On the Evolution of Reproductive Potentials in a Brackish Water Meiobenthic Community

by

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Abstract

The realized and intrinsic rates of increase of several meiobenthic populations are compared. The realized rate of increase is remarkably similar among four species of copepods, which leads to the conclusion that dominance is not a function of rate of increase or parameters influencing this rate. The result is investigated in the light of Vandermeer's (1975) β-competition. There is also a remarkable agreement between the values of the predator *Protohydra leuckarti* and its principal prey *Tachidius discipes*.

The intrinsic rates of natural increase vary more, but are a linear function of temperature in all species investigated. This is in agreement with the theory that natural selection acts against nonlinear dynamic characteristics (Patten 1975). The low intrinsic rate of increase of the nematode *Oncholaimus oxyuris* may be the result of a group selection process.

A. Introduction

In the last few years several mathematical models of complex ecosystems seemed to indicate that increased complexity makes for instability of the system (Gardner & Ashby 1970; May 1972, 1973). This is contrary to the common belief of most ecologists that ecosystems tend to be more stable the larger the number of interacting species they contain. May (1973) brings this apparent contradiction into the light of natural selection by observing that if complex natural systems are in fact stable, this can only be because the interactions occurring in the system, between the species, are highly non-random. It appears that the contradiction is not as keen as May believed, and both Roberts (1974) and De Angelis (1975), by either eliminating biologically meaningless negative densities or by constructing more plausible food web models, recently showed that increased complexity may in fact coincide with increased stability. Nevertheless, it remains obvious that the parameters describing interactions between species have highly non-random values which are the product of natural selection (Maynard-Smith 1974).

Finding it unreasonable to think of selection working upon an ecosystem as a whole, Maynard-Smith (1974) cites two ways in which selection might act to produce complex and stable ecosystems; these are genetic feedback and species ex-

clusion. Actual ecosystems, complex or otherwise, are persistent only because species whose presence would be inconsistent with persistence have been excluded. Genetic feedback, a concept introduced by Pimentel (1961), is still a controversial topic and I will not go into this further, but the main idea is that if two species coexist for some time in an ecosystem, and if they interact, then they are likely to undergo genetic changes caused by this interaction: they will coevolve.

Natural selection operates by differential reproductive success. A convenient indicator of the reproductive potential of a population is the intrinsic rate of natural increase r_m, the rate of increase of a population unrestricted by density effects as described by the equation for exponential growth $dN/dt = r_m N$ (1). This intrinsic rate of increase generally has an inverse hyperbolic relation with generation time and a negative correlation with body size. In this paper I will present some calculations of both the intrinsic and the realized rate of increase of some meiobenthic populations from a brackish water pond in northern Belgium. These populations have been studied from 1968 onwards and most of the material concerning life-cycles has yet to be published.

B. Material and methods

Values of density are provided from fortnightly samples taken over a period of four years. Methods of sampling and extraction are as described by Heip (1973a). In calculations the running average of three samples is used instead of the middle value. Numerous calculations have shown that the value of the rate of increase is not changed substantially by this procedure.

Culture methods for the copepods have been described by Smol & Heip (1974). Both the nematode *Oncholaimus oxyuris* and the polyp *Protohydra leuckarti* were cultured at different temperatures using the nematode *Panagrellus silusiae* as food given in excess of the requirements. A more detailed account on this will be published shortly (Heip, Smol & Absillis, in preparation).

C. Results

It has been shown (Heip 1972, 1973b and in preparation) that all populations which have been investigated show one or more distinct peaks during the year, which can be described by an exponentially increasing and an exponentially decreasing function. These populations belong to the crustacean subclasses Ostracoda and Copepoda, and to the Hydrozoa. The realized rate of increase has been calculated for all peaks for all years, and the mean value for the different populations is given in Table 1. For further illustration the corresponding time needed to double population size, calculated as $t_2 = (\ln 2)/r$, is also given in Table 1.

