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POPULATION REGULATION, CONVERGENCE, AND CANNIBALISM IN *NOTONECTA* (HEMIPTERA)[1]

BRUCE K. ORR,[2] WILLIAM W. MURDOCH,[3] AND JAMES R. BENCE
Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA

Abstract. In a population convergence experiment, the initial densities of adults of the predatory backswimming bug *Notonecta hoffmanni* were set above and below a putative equilibrium density in stock tanks. The experiment was done at two constant rates of food supply (wingless *Drosophila*) for the larger instars (in natural pools *Notonecta* feed mainly on terrestrial arthropods that fall on the water surface). It was predicted that the densities of the resulting populations would converge on an equilibrium set by the rate of food supply for the larger instars. The tanks also contained zooplankton (mainly *Daphnia*), which were the main food supply of the smaller instars of *Notonecta*. The resulting overwintering populations converged towards the appropriate equilibrium densities, via density-dependent and food-dependent fecundity and then cannibalism. However, the populations overshot their equilibria, producing overconvergence. In natural populations such overconvergence might tend to produce 2-yr cycles in abundance. Overconvergence resulted from the insensitivity of the survivorship of the original adults (at least over the short term) to differences in food supply between treatments, allowing them to continue to affect (via cannibalism and reproduction) the eventual density of the new overwintering population. Because *Notonecta* population density was determined by the externally supplied, locally uncoupled food supply, even though the early instars depended for food largely upon dynamic populations of zooplankton, the dynamics of the *Notonecta* population were simpler than a description of the food web might suggest.

Key words: backswimming bug; cannibalism; convergence; cycle; experimental ecology; freshwater; Notonecta; *population dynamics; predation.*

INTRODUCTION

Interactions among populations in communities containing true predators are potentially very complex. The complexity has several sources. First, true predators typically are polyphagous and thus link the dynamics of a number of prey species. Second, and especially in freshwater communities, the size and species of prey in the predator's diet typically change as it grows (e.g., Werner and Gilliam 1984, Bence and Murdoch 1986, Murdoch and Bence 1987). Third, true predators are often cannibalistic, raising the potential for complex internal size- and age-dependent dynamic interactions whose intensity in turn is influenced by the density of a variety of prey species (Fox 1975*a*, Polis 1981). Although much progress has been made in the last decade in modelling interactions between age-distributed populations (e.g., Hastings 1984, Murdoch et al. 1987), these complexities nevertheless pose a daunting challenge to developing useful models involving true predators.

This paper examines some aspects of the dynamics of age-structured polyphagous predators that might render their analysis simpler than the predator's complex food web suggests is possible. Our predator is the backswimming freshwater bug, *Notonecta*, which is in many ways an archetypal freshwater predator. *Notonecta* lives all of its life in freshwater, passing through six instars and a large size range. It is highly polyphagous, and its diet changes with size. Older, larger instars cannibalize younger, smaller instars at a rate influenced by their food supply (Fox 1975*c*). Its generation time is typically longer than those of its prey species, sometimes by as much as an order of magnitude. The delays implicit in *Notonecta*'s age distribution are thus likely to be important dynamically (Murdoch and Bence 1987).

Some features of *Notonecta* make it especially suitable for our purposes. First, we know that *Notonecta* are food limited in their natural stream environment in southern California: they have one generation per year and their density is strongly influenced by the food supply of the reproductive adults (Fox 1975*b*, *c*). Second, extensive studies have been done in our laboratory on *Notonecta*'s predatory behavior (Fox 1973, Scott 1980, Chesson 1981, 1989, Scott and Murdoch 1983), and on the effects of food supply on its development (Fox and Murdoch 1978, Scott 1980), and we have been able to show that these laboratory studies provide an adequate basis for predicting *Notonecta*'s effects upon the population dynamics of its prey species (Murdoch and Scott 1984, Murdoch et al. 1984). Finally, in nature

[1] Manuscript received 16 August 1988; revised 1 March 1989; accepted 4 April 1989.
[2] Present address: College of Natural Resources, Agricultural Experiment Station, Entomology and Parasitology, University of California, Berkeley, California 94720 USA.
[3] Address correspondence to this author.

the larger instars eat mainly terrestrial prey items (insects, etc.) that fall on the surface of the water (Fox 1975*b*), and laboratory studies suggest that larger instars prefer such items to resident planktonic prey (Chesson 1981). This suggests (and we confirm in this paper) that the dynamics of the food supply of the larger instars, and especially of the adults, are uncoupled both from other prey species and from the *Notonecta* themselves, even when the small instars can feed on a complex planktonic fauna.

In our experiments we posed several questions, trying in each case to exploit this decoupling of dynamics to clarify how the various components in the system interact and to determine whether some components can be ignored for certain purposes. We present the results of a "convergence" experiment, in which initial *Notonecta* density is manipulated above and below a putative equilibrium density, and evidence is then sought that the population returns to equilibrium. Those treatments are crossed with the manipulation of the putative equilibrium, which is determined by the food supply for large instars. We ask whether a distinct food supply for large instars, and cannibalism, together suppress the importance of small-instar dynamics (in particular their interactions with their planktonic food supply) in determining the final density of the overwintering *Notonecta* population.

Methods

Laboratory experiments

Experiments were done at 25°C with a 12L:12D light regime. All *Notonecta* and prey were from stock laboratory cultures. With the exception of *Drosophila* all cultures were originally derived from stock tanks in the Santa Ynez Valley in southern California. Experiments were done in 500-mL plastic tubs.

Preference experiments.—Two prey species were offered in initially equal numbers (20 of each species), and were not replaced during each 2-h trial. Before an experiment each *Notonecta* was fed excess mosquito larvae for 24 h, and then starved for 24 h. There was zero mortality in controls without predators. Large *Daphnia* (mean [±SD] length 2.05 ± 0.18 mm), large *Ceriodaphnia* (length 0.78 ± 0.04 mm), adult *Drosophila* (length 2.28 ± 0.21 mm), and instar I *Notonecta* (length 2.81 ± 0.14 mm) were the prey. One experiment measured *Notonecta*'s preference between *Drosophila* and *Daphnia*, and between *Drosophila* and *Ceriodaphnia*. A second experiment measured *Notonecta*'s preference between instar I *Notonecta* and each of these three prey species.

Preference was measured by

$$\alpha_i = \ln(R_i/N_i)/\sum_{j=1}^{k} \ln (R_j/N_j) \qquad (1)$$

where N_i and R_i are number of prey of species i present initially and at the end of the experiment, respectively, k is the number of species, and α_i varies from 0 to 1 (Chesson 1983). When there is no preference $\alpha_i = 1/k$ (i.e., $\alpha_i = 0.5$ in the two-species case).

Feeding rate.—All individuals were starved for 24 h; then for 24 h before the experiment one set of *Notonecta* ("starved") was starved while the second set ("well-fed") was fed excess mosquito larvae. Fifty *Drosophila* were added at the start of the experiment, which ran for 2 h. Prey were not replaced.

The "high" *Drosophila* treatments at the start of the stock tank experiment were given enough *Drosophila* to allocate to each adult *Notonecta* approximately the number of flies eaten per day by well-fed adult notonectids in this laboratory experiment.

