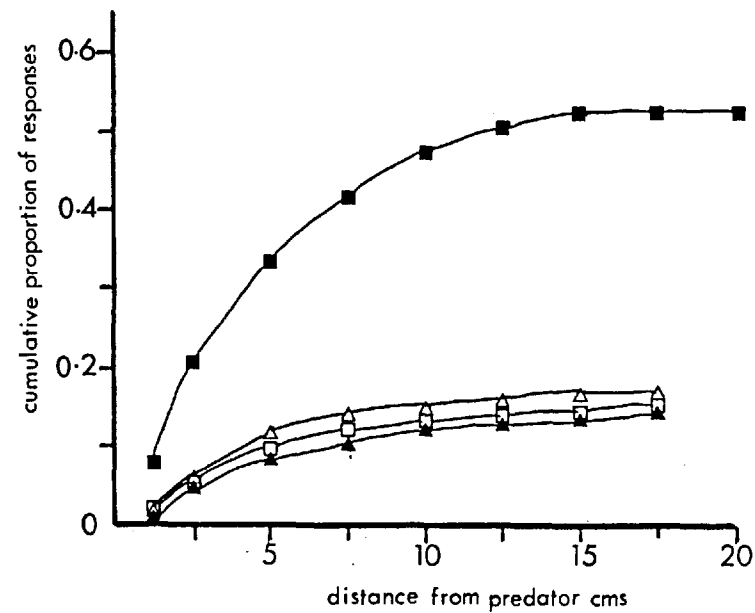
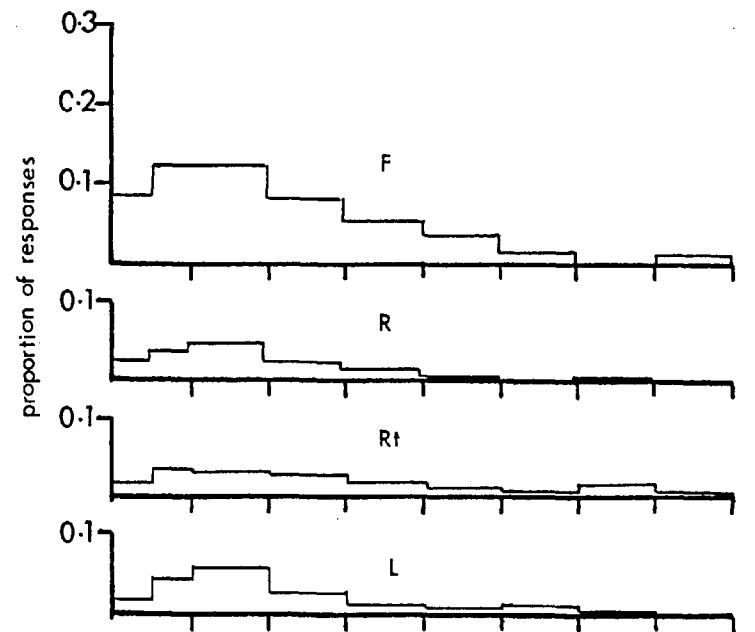
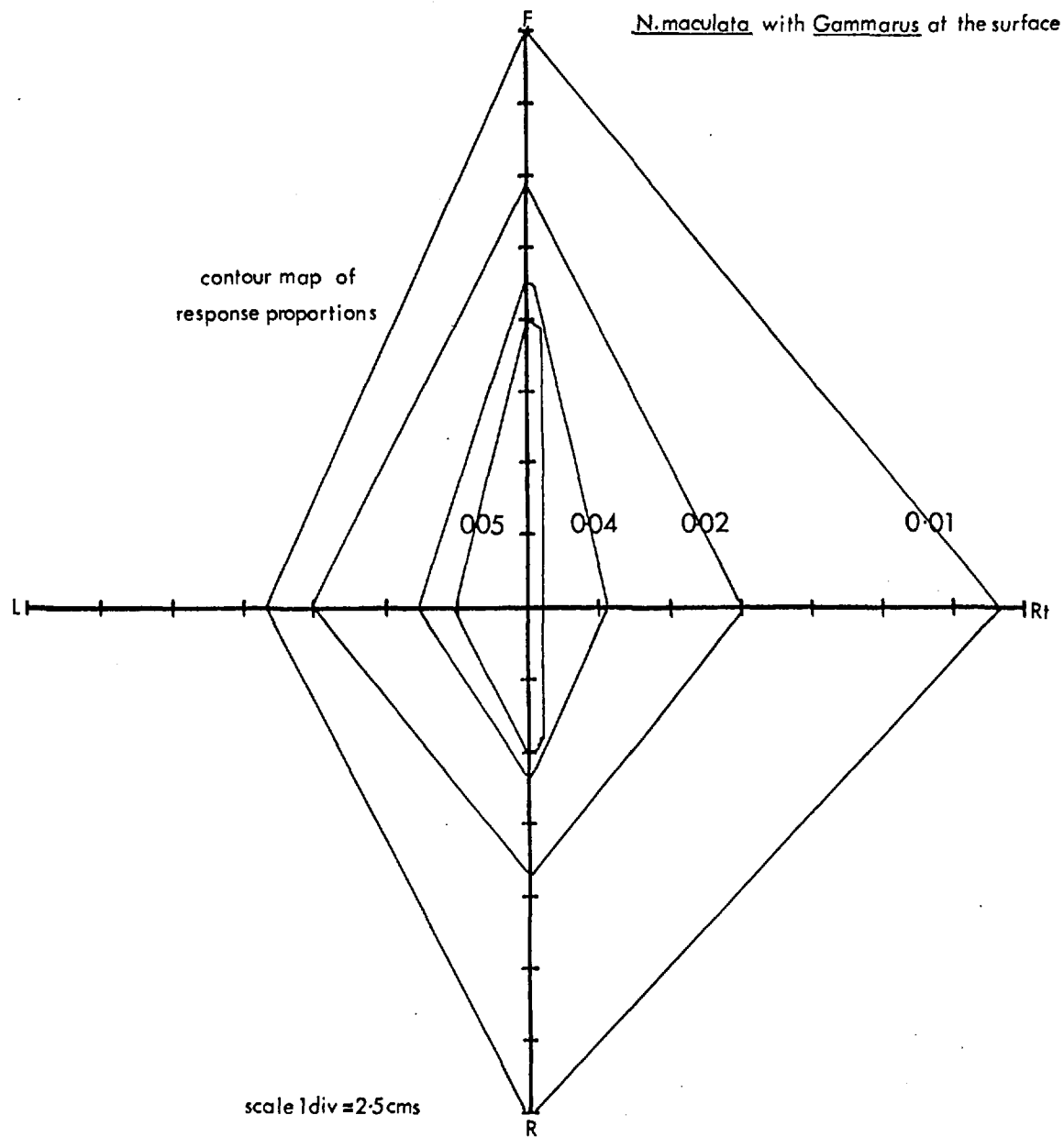
F = Forward; R = Rear; Rt = Right; L = Left.

- A Proportion contours - figures represent proportion of total responses and contours join distances from predator at which equal proportion of responses are made.
- B Proportion of total responses made at different distances from the predator in each direction.
- C Cumulative proportion of responses with distance from predator in each direction.

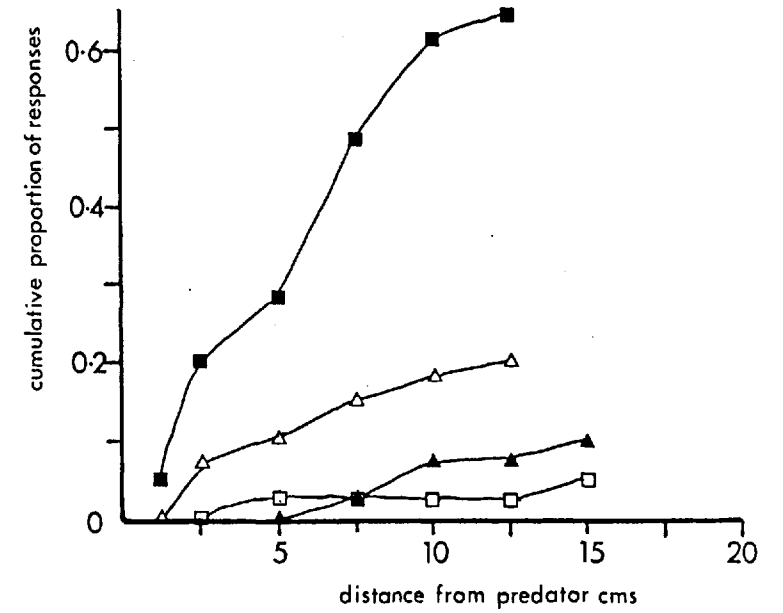
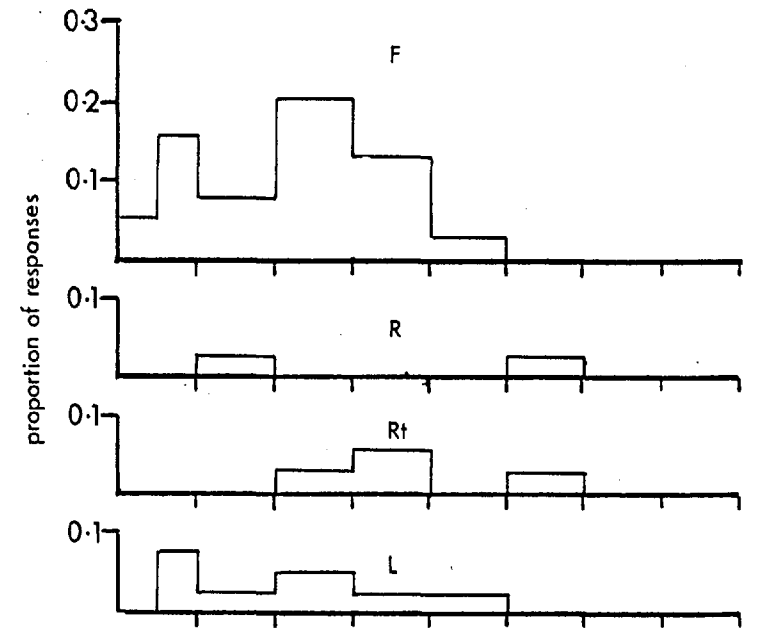
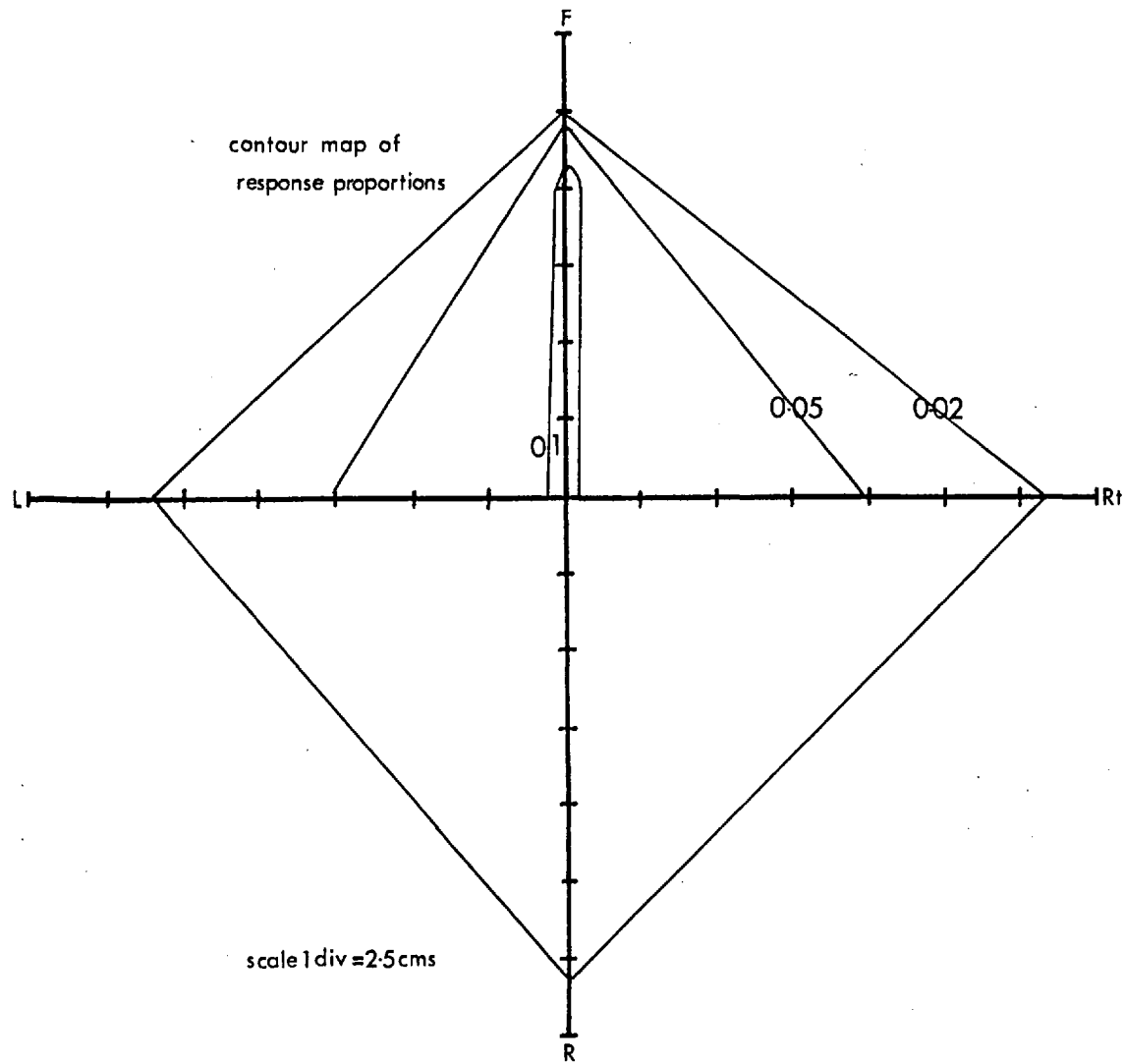
- Forward
- Rear
- Right
- Left



