

On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations

3534

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Abstract

The predator-prey system between the polyp *Protohydra leuckarti* and the harpacticoid copepod *Tachidius discipes* is investigated using the results of a 3 year field survey and laboratory experiments involving the cultivation of the species.

In the field a close relationship between numbers of predator and prey was observed. The possible influence of environmental factors on this relationship is discussed.

A number of mathematical models is compared to investigate the possibility of realistic description of the system. It is concluded that, even during relatively long time intervals, the number of prey can be predicted from the reproductive potential of the prey on the one hand and the rate of predation and predator density on the other hand, using simple deterministic models in which a functional response is incorporated.

Introduction

Protohydra leuckarti Greef 1870 is an important member of the meiobenthic community in many brackish water areas throughout Europe. It has been shown (Muus, 1967; Heip, 1971) that this species attains densities around 40,000-60,000/m² and a high of 200,000/m² has been recorded by Muus (1967). *Protohydra* is known to feed mainly on nematodes and copepods, the two most important constituents of marine and brackish water meiobenthic communities. The impact of predation by *Protohydra* on the density of its prey must be very high, especially in summer, as an individual may easily consume one prey specimen each day (Muus, 1966 and personal observations). This high predation rate has important consequences on the trophic relationships in those communities where *Protohydra* is common. The possibility of competition between this species and other species belonging either to the macrofauna or to the young stages of some fish species has been stressed by Muus (1967). McIntyre (1964) and Marshall (1970) amongst others indicated that the meiobenthos may not play a significant role in

the transfer of food to higher trophic levels, which are of value to man. These studies prove that much of meiobenthic production may be consumed within the meiobenthos itself.

In the community we studied, *Protohydra* is an important species in terms of numbers. In order to assess just how important it is, we chose to investigate its relationship to one of its most important food items, the harpacticoid copepod *Tachidius discipes* Giesbrecht 1882. This species is a well known and widely occurring copepod in brackish water areas throughout Europe, and dominant in all communities where it occurs. Though not the most common species in the investigated habitat, a meso-polyhaline brackish water pond, it is the one most likely to be captured by *Protohydra*. *T. discipes* is indeed epibenthic (Heip, 1973). To come in contact with the copepod, the polyp, which is fixed on a sand grain, makes a periodical, screwing movement through the detritus covering the sediment, appearing at the surface at regular time intervals. Contact is easily established with a prey that happens to be on the surface at the moment the polyp passes through the detritus. Animals living between the sand grains will be captured with more difficulty and perhaps in a different way.

In order to assess the importance of predation by *Protohydra* some simple deterministic models were used. Models describing predator-prey interactions originated with Lotka (1925) and Volterra (1926) who used the following equations:

$$\frac{dH}{dt} = aH - pHP$$

$$\frac{dP}{dt} = -rP + qHP$$

In these equations and further in the text, P denotes the number of *Protohydra* and H the number of *Tachidius*. In these equations each population is limited by the other one and there are no self-limiting density effects. In the absence of the predator the prey population expands exponentially with a rate of a per day. The product of densities PH reflects the approach to predator-prey interactions as molecular processes.

A second set of equations can be obtained when assuming that the prey population would be growing according to the logistic equation rather than exponentially. In this case we may write:

$$\frac{dH}{dt} = aH - \frac{a}{K}H^2 - pHP$$

$$\frac{dP}{dt} = -rP + qHP$$

In this set of equations the term $-\frac{a}{K}H^2$ is a damping term expressing the inhibiting effect of a species on its own growth: this leads to convergent oscillations in which both predator and prey oscillate with decreasing amplitude, the predator oscillation lagging in phase behind the prey.

It is well known that equations as the ones described are often inefficient to describe real predator-prey interactions. One of the main reasons is that the reaction of

predators varies for different prey densities. Solomon (1949) distinguished two different components in the way predators respond to changes in prey density. Firstly, when the prey increases, the individual predator captures more prey per unit of time until some threshold is reached above which the number of prey taken per predator is about constant. Secondly, there is an increased number of prey taken simply because of higher predator densities following the increased prey density itself. Solomon (1949) termed the former the functional response and the latter the numerical response of the predator. These concepts were elaborated by Holling (1965) who developed models in which both types of responses were incorporated. Furthermore, Holling (1966) found that in birds and mammals the functional response is influenced by factors other than prey density and the time required for capturing and handling of the prey. Predation can be influenced by prey palatability and interference between predators through aggression and territoriality. The prey may also learn to avoid the predator.

