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A STUDY OF WINTER FLOUNDER MOVEMENTS[1]

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ABSTRACT

Some aspects of the movements of the winter flounder *Pseudopleuronectes americanus* (Walbaum) were studied by means of tag-recovery data. No gear selectivity by sex was demonstrated for recaptured fish nor was any association found between the size of the individual and distance of recapture from the release site. An analysis of the movements of tagged individuals away from the breeding area indicates some movement to the east of the release point but this may be due to unequal fishing effort. An attempt is made to explain the return of winter flounder to the coast by means of random search postulating the presence of a reflecting barrier.

INTRODUCTION

The migration patterns and movements of fishes have been the subject of numerous investigations, and these have led to several suggestions regarding guiding mechanisms. Studies of fish homing by Hasler (1956), Hasler and Larsen (1955), and Hasler, Horrall, Wisby and Braemer (1958) indicate that the phenomenon is closely associated with orientation to various physical, chemical, and biological stimuli in the environment. Although the concepts of diffusion and oriented dispersion have been developed by Beverton and Holt (1957) as theoretical bases for dispersion and migration, few attempts have been made to apply these to field results. It is the purpose of this paper to analyze some observations pertaining to the movements of winter flounder *Pseudopleuronectes americanus* (Walbaum) away from as well as to the vicinity of a breeding area located on the coast of Rhode Island.

METHODS

Tagging experiments were conducted in Green Hill Pond, Charlestown, Rhode Island, during the winters of 1956–7 and 1957–8. Green Hill Pond is a shallow brackish water pond of approximately 475 acres surface area connected to Rhode Island Sound by an intervening pond and a narrow inlet. This pond has been observed to be a breeding area for winter flounder. A summary of the tagging data is shown in Table 1. Incomplete data on some recaptures prevented use of every tag return for this study. Tags were of the Peterson disc type attached by non-corrosive alloy pins through the nape region of the fish. Tag returns were processed by the U. S. Fish and Wildlife Service. Only lively, uninjured fish over 220 mm in total length were tagged as soon after capture as possible. The gear for capture included fyke nets fished in the pond and a small experimental otter trawl towed from an outboard motor boat. During the last two sampling intervals only the otter trawl was used. It is evident that lower returns were obtained when the fyke net was included for capturing fish, but these lower returns do not affect use of the data for the purposes at hand.

BACKGROUND AND ASSUMPTIONS

A full discussion of the mathematical basis of random diffusion and its application to animal dispersion has been given by Skellam (1951). The method of analysis applied to dispersion is similar to that used by Jones (1959) where it is assumed that movement could be divided into a directional component and an undirected or random component leading to dispersion. In this study all tagged fish were liberated close to a coastline (in the inlet of Green Hill Pond) running in an east-west direction. It is assumed that a directional component of movement, if present, would act in the direction of the coastline.

[1] Support for this investigation was obtained from the U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Woods Hole, Massachusetts, in the form of tags and tag processing, which included payments of rewards.

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TABLE 1. *Summary of Green Hill Pond winter flounder tagging data*

Date	Number tagged	Recaptured to April, 1960	% recovery
Nov/Dec, 1956	254	65	26
Feb/Apr, 1957	205	47	23
Nov/Dec, 1957	288	118	41
Feb/Apr, 1958	205	79	39
Totals	952	309	

If the distribution of catch and fishing effort is uniform in all recapture areas a straightforward interpretation of the parameters describing all movements is possible. Column 2 of the upper part of Table 2 shows that the weights of winter flounder caught are not uniform by code areas. The total effort (Column 3) is also variable, but it appears to be associated with the catch. It is recognized, therefore, that the high catch and correspondingly higher effort in code area 121, located slightly to the east of the release point, could affect the easterly component of directional movement. This must be considered in the interpretation of results.

Some aspects of the life history of the winter flounder are reviewed in light of their importance in the analysis of the tag-return data. Observations by Lobell (1939) as well as those made during this study indicate that adult winter flounder are found in cooler offshore waters during the summer months and in shallow inshore areas during winter and early spring. No adult winter flounder could be found at the original capture site during the summer months. Because of this, the analysis of tag returns is divided into two periods of 5 and 7 months. These are from June to November, during which the fish could be expected in offshore areas; and from November to June, a period which overlaps the breeding season as observed in Green Hill Pond (December–March) as well as the breeding season described by Bigelow and Schroeder (1953) which extends from January to May in New England waters. During this latter period winter flounder are expected to be found in the shallow areas containing the breeding grounds.

