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Feeding rate in juvenile flounder (Platichthys flesus) in relation to prey density

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Abstract

Feeding rate in juvenile flounder was measured at different experimental densities of *Nereis diversicolor*. The results are treated by means of a mathematical model that describes feeding rate as a function of prey density, prey size, fish size and temperature. Feeding rate increases with increasing prey density but at a decelerating rate until a level is reached. The position of the level is lowered with decreasing temperature and fish size and increasing prey size.

Zusammenfassung

Nahrungsaufnahmerate bei jungen Flundern (Platichthys flesus) in Beziehung zur Dichte der Beute

Die Nahrungsaufnahmerate junger Flundern wurde im Experiment bei unterschiedlichen Dichten von *Nereis diversicolor* gemessen. Die Ergebnisse wurden mit Hilfe eines mathematischen Modells interpretiert, das die Nahrungsaufnahmerate als Funktion der Beutedichte, Beutegröße, Fischgröße und der Temperatur beschreibt. Die Nahrungsaufnahmerate steigt mit zunehmender Beutedichte bis zu einem bestimmten Niveau an, aber mit verminderter Rate. Die Höhe des Niveaus wird mit abnehmender Temperatur und Fischgröße und zunehmender Beutegröße herabgesetzt.

Introduction

Feeding rate of fishes depends on environmental factors, and obviously one important factor is the availibility of food. In an evaluation of the impact of predatory fishes on benthic invertebrate populations, it is therefore important to know the relation between feeding rate and density of prey. This note reports on the results of laboratory measurements of feeding rate in juvenile flounder (*Platichthys flesus*) at various densities of prey, *Nereis diversicolor*.

IVLEV (1961) presented a simple mathematical expression of the relationship between predation rate and prey density that provided a good fit to experimental data. His equation is, however, merely descriptive and does not contain any information on the causalities underlying the relationship. In this note I develop a simple mathematical model that describes this relationship by means of variation in hunger of the fish. Furthermore the model takes variation in temperature, prey size and fish size into account, and it is applied to the results of the present experiments.

Material and methods

A. Experimental design

Live specimens of *Nereis diversicolor* were offered at different densities to 0-group flounders. Number and weight of *N. diversicolor* eaten during 24 hours was recorded.

Flounders and worms were collected in the shallow, mesohaline Nivå Bay (Øresund); the flounders in late August 1976 and the worms throughout the experimental period (September–October). Length range of fish used was 80–110 mm, and average weight of worms used ranged from 0.03–0.18 gr (wt). Both increased during the experimental period.

The 72 experiments were conducted in aquaria (37 cm × 55 cm and 22 cm tall) with about 5 cm sediment on the bottom and running water (salinity about 23‰). Temperature ranged from 9 to 15°C.

The fish were adapted to experimental conditions (food, aquaria) during at least one week prior to experiments.

5–200 worms of known total weight were supplied to each aquarium. The worms were allowed to burry themselves (about one hour) before two fish of measured length were added. Number and weight of *N. diversicolor* remaining after 24 hours was recorded. Eight control experiments were run without fish, and the weight decrease of worms found here used to correct the calculated consumed weight. In the controls numbers of worms did not decrease.
In the subsequent analysis a quantitative relationship between the length of a fish and its stomach volume is needed. This relation was found in the following way: A portion of 15–20 *N. diversicolor* was weighed and one by one offered to a fish of measured length until it rejected 10 successive offers. At this point its stomach was considered full. (This could roughly be controlled by checking the degree to which the full stomach expanded the body wall). The residual worms were weighed and the amount of food eaten was calculated. 42 fish of different lengths were fed in this way. Each fish was tested at least twice, and the greatest value found was considered a relative measure of stomach volume (RSV).

B. Numerical methods

The experimental set up does not allow a direct graphical analysis of the results (i. e. to plot number of worms eaten during the 24 h period as a function of prey density) as temperature, fish size (L) and prey size (W) differ between experiments. Furthermore do prey density decrease in the course of the experiments (worms are eaten). The results are therefore treated by means of the following model.

A hypothetical relationship between prey density and feeding rate is outlined in Fig. 1. This hypothesis may be quantified (and therefore tested) in the following way: Assume that instantaneous feeding rate (F) is proportional to prey density (N) and hunger, and further that hunger is proportional to stomach volume (SV) minus stomach content (SC). Hence

$$F = a \cdot (SV - SC) \cdot N \qquad (1).$$

The stomach volume is not known, but the relative measure of it (RSV) is considered proportional to SV. Therefore

$$F = a \cdot (b \cdot RSV - SC) \cdot N \qquad (2),$$

where a and b are proportionality constants.