The calculation of the intrinsic rate of natural increase r_m ideally should use life-tables and requires knowledge of the age-specific survival and fecundity. It is difficult to obtain this information from species with a short life cycle. Heip & Smol (1976b) therefore estimated r_m in copepods from:

$$r_m = \frac{1}{T_1} \ln pN_e \tag{2}$$

Tab. 1. Mean realized rate of increase of all peaks over a four year period (r per day) and corresponding doubling time (t_2 in days)

Hydrozoa	r	t_2
Protohydra leuckarti Greeff, 1870	0.049	14.1
Copepoda		
Halicyclops magniceps (Lilljeborg, 1853)	0.042	16.5
Canuella perplexa T. & A. Scott, 1893	0.045	15.4
Tachidius discipes Giesbrecht, 1882	0.048	14.4
Paronychocamptus nanus (Sars, 1908)	0.044	15.8
Ostracoda		
Cyprideis torosa (Jones, 1850)	0.015	46.2
Loxoconcha elliptica Brady, 1868	0.030	23.1

in which T_1 is the time of first appearance of gravid females of the next generation, p is the percentage of females and N_e is the number of eggs per egg-sac. The value of r_m obtained in this way may not be entirely accurate but it is the best available in the absence of very detailed data which can be used to construct life tables.

Values of the intrinsic rate of natural increase of two harpacticoid copepods as a function of temperature are given in fig. 1. From this figure it is obvious that r_m is a nearly linear function of temperature. This result is robust against large changes in the values of the parameters used in the calculation of r_m. However, the parameters as used in eq. (2) themselves do not show this linear relationship with temperature.
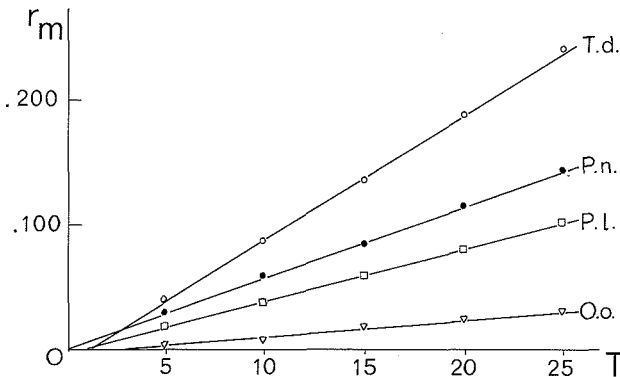

Fig. 1. Intrinsic rate of natural increase as a function of temperature in four meiobenthic populations: T.d. = *Tachidius discipes* (Copepoda); P.n. = *Paronychocamptus nanus* (Copepoda); P.l. = *Protohydra leuckarti* (Hydrozoa); O.o. = *Oncholaimus oxyuris* (Nematoda).

The intrinsic rate of natural increase of the nematode *Oncholaimus oxyuris* has been calculated in essentially the same way and is also shown in fig. 1. Again there

appears to exist a linear relationship between r_m and temperature, in spite of the fact that the parameters used in the calculations are nonlinear functions of temperature (Heip, Smol & Absillis, in preparation).

The intrinsic rate of natural increase of the polyp *Protohydra leuckarti* was calculated from the observed division rate in laboratory experiments at three different temperatures (Table 2). The influence of temperature on the division rate is profound and can be described by $D = 254\ T^{-1.12}(3)$. As this species nearly always reproduces asexually the intrinsic rate r_m is given by $r_m = (\ln 2)/D = 0.69\ /\ (254\ T^{-1.12})$. Selected values of r_m and the corresponding doubling time t_2 are also given in table 2. As in the other species, the relationship between r_m and temperature is nearly linear (fig. 1).

Tab. 2. *Protohydra leuckarti*: Division time, as observed and as calculated from eq. (3), intrinsic rate of natural increase and corresponding doubling time at five different temperatures (after Smol, unpublished).