Wilkinson (1952) defines the reassembly of birds dispersed over a wide stretch of

TABLE 2. *1958 winter flounder summary statistics and tag recovery data by area with a for similar proportions of tag recaptures in the*

Code area	Catch (lb)	Effort (hr)	Tag rec
122	155,203	1,207	1
121	300,209	4,909	2
113	35,404	468	
112	32,162	1,492	
131–133	49,898	2,288	
115–117	26,758	1,589	
Totals	659,634	11,953	6

Code area	Tag recaptures (expected)	Tag rec (obser
122	14	1
121	33	2
113	3	
112	3	
131–133	5	
115, 117	2.5	

$\chi^2 = 7.447$, d.f. = 5, $P \sim .20$.

territory to a breeding station as diasp migration. It has been conjectured by B ton and Holt (1957) that most exampl fish migration are of this type, and they tulate that current direction is a gui factor for the oriented migration of m demersal fishes.

In this study an attempt is made to ex the return of winter flounder to the coa the basis of the model for diasporic m tion without including a guiding factor. plicitly, a case is considered where the are dispersed uniformly over a strip of o of width w bounded on one side by a str coast running east and west which co tutes recognizable territory and on the o by a reflecting barrier consisting of a fathom depth contour located at its o edge. The above requirements are tho to be satisfactory for the following reas

1. No tag returns of Green Hill fish been reported to date outside th fathom contour despite an active tom fishery pursued immediately side of it.
2. The model assumes that the fish retained in the vicinity of the c Marked success of a local fishery fyke nets set close to shore sh before and after the breeding se

TABLE 3. *The proportions of male and female flounder observed and expected on the basis of equal returns from the proportions at tagging*

		Tagged fish		
		Male	Female	Total
Observed		55	153	208
Expected		62.6	145.4	208
	x^2	0.923	.397	1.320

lends support to the above assumption. Results of experimental trawling during this period also support this assumption.

Experimental trawling by the author during the 1958–9 breeding season in Narragansett Bay, Rhode Island, and Massachusetts, indicated that adult winter flounder were consistently more abundant along the margins of the bay than in the middle.

Since the model applies only to finding the coast, further searching is then generally required to establish the location of a specific breeding area. Recognition of a pond inlet is presumed to be due to olfactory perception as demonstrated by Hasler (1954) for homing salmon. However, no empirical evidence is yet available. Assuming that random search continues after the coast is reached and that it is restricted to a narrow belt in the immediate vicinity of the coast, the probability of locating an inlet per unit time would be higher than that required to locate the coast initially. Recovery of one Green Hill tagged winter flounder in each of two nearby salt ponds suggests that the same breeding area is not always successfully located during the succeeding season.

RESULTS

During the course of tagging operations, the sex of 601 tagged winter flounder was reliably recorded. These fish were 30% males and 70% females. Table 3 shows that there is no selectivity by sex at recapture. The high proportion of females does not appear to be due to differential vulnerability nor do these data suggest differences in dispersal pattern by sex for the winter flounder.

Using all the June-to-November data, a simple test for association between the size of the individual fish at tagging and the distance at recapture from the release site does not show any correlation (r=.02, n=110). Even when the partial correlation between size and distance from release site eliminating time at large is calculated, a non-significant ($r_{12.3}$=.056) association exists. According to Warfel and Merriman (1944) immature winter flounder are usually found near shore at all times until a size of at least 100 mm is reached. The above tests apply only to adult fish.

The distribution of 78 tag returns during the period June to November up to one year after tagging is shown in Figure 1, and the returns of 60 tagged fish during the period November to June up to one year after tagging is shown in Figure 2. Similar results were obtained for an additional 104 fish taken between 365 and 730 days at large during both periods.