In the case of the *Protohydra-Tachidius* system there is no need for such elaborate considerations of the factors mentioned above which are of great importance in vertebrate predators. There is no active search for the prey, nor active avoidance of the predator. The capture of prey organisms depends on the probability of a contact occurring, which will be largely a function of density. Because the predator does not move in the horizontal plane, at least not to capture its prey, it is the movement of the individual prey which makes it a candidate for consumption. The chance of an individual prey organism to be captured will therefore be a function of predator density.

Material and methods

Samples were collected fortnightly from December 1969 till December 1972. Collection and treatment of samples was carried out as described earlier by Heip (1971, 1972). Animals were cultured at different temperatures as described by Smol and Heip (1974). Calculations were performed on a Hewlett-Packard 9810A desk calculator. In order to smooth the graphs of density the running average of three subsequent samples was used instead of the middle sample value.

Results and discussion

The density of *Protohydra leuckarti* and *Tachidius discipes* as estimated from fortnightly samples collected during 3 years is given in Fig. 1. From this figure it is clear that a close relationship between the two species exists. The peak of *T. discipes* was followed by a first peak of *P. leuckarti* whose height was proportional to the height of the *Tachidius*-peak. A second peak of *Protohydra* occurred in 1970 and 1972 and was related to the bloom of another copepod, *Paronychocamptus nanus*.

The peaks of both species can be described by two exponential equations, one for the ascending and one for the descending numbers. These functions are $H = H_0 \exp a_1' T_1$ and $H = H_1 \exp a_2' T_2$ for *Tachidius* and $P = P_0 \exp r_1' T_1$ and $P = P_1 \exp r_2' T_2$ for *Protohydra*, in which H_0 and P_0 are the numbers at $t = 0$, H_1 and P_1 are peak numbers and a' and r' are realized rates of change, a_2' and r_2' being, of course, negative.

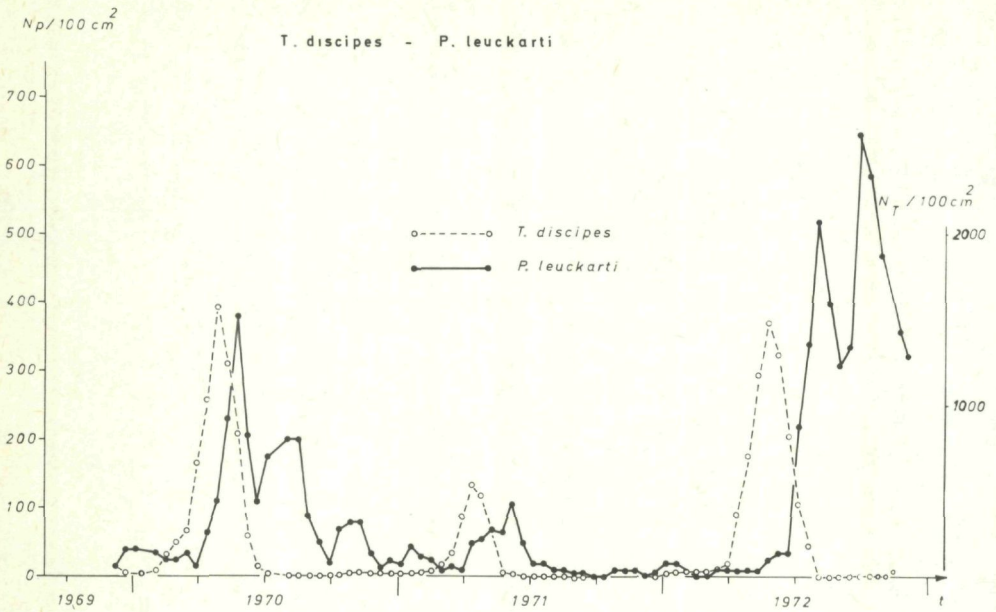
FIG. 1. Density of *P. leuckarti* and *T. discipes* during 3 years.