Temperature ($°C$)	Division time observed	Division time calculated	r_m per day	t_2 days
5	—	41.9	0.017	40.8
10	—	19.3	0.036	19.3
15	12.5 ± 2.5	12.2	0.057	12.2
20	8.4 ± 2.3	8.9	0.078	8.9
25	7.1 ± 1.1	6.9	0.100	6.9

The intrinsic rate of natural increase of the four species investigated seems to be a linear function of temperature. When we consider r_m as such the regression of r_m against temperature yields:

Protohydra leuckarti: $r_m = 0.0042\ T - 0.0048$
Oncholaimus oxyuris: $r_m = 0.0013\ T - 0.0043$
Tachidius discipes: $r_m = 0.0100\ T - 0.0137$
Paronychocamptus nanus: $r_m = 0.0057\ T - 0.0006$

D. Discussion

The fact that the realized rates of increase of the four copepod species investigated are nearly the same is remarkable, more so because differences in the intrinsic rate of increase appear to be much larger. This shows that dominance in these species is not a function of the rate of increase, and this in turn may have consequences on the realism of current models describing competition, when in fact it could be demonstrated that these species are competitors. This is not the case. Nevertheless, it remains certain that dominance is a matter of how long the increase can be maintained and has something to do with tolerance to environmental conditions in the broadest sense, including other populations, and not with the rate of increase, hence not with fertility or generation time.

The same is also apparent from the realized rates of increase of the two ostracod species, where the species with the lowest rate of increase is in fact dominant and the other species occurs much more erratically with much larger fluctuations in density. This might be in agreement with current theory on r- and K-selection, but as the species with the larger r-value is also the smaller one there could be an influence of body size, too. However, in the copepod species body size does not seem to be too important, as the range here is larger than the difference between the two ostracods.

The intensity of interspecific competition is normally expressed as the change in the per capita growth rate of species i due to the presence of an individual of species j relative to the change in the per capita growth rate of species i due to the presence of an individual of species i itself, formally:

$$\frac{\delta(dN_i/N_i dt) / \delta N_j}{\delta(dN_i/N_i dt) / \delta N_i} = \frac{a_{ij}}{a_{ii}} = \alpha_{ij}$$

The interspecific effect of one species is expressed as a fraction of the intraspecific effect of the other species. Vandermeer (1975) made the perfectly valid proposition that, instead of comparing interspecific competitive ability a_{ij} to the intraspecific competitive ability of the other species a_{ii}, we could compare it with the intraspecific competitive ability of the species perpetrating the competition.

$$\frac{\delta(dN_i/N_i dt) / \delta N_j}{\delta(dN_j/N_j dt) / \delta N_j} = \frac{a_{ij}}{a_{jj}} = \beta_{ij}$$

When competition is defined in this way it follows that, when two species are less and less distinguished in terms of the way that one individual depresses the survivorship and fecundity of other individuals, their intrinsic rates must become more and more equal. Ecologically equivalent species coexist only if their r's are relatively equal (Vandermeer 1975). Now we are dealing with realized rates; when these are not themselves the result of the competition it appears justifiable to explain their values as resulting from a selection process permitting coexistence, and use these values in describing the competition. Our data, therefore, seem to validate Vandermeer's approach.

The predator-prey relationship between *Protohydra leuckarti* and its main prey species *Tachidius discipes* has been studied by Heip & Smol (1976a). It is remarkable that the realized rates of increase of these two species are again nearly the same; moreover, there is a remarkable resemblance in the reaction of development time to temperature as expressed with the parameter b of the power equation $D = aT^b$. The value of b is -1.12 for *P. leuckarti* and -1.13 for *T. discipes*. The identical values seem to indicate an interaction during the process which brings them about. Once again, there is a much larger difference in the intrinsic rates of increase of predator and prey. However, the predator increases at a rate which is equal to its intrinsic rate ($r_m = 0.049$ per day taking the mean temperature of 13.2 °C into

account), while the realized rate of increase of the prey is a result of the predation process, and thus a function of the realized rate of increase of the predator.