It is clear from Figures 1 and 2 that winter flounder do not behave similarly during these two periods. The fish appear dispersed during the summer period, and most of the fish are found on the breeding grounds during the winter. Figure 1 does not convey a strong impression of directed movement, but it seems desirable to examine the dispersal phenomenon further.

A x^2 test for similar proportions of returns from columns 2 and 4 of Table 2 gives the following results (x^2=7.45, d.f.=5, P~.20). This information is used to indicate that the distribution of the tagged fish captured during 1958 was not significantly different from that of untagged fish in the major fishing areas when four or more individuals were caught.

Tag returns from other areas were not amenable to the statistical analysis because corresponding catch data were not available. The 17 additional tag returns from other areas during 1958 which provided accurate information on the place of recapture included seven recaptures from the vicinity of Charlestown Pond, Rhode Island, which is adjacent to the tagging site. The other 10 recaptured fish included two from Gayhead, Massachusetts, one from Vinyard Sound, Massachusetts, one from the vicinity of Nan-

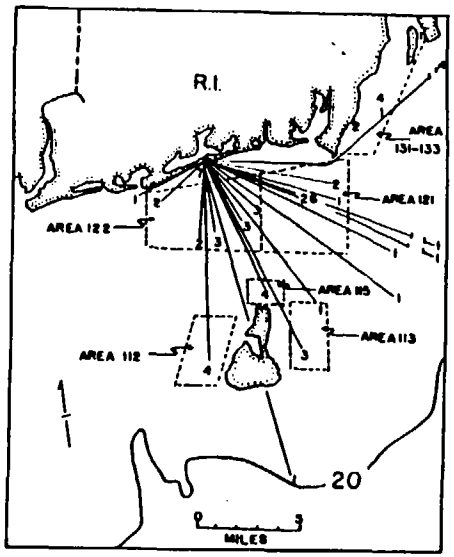

FIG. 1. Distribution of 78 winter flounder recaptured during June to November for a period of less than 365 days at large.

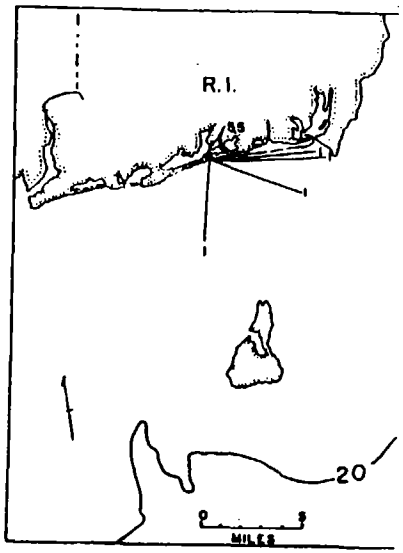

FIG. 2. Distribution of 60 winter flounder recaptured during November to June for a period of less than 365 days at large.

tucket Island, Massachusetts, one from Weekapaug Pond, Rhode Island, four from the Newport area, and one from south of Block Island.

A quantitative interpretation of Figures 1 and 2 is possible using the method of tag return analysis developed by Jones (1959). The formulae derived for estimating V, the directional component of the fishes' velocity, and a^2, the dispersion coefficient, are:

$$V = \frac{\Sigma r \cos \theta}{\Sigma t}$$

and

$$a^2 = \frac{1}{n}\left[\Sigma \frac{r^2}{t} - \frac{(\Sigma r \cos \theta)^2}{\Sigma t}\right]$$

where, for each recapture:

r = apparent straight-line distance travelled,

t = number of days at large,

θ = direction of travel measured from the axis of the coastline,

n = number of recaptures.

