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Help required

Croatia is going to participate in the Winter 1997/98 European Non-estuarine Coastal Waterfowl Survey (NEWS). Counting will br performed during December 1997 and January 1998. As Croatia has a relatively long coastline (5790 km) and a small number of educated and equipped counters, we would like to include collaborators from countries that have a lot of such counters. We kindly ask all interested educated (good knowledge of waterfowl, waders and other waterbirds and seabirds) and equipped (good field telescope and binoculars) counters to contact the following address for information: *Dragan Radovic, Institute of Ornithology, Ilirski trg 9/2, 10000 Zagreb, Croatia.*

Reviews

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Zwarts, Leo. 1997. *Waders and their estuarine food supply.* PhD thesis, Groningen. 386 pp.

After some years of our encountering Leo Zwarts' and co-workers' papers, and being both impressed and confused by the jungle of fact and theory in them, finally the mudflat story as Leo sees it has been assembled. The product is a very readable book-like PhD thesis that holds 16 papers by Zwarts and ten of his co-authors, for which Zwarts received the accolade 'cum laude'.

Even as a teenager, Leo was a fanatic bird watcher. Faced with the choice of what to study, he deliberately ignored his love of biology so as not to make a profession out of his hobby. But obviously, he could not stand the temptation for very long, for he graduated as a psychologist with the strangest curriculum ever. It had the smell of field biology all over it. After several years of field work on the Wadden Sea island Schiermonnikoog as an undergraduate student, he was offered his current position; an estuarine biologist after all. The research he has guided since that time is summarised in his thesis.

All of the articles appeared in scientific journals and none of the texts have been altered. The figures and tables were redone, so that they are all of exactly the same layout now. Most of them are very clear. Zwarts' brother, Jos, made the attractive wader drawings, and Jan van de Kam the very professional photographs of birds and benthos.

Every paper deals with several aspects of the many dynamic interactions between prey and predator species occurring in the estuarine soft-sediment Wadden Sea. A clever introduction explains how all of these highly detailed studies together form a logical story that enhances our understanding of predator prey interactions. The idea of facilitation ('fish helps bird') and predation windows are highlighted in a set of separate boxes within the introduction. The last part of the thesis is in Dutch. It is called 'summary', and it consists of something that is almost a literal translations of the introduction and the two boxes. The style of the

Dutch part is remarkably clear and seems to be written for a larger audience than the rest of the book. In fact, something like it was supposed to be published separately in Dutch. When the financing for that booklet was cancelled, Zwarts found the text to be very appropriate for a Dutch summary. Dutch natives; judge for yourselves.

The main question that Zwarts poses, is 'are wader populations limited by their estuarine food supplies'. He stresses that this question is too large to handle at once. The research he carried out during the last decade has therefore been split up into numerous smaller parts, hence the many seemingly diverse subjects of the papers. They stretch from comparative morphology of benthos to behavioural observations of waders. Upon asking him in person, though, he had to admit that, when starting out with his investigations, he did not have a clue what they would lead to.

They have not lead to answering the big question of carrying capacity, but all the more to understanding why life in and on top of the mud is so hard to predict. He summarises these insights in three statements. First, intake rate by waders cannot be described as a simple function of prey density. Waders are versatile and continuously making decisions in order to optimise their intake rate according to the situation they are faced with. Second, prey density itself does not accurately describe food supply. He introduces the term 'harvestable' to indicate that only part of the prey population is food because it has to be accessible, detectable, digestible, ingestible and profitable. Third, there is a lot of variation in behaviour of individual waders. Measuring only decisions of individual waders and the anti-predator behaviour of the prey does not suffice. Social interactions amongst waders play a major part in determining their intake rate.

The third statement remains largely undealt with in the present thesis. It is mentioned in several discussions, but there is no full chapter going into it. Zwarts commented personally, that quite a lot of time and effort has been spent on observing and experimenting with social interactions, but that the data have yet to be analysed.

Many of Zwarts' papers are long and contain lots of figures. Like no one else he is a master of getting editors to print graphs and even methods and results in 'discussion' sections. His own theory for why his papers are built up this way is: 'we just gathered too many data'. Indeed, at numerous sites in the thesis he refers to unpublished work of himself or a team member. Amongst the unpublished data are more than 1000 hours of observations of Curlews *Numenius arquata*, observations on interference between individual waders, the facilitation experiments mentioned before, and predation by Curlews on *Scrobicularia plana* siphons. Some additional work has just been printed in the form of a special issue of Ardea: 'Oystercatchers and their estuarine food supplies'. We can only hope that they will find the time to analyse and publish more of the wealth of data in stock.