The ostracod *Cyprideis torosa* is a detritus feeder on top of the food chain. It has a relatively low realized rate of increase when compared with the other ostracod *Loxoconcha elliptica* and the copepod species. The nematode *Oncolaimus oxyuris* is a predator on other nematode species and also on top of a food chain. In this species the intrinsic rate of natural increase is very low. Both this species and *C. torosa* seem not to be restricted by either food or predation. It is possible that group selection might play a role in the lowering of reproductive potential. A plausible mechanism for this kind of selection has been described by Gilpin (1975). It has been shown (Rosenzweig & MacArthur 1963) that overexploitation in predator-prey communities arises because there is a selective pressure on the predator to improve its exploitation efficiency. If this is continued too far a point may be reached where the ecological steady state between predator and prey is destroyed and whereafter predator extinction may occur. The destabilization of predator-prey steady state leads to limit cycle oscillations which may effectively cause the predator's extinction by taking it to such low densities that extinction is biologically inescapable. In Gilpin's model, predator populations occupy a number of environmental patches in which overexploitation and extinction of predator populations that are too efficient may occur. Between patches there is migration and gene flow. The populations on each patch are finite, thus the frequency of a gene for cropping efficiency will be subject to genetic drift, a process that will tend to maintain intergroup variance. Genetic drift is necessary for group selection in ensembles of populations which show initially the same genetic structure. If the generation time is lowered the same genetic drift will occur each generation, but the amount of selection is decreased, so lowering the generation time is favorable for group selection. This is of obvious application to meiobenthic populations.

Gilpin (1975) showed that destabilization and predator extinction are very rapid phenomena that occur in ecological as opposed to evolutionary time. If this is true it appears improbable that coevolution would take place, in the sense that it is doubtful that the prey could induce a change in the parameters of the predator population. However, experiments of Pimentel et al. (1965) showed that changes in the competitive ability of a species can occur in a short time. This can be explained by observing that fitness is lowered in the presence of competition, therefore selection acts within competing species to lessen the effect of the competitor on them. This selection should be strongest on the losing competitor because it suffers the greatest depression of fitness. It seems possible that this selection could change the outcome of competition before extinction occurs (Park & Lloyd 1955). A similar mechanism can be conceived in predator-prey relations, and by Occam's razor we need not involve a group selection hypothesis. However, although it is possible that natural selection produces populations with a lowered intrinsic rate of natural increase (Hairston et al., 1970), there is another aspect of the biology of

O. oxyuris which is not easily explained by natural selection. This species, both in the laboratory and in the field, has a low percentage of females in the adult population, around 40 % when sexual maturity is attained and much lower later because males tend to live longer. This phenomenon is hard to explain because selection will always cause either equal sex-ratios or favor females (Emlen 1973); however, the advantages of this low percentage for the population are clear. It lowers the reproductive potential while permitting the species to maintain a relatively high density. Indeed, *O. oxyuris* is at times the dominating species in the nematode community (Heip, Smol & Absillis, in preparation) and such a system in which a top predator is dominant both in numbers and in biomass seems impossible unless a very low turnover of the predator is accompanied by a very rapid turnover of the prey. The latter might indeed be the case, given the very high reproductive potential of some nematode species (Tietjen and Lee 1977).

The fact that the intrinsic rates of increase are linear functions of temperature is in agreement with the hypothesis that linearization of ecosystems is evolutionary adaptative (Patten 1975) in the sense that natural selection acts against nonlinear dynamic characteristics. It seems that systems which express nonlinear dynamic characteristics are not reliable while linear systems are well behaved due to superposition, ecosystem complexity, homeostasis and hierarchical organization. Ecosystem behavior is in the large neighbourhood dynamics about equilibrium and thus linear. Patten (1975) observes furthermore that ecosystems are rich in feedback which again introduces linearization. All these mechanisms should make ecosystems nominally linear in their large-scale holistic dynamics. This might provide some justification for the calculation of linear regressions and offers some hope for future modelling of complex ecosystems.

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