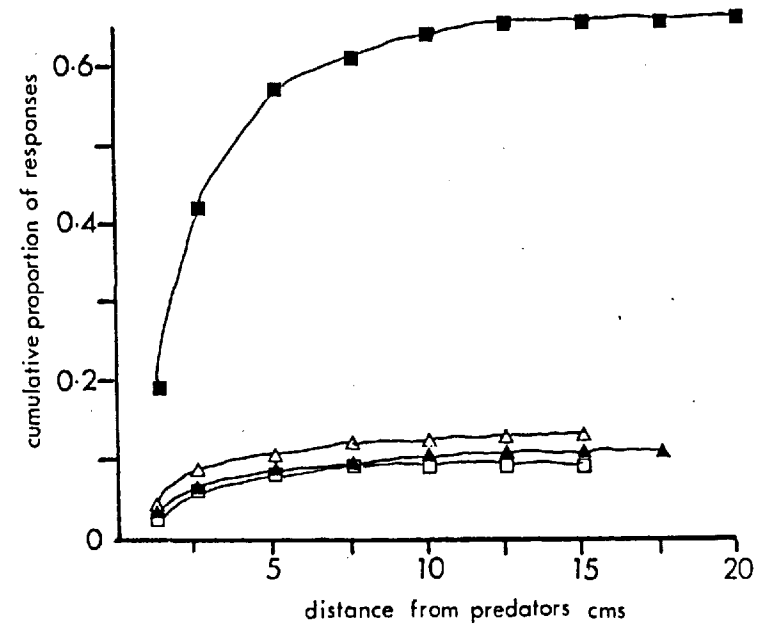
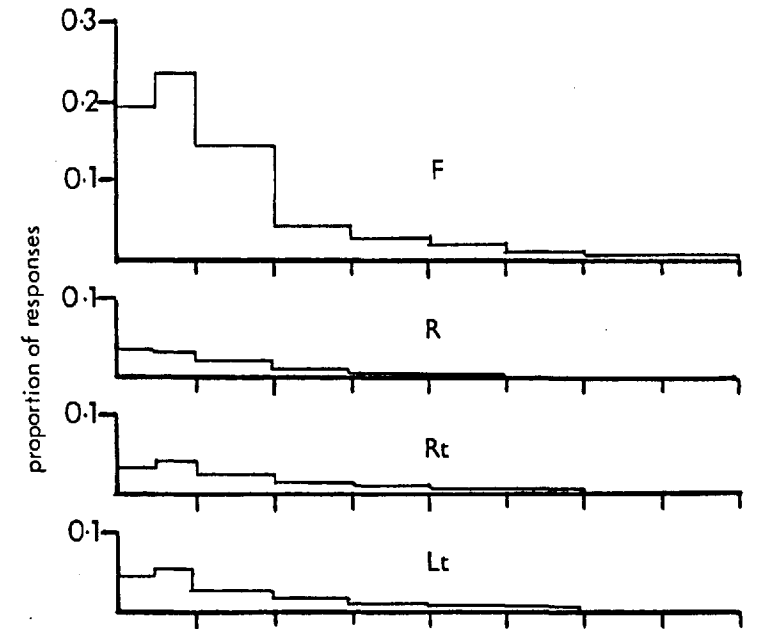
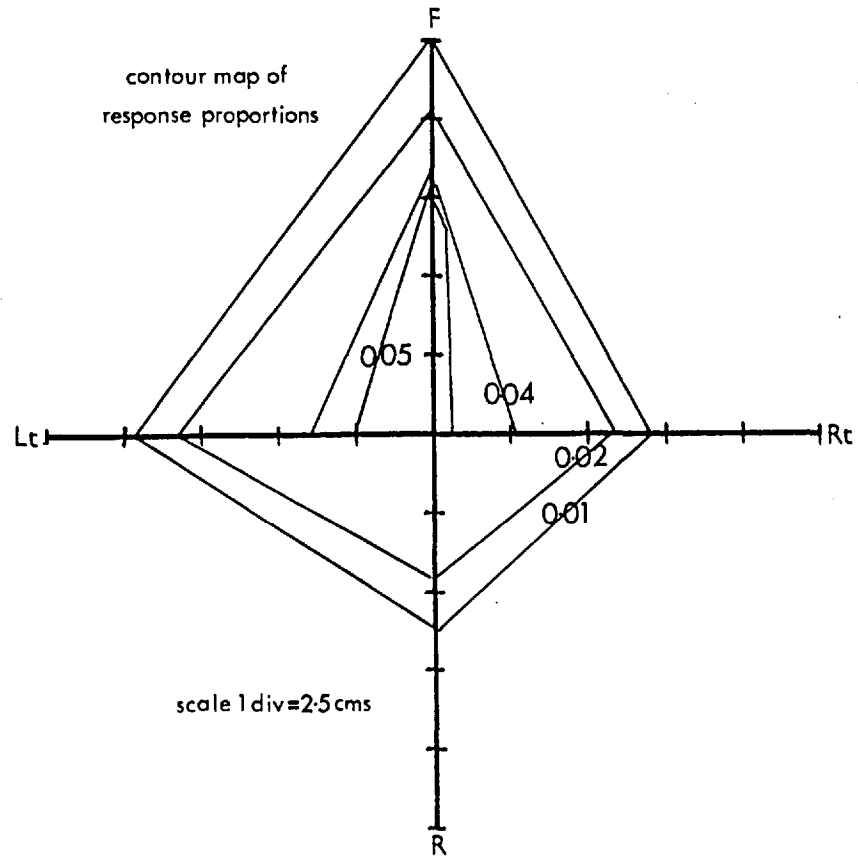




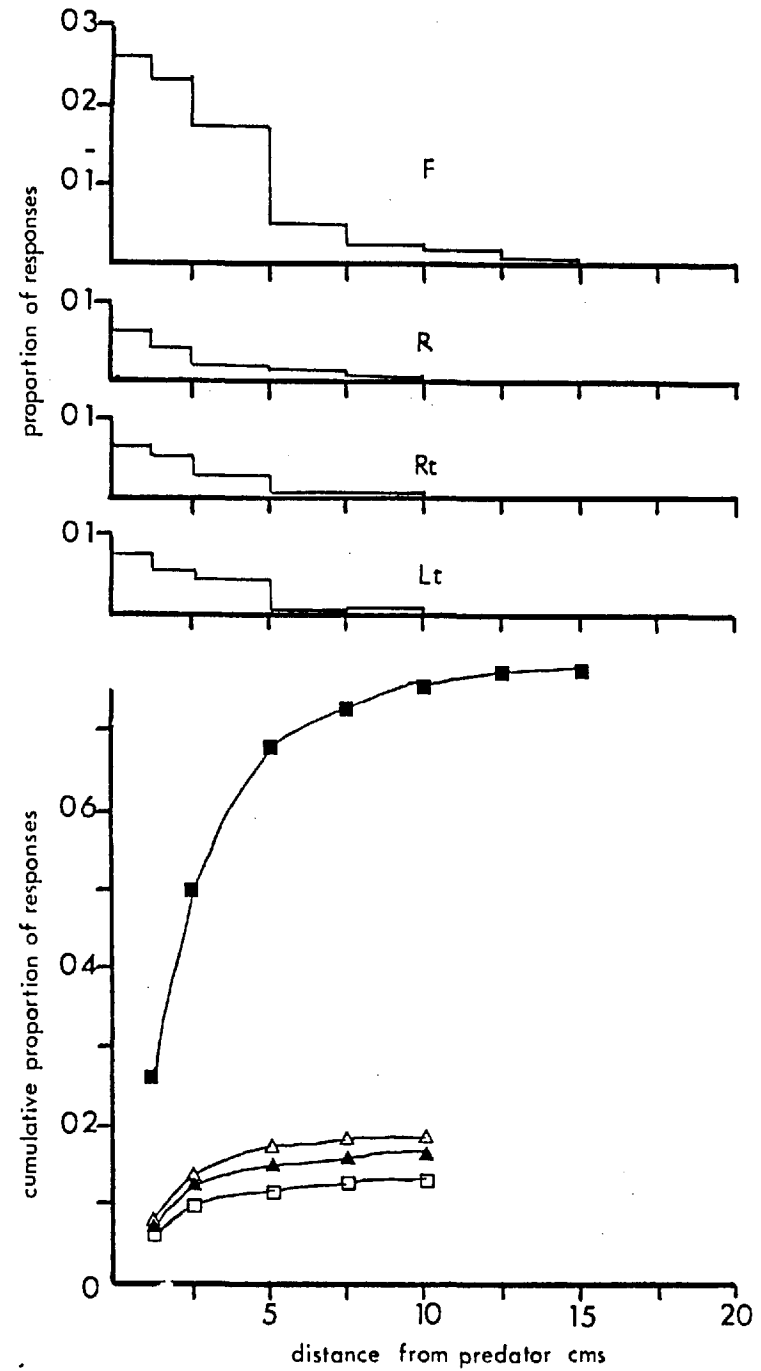
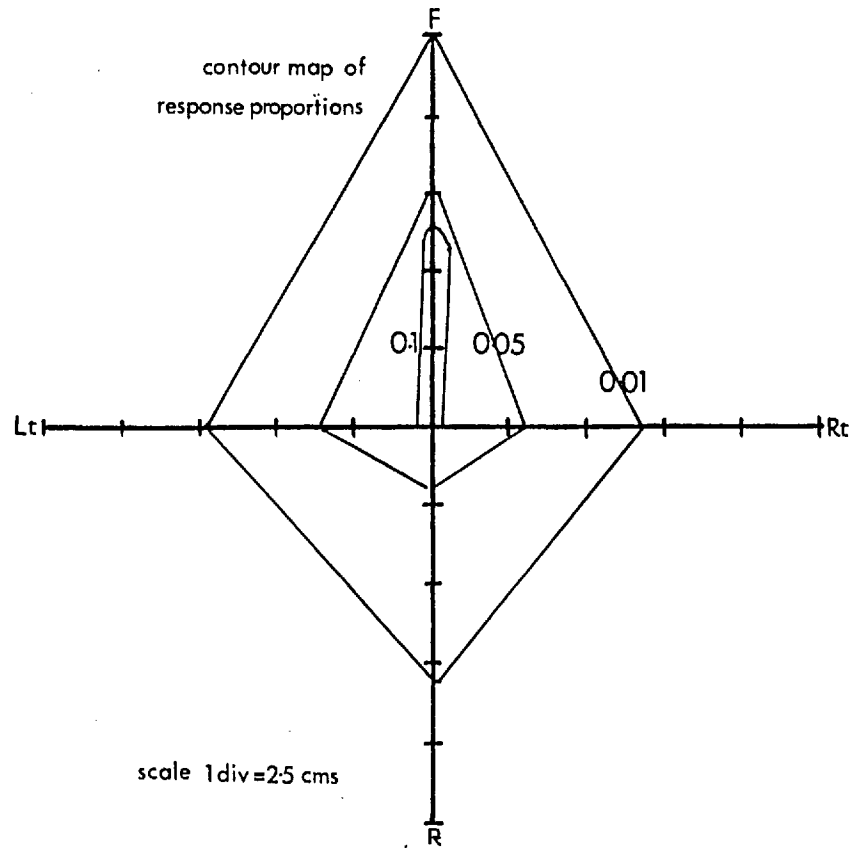
N obliqua with Gammarus at the surface



