Beware of these errors when measuring intake rates in waders

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We describe four errors occasionally made in calculating the gross intake rate of waders (biomass of prey consumed per unit time). These are: (i) measuring feeding rate (number of prey consumed per unit time) from inter-catch intervals (ICIs), which can substantially over-estimate feeding rate, especially when ICIs are variable; (ii) measuring prey size from fragments of opened prey left by the birds in the feeding area, which can lead to substantial over-estimates of prey size; (iii) using linear expressions for the relationship between prey ash-free dry mass (AFDM) and length when a higher-order polynomial expression would provide a better description of the relationship – this can lead to large errors in the estimation of mean prey mass, and (iv) measuring the mean AFDM of consumed prey from the mean length of all those eaten rather than from a frequency histogram based on small size classes – which can also lead to large errors in the estimation of mean prey mass. Errors introduced in these ways, which can sometimes be very large, are illustrated with examples from Oystercatchers *Haematopus ostralegus* eating mussels *Mytilus edulis*.

INTRODUCTION

As considerable effort goes into measuring shorebird gross intake rates (biomass or energy consumed per unit time), it is worth drawing attention to four errors that can arise, despite the fact that intake rates have been measured commonly for over forty years. These errors can sometimes lead to large imprecision in estimates of intake rate because they produce biased measurements in one or both of its two components: feeding rate (number of prey consumed per unit time) and mean ash-free dry mass (AFDM) of consumed prey. We illustrate the magnitude of such errors using examples taken from Eurasian Oystercatchers *Haematopus ostralegus* eating the edible mussel *Mytilus edulis* on the Exe estuary, SW England.

CALCULATING FEEDING RATE FROM INTER-CATCH INTERVALS

Feeding rate is defined as the number of prey consumed per unit time of foraging. It is usually measured directly by selecting a bird at random and recording over a fixed interval (e.g. 30 seconds, 1 minute or 5 minutes) the number of prey swallowed. However, sometimes people calculate feeding rate indirectly by measuring the inter-catch interval (ICI, also known as search-handling time (Stephens & Krebs 1986)) from the end of the swallowing of one prey to the end of the swallowing of the next. The feeding rate (FR) over the fixed interval (FI) is then calculated as:

$$FR = FI/ICI \qquad \text{eqn. 1}$$

One source of error when measuring feeding rate from ICIs is that the bird may go out of view before an ICI has been completed. Since this is more likely to happen with long ICIs than with short ones, there is a danger that the ICIs measured will be biased towards shorter ones, so that feeding rate will be over-estimated. However, corrections can be made for this sort of error using statistics for censored data (Haccou & Meelis 1994).

There is also a fundamental problem with using ICIs to measure feeding rate. Whenever prey are not consumed at exactly equal intervals (i.e. in most circumstances), feeding rate calculated from ICIs is bound to be greater than the true feeding rate as calculated from fixed-length intervals. The more variable the ICI, the greater will be the discrepancy.

Feeding rate might be calculated from ICIs in two different ways. First, equation 1 might be used to calculate the feeding rate equivalent to each individual ICI, and the mean feeding rate calculated from all the individual values: this is the "individual ICI method". The other way is to calculate the mean ICI first, and then to use it in equation 1 to calculate the average feeding rate; this is the "mean ICI method". The individual ICI method results in the most substantial error, but the mean ICI method can also give rise to inaccuracy, especially when sample sizes are small.