Estimates of the directional component of movement (V) and the dispersion coefficient (a^2) from available data are show Table 4. Comparison of the directiona non-directional components during the ods of less than and greater than one y large shows remarkable similarity. T hundred and sixty-five days have been tracted from each recovery period i 365–730-day recovery data. It is clear these data that winter flounder return t locality of tagging with high frequenc

The observed values of V are positiv they average .03 and .001 mile per da the two periods under consideration. tive values of V imply a mean displace of fish to the east. The positive sign these coefficients of directional move are explained by the manner in whic angle θ was measured. Since these a were measured in an east-to-west dire from the axis of the coastline, the relat high catch and correspondingly high returns from code area 121 (east of th release point) provided many angles o than 90°. These, of course, have po values of cos θ. Available informatio the total effort by major fishing areas (

TABLE 4. *Estimates of V and a^2 from available tag-return data*

Period	Number of fish	Directional component miles/day	Dispersion coeff. miles²/day
1. June–Nov (365 days at large)	78	.029	.670
2. June–Nov (365 days at large*)	32	.033	1.10
3. Nov–June (365 days at large)	60	.0004	.030
4. Nov–June (365 days at large*)	72	.0024	.016

* Period 2 and 4 coefficients of directional movement and dispersion have been obtained by subtracting 365 or 730 from each recovery period under the assumption of an annual return to the breeding area by individual fish.

umn 3 of Table 2) indicates a relationship between total effort and the catch of tagged or untagged individuals. The correlation coefficients are 0.85 and 0.88 respectively. Although a directional component of movement to the east is demonstrable from these data, it is suggested that it may be due to the unequal distribution of the catch and the related fishing effort.

Estimates of the dispersion coefficient a^2 are shown for available data in the last column of Table 4. These refer to the amount of undirected movement of fishes relative to one another during each period. The figures obtained in this study (1.1 and .67 miles² per day) compare favorably with a value of 1.5 miles² per day calculated for plaice by Beverton and Holt (1957). However, these values are considerably lower than those obtained by Jones (1959) for haddock. As with the directional component of movement, the non-directional component is consistently smaller during the cooler period of the year. This is thought to be associated with the smaller dimensions of the inshore environment.

The greatest apparent straight-line distance from release site to tag-recovery site was about 54 miles. The average apparent straight-line distance from tagging site to recovery area was 10 miles. The distances of tag recaptures from the original tagging site are comparable to those reported in a previous flounder study by Perlmutter (1947). The data at hand also support Perlmutter's statement that a winter flounder fishery is sustained by products of local spawning due to the fact that most observed movements have been restricted to relatively short distances. However, the magnitude of the contribution from particular breeding areas is not known at present.

It is conjectured that reassembly at the breeding grounds prior to and during the breeding season may be similar to diasporic migration defined by Wilkinson (1952). Gerking (1959), in a comprehensive summary of the movements of fish populations, states that probably no single mechanism will account for the homing response of fishes. The above is believed to be true in this instance also. However, since his survey made no mention of random searching it seems proper to examine this crude but perhaps logical method by which shallow water and the vicinity of the breeding grounds may be reached. Riley's (1956) investigation of Long Island Sound revealed only a weak and variable current in the vicinity of most tag recaptures, so it does not appear reasonable to postulate orientation to currents. Further, neither this investigation nor the investigations of the movements of marine demersal fishes summarized by Gerking (1959) provide information on other guiding mechanisms.

As mentioned previously, an idealized case is established where winter flounder are dispersed uniformly over a strip of ocean of width w bounded on one side by a depth contour which constitutes a reflecting barrier, and the other side contains the coastline which retains the fish on its arrival. It is assumed that, once the vicinity of the shore has been reached, winter flounder will search randomly along a narrow strip until an inlet is located by olfactory perception or some other means.

The width w of the bounded portion of the ocean is taken to be 15 miles. This distance coincides roughly with the presence of the 20-fathom contour beyond which tagged fish were not reported. Consider a random search for the coastline beginning at time zero. The percentage returning as a function of time is required under the assumption of random search. The empirical values of the coefficient of disperson $a^2=1.1$ miles² per day and $w=15$ miles are used. The fraction of fish still searching at time t can be obtained from:

$$\frac{2}{w^2}\sum_{n=1}^{\infty}\frac{1}{\alpha_n^2}e^{(-a^2\alpha_n^2 t)}$$

Derivation of the above is given in the appendix and is similar to the equation derived independently by Wilkinson (1952) for diasporic migration.