Cannibalism rate.—We counted the number of instar I *Notonecta* eaten by instar IV and (young) adults over 24 h in the presence of various combinations of alternative prey. All treatments contained *Ceriodaphnia* and *Notonecta* instar I. The *Ceriodaphnia* served as food for the instar I to prevent them from dying of starvation during the experiment, and has negligible effects on cannibalism by large *Notonecta* (Scott 1980, see also Table 2). We examined cannibalism rate on instar I *Notonecta* when only instar I and *Ceriodaphnia* were present as prey and when, in addition, either *Daphnia* or *Drosophila* were provided as alternative prey for the large *Notonecta*. For 24 h before the experiment, cannibals and instar I nymphs were fed excess amounts of the alternative prey that they would encounter during the experiment.

During the first 12 h of the 24-h experimental period an excess (≈500) of *Ceriodaphnia* was maintained in all treatments. Alternative prey for adults were given far in excess of the feeding rate (250 *Daphnia* or 125 *Drosophila* initially, with smaller batches added every 2 h to replace prey that were eaten). Two large *Notonecta* and 10 instar I were added to each tub initially. Notonectids were censused every hour for the first 12 h, and then again at 24 h. Dead instar I and those that molted to instar II were removed and replaced.

Stock tank experiments

Outdoor galvanized steel stock tanks (1.8 × 0.6 × 0.6 m) lined with fiberglass were filled to a depth of 0.5 m with 500 L deionized tap water in March 1981, with water lost to evaporation replaced weekly thereafter. Beginning in March inocula of algae (mainly *Chlamydomonas* and *Chlorella*) and the local community of zooplankton (*Daphnia*, *Ceriodaphnia*, ostracods, and some rarer species) were added over 4 mo and allowed to grow. Before the experiment, in early July, 20 (of 25) tanks with the most similar communities of algae and zooplankton were selected, and their contents mixed (among tanks) to reduce initial variability. Eight of these 20 tanks were selected, randomly, for use in the experiment described here.

Each tank was covered with fiberglass screening after it was first filled in March. Tanks were inspected several

times a week and extraneous predators (mainly odonate naiads and beetle larvae) were removed.

The experiment lasted 90 d. At the start of the experiment (on 16 July) each tank was stirred and then divided in half by a resin-coated plywood barrier placed perpendicular to the long sides. Rubber fittings around the edge of the plywood prevented movement of zooplankton between the two sides. *Notonecta* were then added.

Most *Notonecta hoffmanni* in southern California overwinter as adults. The entire life cycle (egg, five nymphal instars, adult) is spent in the water, and adults rarely fly. Reproduction begins in early spring and may continue through early fall if food supply and temperatures are favorable (Fox 1973, Scott 1980). Under favorable conditions (25°, and excess food) eggs hatch in 15 d, development from first instar to adult may occur in <45 d, but development rate is temperature and food dependent (Fox 1973, Fox and Murdoch 1978).

Experimental design

In a 2 × 2 factorial experiment ($n = 4$ per treatment), two food treatments, high (200 *Drosophila*/d) and low (50 *Drosophila*/d) were assigned among the eight tanks at random, and were crossed with two initial *Notonecta* density treatments, low (two pairs of adults) and high (eight pairs of adults), assigned at random to the two sides of each tank. (The same number of first instars were also added, but virtually all were cannibalized and we do not discuss these inocula further.) A given tank thus had the same number of *Drosophila* on both sides, but low *Notonecta* density on one side, and high on the other. The initial *Notonecta* densities were well within the range of natural densities in local stock tanks and stream pools. *Drosophila* were added daily inside floating cages that constrained them to the water surface, after those remaining from the previous day had been removed. Each cage had styrofoam sides made from the bottom half of an egg carton, no floor (allowing *Notonecta* access to the *Drosophila*), and a roof of 0.25-mm Nitex screening.

Daily mean water temperature was relatively constant during the first two-thirds of the experiment (21°–26°), but dropped into the 16°–21° range by day 70. Daily fluctuations in water temperature were typically in the range of 6°–8°, while variation between tanks was 1°–2°.

Notonecta were censused every 3–4 d. First, all visible *Notonecta* were counted. We then netted *Notonecta* into buckets of water, instars I and II being kept separately. Netting then continued until five consecutive sweeps yielded no additional *Notonecta* or exuviae. If the visual count or the previous census indicated there were still individuals not accounted for, the census procedure was repeated. Individuals were then classified by instar and sex (adults only), and returned to the tank. Dead adults were also sexed, and classified as old or new generation based on the condition and coloration of the hemelytra. The number of hatched and unhatched eggs present on buoyed removable strips of black plastic Vexar was counted. Vexar is a preferred substrate for egg laying by *Notonecta* (L. R. Fox 1970 and *personal observation*). Some eggs were laid on the sides of the tank and were not counted.

After *Notonecta* and Vexar strips were removed, the water was stirred to mix the contents evenly. Zooplankton densities were then sampled by placing a 500-mL jar halfway down the water column, inverting the jar, and placing the contents in a bucket. This was done nine times on each tank side, the samples being evenly spaced on a 3 × 3 sampling grid. A 500-mL subsample of the water in the bucket was taken, filtered through 153-μm mesh, and preserved in 95% ethanol. The water and animals remaining in each bucket were then poured back into the tank. This procedure was repeated and a second sample was preserved.

Daphnia was almost the sole zooplankter eaten by *Notonecta* and at the start of the experiment there were no significant differences in *Daphnia* density among treatments (ANOVA F tests, all $P > .1$). The *Daphnia* population on both sides of one tank crashed to extinction by day 8, and never reappeared; this tank is excluded from all analyses. Considering all other experimental tanks there were no significant differences in mean *Daphnia* density between treatments during (the mean over the entire experiment) or at the end of the experiment (ANOVA F tests, all $P > .1$).

Observations on feeding of *Notonecta* were made during 10-min periods at various times throughout the experiment. Records were made, by instar, of the number of *Notonecta* feeding, and the prey type they were consuming.

Calculation of Notonecta *vital rates*

For each instar, i, during each intercensus period, $t - 1$ to t, we wish to estimate the number recruiting (molting) into the instar, $M_{i,t}$, the number dying, $D_{i,t}$, and egg production, E_t. The relevant numbers collected at each census are the number alive in each instar, $N_{i,t}$, the number of corpses, $C_{i,t}$, the number of exuviae (cast skins), $S_{i,t}$, and the number of new and hatched eggs. (Note that we denote census date for numbers observed at a census, or numbers recruited or lost between two censuses, with a lower case t.)

To reduce errors we make use of cumulative counts in our estimates. Cumulative totals of the number of corpses, $C_{i,T}$, and exuviae, $S_{i,T}$, in each instar, and of the number of unhatched and hatched eggs were either directly observed or calculated as simple sums. For each census we also estimated the cumulative number ever recruited to the instar, $M_{i,T}$, and the cumulative number ever to have died in the instar, $D_{i,T}$. (To contrast these cumulative counts with the numbers actually counted or estimated at each census [previous paragraph] we replace t by T as the subscript referring

TABLE 1. Preference of *Notonecta* between *Drosophila* and *Daphnia*. The values given are the mean number of prey of each type eaten during 2-h trials and the mean preference for *Drosophila* (α_{dros}), both ±1 SE. (Instar I trials were run for 6 h to obtain adequate numbers eaten.)