A mathematical demonstration of the way in which the errors arise is set out in Appendix 1. We also present the following examples and accompanying diagram (Fig. 1 (A)–(C)):

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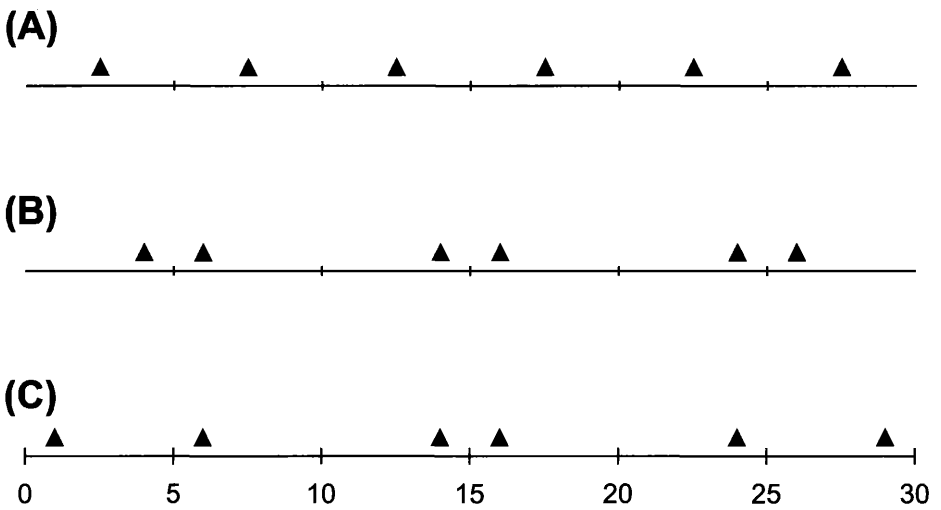

Fig. 1. Diagram of the prey captures (triangles) made by a bird foraging over five-minute intervals. In **(A)**, prey are caught at regular time intervals while in **(B)** and **(C)** they are caught at irregular intervals.

(A) The horizontal line represents the passage of time. It is subdivided into six 300-second intervals; one prey is consumed at the mid-point of each interval. We assume that prey are consumed instantaneously. The mean feeding rate is 1 prey per 300 seconds. There are five ICIs, each of 300 seconds. From eqn. 1, the feeding rate measured over 300 seconds is therefore 300/300; i.e. 1 prey per 300 seconds. As prey captures are distributed at regular intervals over time, the feeding rate is 1 prey per 300 seconds whether the mean ICI method (i.e. (5*300)/(5*300)) or the individual ICI method (i.e. (1+1+1+1+1)/5) is used.

(B) The same calculation is now repeated but with the prey captures distributed in a different pattern along the line. In Fig. 1(B), the prey captures occur at 4, 6, 14, 16, 24 and 26 minutes. Based on five-minute intervals, the feeding rate is 1 prey per 300 seconds. However, using the mean ICI method, the feeding rate is 1.136 per 300 seconds while the individual ICI method gives a feeding rate of 1.75 per 300 seconds.

(C) In the third example in Fig. 1(C), prey captures occur in another pattern, being taken at 1, 6, 14, 16, 24 and 29 minutes. Now the mean ICI method gives a feeding rate of 0.94 per 300 seconds while the individual ICI method gives a feeding rate of 1.15 per 300 seconds.

Examples (B) and (C) give a spread of situations either side of the regular one. Using the mean ICI method, the average feeding rate in (B) and (C) together is (1.136+0.94)/2 = 1.038 per 300 seconds. This is close to the true rate of 1, but is nonetheless an over-estimate. The individual ICI method, however, gives an average feeding rate of (1.75+1.15)/2 = 1.45 per 300 seconds, which is a very large over-estimate of the true value.

Table 1 gives a real-world example from Oystercatchers eating mussels in which the two methods of calculating feeding rate from ICIs and measuring it directly over 300 second periods are compared. The data were collected during the day and at night on the Exe estuary during two "winters" running from September to March (Sitters 2000). The individual ICI method gives estimates of feeding rate that are 40–50% higher than those recorded directly over 300 second periods. The mean ICI method over-estimates feeding rate by 10–20%. Clearly, both methods lead to substantial over-estimates of feeding rate. This is so, despite the fact that the data were obtained from the same video sequences.