N. maculata with mosquito larvae at the surface



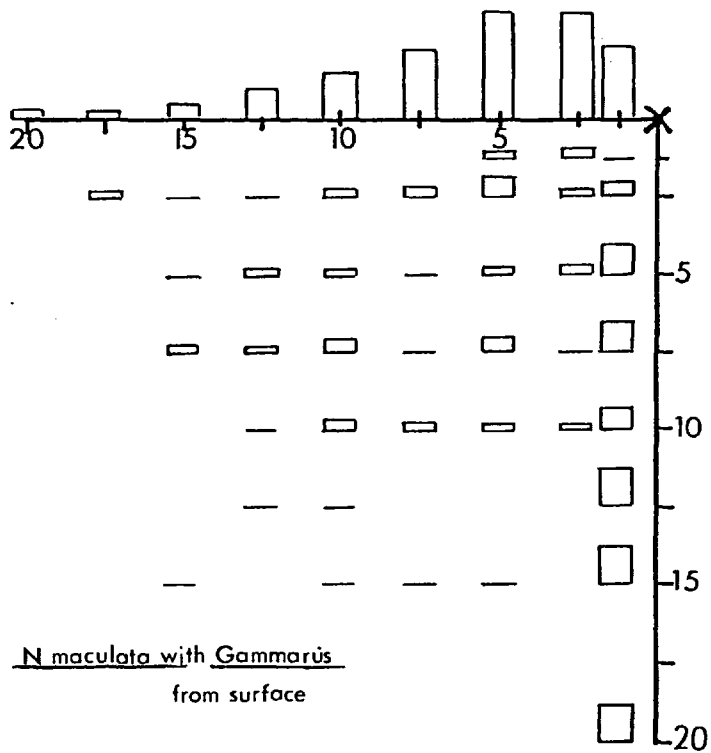
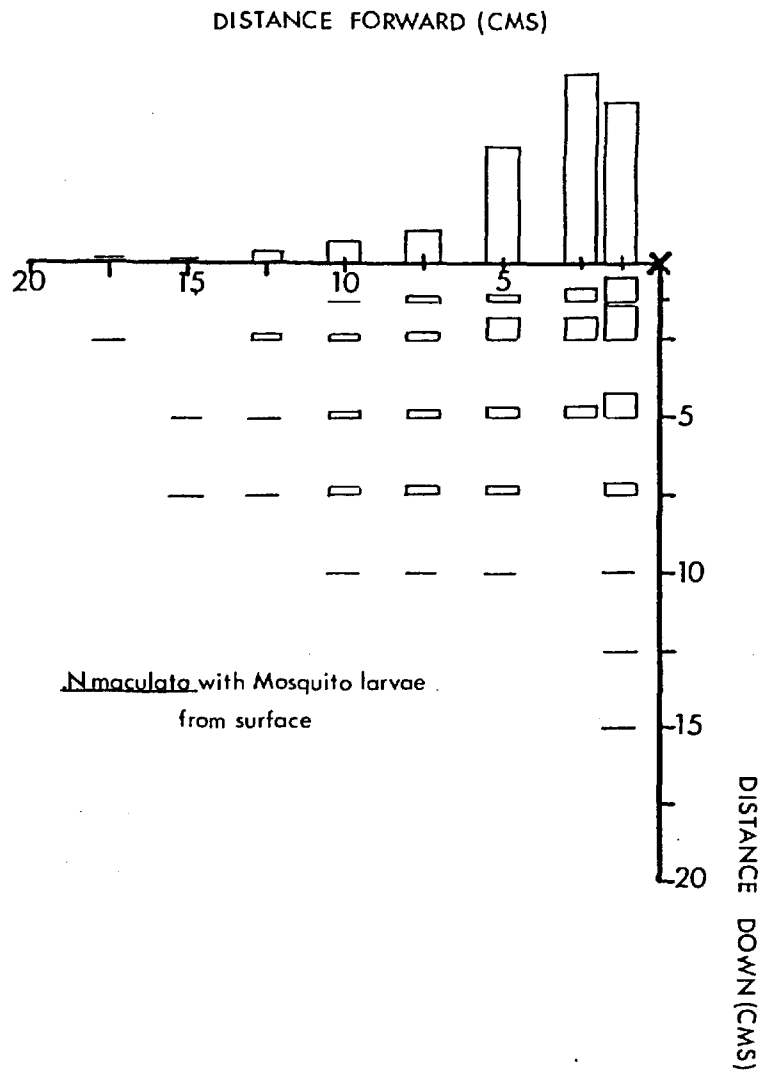
N obliqua with mosquito larvae at surface

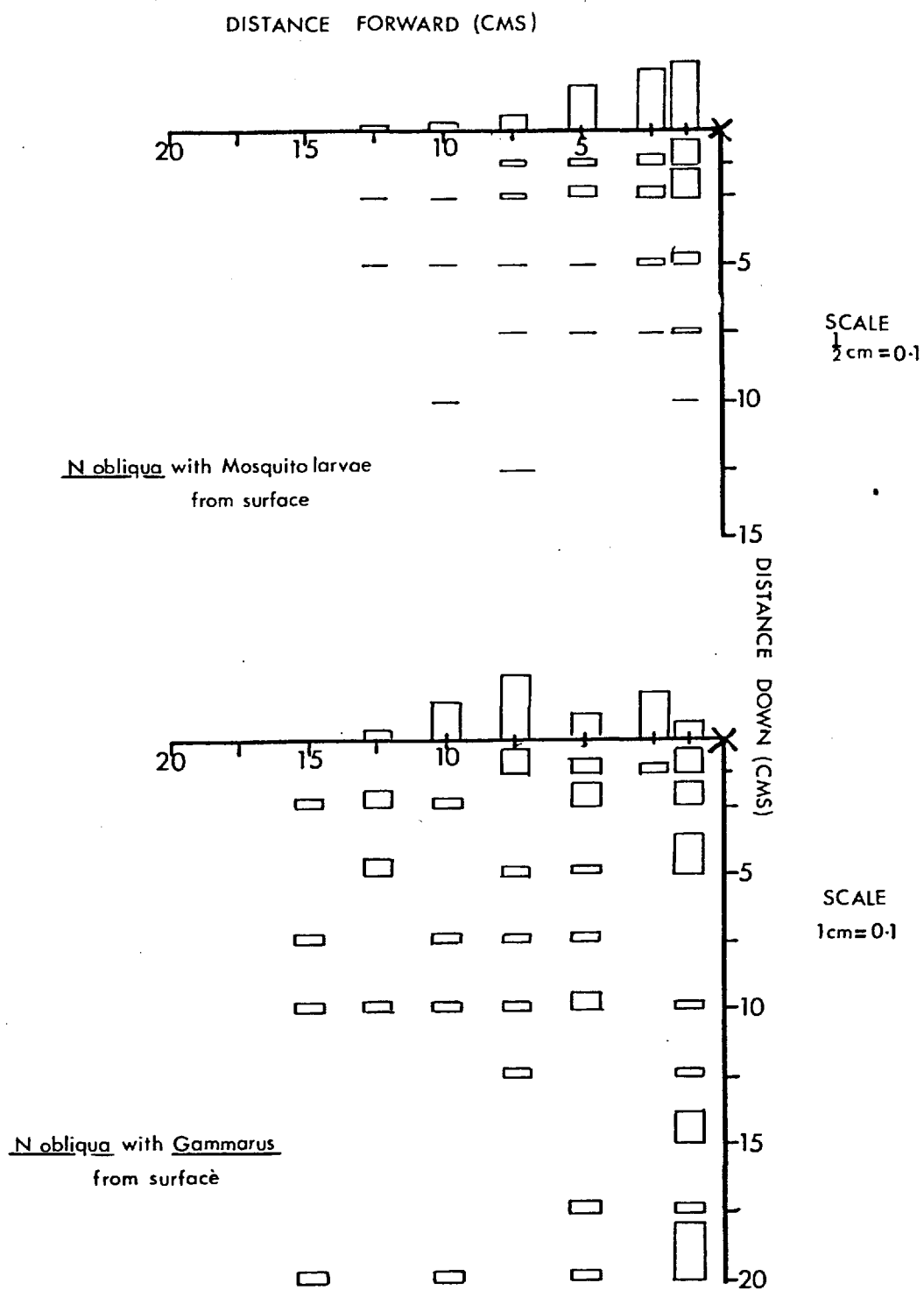


Appendix XIII

Reaction area from the surface of N. maculata and
N. obliqua feeding on mosquito larvae and Gammarus.

Height of bars indicates proportion of total responses
made at that distance from the predator (marked X).

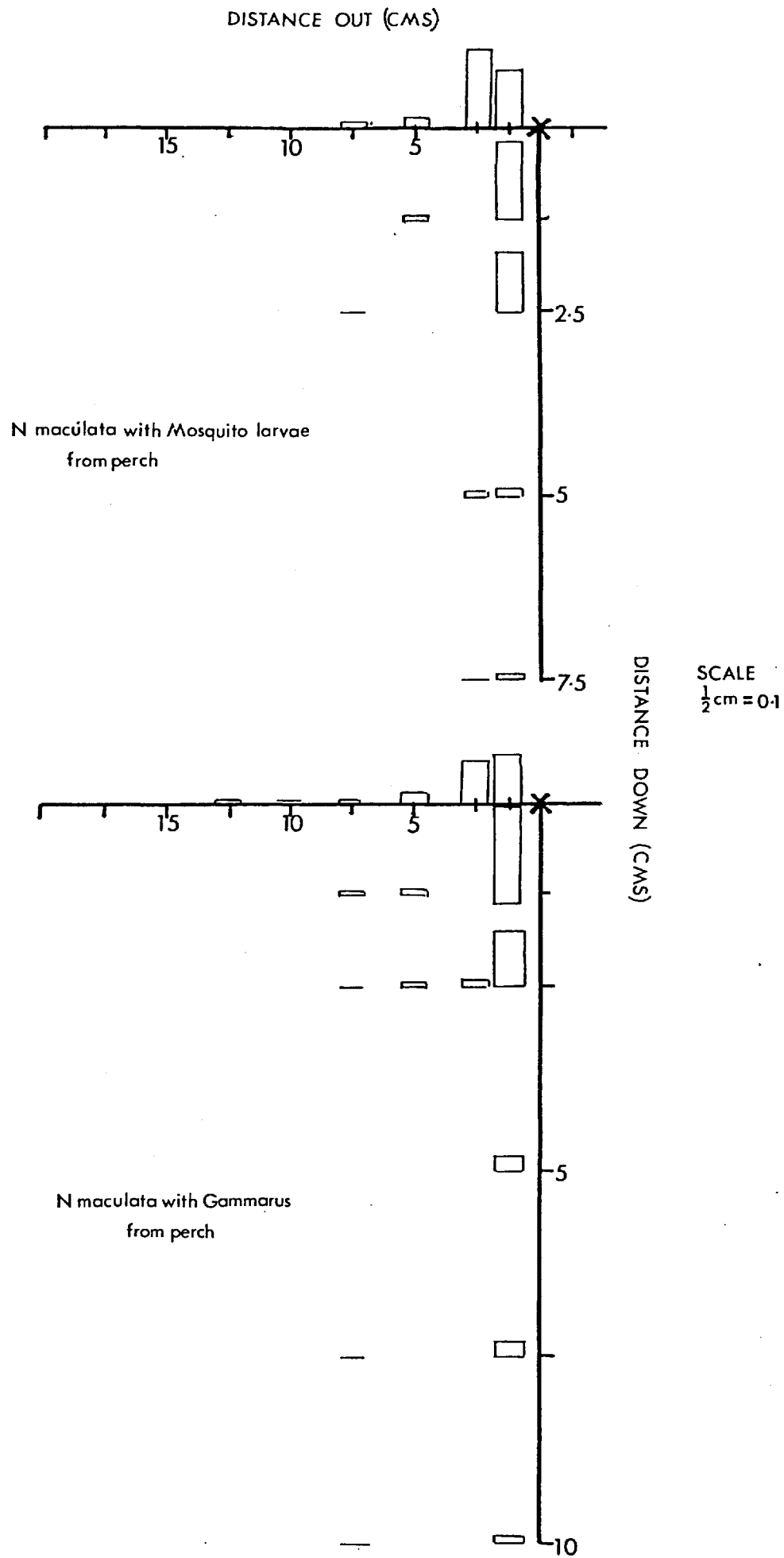


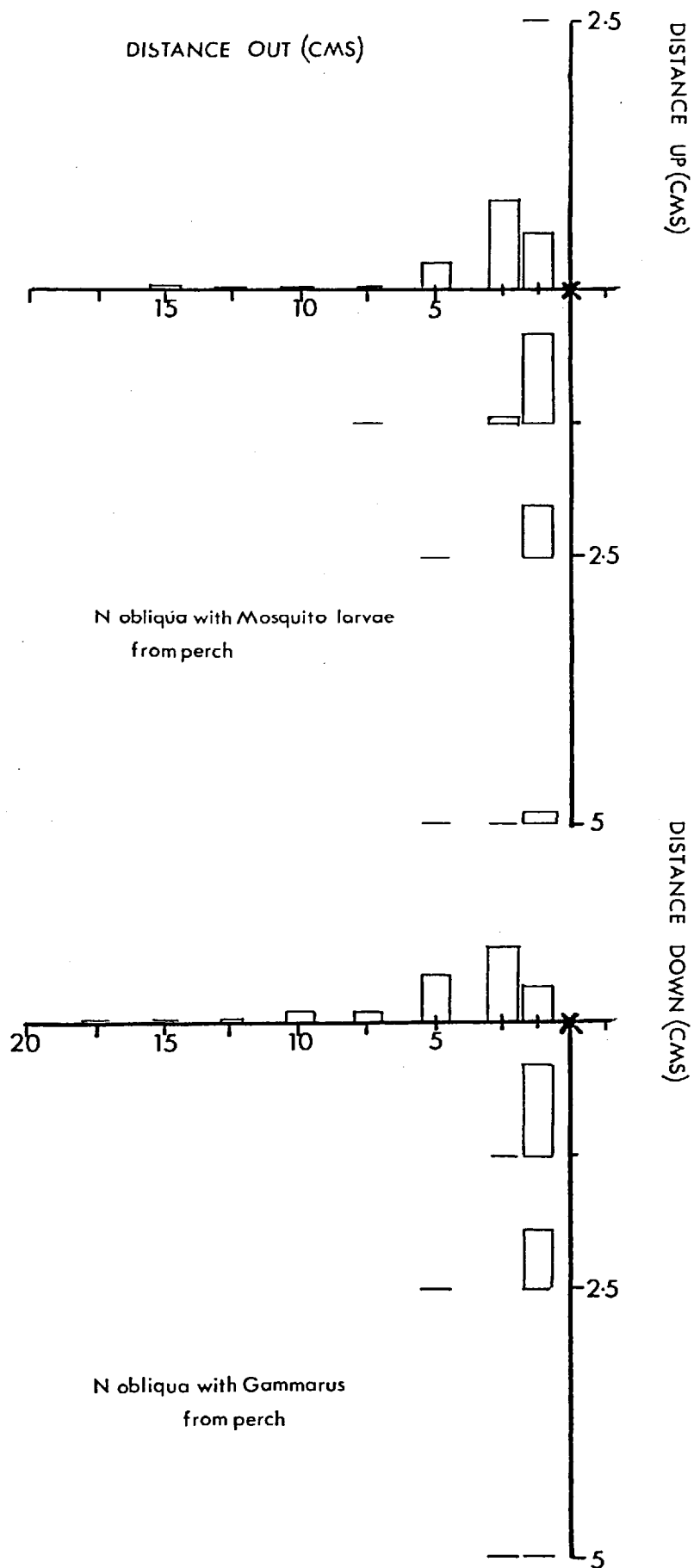


Appendix XIV

Reaction area from perch sites by N. maculata and
N. obliqua feeding on mosquito larvae and Gammarus.