Figure 3 shows the return probability plotted as a function of time of search using two boundary widths. Similar calculations using a boundary width of 10 miles were also made because the majority of the fish were recaptured within this apparent straight-line distance from the point of release. It is evident from this figure that approximately 75% returns to shore are achieved after 90 days of searching in the case of the maximum strip width of 15 miles. If we assume a reflecting barrier at 10 miles, the return probability is more than 90% after 90 days of searching. These results are considered reasonable since the search period of 90 days lies within the time that winter flounder were actually observed to enter Green Hill Pond, and this period is less than the observed breedin son. Diasporic migration with no ass tions about orientation to outside st seems a reasonable explanation for r ment back to the coast.

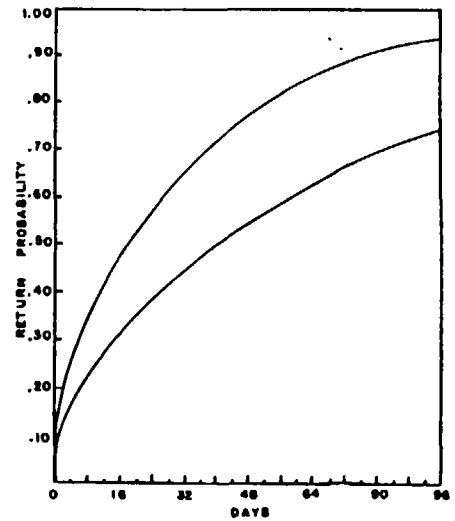

FIG. 3. Return probability in diasporic migration as a function of time, for $w=15$ and 10 and $a^2=1.1$.

APPENDIX

Grateful acknowledgment is made t fessor R. H. Goff, Mechanical Engin Department, University of Rhode Islan this derivation.

The random movement of fishes is c ered to be approximated by the hea fusion equation,

$$K\frac{\delta^2\phi}{\delta x^2}=\frac{\delta\phi}{\delta t}$$

with the boundary conditions ($x=0, \frac{\delta}{\delta}$ for reflection by the depth contour and $\phi=0$ for absorption by the coast). W with the initial condition ($t=0, \phi=\phi$. Assume $\phi=X(x)T(t)$

$$KT\frac{d^2X}{dx^2}=X\frac{dT}{dt}$$

$$\frac{1}{X}\frac{d^2X}{dx^2}=\frac{1}{KT}\frac{dT}{dt}=-\alpha^2,\quad \frac{d^2X}{dx^2}+\alpha^2X$$

$$X=A_1\cos\alpha x+A_2\sin\alpha x$$

$$\frac{dT}{dt}+\alpha^2KT=0,\quad T=B_1e^{-K\alpha^2t}$$

Since $\phi=XT$

$$\phi=e^{-K\alpha^2t}[C_1\cos\alpha x+C_2\sin\alpha x]$$

for $\frac{\delta\phi}{\delta x}=0$, when $x=0, C_2=0$

hence $\phi=Ce^{-K\alpha^2t}\cos\alpha x$

for $\phi=0$ when $x=w$ $\alpha=\frac{\pi(2n-1)}{2w}$ $n=1$

Then $\phi_n=C_ne^{-K\alpha^2t}\cos\alpha_nx$ where $\alpha_n=\frac{\pi}{}$

for $\phi=\phi_0$ when $t=0$ we must use $\phi=$

$$\phi_0=\sum_{n=1}^{\infty}C_n\cos\alpha_nx=\sum_{n=1}^{\infty}C_n\cos\frac{(2n-1)\pi}{2w}$$

Multiplying both sides by $\cos\frac{(2K-1}{2w}$

and integrating from $0\rightarrow w$

$$\int_0^w \phi_0 \cos\frac{(2K-1)\pi}{2w}x\,dx = \sum_{n=1}^{\infty} C_n \int_0^w \cos\frac{(2n-1)\pi}{2w}x \cos\frac{(2K-1)\pi}{2w}x\,dx$$

$$= 0,\ K \neq n$$

$$= \frac{w}{2},\ K = n$$

$$\phi_0 \frac{2w}{(2n-1)\pi} \sin\frac{(2n-1)\pi}{2w}x \Big|_0^w = C_n\frac{w}{2}$$

$$\phi_0 \frac{2w}{(2n-1)\pi}(-1)^{n+1} = C_n\frac{w}{2},$$

$$\phi_0 \frac{1}{\alpha_n}(-1)^{n+1} = C_n\frac{w}{2}$$

$$C_n = \frac{2\phi_0}{w}\frac{1}{\alpha_n}(-1)^{n+1}$$

$$\phi = \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n} e^{-K\alpha_n^2 t}\cos\alpha_n x$$