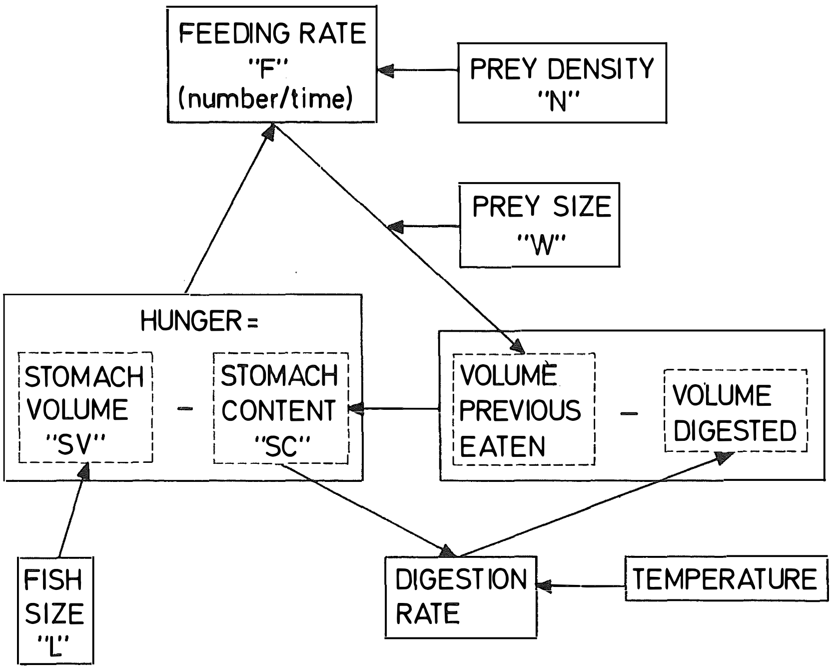

Figure 1

Hypothetical relationship between feeding rate and prey density, prey size, fish size and temperature

RSV is a (known) function of fish size. SC increases during the experiments and is equal to amount (i. e. volume or weight) of food previously eaten minus amount digested. The amount of food previously eaten is obviously a function of consumption rate (F) and average prey size (weight, W). The amount of food digested depends on digestion rate, which is a function of temperature and SC. In a series of laboratory measurements on juvenile flounder (KiØRBOE, 1978) I have found that a proper description of the relation between digestion rate and stomach content is

$$\text{digestion rate} = r_t \cdot SC \quad (3),$$

where r_t is a temperature dependent proportionality constant. This constant was estimated at 10 and 15 °C, i. e. near the extremes of temperature used in the present experiments ($\hat{r}_{10} = 0.14$ and $\hat{r}_{15} = 0.21\ h^{-1}$).

Equation (2) can now be formulated as

$$F = a \cdot (b \cdot RSV\ (L) - SC\ (F, W, r_t, SC)) \cdot N.$$

This is the basic expression which, by means of computer iteration, is expanded to take account of the increasing SC and decreasing N.

The principle of this expansion shall be summarized. The 24 h period is split up into a number of small time intervals. Beginning with SC = O and N equal to initial prey density, the number of worms eaten during the first time interval (f_1) can be calculated from eq. (2). Number of worms eaten during the next time interval (f_2)

can be calculated from eq. (2) using the new N (initial density corrected for worms eaten) and the new SC, which is the difference between amount previously eaten ($f_1 \cdot W$) and the amount digested. As temperature is known the amount digested can be calculated from eq. (3). In this way the calculations proceed during all the small time intervals, and the total number of worms eaten during the 24 h period is thus the sum of the f_i values.

By means of the least squares' method the expanded model can be fitted to the experimental results, and the constants a and b estimated.

Results

In Fig. 2 RSV values are plotted as a function of fish length on a log-log scale. Linear regression analysis is applied and a quantitative relationship is establihed. This relation, together with the previously mentioned measurements of digestion rate, is utilized in the model as lined out above.