Height of bars indicate proportion of total responses
made at that distance from the predator (marked X)





Appendix XV

Histograms showing the proportion of

Rest Time (A)

and Handling Time (B)

spent at different positions in the waterbody by

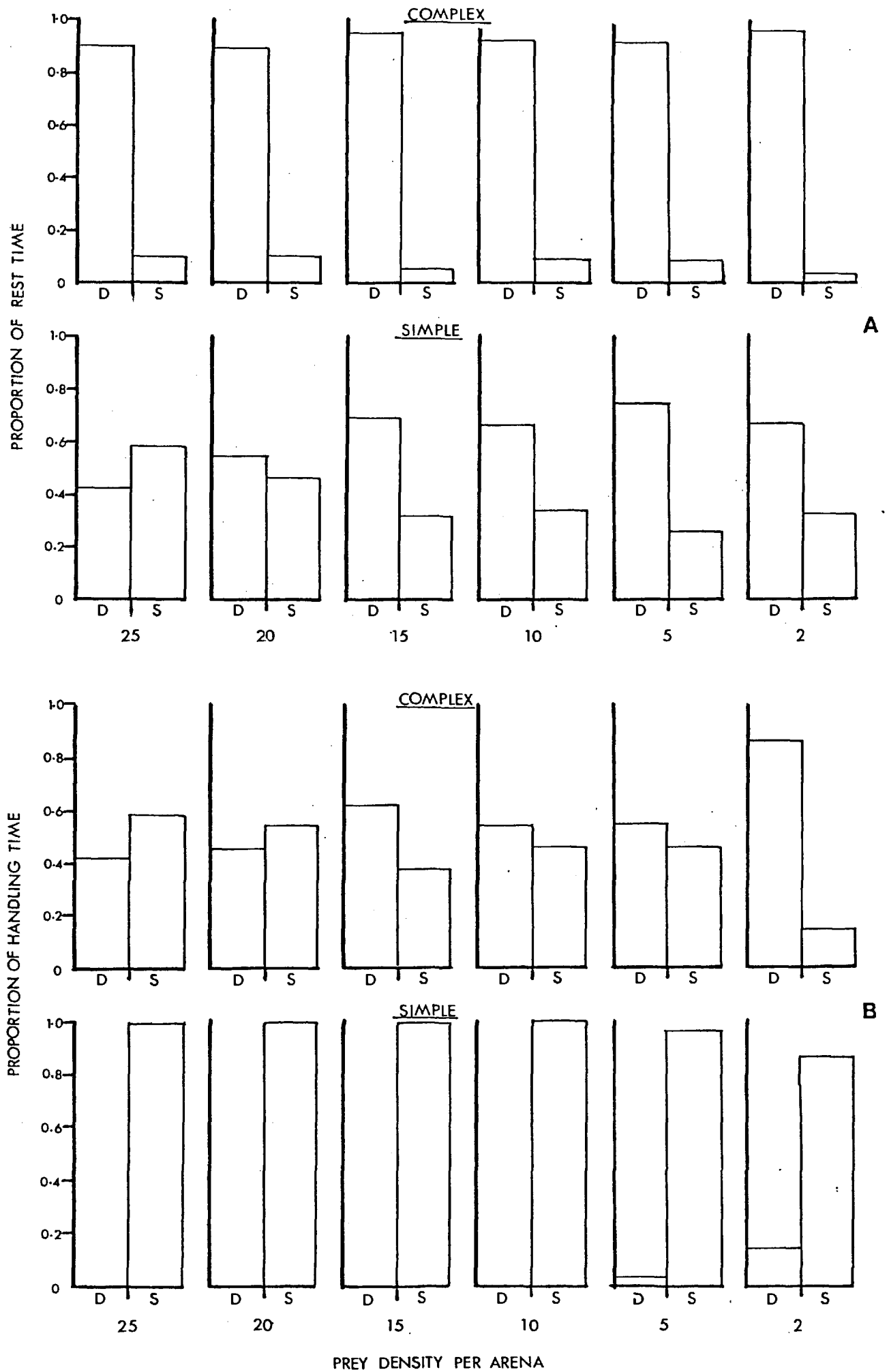
N. glauca, N. maculata and N. obliqua feeding on six

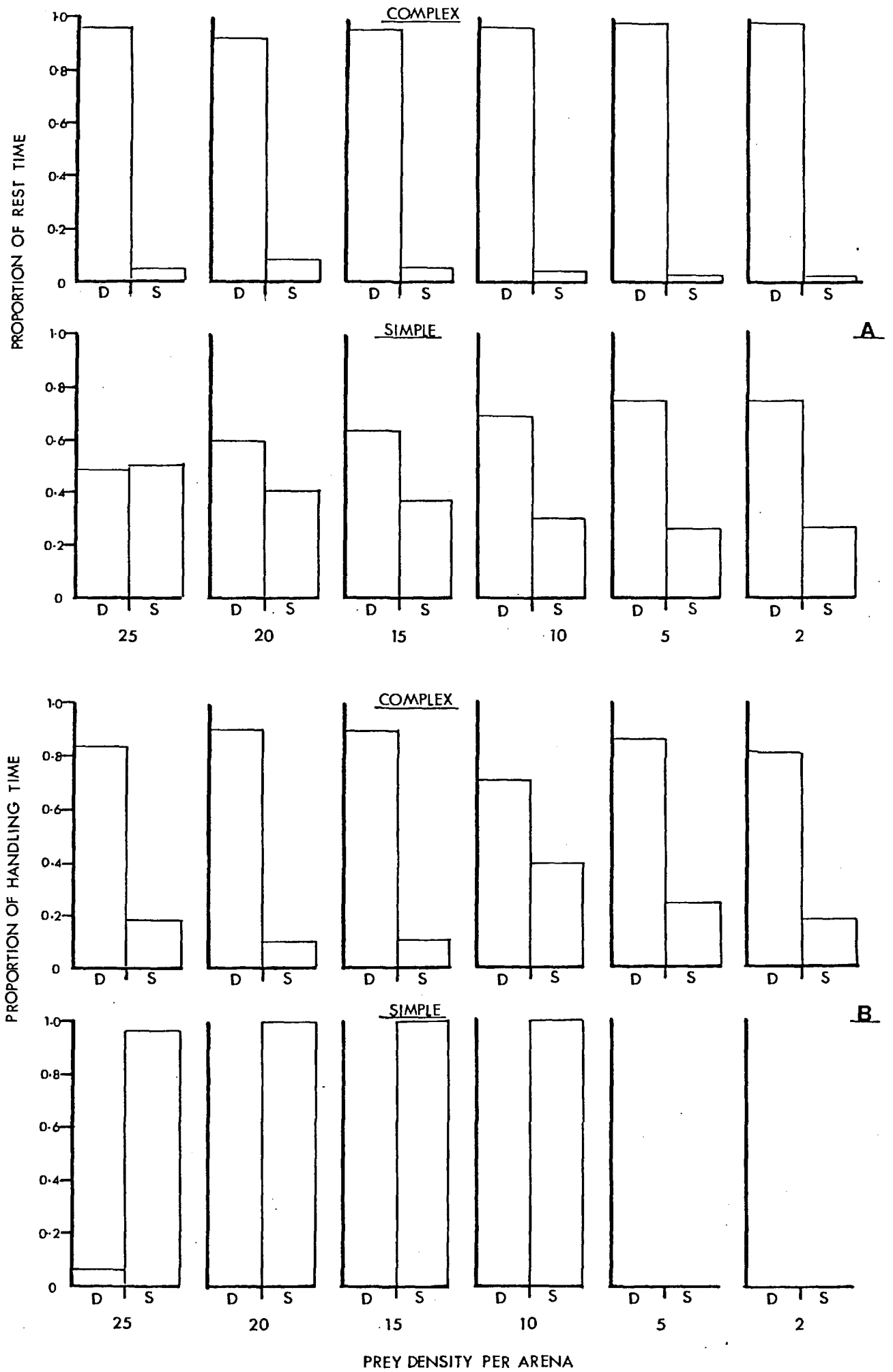
densities of Musca domestica and Gammarus pulex