The mean ICI method can only give an estimate of the true rate and this estimate is only reliable when, in relation to the variance, the sample size is large (Appendix 1). Moreover the sample size may have to be very large indeed. Fig. 2 shows the difference between FR measured directly over 300 second periods and the values obtained from the same birds using each of the two ICI methods. Each datum was obtained either at night or during the day during one month from September to March inclusive; there was no statistically significant difference between the night-time and day-time data. The number of ICIs measured during the day or during the night in a single month varied between 3 and 75. Fig. 2 shows that, with both ICI methods, the amount by

Table 1. The number of mussels consumed per 5 minutes (Feeding rate; FR) of Oystercatchers eating mussels by ventral hammering on the Exe estuary during the day and night as measured (i) by the number consumed over *N* five-minute periods and (ii) from inter-catch intervals (ICI), using either the individual or mean methods: see text for further explanation of these two methods. A standard error cannot be calculated for the mean ICI method. The data are from Sitters (2000).

	Number consumed per 5 min			FR from individual ICIs			FR from mean ICIs	
	Mean	*N*	S.E.	Mean	*N*	S.E.	Mean	*N*
Day	0.941	136	0.057	1.420	88	0.077	1.111	88
Night	0.818	429	0.031	1.138	315	0.033	0.896	315

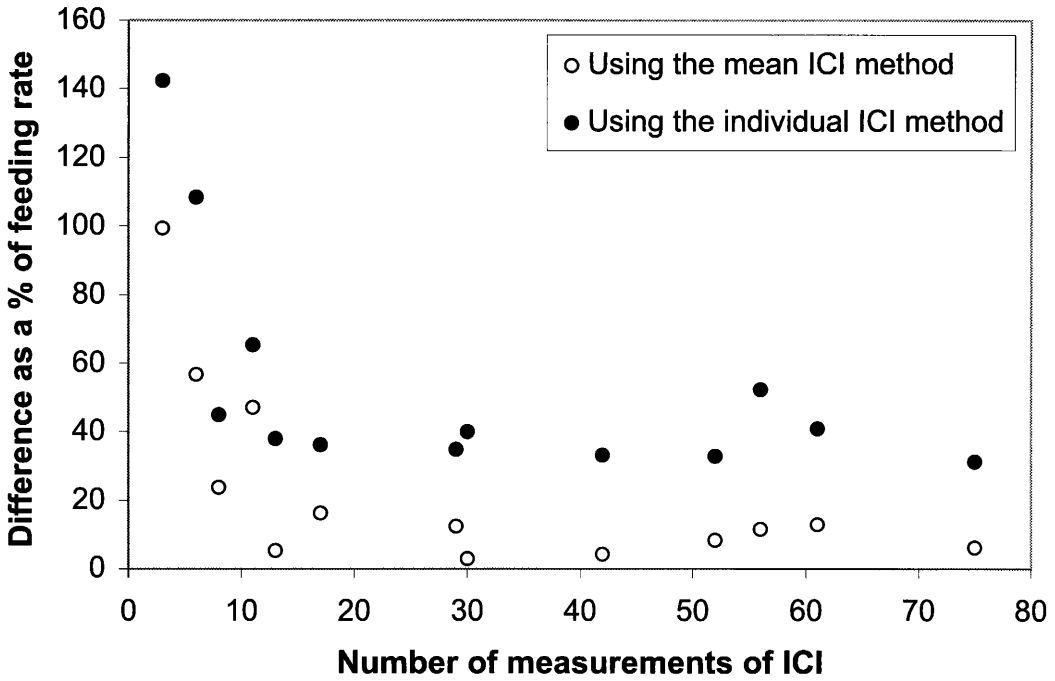

Fig. 2. The difference between measuring the feeding rate directly as the number of prey consumed per unit time (FR_{direct}) and calculating it from inter-catch intervals (FR_{ICI}) using either the mean ICI method (open symbol) or individual ICI method (closed symbol): see text for further explanation of these two methods. The difference between the values from the two methods is expressed as a percentage of the directly measured feeding rate: i.e. difference = $((FR_{ICI} - FR_{direct}) \times 100)/FR_{direct}$. The data are from Oystercatchers eating mussels by ventral hammering on the Exe estuary, with the feeding rate measured as the number of mussels consumed per 300 s (Sitters 2000). Note that all the values are positive. Therefore both methods always over-estimated the 'true' feeding rate obtained by measuring the number of mussels consumed per 5 minutes directly.

which the ICI method over-estimated the directly measured feeding rate fell sharply as the sample size for ICIs increased to about 30. However, there was little evidence that, with still larger sample sizes, the inaccuracy of even the mean ICI method improved by much. Indeed, even with a sample size of 315, the mean ICI still over-estimated the directly observed feeding rate by 10% (Table 1).