TABLE I
Parameters related to the peaks of *P. leuckarti*
and *T. discipes* in three subsequent years

<i>Protohydra leuckarti</i>								
Year	t_0	P_0	r_1	t_1	P_1	r_2	t_2	P_2
1970	April 8	21	0.055	June 2	440	-0.063	July 1	73
1971	March 28	14	0.041	June 4	88	-0.030	Aug. 25	8
1972	May 7	8	0.052	June 5	36	-0.005	July 5	30
Mean	April 14	14	0.049	June 4	188	-0.033	July 21	37
<i>Tachidius discipes</i>								
Year	t_0	H_0	a_1	t_1	H_1	a_2	t_2	H_2
1970	Feb. 11	47	0.040	May 20	2,780	-0.103	Aug. 5	0
1971	Jan. 6	6	0.049	April 20	758	-0.081	June 23	0
1972	Jan. 5	5	0.040	May 27	1,594	-0.030	Aug. 16	0
Mean	Jan. 27	18	0.043	May 14	1,730	-0.064	July 25	0

The values of these parameters as obtained from the regression of numbers *versus* time and the mean of the values over 3 years are given in Table I. The date at which *Protohydra* starts to increase lags well behind that for *Tachidius* (77 days on the average), the same holds for the date of peak occurrence, where the lag is, however, reduced to 21 days. Minimum numbers after the peak are attained at about the same time for both species.

From the mean values in Table I, a mean peak can be drawn. (Fig. 2). Since the product HP in the Lotka-Volterra equations is not a good representation of real predator-prey systems (Rosenzweig 1971), an even simpler equation was taken as a starting point, in which the number of prey changes during dt as :

$$\frac{dH}{dt} = aH - mP \tag{1}$$

where m denotes the number of prey taken per predator per day.

The rate of change during dt depends on two terms, an increase proportional to the prey density (the first term), and a decrease proportional to the predator density (the second term). Density of the predator can be described by the exponential function $P_t = P_0 e^{r't}$, substitution in eq. (1) gives :

$$\frac{dH}{dt} = aH - mP_0 r't \tag{2}$$

If m is constant $m = m_1$, the following differential equation is obtained :

$$\frac{dH}{dt} = aH - m_1 P_0 e^{r't} \tag{3}$$

The solution of this equation is :

$$H_t = H_0 e^{at} - \frac{m_1 P_0}{a - r'} (e^{at} - e^{r't}) \tag{4}$$

In eq. (4) the value of five different parameters and time has to be determined. From the mean peak we already obtained the values $H_0 = 485$, $P_0 = 14$ and $r' = 0.049/\text{day}$. The value of m_1 has been estimated as $m_1 = 1$ according to personal observations and those of Muus (1966) that *Protohydra* consumes about one large prey individual each day, at least at high temperatures. Because total numbers, including copepodites (but not nauplii) are considered it is reasonable to assume that m_1 might be somewhat higher but as there are other prey species available to the polyp, the value of m_1 again decreases. Therefore $m = 1$ seems to be a fair estimate especially since its numerical value is not critical for the general behaviour of the system.

The only parameter value remaining unknown is the intrinsic rate of natural increase of the prey. To obtain a realistic description of the system it is necessary to incorporate

the influence of temperature into the calculation of this intrinsic rate. For an exponentially increasing population:

$$H_t = H_0 e^{at}$$

from which

$$a = \frac{1}{t} \ln \frac{H_t}{H_0}$$

Protohydra - Tachidius
Mean numbers

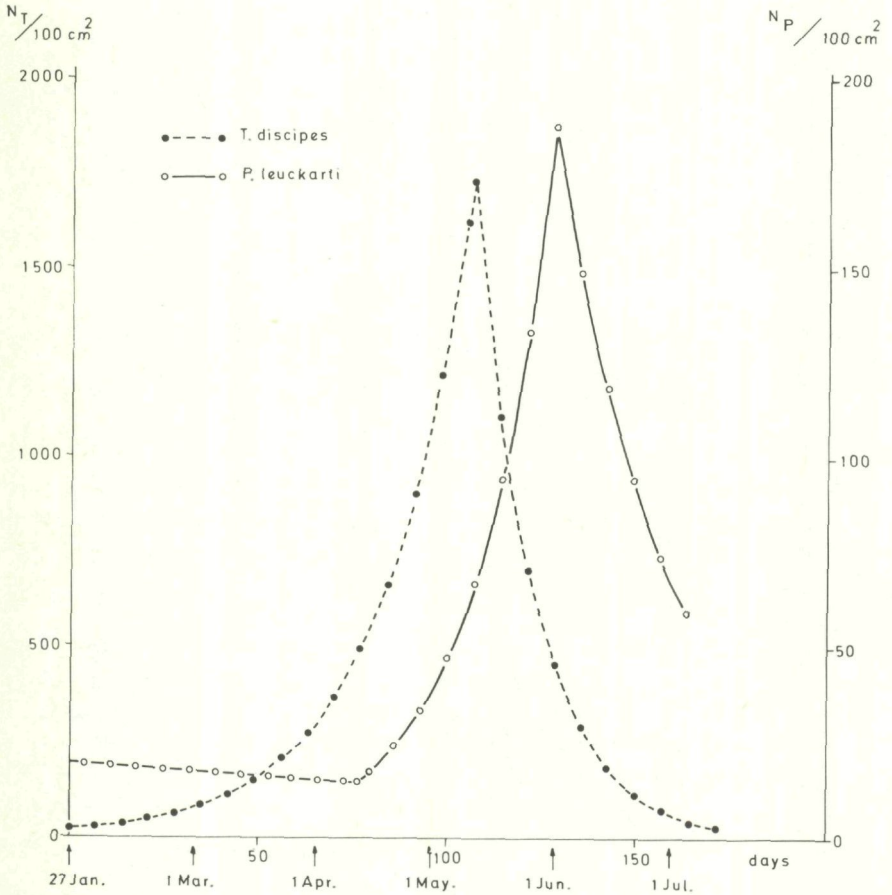


FIG. 2. Mean density of *P. leuckarti* and *T. discipes* as described by exponential growth using the parameters calculated in Table I.

In the last equation H_t is the number of progeny, equal to $H_t = p H_0 N_e$ in which p is the fraction of females in the original population and N_e is the number of eggs per female.

When $t = t_G$, the generation time, the intrinsic rate of increase becomes :

$$a = \frac{1}{t_G} \ln p N_e \quad (5)$$

To incorporate the influence of temperature it is necessary to examine the dependence on temperature of the three parameters used. In another paper (Heip and Smol, 1976) it is shown that neither the sex-ratio nor the number of eggs vary with temperature, while the generation time is very strongly influenced. The generation time of *T. discipes* as a function of temperature can be described as follows :

$$t_G = 527 T^{-1.13} \quad (6)$$

substitution of this equation into eq. (5) gives :

$$a = \frac{\ln p N_e}{527 T^{-1.13}}$$

As the fraction of females $p = 0.67$, and the mean number of eggs in an egg-sac is 41, the intrinsic rate of natural increase becomes :

$$a = \frac{\ln (0.6 \times 41)}{527 T^{-1.13}}$$

$$a = \frac{0.0063}{T^{-1.13}} \quad (7)$$

Substitution of eq. (7) into eq. (4) would yield an expression with two independent variables, temperature T and time t . It would be possible to calculate the mean of observed temperatures at each date. It was, however, preferred to calculate the regression of temperature against time by Fourier-analysis over 3 years, yielding the following equation :

$$T = 11.2 + 8.3 \sin (t - 117) \quad (8)$$

in which $t_0 = 31$ December.