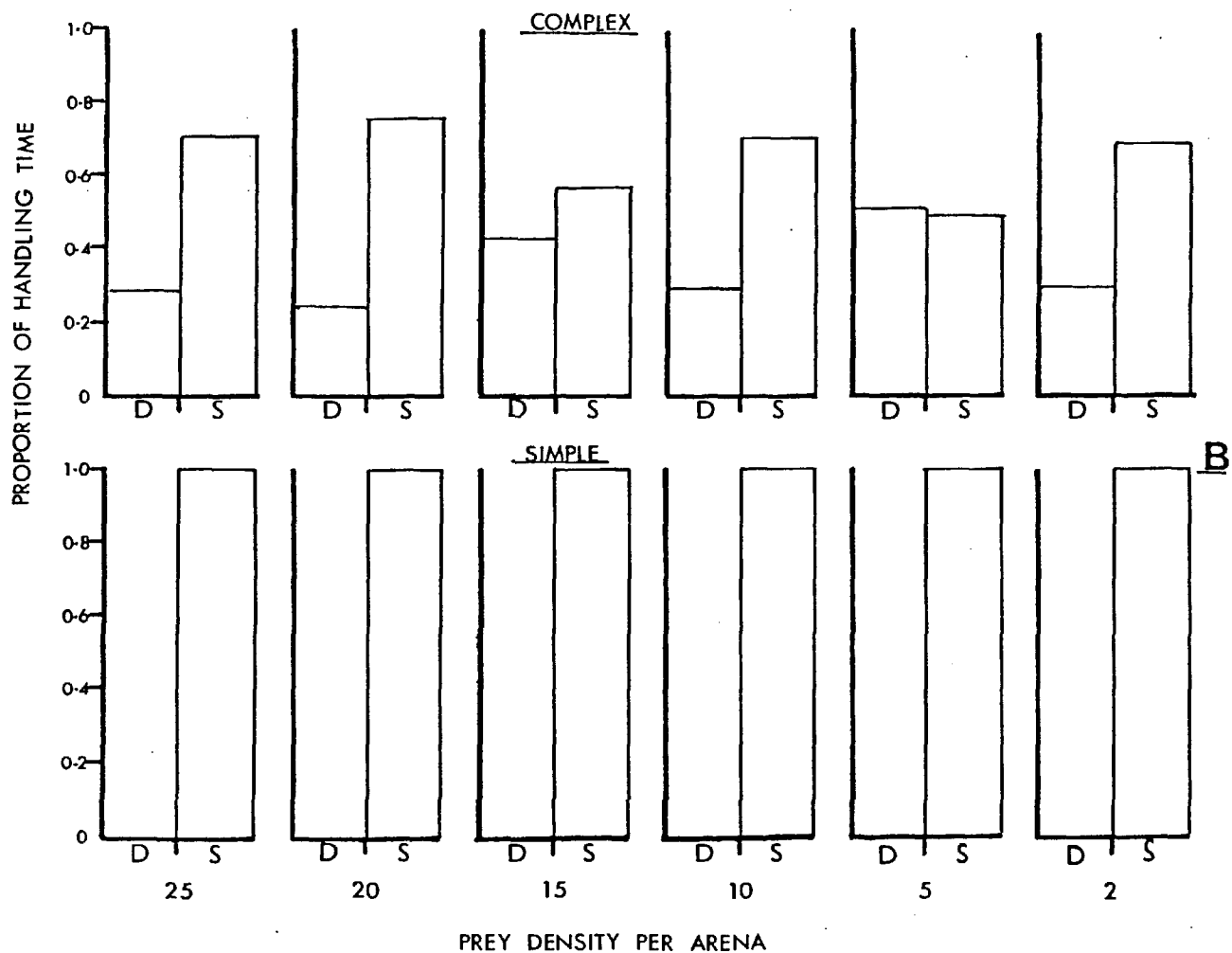
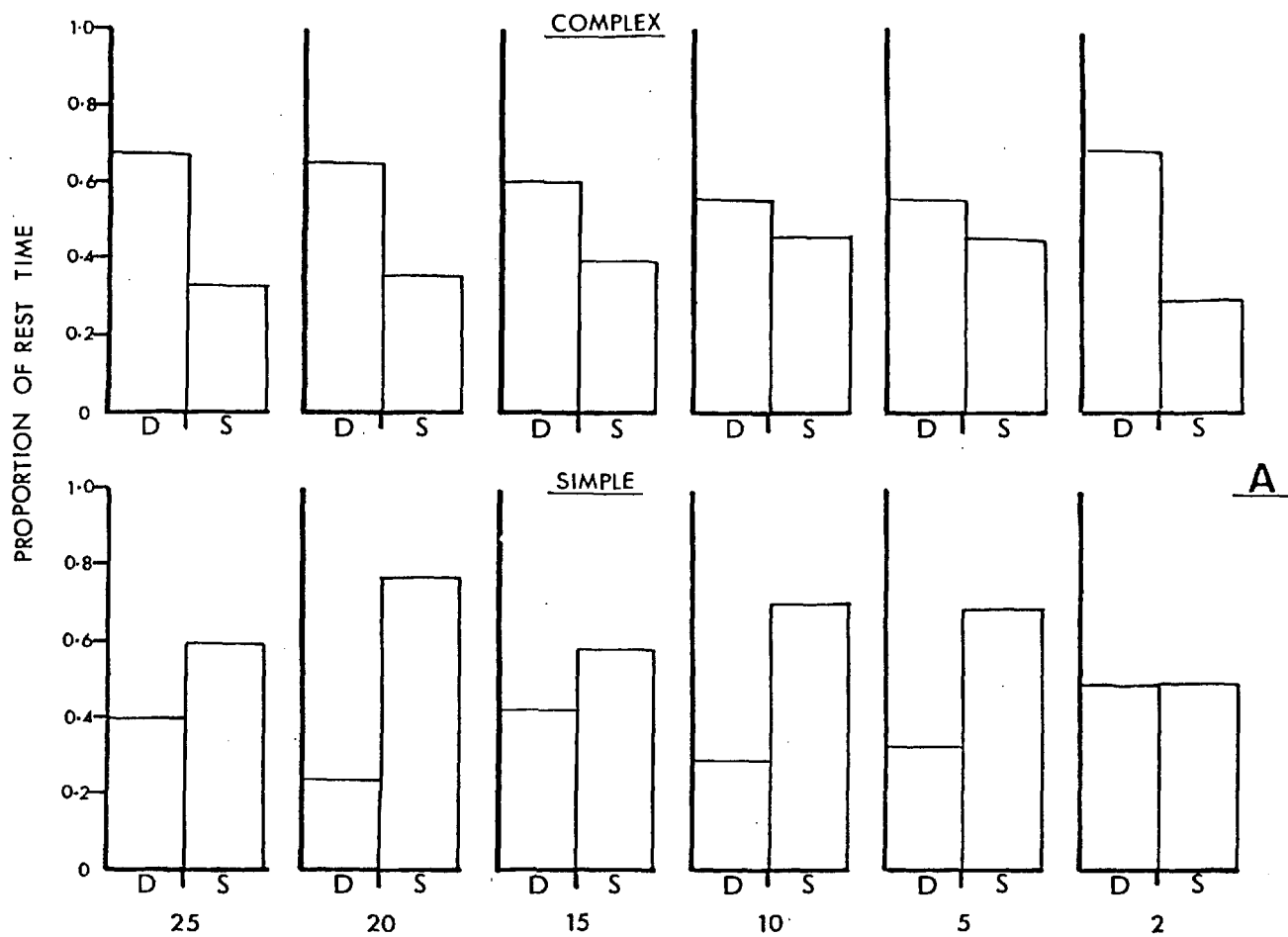
(25, 20, 15, 10, 5 and 2) in both simple and complex environments.

