Flexibility of feeding traits and the distribution of marine benthic invertebrates, particularly bivalves.

First draft.

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General introduction

Recently I started as a post-doc at the Royal Netherlands Institute of Sea Research. My main task will be to study the flexibility of the feeding organs and the associated efficiency of feeding and absorption of nutrients by some marine invertebrates. Because of my experience from past projects, I prefer to work with bivalved molluscs (mussels, cockles, oysters etc). The main feeding organs of this group of species are the gills and palps. Contrasting the general idea, gills of bivalves are not very important for respiration but are mainly used to collect (food) particles from the water. Because bivalves cannot select edible particles immediately from the water they take in all the material that is present in the water, thus, edible as well as inedible particles. Before the particles are ingested, selection takes place to remove the unsuitable ones. During this process, edible particles are separated from the inedible items (e.g. silt and sand). The edible particles are ingested and the unsuitable particles are voided as pseudofaeces. The main organs that are involved in selection are the palps, however, depending on the type of gills, some species can already select on the surface of the gills. Both, gills and palps are thus very important in determining what the quality and quantity of ingested material will be.

Regulation of selection and rate of filtration are very important to optimise or maximise intake of nutrients. Some researchers think that bivalves are only able to regulate what comes in by adjusting the opening of the shell. In case of too many collected particles, which will cloth the gills, palps and mouth, the opening of the shell will be reduced and less water flows through the mantle cavity. Some researchers think that that is the only mechanism involved in regulating intake rate. Others believe that the rate at which the gills pump the water through the mantle cavity can be reduced as well, independent of the opening of the shell. There is a third group of researchers that believe that bivalves are much more flexible and can regulate or adjust many more traits, e.g. adjusting sizes of gills and palps.
It is already known for some time that the relative size of gills and palps depends on the turbidity of the water or the amount of particulate inorganic matter (e.g. sand and silt) (Theisen, 1982; Payne et al., 1995a; Payne et al., 1995b). It is thought that too many material in the water will cloth the feeding system. Moreover, the collected material is low-quality food. Therefore, large gills will collect too many particles and the palps need to do much sorting.

From an energetic point of view it can be disadvantageous to maintain large gills if they are not needed. Therefore, if there is a large amount of particulate matter of a low quality, the gills are relatively small and the palps large. It is exactly the other way around if there is relatively few particulate material of good quality. Thus, the sizes of gills and palps, often expressed as the gill to palp ratio depends on the quality and quantity of the particulate material.

Although Theisen (1982) already showed that the g/p ratio could change if, in this case, blue mussels were transplanted from one situation to another, the flexibility and functionality of the changes is not yet investigated. It can be argued that the observed change in the g/p ratio was only a consequence of differential rates of positive growth of the different organs. Flexibility involves, however, more. Under some circumstances negative growth of gills and palps can be expected. The only information concerning that aspect came from work we did a couple of years ago in Australia with two species of oysters. We found that, indeed, sizes (measured simply as weights) of gills and palps could decrease (Honkoop et al., 2003). Unfortunately, we were not able to link those changes to quality of quantity of particulate material or to describe the functionality of those changes.

Aims

The aim of the work I would like to do in the near future is to get more information about the generality of flexibility, i.e. can all bivalves adjust sizes of gills and palps and to what extend? To test this, a number of common bivalves from Wadden Sea and North Sea will be used and different groups will be subjected to different quality and quantity of food, administered continuously at a constant density. When the results are available and flexibility is confirmed (or rejected), the functional aspects of the flexibility will be examined. That means that energetic details are needed.

DEB

What can DEB do for me? In the past I would have estimated costs of growth, reproduction or maintenance using a static approach; the Scope for Growth (SfG) concept (Warren and Davis, 1967) based on the energy balance described by Winberg (Winberg, 1956). Now, for several reasons, I would like to use the DEB approach. First I would like to sketch the general lines.
One of the important things I need information about is the volume-related maintenance costs. If the maintenance costs are known, the next step will be to analyse the maximum filtration rate. The important aspect is to predict for which food situations the maintenance cost can not be paid for, i.e. the animals are not able to collect sufficient nutrients to meet the maintenance requirements. The final aim of this work will be to predict for which circumstances species cannot survive any longer, for example it might be possible that due to human activities the silt content of the water may increase (and thus the quality of the ingested material will decrease) which can cause local extinction of species that cannot adapt and meet the maintenance requirements.
Secondly, I would like to go into a bit more detail and discuss the problems I will meet.

Maintenance costs.

To determine volume specific maintenance costs, I reckon that has to be done according to fig. 3.14 (DEB-book). At different food concentrations growth curves will be fitted and ultimate lengths calculated. This will be used to calculate the maintenance rate constant. According Marr and Pirt (p. 94) this is the volume-specific maintenance rate (the factor of interest) divided by the volume specific costs of growth. Now comes my problem: how to measure the volume specific costs of growth?

Another problem is that those experiments are very time consuming. It can take years to determine maximum lengths.

Might there be an alternative? For example measuring rate of growth at different food conditions and extrapolating to the point of zero-growth? The problem I have with this approach is that at this point there still can be allocation of energy to reproduction and, therefore, maintenance costs are overestimated.

Maximum filtration rate.

This will be measured according to what is presented in Fig 3.6. The parameters of the hyperbolic functional response will be estimated for each size of gills (note that length of the shell, or volume, can not be used). This is necessary to test the hypothesis that the gill-area specific filtration rate is the same for each size of gills. When the maximum feeding rate is known, and information about quality and quantity is known, energy gains can be calculated.

Food quality and quantity.

Characterisation of food in the laboratory is relatively easy. Getting similar information from the field is very hard. Even in a constant environment (if this exists) quality and quantity of food is never constant.

The crudest and commonest way to characterise the quality of food is to measure the amount of organic material and assume that the quality of the organic material is constant and can be completely utilised by an individual. A more complex way is to chemically characterise the organic material. This is only relevant if it is known which compounds or which classes of compounds can be used as source of food. A question to be answered is what additional accuracy will be gained, or what additional part of the seasonal variability of the quality of food will be explained by a chemical characterisation of organic material.

A third possibility to characterise the quality of food is to let the animals decide what can be ingested. This can be done by measuring the absorption efficiency (AE). This is very common practise in the static energy budget approach and, therefore, I’m not sure whether this can be used at all; it is a kind of a line-fitting approach. The method generally used has been described by Conover (1966). In this method the relative amount of organic material in faeces is compared with the relative amount of organic material in food. Assuming that inorganic material is not ingested (which is probably not a valid assumption) it can be calculated how many organic material is ingested. If experimental animals are subjected to water containing natural seston at regular intervals, the AE can be calculated and be used as an estimate for the quality of food.

Final remarks

Formulation of the aim of this project was easy: for which food-conditions can the maintenance requirements of common North Sea and Wadden Sea bivalves not be met and what are the consequences for the populations?

The solution of this problem is, in my opinion, not easy at all. I hope that DEB can contribute considerably to a solution. The rationale to develop the theory of DEB and the mechanistic approach, contrasting the assumption of static energy budgets, are very attractive but, as you may have noticed, the practical problems of how to measure DEB parameters are, for me, still very hard. But, because the mechanistic approach it is worthwhile pursuing experiments within the DEB context. I'm really looking forward getting comment from readers.

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