When this value of T is substituted into eq. (7), we obtain :

$$a = \frac{0.0063}{(11.2 + 8.3 \sin (t - 117))^{-1.13}} \quad (9)$$

In turn, this value is substituted in eq. (4), and all the parameters necessary for the calculation of H_t are determined.

There are, however, two different time scales, one to calculate e^{at} and $e^{r't}$ and one to compute a . When $t = 0$ in the first time scale, $t = 104$ in the second time scale.

The value of H_t as calculated from eq. (4) is shown in Fig. 3. It is obvious that this equation does not describe the observed values very well. Moreover, it can be shown that the general behaviour of this model is within broad limits independent of the value of the parameters and that the curves will never yield the desired shape, *i.e.* with an increasing and a decreasing part.

In order to improve the model the general equation (1) must be changed and a feedback mechanism, in the form of a functional response, is introduced. The cases in which m is not constant but a function of prey density will be considered here. Holling

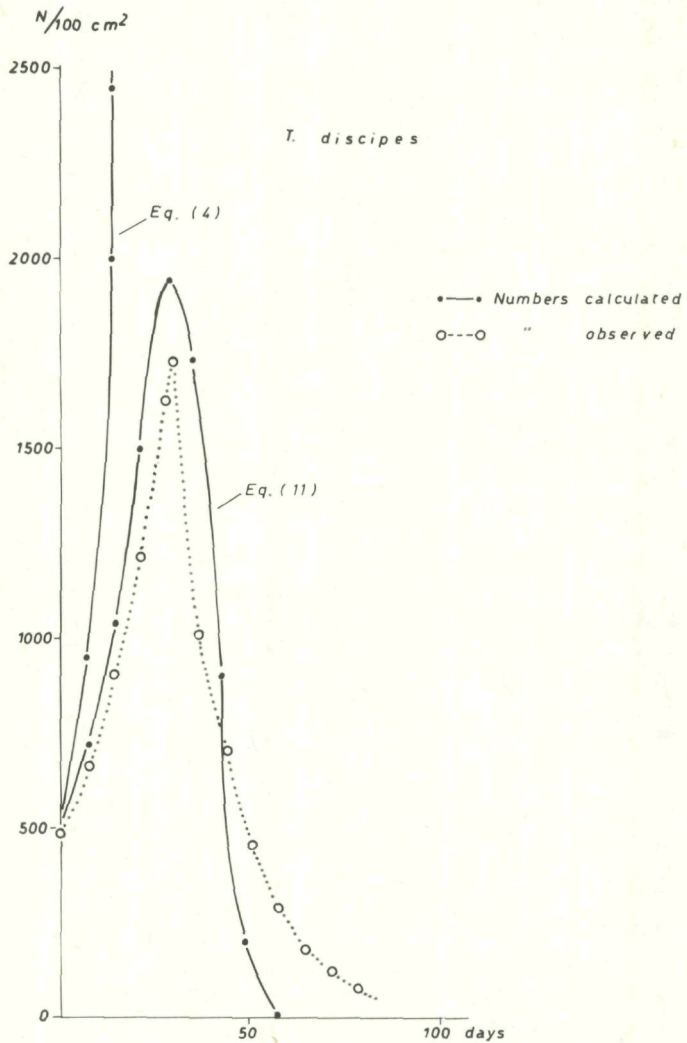


FIG. 3. Mean peak of *T. discipes*, as observed over 3 years and as calculated from equations (4) en (11).

(1965) described three types of functional responses. In type I the number of prey taken per predator increases linearly with the prey density until some threshold is reached after which m remains constant. Holling (1965) suggested that type I responses are unusual, except for filter-feeding crustaceans feeding on algal cells. According to Holling (1965) type II responses are typical for vertebrate predators, where it takes the predator a certain time to kill and eat the prey. However, a model generally used in the description of phytoplankton dynamics assumes such a type II response for the rate at which phytoplankton takes up nutrients (Steele, 1974). Type III responses were found in cases where alternative prey is available and may therefore be important in the system we studied.