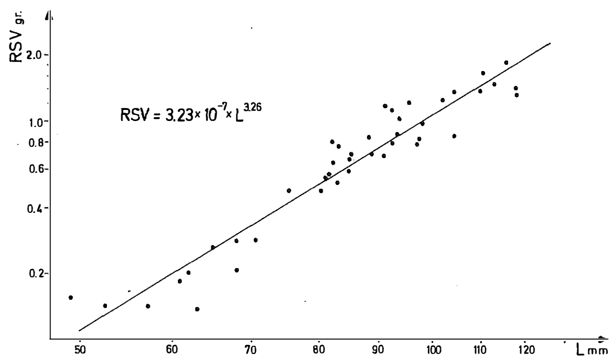

Figure 2

Relative measure of stomach volume (RSV) plottet as a function of length of fish (L) on a log-log scale

The model is fitted to the results of the feeding rate experiments, and the parameters are estimated as $\hat{a} = 0.32$ and $\hat{b} = 0.29$. In Fig. 3 the observed numbers of worms eaten in the experiments are compared to the numbers expected from the model. If the relation between feeding rate and prey density, fish size, prey size and temperature postulated in the model is correct, the points shall scatter around a straight line through (0,0) and with slope equal to one. In spite of minor systematic deviations and rather a great scatter, Fig. 3 shows that the model is in reasonable good accordance with the observations. I therefore accept the "null" (0,0) hypothesis formulated in the model.

The (experimental) reality of the causalities build into the model can also be controlled in an other way. In numerical terms the unexplained variation in Fig. 3 can be expressed as the sum of squared deviations (SSD), where the deviations are the differences between observed and expected numbers of worms eaten. Provided temperature, for example, acts as postulated in the model (or in a very similar way), SSD will increase if variation in temperature is neglected (i.e. if digestion rate is

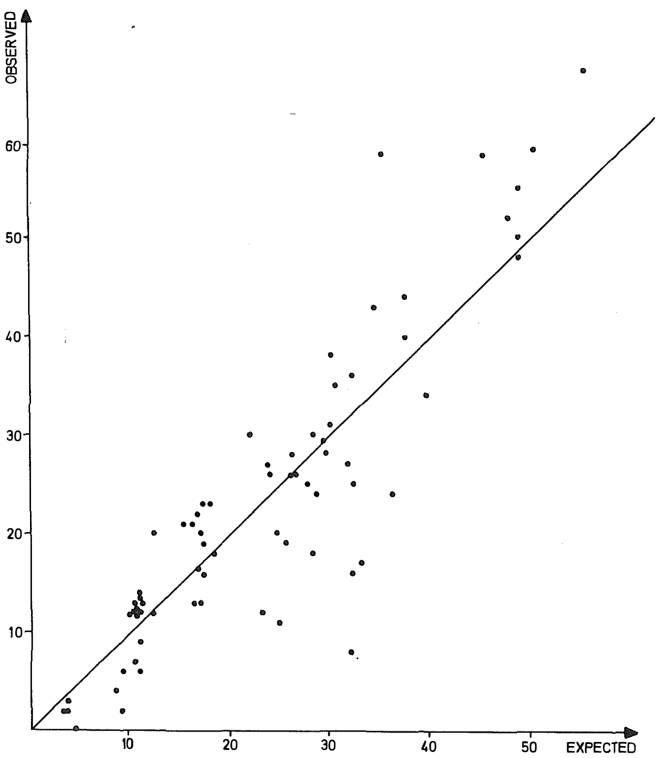

Figure 3

Observed numbers of worms eaten in the experiments plotted as a function of numbers predicted from the model. At perfect agreement between model and observations the points shall lie on the straight line through (0,0) with slope equal to 1.0

considered independent of temperature) when a and b are estimated and the expected values calculated. Likewise SSD will increase if variation in prey size or fish size is neglected, provided the postulated relatlonships are correct (or 'nearly' correct).

Table 1

Changes in SSD when variation in temperature, fish size or prey size is neglected. Variations in the components are expressed as standard deviations in % of their respective mean values (SDEV)

Component	Variation in component. SDEV %	SSD	Change in SSD %
(Intact model)	–	3 714	–
Variation in temperature neglected	11	4 236	+ 14
Variation in fish size neglected	23	4 396	+ 18
Variation in prey size neglected	43	7 110	+ 91

Table 1 gives the SSD value for the intact model and SSD values when variation in one of each of the three variables is neglected. The observed increases in SSD must be compared to the amount of neglected variation. Table 1 therefore also gives the variation in experimental temperature, fish size and prey size, all expressed as standard deviation in percent of their respective mean values. The results in Table 1 are consistent with the relationships postulated in the model.

On basis of the model, the relationship between feeding rate and prey density can now be calculated in situations with different temperature, fish size and prey size. Fig. 4 gives some examples.