We conclude that using either of the ICI method can substantially over-estimate feeding rate, especially when the ICIs are variable – which is usually the case. The over-estimations will be much higher when the individual ICI method is used to calculate feeding rate than when the mean ICI method is used. But, even with the mean ICI method and very large sample sizes, the over-estimation can be large. On the assumption that observations are made of a representative sample of birds, the most accurate way to measure feeding rate is to watch birds for a fixed period and to record the number of prey consumed during that period. This is the only straightforward, error-free method.

MEASURING THE SIZE OF CONSUMED PREY BY COLLECTING OPENED SHELLS

The sizes of consumed prey can sometimes be obtained from the remains of the prey left on the feeding area by the birds. A well-known example is Oystercatchers eating large molluscs, such as mussels or cockles *Cerastoderma edule*. The danger with this method is that the remains of large prey are more likely to be seen and found by the research worker than are those of the smaller ones. As shown by Cayford (1988) for Oystercatchers eating mussels, the remains of large prey may be 2–3 times more likely to be found than those of small prey.

This bias towards finding large prey can lead to very substantial errors in the estimation of the intake rate. It causes the mean AFDM of consumed prey to be considerably over-estimated because of the exponential relationship between the AFDM of a prey and its length (see below).

An example of the kind of misleading results that can be obtained from shell collections is given in Fig. 3. Oystercatchers on mussel bed 4 of the Exe estuary in Nagarajan's (2000) study took smaller mussels as the winter progressed. This was ascertained by watching the birds and estimating mussel size as a proportion of bill length and correcting for individual observer bias, as discussed in Goss-Custard *et al.* (1987). However, Nagarajan also collected mussels opened by the birds for purposes other than measuring the size of consumed prey (Nagarajan *et al.* 2002). This comparison showed that, whereas the visual observations showed that Oystercatchers actually took progressively smaller mussels towards mid-winter and then took larger ones again towards spring, the mean length of the opened shells of mussels opened by the birds and collected from the feeding area did not change because only the larger ones were being found. In mid-winter, the two estimates of the mean lengths of the mussels taken by Oystercatchers differed by as much as 10 mm. This would make an enormous difference to the estimate of the mean AFDM of the mussels consumed and, therefore, the intake rate at that time of year.

The conclusion is that one should be very careful that estimates of prey length are not biased towards either large or small prey. In the case of Oystercatchers eating mussels, this will usually mean that prey lengths are probably best determined by observation. This is more difficult with Oystercatchers eating edible cockles *Cerastoderma edule* because