Instar	Number of prey eaten		Preference†		
	Alternative prey (*Daphnia*)	*Drosophila*	α_{dros}	t	(df)
I	6.1 ± 1.4	1.7 ± 0.2	0.2 ± 0.06	3.83**	(9)
II	9.6 ± 0.5	1.0 ± 0.2	0.08 ± 0.02	21.00***	(9)
III	14.8 ± 1.7	2.3 ± 0.4	0.11 ± 0.05	7.80***	(7)
IV	9.6 ± 0.9	4.4 ± 0.7	0.28 ± 0.05	4.40**	(9)
V	5.7 ± 2.1	9.1 ± 2.0	0.64 ± 0.11	1.27	(7)
Adult	1.7 ± 0.4	7.6 ± 2.0	0.74 ± 0.10	2.40*	(9)
	Alternative prey (*Ceriodaphnia*)	*Drosophila*			
II	3.3 ± 0.9	2.2 ± 0.3	0.55 ± 0.12	0.42	(9)
IV	0.4 ± 0.2	8.3 ± 0.03	0.94 ± 0.03	14.67***	(9)
Adult	0.6 ± 0.2	5.2 ± 1.6	0.82 ± 0.08	4.00**	(9)

† Significant deviations from random selection ($\alpha_{dros} = 0.5$) were tested by t tests. There were 8–10 replicate trials for each instar.

* $.01 < P < .05$; ** $.001 < P < .01$; *** $P < .001$.

to census date.) The number entering into an instar or dying within an instar within a census period is then obtained simply by subtracting the cumulative number at census $t - 1$ from that at census t. Over the entire experiment only a few individuals that were counted as instar I could not be accounted for, either as eventual survivors or as corpses. Nor did our censuses of later stages ever exceed the number expected from counted recruits to earlier stages. Thus all stages (except eggs) were counted with virtually no error.

The cumulative number of exuviae of the preceding instar gives a minimum estimate of the number ever recruited into an instar by time t, $M_{i,T}$. However, this may be an underestimate, especially for the smallest instar. We therefore first calculate $M_{i,T}$ for the largest instar, the adults. This is simply the number present at time t plus the cumulative number of adult corpses found up to time t, with the constraint that the cumulative number can never decrease, and if it does, the number from the previous census is retained. Each adult typically was counted many times in its life, and there was never an inconsistency in the estimates of the number recruiting to the adult stage based on fifth-instar exuviae vs. direct counts of adults.

$M_{i,T}$ was then calculated for progressively smaller instars by noting that the estimated cumulative number recruited to the instar is the sum of the number alive in the instar at time t ($N_{i,t}$), plus the number that ever recruited out of it ($M_{i+1,T}$) plus the number that ever died in the instar ($D_{i,T}$):

$$M_{i,T} = N_{i,t} + D_{i,T} + M_{i+1,T}. \quad (2)$$

$N_{i,t}$ is again known without error, and $M_{i+1,T}$ has just been calculated. A minimum estimate of $D_{i,T}$ is provided by the cumulative number of corpses, and again the only source of error is current corpses that have not been found. A further check is now possible, since $M_{i,T}$ calculated in this way should not be smaller than its estimate based on the cumulative numbers of exuviae and corpses, and should not decline through time. For instars II and older, only 1 or 2% of estimates ever presented such inconsistencies, and these concerned only one or two individuals. In these cases, Eq. 2 was balanced by increasing the estimated number of cumulative deaths in the instar.

Inconsistencies were more common in instar I, due mainly to delayed recovery of corpses and exuviae. A second, minimum, estimate of recruitment to instar I was provided by the cumulative number of hatched eggs. On the occasions that the egg count gave a higher estimate than Eq. 2, the egg count was used.

TABLE 2. Number of each prey type ($\bar{X}$ ±1 SE) eaten in 2 h (E_A = number of alternative prey eaten, E_1 = number of instar I eaten) and mean preference (α_1) for instar I by large *Notonecta* given a choice between 10 instar I nymphs and 30 individuals of an alternative prey type.

Predator	Alternative prey	N	E_1	E_A	α_1	t
Instar IV	*Drosophila*	6	1.7 ± 0.6	14.5 ± 2.9	0.26 ± 0.08	2.1†
Adult	*Drosophila*	6	0.3 ± 0.2	6.7 ± 1.5	0.12 ± 0.08	4.75**
Adult	*Daphnia*	6	1.7 ± 0.2	13.5 ± 3.0	0.28 ± 0.09	7.5***
Adult	*Ceriodaphnia*	5	1.6 ± 0.4	0	1.00	···

† $.05 < P < .10$; ** $.001 < P < .01$; *** $P < .001$.

Results

Preference and cannibalism rates

Laboratory experiments measured *Notonecta*'s preferences among the major prey species present in the stock tanks, and also measured the effect of these prey on cannibalism by large upon small *Notonecta*. These experiments were designed to improve our interpretation of cannibalism in the stock tanks. *Drosophila, Daphnia,* and *Ceriodaphnia* were the three prey types available in the tanks.

The early instars of *Notonecta* strongly preferred *Daphnia* over the larger *Drosophila*, but preference for *Drosophila* increased with *Notonecta* size, the changeover occurring in instar V (Table 1). All three instars we tested (II, IV, adult) preferred *Drosophila* to *Ceriodaphnia*, which is much smaller than *Daphnia*; the preference was strong in the larger two instars, but not statistically significant for instar II. These results are consistent with other research indicating that prey size relative to predator size is a key variable determining preference by *Notonecta* (Scott and Murdoch 1983).

These results, combined with those of Chesson (1981) and Scott and Murdoch (1983), show that, among the three species given, *Daphnia* is the preferred prey for instars I–IV, that instar V tends to prefer *Drosophila* (but not significantly),while adults prefer *Drosophila*. *Ceriodaphnia* is the least preferred by all stages of *Notonecta*, with preference for *Ceriodaphnia* decreasing with size of the predator.

A reasonable expectation is that the preference of adult notonectids for smaller conspecifics should be highest when *Ceriodaphnia* is the only other prey available, and lowest when *Drosophila* is present. This prediction was confirmed in a laboratory experiment (Table 2). Preference of adult *Notonecta* for first-instar *Notonecta* was lowest when *Drosophila* were present, intermediate when *Daphnia* were present, and highest when *Ceriodaphnia* was the alternative prey. Instar-IV nymphs were tested only with *Drosophila* as the alternative prey and preferred *Drosophila* to instar-I notonectids.

Two factors in addition to preference will influence the cannibalism rate in the presence of alternative prey. First, hunger strongly affected the number of prey eaten: starved adult *Notonecta* presented only with *Drosophila* ate more than twice as many of this prey per day ($\bar{X} \pm$ SE = 31.7 ± 4.2 prey/d, $N = 6$) as did well-fed adults (13.4 ± 3.7 prey/d, $N = 10$), t test, $P < .01$. Second, larger preferred prey lowered the attack rate on the alternative prey more than would have been predicted on the basis of preference alone, because handling time is longer (Chesson 1989). The effects of these two factors are apparent in the next set of results.