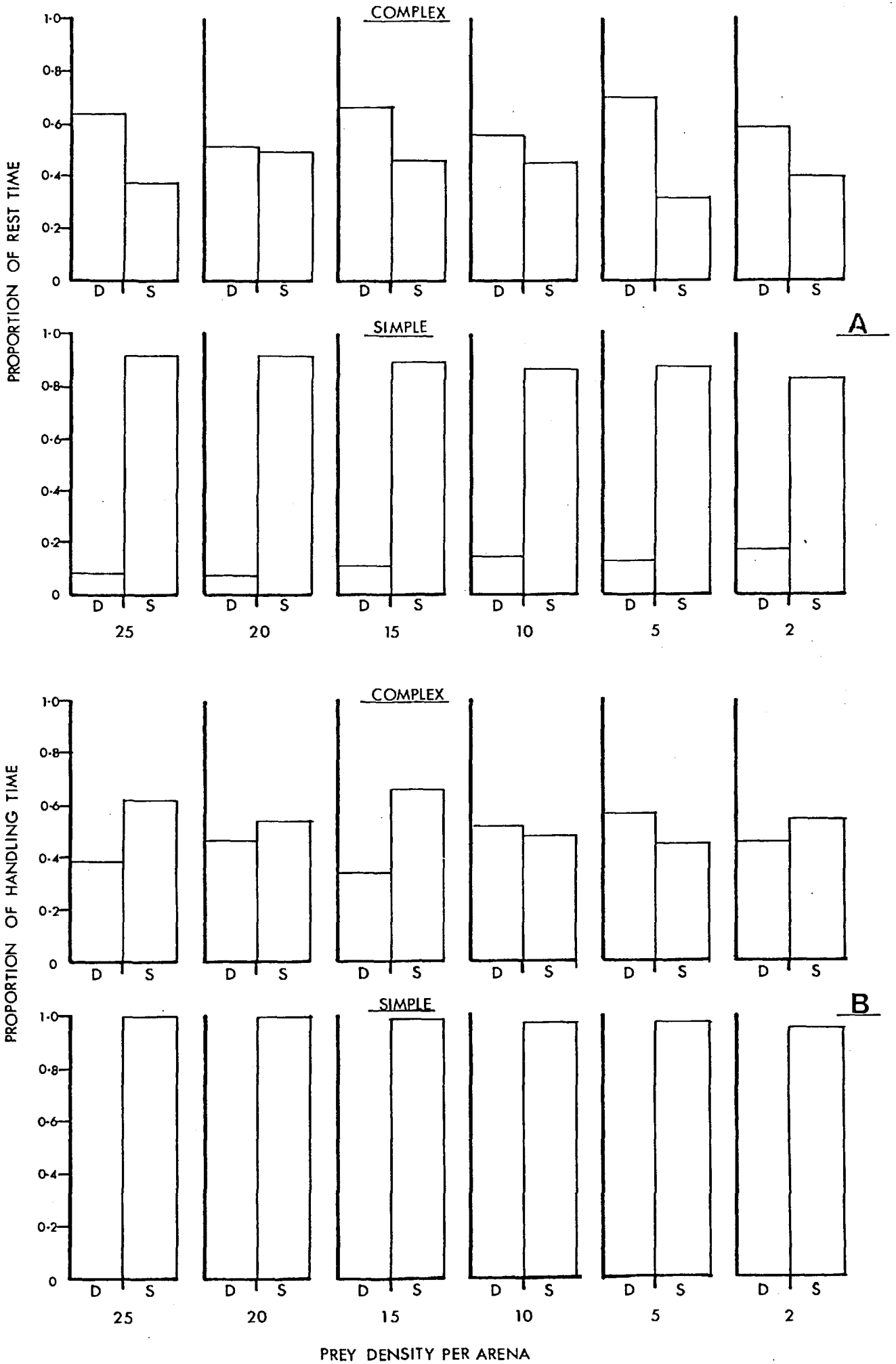
D - Positions at depth

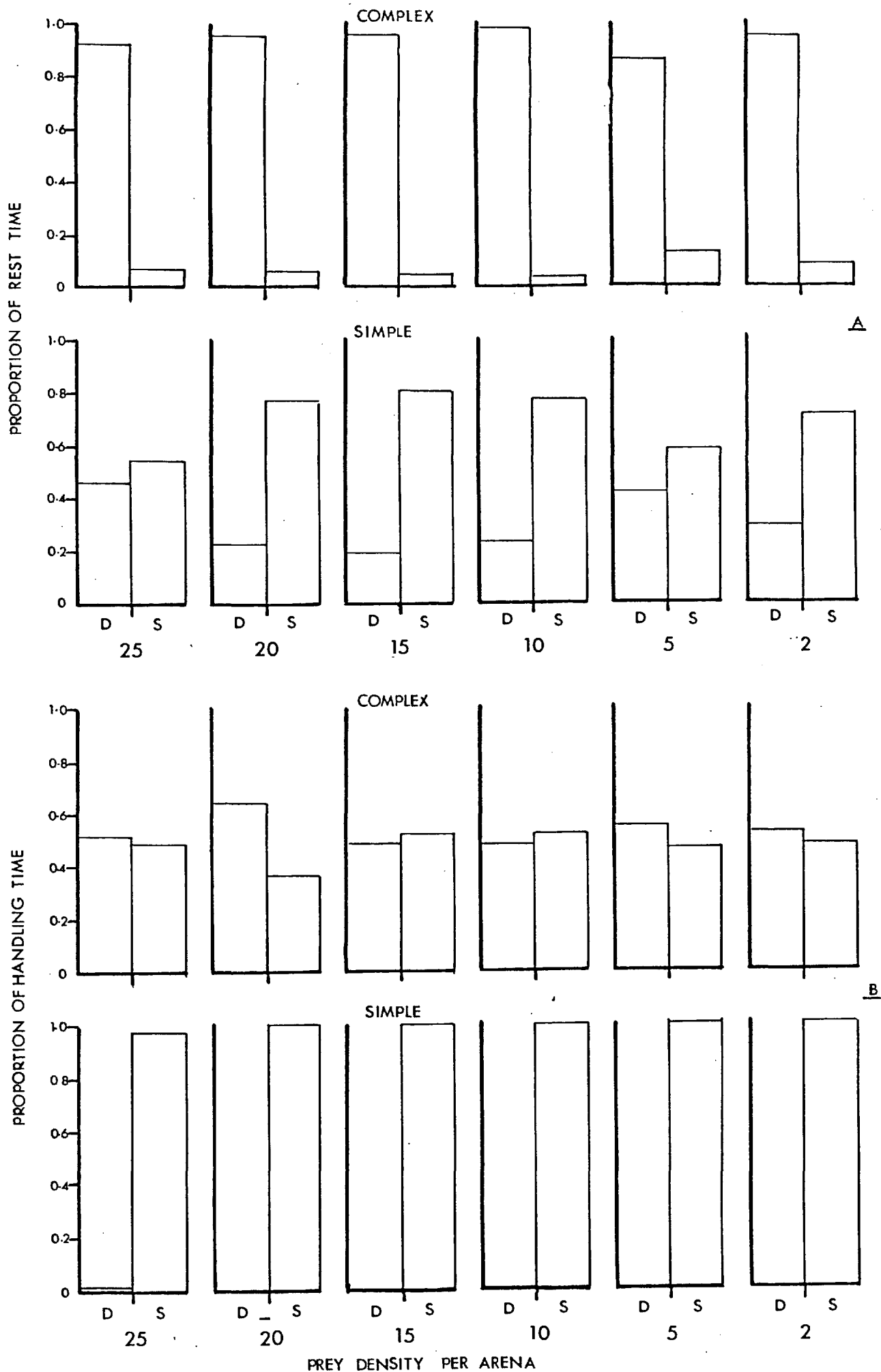
S - Positions at surface

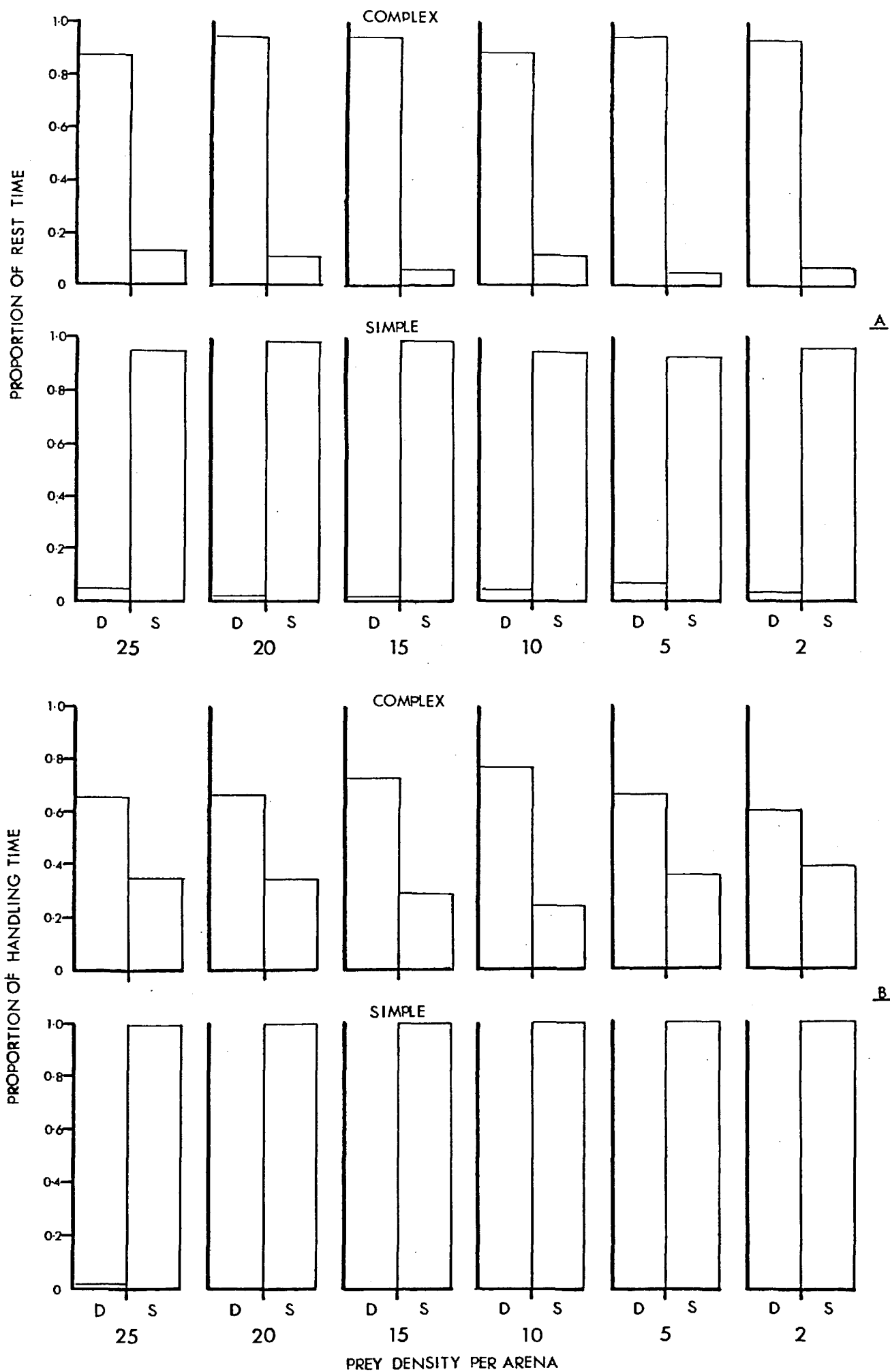












Appendix XVI(a) Tests of significance for differences between proportion of time at surface and depth for pooled data from all densities so distribution approximates to normal.

Use general formula $d = \frac{a}{n} - P$ (Bailey 1959)

where $\frac{a}{n}$ is measured proportion $\frac{\sqrt{P(1-P)}}{n}$

P = expected proportion = 0.5

(i.e. no preference)

H₀ - proportion of time at depth ($\frac{a}{n}$) = 0.5 no preference (P).

N. glauca

		Proportion at	Expected	d	Sig-to-reject.
		Depth	Proportion		No
<u>Rest</u>					
<u>Complex</u>	<u>Musca</u>	0.917	0.5	6.12	0.001
	<u>Gammarus</u>	0.957	0.5	6.71	0.001
	<u>Mosquito</u>	0.83	0.5	4.85	0.001
<u>Simple</u>	<u>Musca</u>	0.685	0.5	2.71	0.01
	<u>Gammarus</u>	0.646	0.5	2.14	0.05
	<u>Mosquito</u>	0.671	0.5	2.51	0.02
<u>Handling</u>					
<u>Complex</u>	<u>Musca</u>	0.536	0.5	0.53	n.sig.
	<u>Gammarus</u>	0.837	0.5	4.95	0.001
	<u>Mosquito</u>	0.73	0.5	3.38	0.001
<u>Simple</u>	<u>Musca</u>	0.016	0.5	7.11	0.001
	<u>Gammarus</u>	0	0.5	7.34	0.001
	<u>Mosquito</u>	0.16	0.5	4.99	0.001

Comparison between Rest and Handling at depth.

<u>Complex</u>	<u>Musca</u>	R → H
		0.001
	<u>Gammarus</u>	R → H
		0.05
	<u>Mosquito</u>	R → H
<u>Simple</u>	<u>Musca</u>	R → H
		0.001
	<u>Gammarus</u>	R → H
		0.001
	<u>Mosquito</u>	R → H

Comparison of time at depth with different prey.

<u>Rest</u>	<u>Complex</u>	<u>Simple</u>
	<u>Gammarus</u>	<u>Musca</u>
	n.	
	sig.	
0.01	<u>Musca</u>	<u>Gammarus</u>
	n.	
	sig.	
	<u>Mosquito</u>	<u>Mosquito</u>
		n.sig.
<u>Handling</u>	<u>Gammarus</u>	<u>Mosquito</u>
	n.sig.	
0.001	<u>Mosquito</u>	0.01
	0.01	<u>Musca</u>
	0.05	
	<u>Musca</u>	<u>Gammarus</u>
		n.sig.

R = rest, H = handling.

Comparison time at depth between environments
S = Simple. C = Complex.

<u>Rest</u>	<u>Musca</u>	S+C	<u>Handling</u>	<u>Musca</u>	S+C
		0.001			0.001
	<u>Gammarus</u>	S+C		<u>Gammarus</u>	S+C
		0.001			0.001
	<u>Mosquito</u>	S+C		<u>Mosquito</u>	S+C
		0.01			0.001

Appendix XVI(a)(Continued)N. maculata

		Proportion at depth	Expected Proportion	d	Sig. to reject Ho
<u>Rest</u>	<u>Musca</u>	0.622	0.5	1.79	0.1
<u>Complex</u>	<u>Gammarus</u>	0.584	0.5	1.3	n.sig.
	<u>Mosquito</u>	0.571	0.5	1.04	n.sig.
<u>Simple</u>	<u>Musca</u>	0.366	0.5	1.97	0.05
	<u>Gammarus</u>	0.127	0.5	5.48	0.001
	<u>Mosquito</u>	0.132	0.5	5.4	0.001
<u>Handling</u>	<u>Musca</u>	0.348	0.5	2.23	0.05
<u>Complex</u>	<u>Gammarus</u>	0.55	0.5	0.73	n.sig.
	<u>Mosquito</u>	0.523	0.5	0.37	n.sig.
<u>Simple</u>	<u>Musca</u>	0	0.5	7.35	0.001
	<u>Gammarus</u>	0.026	0.5	7.31	0.001
	<u>Mosquito</u>	0.091	0.5	6.01	0.001

Comparison between time of rest
and handling at depth.

Comparison of time at depth with
different prey.

<u>Complex</u>	<u>Musca</u>	R+H		<u>Rest</u>	<u>Complex</u>		<u>Simple</u>	
		0.001			<u>Musca</u>	n.sig.	<u>Musca</u>	0.01
	<u>Gammarus</u>	R H			<u>Gammarus</u>		<u>Gammarus</u>	n.sig.
	<u>Mosquito</u>	R H			<u>Mosquito</u>		<u>Mosquito</u>	n.sig.
<u>Simple</u>	<u>Musca</u>	R+H		<u>Handling</u>	<u>Gammarus</u>	n.sig.	<u>Mosquito</u>	n.sig.
		0.001		0.1	<u>Mosquito</u>	0.05	<u>Gammarus</u>	n.sig.
	<u>Gammarus</u>	R+H			<u>Musca</u>		<u>Musca</u>	n.sig.
		0.05						
	<u>Mosquito</u>	R H						

R = rest. H = handling.

Comparison of time at depth between environments.

<u>Rest</u>	<u>Musca</u>	S+C	<u>Handling</u>	<u>Musca</u>	S+C
		0.001			0.001
	<u>Gammarus</u>	S+C		<u>Gammarus</u>	S+C
		0.001			0.001
	<u>Mosquito</u>	S+C		<u>Mosquito</u>	S+C
		0.001			0.001

S = Simple, C = Complex.

Appendix XVI(a)(Continued)

N. obliqua

		Proportion of time at depth	Expected Proportion	d	Sig. to reject Ho
<u>Rest</u>					
<u>Complex</u>	<u>Musca</u>	0.937	0.5	6.42	0.001
	<u>Gammarus</u>	0.921	0.5	6.18	0.001
	<u>Mosquito</u>	0.866	0.5	5.38	0.001
<u>Simple</u>	<u>Musca</u>	0.3	0.5	2.94	0.01
	<u>Gammarus</u>	0.038	0.5	6.78	0.001
	<u>Mosquito</u>	0.041	0.5	6.75	0.001
<u>Handling</u>	<u>Musca</u>	0.53	0.5	0.44	n.sig.
<u>Complex</u>	<u>Gammarus</u>	0.676	0.5	2.58	0.01
	<u>Mosquito</u>	0.65	0.5	2.2	0.05
<u>Simple</u>	<u>Musca</u>	0.004	0.5	7.29	0.001
	<u>Gammarus</u>	0	0.5	7.34	0.001
	<u>Mosquito</u>	0.039	0.5	6.77	0.001

Comparison between rest and handling at depth. Comparison of time at depth with different prey.

				<u>Complex</u>		<u>Simple</u>
<u>Complex</u>	<u>Musca</u>	R→H		<u>Musca</u>		<u>Musca</u>
		0.001			0.001	
	<u>Gammarus</u>	R→H		<u>Gammarus</u>	n.sig.	<u>Mosquito</u>
		0.002				
	<u>Mosquito</u>	R→H		<u>Mosquito</u>		<u>Gammarus</u>
		0.01				
<u>Simple</u>	<u>Musca</u>	R→H		<u>Gammarus</u>		<u>Mosquito</u>
		0.001			n.sig.	
	<u>Gammarus</u>	R H		<u>Mosquito</u>	0.01	<u>Gammarus</u>
			0.1		0.05	
	<u>Mosquito</u>	R H		<u>Musca</u>		<u>Musca</u>

R = rest. H = Handling.

Comparison of time at depth between environments.

<u>Rest</u>	<u>Musca</u>	S+C	<u>Handling</u>	<u>Musca</u>	S+C
		0.001			0.001
	<u>Gammarus</u>	S+C		<u>Gammarus</u>	S+C
		0.001			0.001
	<u>Mosquito</u>	S+C		<u>Mosquito</u>	S+C
		0.001			0.001

Appendix XVI(b) Comparison of proportion of time at depth betweenpredators using $d = r_1 - r_2$

$$\sqrt{r(1-r)}\left(\frac{2}{n}\right) \text{ where } r_1 \text{ and } r_2 \text{ are the}$$

two proportions, r the mean proportion of the two, n

the total sample number (Parker 1973).

Significance of differences shown.

<u>Rest</u>		<u>Complex</u>		<u>Simple</u>	
<u>Musca</u>	0.001	$\begin{bmatrix} O & 0.937 \\ G & 0.917 \\ M & 0.622 \end{bmatrix}$	n.sig. 0.001	$\begin{bmatrix} G & 0.685 \\ M & 0.366 \\ O & 0.3 \end{bmatrix}$	0.001 n.sig.
<u>Gammarus</u>	0.001	$\begin{bmatrix} G & 0.957 \\ O & 0.921 \\ M & 0.589 \end{bmatrix}$	n.sig. 0.001	$\begin{bmatrix} G & 0.646 \\ M & 0.127 \\ O & 0.038 \end{bmatrix}$	0.001 n.sig.
<u>Mosquito</u>	0.002	$\begin{bmatrix} O & 0.536 \\ G & 0.83 \\ M & 0.571 \end{bmatrix}$	n.sig. 0.001	$\begin{bmatrix} G & 0.671 \\ M & 0.132 \\ O & 0.041 \end{bmatrix}$	0.001 0.1
<u>Handling</u>					
<u>Musca</u>	0.1	$\begin{bmatrix} G & 0.536 \\ O & 0.53 \\ M & 0.348 \end{bmatrix}$	n.sig. 0.1	$\begin{bmatrix} G & 0.016 \\ O & 0.004 \\ M & 0 \end{bmatrix}$	n.sig.
<u>Gammarus</u>	0.001	$\begin{bmatrix} G & 0.837 \\ O & 0.676 \\ M & 0.55 \end{bmatrix}$	0.1 n.sig.	$\begin{bmatrix} G \\ O \\ M \end{bmatrix}$	n.sig.
<u>Mosquito</u>	0.05	$\begin{bmatrix} G & 0.73 \\ O & 0.65 \\ M & 0.523 \end{bmatrix}$	n.sig. n.sig.	$\begin{bmatrix} G & 0.16 \\ M & 0.091 \\ O & 0.039 \end{bmatrix}$	0.05 n.sig. n.sig.

O = N. obliquaM = N. maculataG = N. glauca

n = 54

Appendix XVII

Differences in net energy gains from prey combination tests between the three predators, N. maculata (M) N. glauca (G) and N. obliqua (O), tested by T test. Significance of differences shown.

	Combination							
	5,5,10.	5,20,10,	5,20,50.	5,5,50.	20,5,10.	20,5,50.	20,20,10.	20,20,50
<u>Complex</u>	$\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.1 $\begin{matrix} M \\ G \\ O \end{matrix}$ n.sig.	0.05 $\begin{matrix} M \\ G \\ O \end{matrix}$ n.sig.	$\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.02 $\begin{matrix} M \\ G \\ O \end{matrix}$ n.sig.	$\begin{matrix} M \\ G \\ O \end{matrix}$ n.sig.	0.05 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	$\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.
<u>Simple</u>	0.05 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.002 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.	0.001 $\begin{matrix} M \\ O \\ G \end{matrix}$ n.sig.