To find total at time "t" we must find $\int_0^w \phi\,dx$

$$\int_0^w \phi\,dx = \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n} e^{-K\alpha_n^2 t}\int_0^w \cos\alpha_n x\,dx$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n} e^{-K\alpha_n^2 t}\left|\frac{1}{\alpha_n}\sin\alpha_n x\right|_0^w$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n^2} e^{-K\alpha_n^2 t}(-1)^{n+1}$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{1}{\alpha_n^2} e^{-K\alpha_n^2 t}$$

Total at $t = 0 = \phi_0 w$

The fraction at time "t" $= \frac{2}{w^2}\sum_{n=1}^{\infty}\frac{1}{\alpha^2_n} e^{-K\alpha_n^2 t}$

Substitution of a^2 for K gives the form described in the body of the report.

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COMPETITION BETWEEN *EUCYCLOPS AGILIS* AND *DAPHNIA PULEX*[1]

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ABSTRACT

Daphnia pulex suppressed the population development of *Eucyclops agilis* in mixed cultures. It appears that this reduced reproductive rate was due to the presence of *Daphnia* and not to metabolic products.

INTRODUCTION

In an earlier work it was shown that *Simocephalus vetulus* had a depressing effect on the number of *Cyclops viridis* occupying the same culture (Parker 1960). Reports by Fryer (1957a, 1957b) indicate that *Cyclops viridis* is predatory; among 51 guts examined he found approximately 22% with oligochaetes, 18% with cyclopoid copepods, 16% with dipteran larvae, and 6% with cladocerans. These figures suggest that the results obtained with *C. viridis* and *S. vetulus* may have been atypical since the copepods were forced to exist on an unnatural diet. Another possibility is that not all of the animals used were *C. viridis* since only a few were sent away for taxonomic verification; nevertheless, Fryer states that in general the large cyclopoids are carnivorous so that if members of other large species were present it is likely that they too were naturally carnivorous. This criticism pointed to the need of further work with a known herbivorous copepod; consequently, *Daphnia pulex* and *Eucyclops agilis* were the subject of the study reported here. *Eucyclops agilis* guts (106) were examined by Fryer and he found 67% with diatoms, 49% with filamentous green algae, and 32% with unicellular algae and broken colonies.

METHODS

Fundamentally the questions to be considered are two, 1) will *Daphnia pulex* suppress the *Eucyclops agilis* population and, if so, 2) how is this brought about; is competition direct or indirect? Toward these end cultures were established; 18 contai gravid daphnid, 18 contained 1 gravid poid, and 144 contained 1 gravid da and 1 gravid cyclopoid, in 50 ml of fil lake water in every case. All cultures kept under continuous light in a wate at 20°C and were fed weekly with 1 m suspension of *Chlamydomonas mo* having a Klett photometer reading o This experiment ran for a period of 9 and there were 10 treatments among th cultures. These 10 treatment group described below:

Group	Treatment
0[1]	Pure *Daphnia*
0	Pure *Eucyclops*
I	*Daphnia* removed from mixed cult after 1 week
II	*Daphnia* removed from mixed cult after 2 weeks
III	*Daphnia* removed from mixed cult after 3 weeks
IV	*Daphnia* removed from mixed cult after 4 weeks
V	*Daphnia* removed from mixed cult after 5 weeks
VI	*Daphnia* removed from mixed cult after 6 weeks
VII	*Daphnia* removed from mixed cult after 7 weeks
VIII	*Daphnia* removed from mixed cult after 8 weeks

Two cultures were terminated weekly each group and the copepods were co in three categories: nauplii and copep with and without egg sacs. If a suppre of *Eucyclops* occurred and was due prin to the physical presence of *Daphnia*. would expect that the *Eucyclops* po tions would respond promptly afte removal of *Daphnia*.

[1] This research was supported in part by a National Science Foundation Research Grant (G-8911).