Practising science is notorious for its lack of solving problems. When doing it right, one always ends up with more problems than there were to start with. Constructing a model that accurately captures estuaries like the Wadden Sea, and solves the carrying capacity problem, seems even more difficult now than apprehended before. Just counting prey and predators is not enough. To get a thorough understanding of the complicating factors, we refer to the thesis itself. As an appetiser we present here short summaries of each chapter.

In our opinion, this thesis offers a great deal of essential information for waderologists as well as soft sediment benthos adepts. Even those that are already familiar with the papers will find more in them than before, now that they are all together and accompanied by the enlightening introduction and the improved figures.

Separate papers reviewed.

Chapter 1: Seasonal variation in body weight of the bivalves Macoma balthica, Scrobicularia plana, Mya arenaria and Cerastoderma edula in the Dutch Wadden Sea.

Zwarts starts at the bottom of the problem of waders and their food supply by simply monitoring and recording the flesh weight of the most abundant bivalves in the Wadden Sea for eleven years. This work shows the high variability of body weights with seasons and years of the prey items the waders depend on. It shows that one *Macoma* is not the same in spring as it is the fall.

Chapter 2: How the food supply harvestable by waders in the Dutch Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates..

In this review-like paper, the information on the prey species is more comprehensive than the mere body weights of chapter 1. Seasonal and yearly variation in energy density, body weight, total biomass and depth distribution are outlined with a wader point of view. The results are discussed in terms of accesibility, detectability, ingestibility and digestibility, profitability and finally harvestability. 'Available + profitable = harvestable' is in short the point that is made. The information gathered predicted that birds take different prey under different conditions and perhaps move away to better sites when intake cannot be met with output. Both phenomena have been observed. The distribution over NW Europe based on the prey availability is not fully satisfactory due to lack of detailed information on other regions than the Wadden Sea.

Chapter 3: Burying depth of the benthic bivalve Scrobicularia plana (Da Costa) in relation to siphon cropping.

Burying depth of prey is one of the factors determining harvestability. Deeper buried specimens can be undetectable, inaccessible and/or unprofitable. The maximum of burying depth is constrained, however, e.g. in bivalves by the length of the siphon. Therefore it was hypothesised that the choice of burying depth, which shows a lot of variation within many species of benthos, is the result of a trade-off between predator avoidance and feeding. This paper shows for *Scrobicularia plana* not only that, but also that siphon cropping (by e.g. shrimp and young flatfish) changes the outcome of this trade-off, thus increasing food supply for waders. This kind of indirect positive feedback has recently been termed facilitation (e.g. Strong, 1997) ; the common phenomenon known from botany.

Chapter 4: Siphon size and burying depth in deposit- and suspension feeding benthic bivalves.

Whenever benthic bivalves succeed in attaining a safe depth refuge, they do not increase it any more. They only come up if they are in a bad condition and are attacked heavily by siphon croppers. This, however, could not and can not explain all of the observed seasonal and geographical differences. Moreover, controlled experiments are necessary to prove that the correlations presented here are causal. A shortcoming of this paper is that the authors do not consider fitness consequences, e.g., it is implicitly assumed that larger is always better. But clams may want to avoid growing into any predation window (Oystercatchers *Haematopus ostralegus*?) as much as growing out of some (Knots *Calidris canutus*?).

Chapter 5: Feeding radius, burying depth and siphon size of Macoma balthica and Scrobicularia plana.

Differences in choice of burying depth in relation to size, siphon weight and body weight are found for these two species. The linear relationship between shell size and feeding radius is not explained functionally, but only with allometric regressions. The paper ends with the suggestion that perhaps there is a general rule for bivalve siphons to weigh 0.6% of the body weight per cm. This is stated without any consideration of what could cause such a rule.

Chapter 6: The macrobenthos fraction accessible to waders often represents marginal prey.

When taking burying depth into account, the body conditions of the shallow living animals is found to be worse than that of the deeper ones. This means that the prey taken by waders has a lower body condition than the population mean. The fittest seem actually to be the fittest here, as in the common misinterpretation of Darwin's catchy phrase.

Chapter 7: Does an optimally foraging Oystercatcher obey the functional response?

Burying decreased handling time, and thus profitability. As expected, at high intake rates, deep prey were ignored. Unexpectedly, the Oystercatcher's intake rate exceeded the predicted one at high prey densities, probably because it selected those prey with slightly opened valves. Explanations not considered are other distinctions in profitability (prey differ in energy yield not just due to size, or handling time goes down, which suggests learning). Using a single predator controls for individual differences, but conflicts with generality.

Chapter 8: Prey size selection and intake rate.