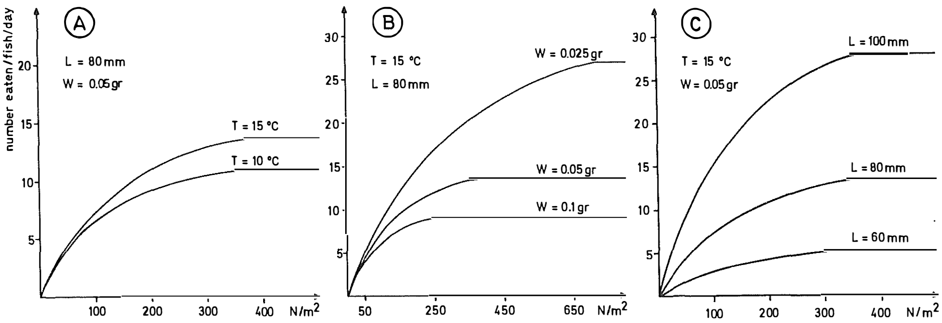

Figure 4

Calculated number of *Nereis* eaten / fish / day as a function of prey density at (A) various temperatures, T; (B) various prey sizes, W; and (C) various fish sizes

Discussion

The relation between feeding rate and prey density (i.e. the functional response) found for juvenile flounder predating on *N. diversicolor* is a HOLLING type II response (HOLLING, 1959): Feeding rate increases with increasing prey density but at a decellerating rate until a level is eventually reached. This shape of the functional response has been found for a varity of organisms (see reviews by MURDOCH and OATEN, 1975 and HASSEL et al., 1976) including fish (IVLEV, 1961 and WARE, 1972). In the present case this shape could be ascribed to variations in hunger, and hunger could be related to fish size, prey size and temperature.

Two predictions can be made from the model. They are not in themselves exiting, but they are controllable and may therefore illustrate the reliability of the present findings. First, it can be estimated that a flounder of e.g. 60 mm length at 15 °C has a daily maximum consumption equal to 31% of its own weight. MUUS (1967) predicted, on theoretical grounds, a maximum of about 30% for a flounder of about that size. Second, the maximum realized stomach volume estimated from the model ($\hat{b} \cdot RSV$) is a little less than that found for equally sized 0-group plaice (*Pleuronectes platessa*) by BREGNEBALLE (1961). Accordingly, GROOT (1971) found that the esophagus and stomach make up a lesser part of the alimentary channel in flounder compared to place.

Even though the model is consistent with the findings of other authors and provides a fairly good description of the present results, it is not directly applicable to natural conditions. Natural situations are more complex than the experimental situation, especially because there will almost always be more than one prey species available. Selective predation may therefore alter the relation between prey density and the rate of predation on a given species. However, one has to analyse and understand the simple situation before the more complex ones. The experimental situation must successively be made more complex (and realistic) and the results of these successive steps build into the model, until a more comprehensive understanding is achieved. Attempts are being made to include selective predation and growth of the predator into the model.

References

BREGNEBALLE, F.: Plaice and Flounder as Consumers of the Microscopic Bottom Fauna. Medd. Danm. Fiskr. Havunders. N.S. **3** (6), 133–182 (1961)

GROOT, S. J. De: On the Interrelationships Between Morphology of the Alimentary Tract, Food and Feeding Behaviour in Flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. **5**, 121–196 (1971)

HASSEL, M. P., J. H. LAWTON and J. R. BEDDINGTON: The Components of Arthropod Predation. I. The Prey Death Rate. J. Anim. Ecol. **45**, 135–164 (1976)

HOLLING, C. S.: The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. Can. Ent. **91**, 293–320 (1959)

IVLEV, V. S.: Experimental Ecology of the Feeding of Fishes. 302 pp. New Haven: Yale University Press (1961)

KIØRBOE, T.: Laboratory Measurements of Digestion Rate in 0-group Flounder (*Platichtys flesus*) at two temperatures. Ophelia **17** (1), 155-161 (1978)

MURDOCH, W. W. and A. OATEN: Predation and Population Stability. Adv. Ecol. Res. **9**, 1–131 (1975)

MUUS, B. J.: The Fauna of Danish Estuaries and Lagoons. 316 pp. København: Høst & Søn (1967)

WARE, D. M.: Predation by Rainbow Trout (*Salmo gairdneri*): the Influence of Hunger, Prey Density, and Prey Size. J. Fish. Res. Bd. Canada **29**, 1193–1201 (1972)