Cannibalism rates of *Notonecta* instars IV and young adults upon *Notonecta* instar I were measured over 24 h: (1) in the presence of *Ceriodaphnia* alone, (2) with *Ceriodaphnia* plus *Daphnia*, and (3) with *Ceriodaphnia* plus *Drosophila*. (*Ceriodaphnia* was provided as food for instar I and had almost no effect on cannibalism, see Methods). The results are as expected (Fig. 1); alternative prey (*Daphnia* and *Drosophila*) significantly reduced the number of instar I cannibalized in 24 h by both adults and instar IV (two-way ANOVA, main effect of alternative prey: $F_{2,18} = 21.05$, $P < .001$). The cannibalism rate of adults was lowest in the presence of *Drosophila*, which was more preferred by adult *Notonecta* and required a longer handling time (4.8 min) than *Daphnia* (1.5 min). Cannibalism by instar IV was also more suppressed by *Drosophila* than by *Daphnia*, even though the latter was preferred (Table 1). The reason appears to be that handling time of instar IV is six times as long on *Drosophila* (12 min) as on *Daphnia* (2 min), and the former presumably also lowers hunger more than *Daphnia* does. There was no difference in the number of instar I eaten by adults vs. instar IV (two-way ANOVA, main effect of *Notonecta* stage: $P > .1$).

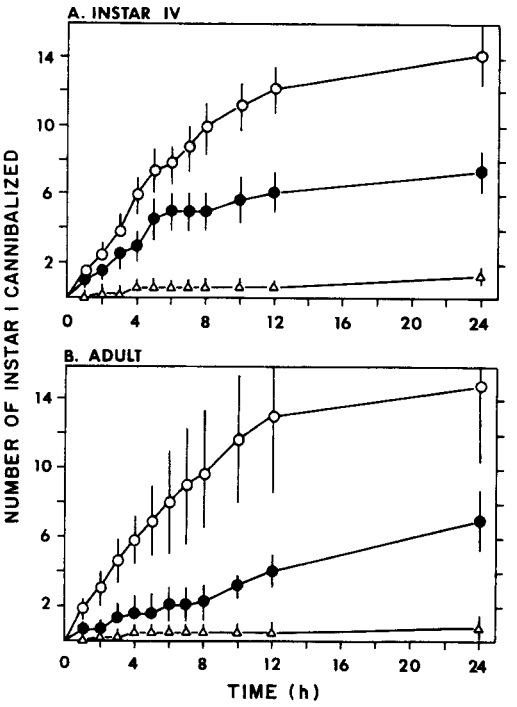

FIG. 1. Cumulative numbers of instar I eaten over a 24-h period (means ± 1 SE) by (A) instar IV and (B) adult *Notonecta*. Alternative prey were *Ceriodaphnia* alone (○), *Ceriodaphnia* plus *Daphnia* (●), and *Ceriodaphnia* plus *Drosophila* (△).

Observations made during the stock tank experiment showed that diets in the field followed the pattern of preferences established in the laboratory (Table 3). *Daphnia* was the major item in the diets of early *Notonecta* instars but was rarely eaten by larger instars,

TABLE 3. Percentage of observed *Notonecta* meals in stock tanks composed of each prey type. *N* is the number of feeding observations. "Other" includes miscellaneous prey such as chironomids and corixids.

Predator	Prey type					
	Droso-phila	Cladoc-era*	Ostra-coda	*Noto-necta*	Other	*N*
Instar I	5.4	78.3	9.8	1.1	5.4	992
Instar II	2.4	86.3	4.2	2.4	4.8	168
Instar III	11.7	59.2	0.8	18.3	10.0	120
Instar IV	23.3	23.3	3.3	26.7	23.3	30
Instar V	44.1	2.9	0	41.2	11.8	34
Adult	50.0	2.3	0	29.6	18.2	44

* Nearly all of the Cladocera eaten were *Daphnia*, but in a few cases when smaller Cladocera were being consumed we could not determine whether these were *Ceriodaphnia* or *Daphnia*.

while the opposite was true of *Drosophila*. The three smaller *Notonecta* were the main predators of *Daphnia*, while large predators were the main cannibals of young *Notonecta*. *Ceriodaphnia* were rarely eaten.

These results from the tanks can be used only to confirm the general patterns of feeding established in the laboratory, and cannot be used to estimate absolute cannibalism rates or preference values: the number observed feeding varied greatly from time to time and among instars; although we made frequent observations, few *Notonecta* were seen feeding on any particular date; we do not know the abundance of *Daphnia* actually available in *Notonecta*'s foraging zone (mainly the top few centimetres of the water column); finally, handling times varied greatly among prey types and predator instars and we do not have adequate data on handling times in the field.

For an index of the potential cannibalism rate of populations of *Notonecta*, we used the cannibalism rates by instars III to adult as estimated in the laboratory. These instars are cannibalistic in the laboratory and field, instar V having the highest cannibalism rate (present results, Fox 1973, Scott 1980). Young adults and instar IV cannibalized at about the same rate (Fig. 1), but adult feeding rate declines with age and old adults cannibalize weakly (Scott 1980, Chesson 1981). Cannibalism rates from Scott's (1980) experiments averaged over treatments with preferred and nonpreferred alternative prey available, were used to assign a cannibalism index to each of the larger instars, setting adults = 1, on the assumption that the adult group consisted of equal numbers of old and young. The other indices are then: instar III: 0.5, instar IV: 1.3, instar V: 2.6.

Stock tank experiments

Notonecta *phenology.*—The original adult population declined steadily in numbers through the experiment (Fig. 2). Close to half survived to the end in most populations, and there was no significant effect of either food supply (i.e., *Drosophila*) or their own density on the number surviving (Table 4). Although the percentage of adults surviving was highest in the high food–low adult density treatment, this result was based on only 12 individuals.

Per capita reproduction was somewhat higher in every treatment during the initial period of egg production (until the 10th census, reflecting ≈15 d of egg production) than during the remainder of the experiment, but this difference was not statistically significant (Table 5).

The earliest first instars produced from eggs laid during the experiment (the new cohort) appeared after the census on day 14; the first to survive to the adult stage appeared around day 60, as indicated by the increase in the total number of old plus new adults in low-density treatments, most obviously in the high-food treatment (Fig. 3). Most of the cohort had either died or reached the adult stage by the end of the experiment. None of the new adults could have produced first instars before the end of the experiment given the time required for maturation of the adult and the development of eggs (Fox 1973, 1975*b*). Reproduction (as measured by recruitment of first instars, see Methods: Calculation of *Notonecta* Vital Rates) extended somewhat later into the season in high food treatments (Fig. 4). Populations within a treatment showed broadly similar phenology, but differed in detail.

Population convergence, overconvergence, and food supply

Within each tank one side had a high initial *Notonecta* density and the other had a low initial density. There are several different components of these populations that might converge to a putative equilibrium density, including total *Notonecta* at the end of the experiment, and potential number of adults in the new cohort surviving to overwinter. The latter is the better choice for our purposes since old adults (i.e., survivors from the initial cohort) lose vigor and stop reproducing

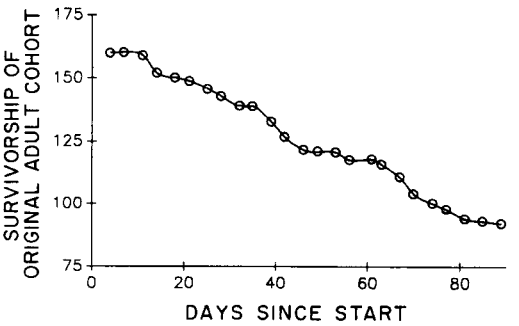

FIG. 2. The number of the original cohort of adult *Notonecta*, summed over all tanks, surviving from the start of the experiment to successive census days.

TABLE 4. Effect of prey (*Drosophila*) density and adult *Notonecta* density on the survivorship of the original cohort of adult *Notonecta* in the stock tanks.