Prey size selection of Oystercatchers is predicted using searching behaviour and profitability of prey types. Field observations confirm predictions. This is generally true for other studies cited as well, except that the size classes just above the predicted lower threshold are underrepresented in the diet. Data on 197 studies on intake rate are included. A plea for more state- and risk-dependent foraging models (in contrast to rate maximisation models) ends the chapter, but this conflicts to some extent with the observed correlation between predictions and field observations based on rate maximisation.

Chapter 9: Causes of variation in prey profitability and its consequences for the intake rate of Oystercatchers Haematopus ostralegus.

Reviewing about 70 studies of Oystercatcher feeding behaviour, it becomes clear that predicting diet choice on the basis of prey characteristics is possible, but sometimes difficult. Handling time is influenced by prey size, burying depth, opening technique, proportion of prey taken, armouring of prey, and possibly more. Experience and interference (surprisingly no chapter treats this extensively) may further complicate predictions. Oystercatchers are mainly limited by their food supplies in harsh winters, when unfortunately little field work is done!

Chapter 10: Why Oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period.

Digestion is a constraining factor in Oystercatcher ecology. As processing rates are usually lower than intake rates, digestive pauses are taken. In making the best of a bad job, Oystercatcher stuff themselves before going to the high tide roost! This physiological constraint thus has an impact on distribution of predation pressure in time and space, and therefore on the prey. To what extent maximisation models and their predictions are affected, could be subject of future research.

Chapter 11: Predicting seasonal and annual fluctuations in the local exploitation of different prey by Oystercatchers Haematopus ostralegus: a ten-year study in the Wadden Sea.

Even though Zwarts himself states that predictions concerning waders and food are difficult, they are not by any means impossible. Diet composition of Oystercatchers at the study site, both between and within years, is accurately predicted. Oystercatcher diet and numbers responded strongly to harvestable food levels. This demonstrates their flexibility and mobility as foragers on the one hand, but their dependence on variation in prey types and foraging areas on the other. This renders them potentially a valuable indicator of disturbance of mudflat ecology. However, food shortage does not seem to be a problem most of the time. But in cold winters with ice cover and low levels of harvestable food, mortality increases to over 30%. This is when human impact on prey, like shellfisheries, hit them hardest.

Chapter 12: Why Knot Calidris canutus take medium-sized Macoma balthica when six prey species are available.

Reasons for Knots ignoring particular classes of alternative prey are discussed. The 'random touch model' used here can now be tested again the 'remote sense' model (Piersma et al., 1995). This might well decrease the difference between calculated and observed diet. Many studies would benefit from the interesting treatment of 'wrong decision making': what difference does it all really make to our study subject, and can we expect it to adjust its decisions? Unfortunately no data are presented (or existing?) on maximum digestion rates as an apparently crucial constraining factor, and only a comparison with Whimbrel *Numenius phaeopus* and Oystercatcher was possible.

Chapter 13: Annual and seasonal variation in the food supply harvestable by Knot Calidris canutus staging in the Wadden Sea in late summer.

Knots staging in the Wadden Sea, preparing for migration south, have a problem with unpredictable variability of food levels, due to correlated recruitment over years, sites and species. However, Knots seem to be able to find and return to sites which yield a high intake rate. Knots did not measurably influence the densities of prey. The authors' conclusion can therefore be extended as follows: for Knots preparing for migration to Africa, food is in some years limiting on a small scale (of kilometres), but not in most (if not all) years on the scale of the entire Wadden Sea.

Chapter 14: Seasonal trends in burrow depth and tidal variation in surface feeding of Nereis diversicolor.

and

Chapter 15: Versatility of male Curlews (Numenius arquata) preying upon Nereis diversicolor: deploying contrasting capture mode dependent on prey availability.

Feeding mode in Curlews varies with prey availability: walking slowly when searching for burrow entrances of deep living worms, walking more quickly when searching for surface feeding worms. Individuals may use both modes, and continuously monitor their environment while foraging. In an inventive experiment, Ragworm accessibility was raised by spreading out minced meat, which attracts the worms. Feeding behaviour and intake rate of the Curlew changed according to expectations.

Chapter 16: How Oystercatchers and Curlews successively deplete clams.

Resource partitioning between Oystercatcher and Curlew is treated by predicting optimal size selection, based on profitability. Unfortunately the effect of depth on handling time was insufficiently included in the experimental measurements. As larger prey live deeper, their profitability has been overestimated, and predicted optimal prey size will be too large Generalisation from the single female Curlew '20 Yellow' towards the average Curlew interferes with Zwarts' own comment on individual differences. It also fails to explain that 'the majority of male Curlews never take clams, nor do some females'. This type of resource partitioning must certainly be important as well!

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