Appendix XVIII

Differences in proportion of time spent handling in the two environments during combination experiments, data pooled over all combinations.

Test using $d = \frac{r_1 - r_2}{\sqrt{r(1-r) \frac{2}{n}}}$ r_1, r_2 - proportions
 r = average of two proportions
 n = sample size
 d = standardised normal deviate.

<u>N. glauca</u>	Complex	0.573	d = 0.121	n.sig.
	Simple	0.563		
<u>N. maculata</u>	Complex	0.691	d = 1.95	sig. 0.05
	Simple	0.83		
<u>N. obliqua</u>	Complex	0.405	d = 2.316	sig. 0.02
	Simple	0.598		

Appendix XIX

A) Comparison of the proportion of time spent at depth with expected proportion (no preference) during prey combination experiments.

Due to small sample size, data is pooled over all combinations to give a general idea of significance of the differences in proportions, with normal distribution, approximation.

<u>N. glauca</u>		Depth	Expected Proportion	n	d	sig.
Complex	Rest	0.895	0.5	72	6.7	0.001
	Feeding	0.743	0.5	72	4.12	0.001
Simple	Rest	0.383	0.5	72	1.98	0.05
	Feeding	0	0.5	72	8.48	0.001
<u>N. maculata</u>						
Complex	Rest	0.60	0.5	72	1.69	0.1
	Feeding	0.318	0.5	72	3.08	0.002
Simple	Rest	0.406	0.5	72	1.59	n.sig.
	Feeding	0	0.5	72	8.48	0.001
<u>N. obliqua</u>						
Complex	Rest	0.857	0.5	72	6.06	0.001
	Feeding	0.363	0.5	72	2.32	0.02
Simple	Rest	0.019	0.5	72	8.16	0.001
	Feeding	0	0.5	72	8.48	0.001

$$\text{Test } d = \frac{\left(\frac{a}{n}\right) - P}{\sqrt{\frac{P(1-P)}{n}}}$$

$\frac{a}{n}$ = proportion at depth
 P = expected proportion i.e. 0.5
 n = total sample number = 72
 d = normal statistic

B) Difference in proportion of time spent at depth between Simple (S) and Complex (C) environments and during Rest (R) and Feeding (F) in prey combination experiments. Significance shown.

<u>N. glauca</u>		0.02	<u>N. maculata</u>		0.001	<u>N. obliqua</u>		0.001
Complex	R→F	0.001	Complex	R→F	0.001	Complex	R→F	0.001
	R→F			R→F			R→F	
Simple			Simple			Simple		n.sig.
0.001			0.02			0.001		
Rest	C→S		Rest	C→S		Rest	C→S	
0.001			0.001			0.001		
Feed	C→S		Feed	C→S		Feed	C→S	

Appendix XX Predictions of proportions of each prey type captured based on models in Chapter V.

Each combination group comprises of 4 separate combinations e.g. 5 Musca comprises of the following combinations 5, 5, 10; 5, 20, 10; 5, 20, 50; and 5, 5, 50. Musca, Gammarus, mosquito larvae respectively.

The predictions of the models are made on the basis of averaging data for a particular activity over the 4 separate combinations to give a value for the larger combination group e.g.

$$\frac{\sum \text{Proportion of time at depth for 4 combinations}}{4}$$

Expected values are obtained within each combination group for each prey type and these are adjusted to give expected proportion of each prey type captured under the criteria of each model in each combination group.

All models assume no prey preference unless otherwise stated, capture at every encounter, and random encounters.

Model 1. - Based on position at Rest - data during rest

Complex	<u>Musca</u>	-	$\frac{\sum \text{Proportion time at surface}}{4}$
	<u>Gammarus</u>	-	$\frac{\sum \text{Proportion of time at depth x proportion visits to bottom perches}}{4}$
	<u>Mosquito</u>	-	$\frac{\sum \text{Proportion of time at depth x proportion visits to middle and near surface perches}}{4}$
Simple	<u>Musca</u>	[	$\frac{\sum \text{Proportion time at surface}}{4}$
	<u>Mosquito</u>		
	<u>Gammarus</u>		$\frac{\sum \text{Proportion time at depth}}{4}$

Values are then converted to expected proportions of total captures.

Appendix XX (Continued)

Model 1.(Continued)

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	Mosquito		<u>Musca</u>	<u>Gammarus</u>	Mosquito
Combination	Complex				Simple			
5	<u>Musca</u>	0.105	0.378	0.515		0.292	0.415	0.292
20	<u>Musca</u>	0.105	0.356	0.544		0.323	0.354	0.323
5	<u>Gammarus</u>	0.14	0.362	0.499		0.276	0.449	0.276
20	<u>Gammarus</u>	0.07	0.372	0.565		0.338	0.323	0.338
10	<u>Mosquito</u>	0.105	0.378	0.515		0.312	0.375	0.312
50	Mosquito	0.105	0.356	0.544		0.303	0.394	0.303

N. maculata

	Complex				Simple			
5	<u>Musca</u>	0.353	0.408	0.24		0.287	0.426	0.287
20	<u>Musca</u>	0.371	0.349	0.28		0.308	0.384	0.308
5	<u>Gammarus</u>	0.382	0.361	0.257		0.271	0.458	0.271
20	<u>Gammarus</u>	0.341	0.395	0.264		0.324	0.352	0.324
10	<u>Mosquito</u>	0.32	0.417	0.256		0.246	0.408	0.296
50	Mosquito	0.41	0.336	0.254		0.299	0.402	0.299

N. obliqua

	Complex				Simple	
5	<u>Musca</u>	0.16	0.418	0.42		Time at surface 1.0
20	<u>Musca</u>	0.126	0.35	0.52		Expect all combinations
5	<u>Gammarus</u>	0.107	0.393	0.499		Musca 0.5 Mosquito 0.5
20	<u>Gammarus</u>	0.179	0.38	0.446		
10	<u>Mosquito</u>	0.164	0.407	0.429		
50	Mosquito	0.122	0.363	0.515		

Appendix XX (Continued)

Model 2. - Selection based on greatest net energy gain from single prey experiments. Prey returning greatest net energy gain at densities in each combination should be selected for that combination.

	Expected proportion of each prey for combination group			Σ <u>Expected proportion prey for each combination in group</u> 4		
	Complex			Simple		
	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>	<u>N. glauca</u>	<u>N. maculata</u>	<u>N. obliqua</u>
5 <u>Musca</u>	0.5M 0.5G	1.0G	0.25M 0.75G	1.0M	1.0G	0.75M 0.25G
20 <u>Musca</u>	1.0M	1.0M	1.0G	1.0M	1.0G	0.5M 0.5G
5 <u>Gammarus</u>	0.5M 0.5G	1.0M	0.25M 0.75G	1.0M	1.0G	1.0M
20 <u>Gammarus</u>	1.0M	1.0G	1.0G	1.0M	1.0G	0.25M 0.75G
10 Mosquito	0.75M 0.25G	0.5M 0.5G	0.125M 0.875G	1.0M	1.0G	0.625M 0.375G
50 Mosquito	0.75M 0.25G	0.5M 0.5G	0.125M 0.875G	1.0M	1.0G	0.625M 0.375G

M = Musca, G. = Gammarus

Model 3. - All combinations with all densities - selection of Musca

Appendix XX (Continued)

Model 4. - 1st capture as in Model 1. Subsequent captures based on position during handling. Values calculated as in Model 1. except data is from during handling.

N. glauca

Complex	<u>Musca</u>	<u>Gammarus</u>	Mosquito	Simple	<u>Musca</u>	<u>Gammarus</u>	Mosquito
5 <u>Musca</u>	0.233	0.26	0.505		0.5	0	0.5
20 <u>Musca</u>	0.28	0.245	0.472		0.5	0	0.5
5 <u>Gammarus</u>	0.287	0.205	0.506		0.5	0	0.5
20 <u>Gammarus</u>	0.225	0.306	0.463		0.5	0	0.5
10 <u>Mosquito</u>	0.238	0.253	0.505		0.5	0	0.5
50 <u>Mosquito</u>	0.275	0.253	0.473		0.5	0	0.5

N. maculata

5 <u>Musca</u>	0.655	0.216	0.129		0.5	0	0.5
20 <u>Musca</u>	0.702	0.18	0.116		0.5	0	0.5
5 <u>Gammarus</u>	0.702	0.179	0.118		0.5	0	0.5
20 <u>Gammarus</u>	0.655	0.219	0.126		0.5	0	0.5
10 <u>Mosquito</u>	0.697	0.218	0.09		0.5	0	0.5
50 <u>Mosquito</u>	0.66	0.186	0.15		0.5	0	0.5

N. obliqua

5 <u>Musca</u>	0.698	0.132	0.17		0.5	0	0.5
20 <u>Musca</u>	0.576	0.158	0.206		0.5	0	0.5
5 <u>Gammarus</u>	0.6	0.205	0.195		0.5	0	0.5
20 <u>Gammarus</u>	0.686	0.093	0.22		0.5	0	0.5
10 <u>Mosquito</u>	0.628	0.181	0.19		0.5	0	0.5
50 <u>Mosquito</u>	0.646	0.114	0.239		0.5	0	0.5

Appendix XX (Continued)

Model 5. - Based on relative prey abundance. Assuming equal likelihood of encounters with each prey type.

Expected value = $\frac{\sum n}{4}$ for each combination in combination group for prey type
for each prey type
in each combination group where n = density of prey type.

Values then converted to give expected proportion of total captures for each prey type in each combination group.

	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	
5 <u>Musca</u>	0.136	0.293	0.57	
20 <u>Musca</u>	0.364	0.208	0.43	all predators in all environments
5 <u>Gammarus</u>	0.293	0.136	0.57	
20 <u>Gammarus</u>	0.208	0.364	0.43	
10 <u>Mosquito</u>	0.34	0.34	0.32	
50 <u>Mosquito</u>	0.159	0.159	0.678	

Model 6. - 1st as in 1 or 7. 2nd as in 3.

Model 7. - Based on probability of successful capture with random encounters of all prey.

Obtain probability of successful capture for each prey at densities used in combination experiments
from data in single prey experiments.

e.g. Musca density 5

probability of successful capture = $\frac{\text{pursuit success} \times \text{attack success} \times \text{capture success}}{\text{success success success}}$

Appendix XX (Continued)

Model 7. (Continued)

Expected value for each prey in combination group. = $\frac{\sum \text{Probability of successful capture at each density in each combination group}}{4}$

Values then converted to give expected proportion of total captures for each prey type in each combination group.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	<u>Simple</u>	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
<u>Complex</u>								
5	<u>Musca</u>	0.365	0.188	0.446		0.422	0.562	0.515
20	<u>Musca</u>	0.373	0.186	0.441		0.323	0.073	0.604
5	<u>Gammarus</u>	0.362	0.202	0.436		0.384	0.05	0.566
20	<u>Gammarus</u>	0.376	0.172	0.452		0.37	0.083	0.546
10	<u>Mosquito</u>	0.356	0.18	0.463		0.38	0.068	0.551
50	<u>Mosquito</u>	0.383	0.19	0.423		0.373	0.066	0.56
<u>N. maculata</u>					<u>Simple</u>			
<u>Complex</u>								
5	<u>Musca</u>	0.5	0.22	0.28		0.464	0.141	0.395
20	<u>Musca</u>	0.44	0.17	0.39		0.44	0.147	0.412
5	<u>Gammarus</u>	0.5	0.17	0.33		0.462	0.125	0.413
20	<u>Gammarus</u>	0.45	0.19	0.36		0.442	0.163	0.395
10	<u>Mosquito</u>	0.42	0.21	0.37		0.46	0.247	0.392
50	<u>Mosquito</u>	0.53	0.17	0.3		0.444	0.141	0.414
<u>N. obliqua</u>					<u>Simple</u>			
<u>Complex</u>								
5	<u>Musca</u>	0.397	0.266	0.337		0.398	0.239	0.36
20	<u>Musca</u>	0.403	0.264	0.33		0.372	0.249	0.378
5	<u>Gammarus</u>	0.416	0.235	0.348		0.392	0.23	0.376
20	<u>Gammarus</u>	0.385	0.292	0.323		0.379	0.257	0.36
10	<u>Mosquito</u>	0.401	0.266	0.33		0.397	0.25	0.351
50	<u>Mosquito</u>	0.398	0.263	0.338		0.374	0.237	0.388

Appendix XX (Continued)

Model 8. - Combination of models 1 and 7.

Expected value for each prey in combination group. = Expected value from Model 1. x Expected value from Model 7

Values then converted to give expected proportion of total captures for each prey type in each combination group.