A. Total number of adult *Notonecta* in each treatment surviving or dying out of the original adult cohort by the end of the experiment (totals over all replicates).

	High *Notonecta* density			Low *Notonecta* density		
	Alive	Dead	Percent surviving	Alive	Dead	Percent surviving
High *Drosophila*	34	30	53	12	4	75
Low *Drosophila**	25	23	52	7	5	58

B. Log-linear analysis of numbers surviving vs. dying.

Source of variation†	χ^2	df	*P*
Notonecta	1.83	1	.18
Drosophila	0.79	1	.38
Notonecta × *Drosophila*	0.63	1	.43

* Note there were only three tanks in the low *Drosophila* food level; there were four tanks in the high food level.
† A significant main effect indicates survival differed between the two levels of a factor. A significant interaction indicates there were unique effects associated with some treatment combinations of the two factors.

as they age; they probably do not survive and contribute to the production of a new generation the next year (Fox 1975*b*, Scott 1980).

To obtain the total number of overwintering adults, we added to the number of new adults produced the number of extant immatures (most of which were instar V), corrected by expected survivorship to adulthood, based upon the average through-stage survival rates over the experiment. This potential number of new adults is henceforth the "overwintering" population.

There was convergence in the overwintering populations in both food (*Drosophila*) treatments: the relative difference in the number of overwinterers between the high- and low-density treatments was less at the end than at the beginning of the experiment for both food treatments (Table 6A). (This was determined by showing that the final logarithmic differences were, on average, significantly smaller than the initial logarithmic difference, namely 1.39.)

There was also overconvergence in both food treatments. In fact, for every pair of populations housed on opposite sides of a single tank, the low-density population produced more overwinterers than the high-density population (Table 6A).

If we consider total adults (i.e., including old adults: Fig. 3, bottom panels show an example) or total "big" *Notonecta* (instars IV–VI), statistically significant convergence is still evident (Table 6B). The clear overconvergence seen in the overwintering population, however, was not seen in total adults or big *Notonecta* (Table 6B). The failure to see overconvergence in total adults arises from the following combination. New adults overconverged, but old adults showed no convergence: their survival was independent of *Notonecta* density or food level (Table 4).

TABLE 5. Fecundity (viable eggs per day per female) as estimated from recruitment of instar I. For these analyses, the experiment was broken into the two time periods. The first is the initial period of egg production, which includes approximately the first 15 d of egg production, the second is the remainder of the experiment.

A. Fecundity for each treatment ($\bar{X} \pm 1$ SE)

	First time period		Second time period	
	Low *Notonecta* density	High *Notonecta* density	Low *Notonecta* density	High *Notonecta* density
Low *Drosophila*	2.35 ± 0.38	0.92 ± 0.22	1.62 ± 0.14	0.89 ± 0.24
High *Drosophila*	3.38 ± 0.22	1.85 ± 0.17	2.13 ± 0.49	1.71 ± 0.21

B. Summary of repeated-measures ANOVA on log-transformed fecundity

Source of variation	*F*	df	*P*
Time period	2.4	1,5	.18
Notonecta density	23.4	1,5	.005
Drosophila level	24.1	1,5	.004
Time period × *Notonecta* density	4.0	1,5	.10
Time period × *Drosophila* level	0.2	1,5	.71
Notonecta density × *Drosophila* level	3.1	1,5	.14
Time periods × *Notonecta* density × *Drosophila* level	0.1	1,5	.74

TABLE 6. Demonstration of convergence and overconvergence in density by experimental *Notonecta* populations set initially at high or low density, and given either a high or low food supply.

A. Estimated number of overwintering adult *Notonecta* in each tank and treatment, and tests of convergence between high and low *Notonecta* density treatments.

Food treatment	Tank no.	High *Notonecta* side (initial $N = 16$)	Low *Notonecta* side (initial $N = 4$)	Difference of logs (initially = 1.39)
High *Drosophila*	10	7.3	14.2	−0.66
	13	8.6	12.6	−0.38
	21	4.9	12.2	−0.89
	25	8.3	11.0	−0.28
	$\bar{X} \pm$ SE	7.3 ± 0.83	12.5 ± 0.66	−0.56 ± 0.14
Low *Drosophila*	2	3.2	5.9	−0.61
	6	1.2	6.7	−1.71
	17	1.4	3.3	−0.85
	$\bar{X} \pm$ SE	1.9 ± 0.6	5.3 ± 1.03	−1.06 ± 0.33

Tests on differences of log densities between initially high- and initially low-density sides of each tank. High- and low-*Drosophila* treatments are combined.

	H_1	t_6	P
Convergence	$\mu < 1.39$	−12.1	<.001
Overconvergence	$\mu < 0$	−4.3	<.001

B. Number ($\bar{X} \pm 1$ SE) of total adult and big (instars IV–VI) *Notonecta* in each treatment at the end of the experiment.

	High *Notonecta* density		Low *Notonecta* density	
	Adult	Big	Adult	Big
High *Drosophila*	12.3 ± 2.0	17.0 ± 1.1	14.5 ± 1.2	15.8 ± 1.0
Low *Drosophila*	9.0 ± 1.7	10.7 ± 1.3	5.0 ± 0.6	8.0 ± 0.6

Tests on differences of log densities between initially high- and initially low-density sides of each tank. High- and low-*Drosophila* treatments are combined.

		Adult		Big	
	H_1	t_6	P	t_6	P
Convergence	$\mu < 1.39$	−22.0	<.001	−7.69	<.001
Overconvergence	$\mu < 0$	+2.86	>.1	+0.81	>.1

Mechanisms of convergence and overconvergence

Since these were closed populations, dynamics were determined entirely by natality and mortality. No eggs were ever observed to be eaten by *Notonecta,* and egg viability was consistently high (92%) and unaffected by the treatments (two-way ANOVA, $P > .1$ for treatment and interaction effects). Thus the recruitment of instar I to the population reflected the production of eggs.

Fecundity (viable eggs per female per day) contributed to convergence and overconvergence. It was responsive to both adult density and food supply, especially in the low-food treatments, both during the early part of the experiment and in the later part, when egg production seemed somewhat lower (Table 5). During the initial period, the low-*Notonecta* adults at high food had fecundity (3.4 ± 0.2 eggs/d) exceeding the maximum we have observed in the laboratory (in *Notonecta* fed excess food at 25°C Fox [1975*b*] reports a maximum of 2.3 ± 1.2 eggs/d but in one experiment Fox [1973] observed 3.6 eggs/d), and thus their fecundity was not food limited. The high-*Notonecta* adults at high food had fecundity about half (55%) as high as the low-*Notonecta* treatment and thus may have been somewhat food limited. At low food levels, fecundity was 24–50% lower than at the high-food level (Table 5).

Although fecundity was both density dependent and food dependent, we were not able to detect a significant food level × *Notonecta* density interaction ($P = .14$, Table 5B). The results suggest, however, that density-dependent fecundity had more pronounced effects in the low-food tanks: during the first time period, in the high-food treatments fecundity in the high-density populations was 55% of that in the low-density populations, whereas in the low-food populations this figure was 39%. The comparable numbers in the second time period were 80 and 55%. These differences played a role in convergence of the overwintering populations: over the entire experiment, in the high-food tanks, the high-*Notonecta* density produced nearly three times as many instar I recruits as the low-*Notonecta* density, while at low food the numbers produced at the two *Notonecta* densities were roughly equal (Fig. 5). Note that at both food levels the high-*Notonecta* density started with four times as many adult females, yet produced less than four times as many instar I recruits as the corresponding low-density treatment.