In type I responses m varies linearly with H and is given by :

$$m = \frac{m_1 H}{2H_1}$$

in which H_1 is the prey density at which $m = 0.5 m_1$. The general equation now becomes :

$$\frac{dH}{dt} = aH - \frac{m_1 H}{2H_1} P_0 e^{rt} \quad (10)$$

which has been solved :

$$H_t = H_0 \exp \left(at - \frac{m_1 P_0}{2r'H_1} (e^{rt} - 1) \right) \quad (11)$$

In eq. (11) only one new parameter, H_1 , the density at which $m = 0.5 m_1$ appears. This density can be calculated very roughly as follows (Heip, 1974) : when we assume that the copepod makes a horizontal displacement of 5 cm/hr, the surface covered by the organism during a 12 hr active period is 0.1 mm (copepod breadth) \times 60 cm (displacement) = 0.6 cm². It therefore takes 10,000/0.6 = 17,000 copepods to cover 1 m² on the average during a day. This figure might well be the threshold level at which every predator has a chance of obtaining one prey item every day. From this, we obtain $H_1 = 85$ per 100 cm², but again, the value is not critical for the behaviour of the system.

With this value of H_1 and the values of the other parameters as used in eq. (4), H_t can be calculated according to eq. (11). The curve thus obtained is shown in Fig. 3. It is obvious that this equation gives a fairly realistic representation of the system. Only when density becomes low after the peak some aberration occurs, which is probably due to the predator switching to other prey species. This switch would result in densities of *Protohydra* which are higher than could be inferred from *Tachidius*-density alone, and would predict *Tachidius*-densities which are consequently too low. Most probably this switching is a real phenomenon because in 2 years a second peak of *Protohydra* occurred after *Tachidius* disappeared : this mechanism might provide a means for lengthening the predator-prey cycle and could be important in giving the prey organism the chance to complete its life-cycle.

Equations in which the functional response is of type II or type III are given in Table II. Since the differential equations associated with these responses have not been solved, a different approach was used.

When $dH/dt = 0$, the function $H = f(t)$ has an extremum. Solving $dH/dt = 0$ for t gives the time of this extremum, which yields information on at least two aspects of a good fit to the observed system, namely the existence of a peak and the time at which it occurs.

TABLE II

The number of prey taken per predator per day as a function of the number of prey occurring [$m = f(H)$], in three types of functional response and the time at which peak density is reached ($dH/dt = 0$) for an exponentially — and a logistically increasing population. (See text for explanation of parameters)

	Type I	Type II	Type III
$m = f(H)$	$m = \frac{m_1 H}{2H_1}$	$m = \frac{m_1 H}{H + H_1}$	$m = \frac{m_1}{1 + b(H_1 - H)}$
Time at which $dH/dt = 0$ (in days)	27.9 29.4	31.0 32.9	27.9 29.4
	Observed: 30 days		

In table II this time has been calculated for both an exponentially and a logistically growing population. It can be seen that, with the parameters obtained from the mean peak and the culture experiments as previously described, the prediction of the time a peak will occur is very accurate and close to the observed value of $t = 30$ days, and this with all the equations used. We may therefore conclude that in this predator-prey system, which is uncomplicated but nevertheless realistic, a simple feed-back mechanism involving the functional response of a predator to the density of its prey is sufficient to obtain realistic estimates of at least the moment of peak density, and, in the one case where it could be examined, also of the density of the prey. We may also conclude that there is no good estimate of the time of extinction of the prey because of switching by the predator. Steele (1974) has shown that one-predator-two-prey systems are not stable because the prey species converge until they reach the point where the predator has the same response to both of them. The prey then become functionally identical. This is however not necessarily the case if convergence is impossible because of different temperature requirements of the prey species causing a separation in time.

It was established that the peak of *Tachidius discipes* may be described from the known intrinsic rate of the prey's natural increase and from the predator density. The impact of *Protohydra* on *Tachidius* can also be calculated in a different way to show how much of the production of *Tachidius* is taken by *Protohydra*. Heip (in preparation) proposes the following equation to calculate the numbers eliminated from an exponentially changing population during a time interval t , from the known realized rate of increase a' and the mortality or natality:

$$H_e = H_0 \frac{d}{a'} (e^{a't} - 1)$$

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