N. glauca		Musca	Gammarus	Mosquito	Simple	Musca	Gammarus	Mosquito
Complex								
5	Musca	0.236	0.137	0.627		0.411	0.087	0.502
20	Musca	0.291	0.127	0.582		0.32	0.078	0.6
5	Gammarus	0.284	0.112	0.603		0.372	0.079	0.549
20	Gammarus	0.244	0.151	0.604		0.371	0.08	0.549
10	Mosquito	0.232	0.126	0.642		0.376	0.079	0.545
50	Mosquito	0.297	0.14	0.564		0.366	0.083	0.55
N. maculata								
Complex					Simple			
5	Musca	0.53	0.205	0.264		0.433	0.197	0.37
20	Musca	0.486	0.149	0.304		0.425	0.197	0.39
5	Gammarus	0.555	0.151	0.293		0.425	0.194	0.38
20	Gammarus	0.46	0.186	0.353		0.436	0.174	0.39
10	Mosquito	0.405	0.214	0.38		0.436	0.191	0.37
50	Mosquito	0.611	0.14	0.247		0.424	0.18	0.39
N. obliqua								
Complex					Simple			
5	Musca	0.2	0.352	0.447		0.525	0	0.475
20	Musca	0.159	0.287	0.553		0.496	0	0.504
5	Gammarus	0.142	0.298	0.559		0.51	0	0.49
20	Gammarus	0.211	0.34	0.447		0.512	0	0.488
10	Mosquito	0.207	0.344	0.45		0.53	0	0.47
50	Mosquito	0.15	0.299	0.55		0.49	0	0.51

Appendix XX (Continued)

Model 9. - Combination of Models 1 and 5. Proportions estimated in similar way to Model 8.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	Mosquito		<u>Musca</u>	<u>Gammarus</u>	Mosquito
<u>Complex</u>	5 <u>Musca</u>	0.033	0.264	0.703	<u>Simple</u>	0.120	0.371	0.509
	20 <u>Musca</u>	0.109	0.214	0.676		0.359	0.215	0.426
	5 <u>Gammarus</u>	0.109	0.131	0.759		0.272	0.201	0.527
	20 <u>Gammarus</u>	0.036	0.346	0.608		0.185	0.43	0.383
	10 <u>Mosquito</u>	0.106	0.39	0.503		0.319	0.382	0.298
	50 <u>Mosquito</u>	0.038	0.129	0.833		0.152	0.199	0.649
<u>N. maculata</u>								
<u>Complex</u>	5 <u>Musca</u>	0.157	0.393	0.450	<u>Simple</u>	0.119	0.38	0.49
	20 <u>Musca</u>	0.41	0.227	0.367		0.346	0.247	0.407
	5 <u>Gammarus</u>	0.365	0.159	0.473		0.268	0.21	0.522
	20 <u>Gammarus</u>	0.235	0.474	0.288		0.201	0.384	0.414
	10 <u>Mosquito</u>	0.327	0.427	0.246		0.304	0.422	0.27
	50 <u>Mosquito</u>	0.224	0.182	0.592		0.149	0.204	0.646
<u>N. obliqua</u>								
<u>Complex</u>	5 <u>Musca</u>	0.052	0.32	0.627	<u>Simple</u>	0.192	0	0.808
	20 <u>Musca</u>	0.132	0.214	0.683		0.458	0	0.542
	5 <u>Gammarus</u>	0.082	0.137	0.78		0.338	0	0.662
	20 <u>Gammarus</u>	0.098	0.452	0.626		0.326	0	0.674
	10 <u>Mosquito</u>	0.166	0.48	0.415		0.515	0	0.485
	50 <u>Mosquito</u>	0.044	0.136	0.819		0.188	0	0.812

Appendix XX (Continued)

Model 10. - Combination of Models 7 and 5. Proportions estimated in similar way to Model 8.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	<u>Simple</u>	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
<u>Complex</u>								
	5 <u>Musca</u>	0.138	0.153	0.709		0.055	0.049	0.796
	20 <u>Musca</u>	0.373	0.106	0.522		0.299	0.038	0.662
	5 <u>Gammarus</u>	0.277	0.072	0.651		0.255	0.0158	0.729
	20 <u>Gammarus</u>	0.234	0.188	0.578		0.228	0.089	0.677
	10 <u>Mosquito</u>	0.367	0.185	0.448		0.393	0.07	0.536
	50 <u>Mosquito</u>	0.16	0.081	0.757		0.131	0.023	0.845
<u>N. maculata</u>								
<u>Complex</u>					<u>Simple</u>			
	5 <u>Musca</u>	0.255	0.213	0.532		0.19	0.125	0.683
	20 <u>Musca</u>	0.487	0.082	0.429		0.436	0.083	0.481
	5 <u>Gammarus</u>	0.465	0.057	0.477		0.349	0.043	0.607
	20 <u>Gammarus</u>	0.307	0.207	0.485		0.288	0.185	0.526
	10 <u>Mosquito</u>	0.416	0.219	0.364		0.409	0.151	0.379
	50 <u>Mosquito</u>	0.341	0.07	0.588		0.188	0.06	0.751
<u>N. obliqua</u>								
<u>Complex</u>					<u>Simple</u>			
	5 <u>Musca</u>	0.167	0.24	0.592		0.164	0.212	0.623
	20 <u>Musca</u>	0.424	0.159	0.416		0.389	0.144	0.617
	5 <u>Gammarus</u>	0.346	0.091	0.56		0.319	0.086	0.594
	20 <u>Gammarus</u>	0.247	0.279	0.457		0.242	0.285	0.472
	10 <u>Mosquito</u>	0.41	0.271	0.317		0.406	0.256	0.337
	50 <u>Mosquito</u>	0.188	0.126	0.685		0.167	0.102	0.73

Appendix XX (Continued)

Model 11. - Combination Models 8 and 5. Proportions estimated in similar way to Model 8.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
<u>Complex</u>	5 <u>Musca</u>	0.027	0.113	0.859	<u>Simple</u>	0.052	0.068	0.703
	20 <u>Musca</u>	0.094	0.091	0.815		0.298	0.043	0.658
	5 <u>Gammarus</u>	0.08	0.054	0.865		0.252	0.023	0.724
	20 <u>Gammarus</u>	0.035	0.155	0.81		0.225	0.085	0.69
	10 <u>Mosquito</u>	0.076	0.186	0.738		0.387	0.085	0.527
	50 <u>Mosquito</u>	0.032	0.053	0.916		0.132	0.029	0.838
<u>N. maculata</u>								
<u>Complex</u>	5 <u>Musca</u>	0.33	0.14	0.52	<u>Simple</u>	0.18	0.177	0.642
	20 <u>Musca</u>	0.248	0.119	0.585		0.439	0.105	0.456
	5 <u>Gammarus</u>	0.33	0.108	0.56		0.338	0.07 0.591	
	20 <u>Gammarus</u>	0.314	0.12	0.56		0.282	0.197	0.52
	10 <u>Mosquito</u>	0.285	0.146	0.57		0.447	0.196	0.356
	50 <u>Mosquito</u>	0.368	0.119	0.511		0.187	0.078	0.735
<u>N. obliqua</u>								
<u>Complex</u>	5 <u>Musca</u>	0.07	0.268	0.661	<u>Simple</u>	0.209	0	0.791
	20 <u>Musca</u>	0.163	0.166	0.67		0.454	0	0.546
	5 <u>Gammarus</u>	0.102	0.099	0.79		0.348	0	0.652
	20 <u>Gammarus</u>	0.123	0.344	0.532		0.338	0	0.662
	10 <u>Mosquito</u>	0.21	0.337	0.435		0.548	0	0.455
	50 <u>Mosquito</u>	0.045	0.106	0.847		0.18	0	0.816

Appendix XX (Continued)

Model 12. - Combination of Models 4 and 5. Proportions estimated in a similar way to Model 8.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>	<u>Simple</u>	<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
<u>Complex</u>								
	5 <u>Musca</u>	0.081	0.192	0.726		0.193	0	0.807
	20 <u>Musca</u>	0.286	0.143	0.57		0.458	0	0.542
	5 <u>Gammarus</u>	0.209	0.069	0.72		0.339	0	0.661
	20 <u>Gammarus</u>	0.23	0.313	0.55		0.326	0	0.774
	10 <u>Mosquito</u>	0.25	0.26	0.492		0.515	0	0.485
	50 <u>Mosquito</u>	0.209	0.099	0.79		0.189	0	0.811
<u>N. maculata</u>					<u>Simple</u>			
<u>Complex</u>								
	5 <u>Musca</u>	0.118	0.107	0.775		0.193	0	0.807
	20 <u>Musca</u>	0.282	0.065	0.65		0.458	0	0.542
	5 <u>Gammarus</u>	0.223	0.034	0.74		0.339	0	0.661
	20 <u>Gammarus</u>	0.187	0.12	0.687		0.326	0	0.774
	10 <u>Mosquito</u>	0.297	0.147	0.557		0.515	0	0.485
	50 <u>Mosquito</u>	0.137	0.045	0.818		0.189	0	0.811
<u>N. obliqua</u>					<u>Simple</u>			
<u>Complex</u>								
	5 <u>Musca</u>	0.41	0.166	0.423		0.192	0	0.807
	20 <u>Musca</u>	0.587	0.092	0.32		0.458	0	0.542
	5 <u>Gammarus</u>	0.538	0.122	0.339		0.339	0	0.661
	20 <u>Gammarus</u>	0.534	0.128	0.338		0.326	0	0.774
	10 <u>Mosquito</u>	0.639	0.18	0.18		0.515	0	0.485
	50 <u>Mosquito</u>	0.362	0.064	0.574		0.189	0	0.811

Appendix XX (Continued)

Model 13. - Combination of Models 10 and 4. Proportions estimated in a similar way to Model 8.

<u>N. glauca</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>		<u>Musca</u>	<u>Gammarus</u>	<u>Mosquito</u>
<u>Complex</u>	5 <u>Musca</u>	0.075	0.093	0.83	<u>Simple</u>	0.162	0	0.837
	20 <u>Musca</u>	0.277	0.069	0.654		0.311	0	0.689
	5 <u>Gammarus</u>	0.188	0.034	0.78		0.259	0	0.741
	20 <u>Gammarus</u>	0.223	0.14	0.64		0.228	0	0.772
	10 <u>Mosquito</u>	0.246	0.129	0.626		0.423	0	0.577
	50 <u>Mosquito</u>	0.105	0.05	0.85		0.134	0	0.866
<u>N. maculata</u>								
<u>Complex</u>	5 <u>Musca</u>	0.5	0.128	0.372	<u>Simple</u>	0.217	0	0.783
	20 <u>Musca</u>	0.785	0.05	0.166		0.475	0	0.525
	5 <u>Gammarus</u>	0.731	0.029	0.24		0.365	0	0.635
	20 <u>Gammarus</u>	0.63	0.12	0.25		0.354	0	0.646
	10 <u>Mosquito</u>	0.8	0.093	0.108		0.553	0	0.447
	50 <u>Mosquito</u>	0.506	0.055	0.44		0.2	0	0.8
<u>N. obliqua</u>								
<u>Complex</u>	5 <u>Musca</u>	0.469	0.125	0.405	<u>Simple</u>	0.192	0	0.808
	20 <u>Musca</u>	0.643	0.066	0.29		0.458	0	0.542
	5 <u>Gammarus</u>	0.62	0.054	0.325		0.338	0	0.662
	20 <u>Gammarus</u>	0.708	0.06	0.231		0.326	0	0.674
	10 <u>Mosquito</u>	0.702	0.133	0.163		0.515	0	0.485
	50 <u>Mosquito</u>	0.406	0.047	0.547		0.188	0	0.812

Appendix XXI: Goodness of fit tests between prey selection and selection expected from models, using a χ^2 test; 6 x 3 contingency table (d.f. = 10).

N. glauca

<u>complex</u>	model 5	1st capture $\chi^2 = 0.833$ n. sig
		2nd capture $\chi^2 = 0.43$ n. sig
		3rd capture $\chi^2 = 1.058$ n. sig
		4th capture $\chi^2 = 1.17$ n. sig
	model 9	1st capture $\chi^2 = 0.898$ n. sig
	model 12	2nd capture $\chi^2 = 0.663$ n. sig
		3rd capture $\chi^2 = 0.976$ n. sig
	model 10	1st capture $\chi^2 = 2.59$ n. sig
		2nd capture $\chi^2 = 0.57$ n. sig

N. maculata

<u>complex</u>	model 1	1st capture $\chi^2 = 9.01$ (0.9 < P < 0.5)
	model 4	2nd capture $\chi^2 = 4.55$ (0.9 < P < 0.5)
	model 7	1st capture $\chi^2 = 0.584$ n. sig
		2nd capture $\chi^2 = 0.806$ n. sig
		3rd capture $\chi^2 = 2.717$ n. sig
		4th capture $\chi^2 = 3.848$ n. sig
	model 8	1st capture $\chi^2 = 0.939$ n. sig
		2nd capture $\chi^2 = 0.984$ n. sig
	model 10	1st capture $\chi^2 = 0.67$ n. sig
		2nd capture $\chi^2 = 0.65$ n. sig
		3rd capture $\chi^2 = 0.719$ n. sig
	model 11	1st capture $\chi^2 = 0.76$ n. sig
		2nd capture $\chi^2 = 1.03$ n. sig
		3rd capture $\chi^2 = 1.13$ n. sig
<u>simple</u>	model 7	1st capture $\chi^2 = 0.449$ n. sig
	model 8	1st capture $\chi^2 = 0.544$ n. sig
	model 10	1st capture $\chi^2 = 1.877$ n. sig
	model 11	1st capture $\chi^2 = 1.77$ n. sig

N. obliqua

<u>complex</u>	model 5	1st capture $\chi^2 = 1.24$
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