Subsequent mortality of first instars (low-food) and

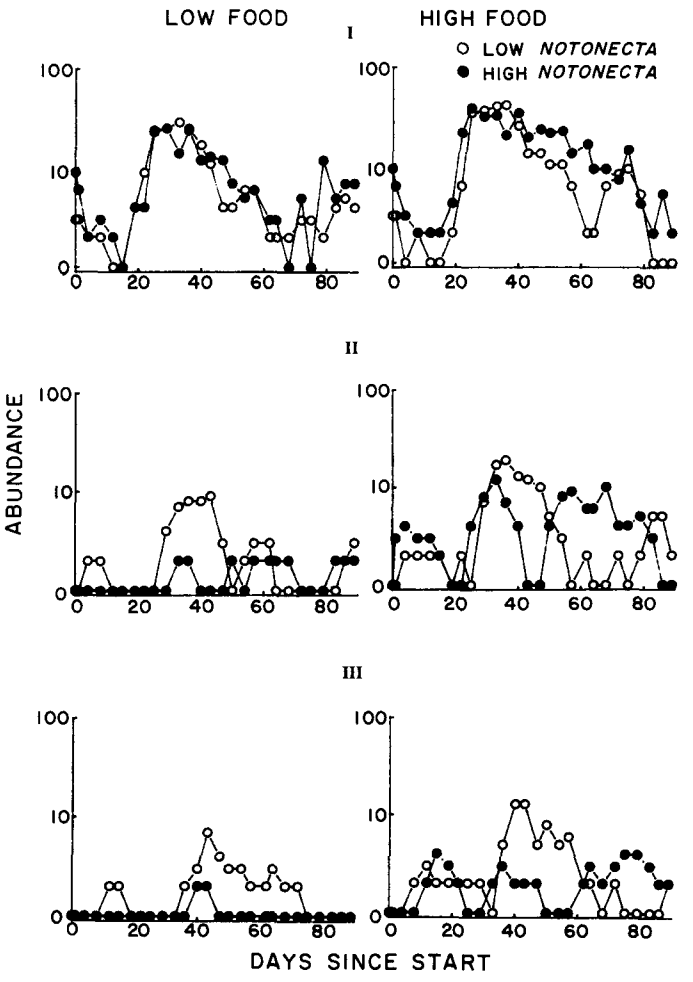

FIG. 3. Examples of the population dynamics (numbers plotted against days since the start of the stock tank experiment), by instar, seen in each treatment. Dynamics for the different initial *Notonecta* densities within a food level come from the opposite sides of the same tank. For all instars the total number present is shown; for instars I and VI this can include some individuals that were present at the start of the experiment as well as new recruits.

first and second instars (high-food) completed the process of convergence (and of overconvergence) (Fig. 5). Through-instar survival (i.e., the fraction entering the instar and surviving to molt) in the first instar was especially low, and was significantly and strongly density dependent (Table 7B). Although survival in instar II was not significantly density dependent overall, it was significantly density dependent in the high-*Drosophila* treatment ($P < .05$, pairwise contrast using common covariance structure [SAS 1985]), where survival in the high-density *Notonecta* treatment was only half of that seen in the low-density populations (Table 7A). Survival was high in the later stages with no indication of significant differences among treatments (Table 7B).

Overconvergence occurred very quickly: as a result of these strongly density-dependent processes, the cumulative numbers recruited were actually higher for the low initial *Notonecta* density treatments than for the high-density treatments by the second instar in low-food tanks, and by the third instar in high-food tanks (Fig. 5). Overconvergence was maintained thereafter (Table 6).

The agent of density-dependent mortality upon instars I and II was cannibalism by large-instar *Notonecta*. The evidence is of several sorts. First, most of

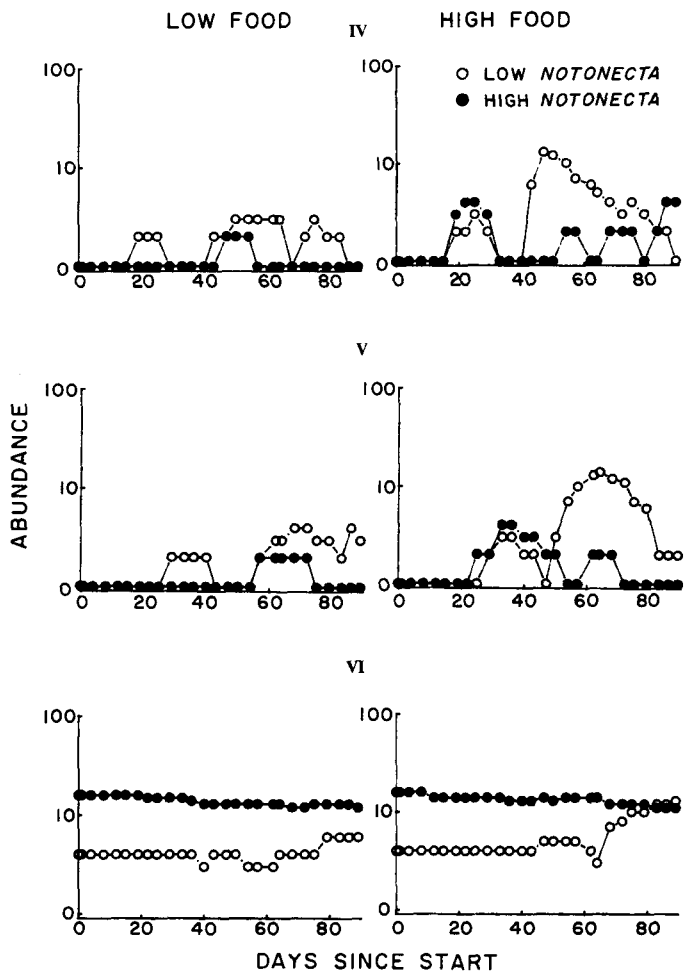

FIG. 3. Continued.

the time, instar I and II corpses had holes characteristic of those made by larger *Notonecta*.

Second, the instantaneous per capita mortality rates of instars I and II were positively related to the abundance of cannibalistic *Notonecta* (Table 8). We tested for this by regressing a mortality index (the proportion of individuals in instar I or II observed during a week that did not survive to the end of that week) against the weighted number of cannibals present (using the cannibalism indices calculated above from laboratory experiments). The results show that mortality of instar I increased significantly with increased density of cannibals in both food treatments, and this was also true for instar II in the high-food treatment, but not the low-food treatment (Table 8). This last result is consistent with our observations on population dynamics and through-instar mortality described above. (Through-instar mortality of instar II was higher in the high-adult-*Notonecta* density treatment than in the low-adult density treatment only in high-food tanks, and convergence was essentially complete by instar II at low food, but continued through to instar III at high food.)

Third, as expected, mortality of instar I increased with increasing density of cannibals significantly faster at low food than at the high food (see comparison of slopes, Table 8); thus the impact of a cannibal was lessened in the presence of alternative food.

It is possible that the small instars were actually eaten after they died from other causes, the most likely alternative cause of death being inadequate food. It appears, however, that food for the early instars was always in excess. First, we showed above that the most important alternative prey for young *Notonecta* was

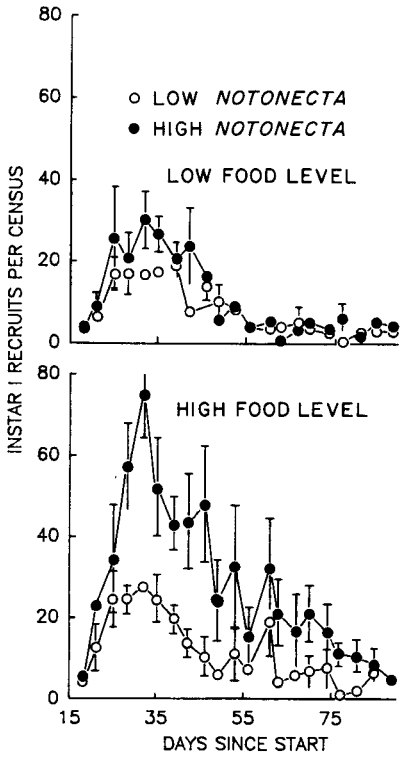

FIG. 4. The estimated instar I recruitment per census (means ± 1 SE) plotted against days since the start of the stock tank experiment.

Daphnia (Tables 1 and 3), and that *Daphnia* density did not vary among treatments (Methods: Experimental Design). Second, based on the time between either peak abundances of successive instars or the appearances of the first few individuals of successive instars, we estimate that instars I and II lasted ≤7 d. Thus they developed as fast as the maximum rate observed in the laboratory at 25° (between 6 and 7 d) and in the presence of greatly excessive food (Fox 1973). Although this rapid development combined with our sampling schedule (twice a week) precludes a formal analysis, there is no evidence that the duration of these instars varied in a systematic way among treatments.

Although the above results are internally consistent, they are puzzling in one regard. A priori we expected that cannibalism on instar II would be more intense at low- than at high-food levels, as it is for instar I. But our result in Tables 7 and 8 can be interpreted as indicating that cannibalism on instar II acted more strongly at the high-food level. We feel that this interpretation is incorrect, and that our failure to see significant effects for the second instar at low food is most likely an artifact due to low statistical power. At the low-food levels fecundity was lower, as was survival through the first instar. As a consequence, very few instar II were recruited in the low-food and high-*Notonecta* populations (Fig. 5); our through-stage survival (and mortality rate) estimates are therefore quite variable in this treatment (see the relevant standard error in Table 7). In addition, for the regressions against the cannibalism index presented above, high values of the cannibalism index were absent from this treatment precisely because the action of previous density-dependent mechanisms led to fewer large *Notonecta* being produced. This restricted range of data probably contributed to the large standard error in the slope parameter for this instar (Table 8).

Based on the temporal changes in mean cannibalism index through time, and on the above regressions, it seems evident that initial differences among treatments in cannibalistic mortality are lost by about day 40 of the experiment (itself an expression of convergence; Fig. 6). The initial differences nevertheless had marked effects on the through-stage survival probabilities for instar I and, at high food, for instar II pooled over the entire experiment. The reason for this is that most recruitment into instars I and II occurred early in the experiment (Fig. 5), when initial differences in potential cannibalism were still high (Fig. 6).

DISCUSSION

There have been surprisingly few convergence experiments done since Eisenberg's (1966) study of pond snails; he showed that the equilibrium was set by the food supply and convergence occurred via food- and density-dependent fecundity. Stimson and Black (1975) and Black (1977) studied convergence in intertidal grazing limpets, whose densities were again resource limited. Lawton et al. (1986) have extended convergence studies to herbivorous insects. That study is so far unique among convergence experiments in that, apparently, predators kept the population below any resource limitation; however, no evidence is available on the mechanisms from this preliminary experiment. The *Notonecta* in the present study were again food limited. Our results provide more detail on the mechanisms of convergence than has been available before.

Populations of *Notonecta* in streams in southern Cal-

TABLE 8. Regressions of mortality rate against cannibalism index. Analyses for both instar I and II were done separately for each food level.

Instar	Food level	Slope ($\bar{X}$ ± SE)*	F	df	P
I	low	0.05 (0.01)	21.7	58	<.0001
	high	0.02 (0.005)	13.6	78	.0004
II	low	0.005 (0.02)	0.04	47	.84
	high	0.015 (0.007)	4.2	64	.04

* F tests for equality of slopes for different food levels: Instar I, F = 5.71, df = 1,136, P = .02; Instar II, F = 0.17, df = 1,111, P = .68.

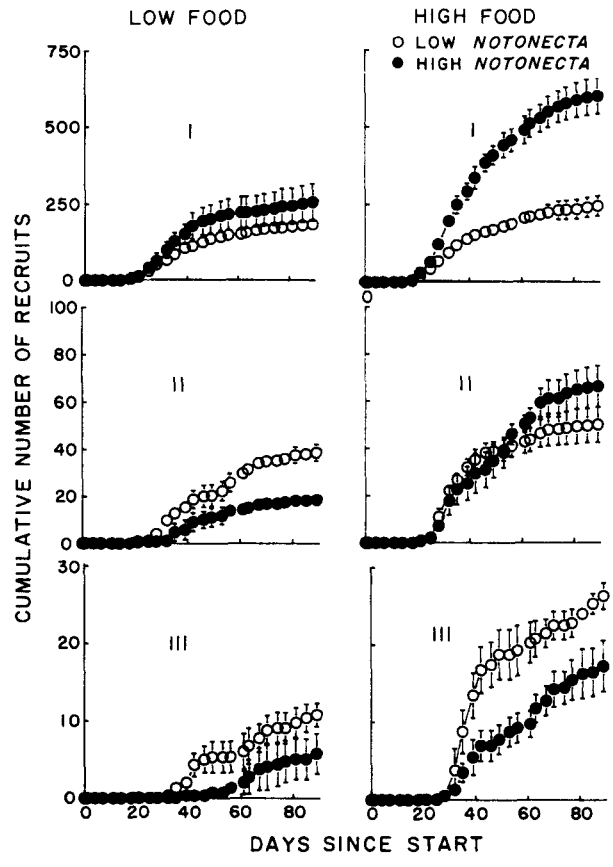

FIG. 5. Cumulative number of recruits (mean ±1 SE) of instars I–III, plotted against days since the start of the stock tank experiment.

ifornia appeared to be strongly food limited but, as in our stock tanks, cannibalism of smaller by larger instars was the immediate mechanism of population regulation (Fox 1975*b*, *c*). Our experiment shows that an important feature of this mechanism is that the densities achieved by the small instars is set, not by their own food supply, but by that of the large instars. Thus, there was always excess food (zooplankton) for the first few instars; they were kept well below any limits set by this food supply because food for large instars (*Drosophila*) was sometimes limited. This situation may be common in other age- or size-structured populations. For example, later instar damselflies may often be food limited, while earlier instars feed on smaller prey that are generally abundant (Crowley et al. 1987).

Convergence to the food equilibrium was through both density-dependent fecundity, and density-dependent early mortality (cannibalism), with the action of cannibalism extending to a later stage (the second instar) at high food. Cannibalism operates so early in the victims' development that it is similar to reduced fecundity in its effects on convergence.

Cannibalism allows larger *Notonecta* to exploit indirectly a food source, the prey of smaller instars, that is otherwise largely unavailable. This could well influence the ultimate abundance of overwintering *Notonecta*, since small *Notonecta* make up a significant fraction of the diet of large *Notonecta*. However, we are unable to measure this effect.

Our results suggest that the dynamics of at least this particular polyphagous and age-structured freshwater predator can be portrayed much more simply than would appear at first sight. The primary reason for this simplicity is that the rate of supply of adult food is dynamically uncoupled from *Notonecta*'s dynamics. In natural systems, as in our experiment, this food supply is also independent of *Notonecta* dynamics: it is mainly arthropods falling onto the water surface. This adult food supply primarily determines the overwintering population of adults each year; it also primarily de-

TABLE 7. The effects of initial *Notonecta* density, and food supply, on instar-specific *Notonecta* survival rates.

A. Through-instar survival of *Notonecta* ($\bar{X} \pm 1$ SE) for each treatment.

		High *Notonecta* density		Low *Notonecta* density	
	Instar	Survival	*N*	Survival	*N*
High *Drosophila*	I*	0.12 ± 0.01	4	0.22 ± 0.03	3
	II*	0.25 ± 0.03	4	0.51 ± 0.06	3
	III	0.69 ± 0.14	4	0.71 ± 0.05	3
	IV	0.62 ± 0.10	4	0.92 ± 0.04	3
	V	0.76 ± 0.11	4	0.65 ± 0.05	3
Low *Drosophila*	I*	0.08 ± 0.02	3	0.21 ± 0.01	3
	II	0.32 ± 0.23	3	0.26 ± 0.05	3
	III	0.48 ± 0.29	3	0.57 ± 0.02	3
	IV	0.63 ± 0.37	2	0.92 ± 0.08	3
	V	1.0 ± –	1	0.56 ± 0.29	3

B. Repeated-measure ANOVA of through-instar survival. Tank is treated as a random factor nested within *Drosophila* treatment and the mean square associated with it is used as the error term for tests of the main effect of *Drosophila*. All tests used arcsine square root transformations.

Source of variation	df	ss	*F*	*P*
		Instar I		
Notonecta density	1	0.10	70.2	.0004
Drosophila	1	0.0043	0.96	.37
Drosophila × *Notonecta*	1	0.0021	1.56	.27
Tank	5	0.022	3.2	.11
Error	5	0.0069	...	...
		Instar II		
Notonecta density	1	0.054	0.85	.39
Drosophila	1	0.043	1.26	.31
Drosophila × *Notonecta*	1	0.076	1.19	.32
Tank	5	0.17	0.54	.75
Error	5	0.32	...	...
		Instar III		
Notonecta density	1	0.001	0.01	.93
Drosophila	1	0.16	0.97	.37
Drosophila × *Notonecta*	1	0.017	0.09	.77
Tank	5	0.84	0.90	.54
Error	5	0.92	...	...
		Instar IV		
Notonecta density	1	0.31	1.96	.23
Drosophila	1	0.059	0.87	.39
Drosophila × *Notonecta*	1	0.0035	0.10	.76
Tank	5	0.33	0.43	.81
Error	4	0.63	...	...
		Instar V		
Notonecta density	1	0.26	2.66	.20
Drosophila	1	0.02	0.08	.80
Drosophila × *Notonecta*	1	0.07	0.77	.44
Tank	5	1.34	2.78	.21
Error	3	0.29	...	...

* Indicates cases where survival differed between high and low *Notonecta* density within a food treatment ($P < .05$); these pairwise tests differ from an ordinary one-sample *t* test only in that the common variance from the ANOVA (see Table 7B) was used in the tests. These pairwise tests were done separately for each instar at each *Drosophila* level.

termines the peak population (which consists largely of small instars) and the general level of *Notonecta* density between peak abundance and the end of the season.

Notonecta's dynamics resemble, at least in one respect, those of open populations (i.e., those, such as barnacles, whose recruits come from elsewhere) in that the equilibrium is determined, in part, by an external "forcing function." In *Notonecta,* the supply of food comes from outside the local system, and the recruitment of new individuals depends, in large part, upon this food supply, as does the final equilibrium density. In open populations, the recruitment of new individuals comes from outside the local population, and this uncoupled input can affect the equilibrium (e.g., Roughgarden et al. 1985, Bence and Nisbet 1989). Examples come from reef corals (Hughes 1984), reef fish (Warner and Hughes 1989), intertidal barnacles (Gaines and Roughgarden 1985), and some aquatic insects, like mosquitoes, with a flying adult stage (Frogner 1980).

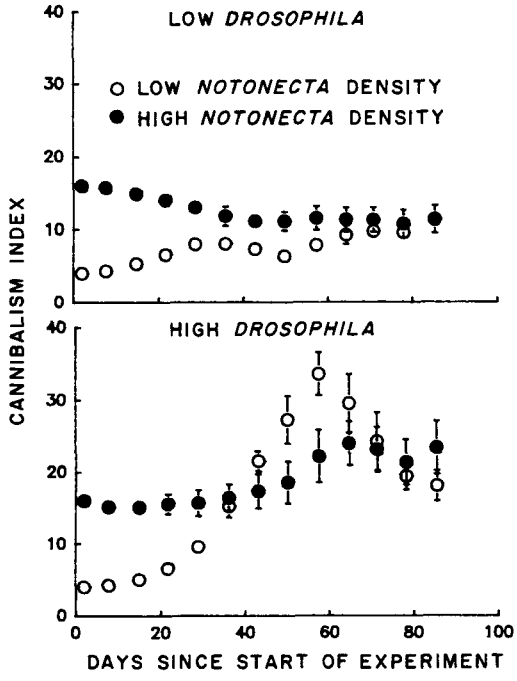

FIG. 6. Mean (±1 SE) cannibalism index (see Results: Mechanisms of Convergence and Overconvergence) plotted against days since the start of the stock tank experiment.

It is not clear how unusual these features of *Notonecta* dynamics are in other closed populations. For example, the rate of adult food supply to some other freshwater predators, such as water striders, or surface-feeding fish species can be largely independent of the dynamics of the predators (e.g., Moyle 1976, Murdoch and Bence 1987), but there are other predatory species that feed entirely upon resident prey species.

A secondary, but interesting, component of the regulation of density involves time lags in the *Notonecta* population itself. Although the density of the large-instar population is regulated by food supply, this regulation occurs during the production of eggs or the survival from cannibalism of the resulting small instars. Thus, regulation occurs through the food supply that was available to an earlier cohort of larger individuals. Particularly important, however is that only the fecundity of that cohort is sensitive to food supply; its survival seems relatively unresponsive to variation in food (perhaps, in part, because it can cannibalize its own products [Polis 1981]). It is this insensitivity that causes overconvergence: when the old adults are above the equilibrium, they survive and suppress the subsequent cohort, causing it to undershoot the equilibrium. As a result, an abundant adult cohort produces a small succeeding overwintering cohort, while a low-density adult cohort produces a relatively large overwintering cohort. Thus, if food supply were to remain relatively constant, alternating high and low populations could result. There are now several examples in nature of cyclic fluctuations in population density that appear to result from one cohort suppressing future recruits (Gaines and Roughgarden 1985, McCauley and Murdoch 1987, Nisbet and Bence 1989). The nature of such cycles appears to depend upon a variety of factors, and we intend to explore the possibility for cyclic fluctuations in *Notonecta*'s population density through modelling of its dynamics.

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