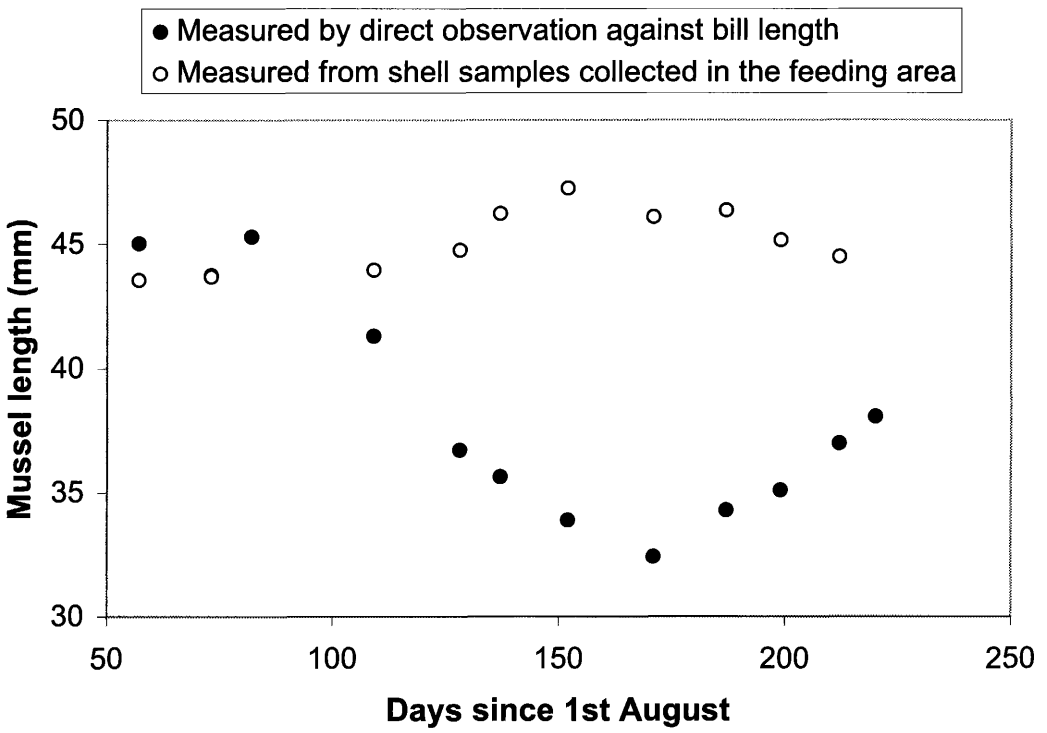

Fig. 3. The mean lengths of the mussels taken by Oystercatchers as measured by (a) direct visual observation against bird bill length (solid symbols) and (b) from samples of shells opened by Oystercatchers and collected from the feeding area (open symbols).

of the generally narrower range in size and round shape of this shellfish, so that prey size may usually have to be estimated from collections of opened prey. But if this is done, every effort should be taken to avoid bias towards large cockles. The best solution is probably to measure the bias experimentally by one person putting out cockles of the appropriate range of sizes and a second person to attempt to retrieve them, as was done by Cayford (1988) for mussel-eating birds.

Biases can also occur when measuring the lengths of other kinds of prey taken by other wader species, as has been thoroughly investigated recently by Lee & Hockey (2001). Every effort should be made to carry out calibration experiments so that any biases in direct field observation can be detected and corrected. Good examples of the calibration techniques available are given by Zwarts & Esselink (1989) and Zwarts & Dirksen (1990).

NON-LINEAR LENGTH–AFDM RELATIONSHIPS

The usual method for calculating the AFDM of a prey of a given length is to fit an allometric function to the relationship between $\log_e$AFDM and $\log_e$Length: an example from mussels of the Exe is given in Fig. 4(A). Usually, a linear regression is fitted to this relationship and the AFDM of any given prey length calculated from the antilogarithm of the predicted $\log_e$AFDM.

There are two cautionary points that need to be made here. First, the log:log relationship may not be linear and a higher-order polynomial may provide a significantly better fit, as it does to the data in Fig. 4(A). The regression was not forced through the origin as this could have distorted the predicted relationship over the range of mussel lengths, 20–70 mm, in which we were interested, these being the ones most consumed by Oystercatchers on the Exe estuary (Cayford & Goss-Custard 1990). Fig. 4(B) shows that using the quadratic expression, when both axes have been $\log_e$ transformed, causes the predicted *untransformed* relationship between AFDM and mussel length to be closer to linearity over the range (30–65 mm) than does a linear expression of $\log_e$AFDM against $\log_e$Length.

Assuming a linear relationship between $\log_e$AFDM and $\log_e$Length when, in fact, a quadratic expression would be more appropriate, can lead to substantial errors. This can be illustrated by comparing the predicted back-transformed AFDMs from linear and quadratic log:log expressions shown in Fig. 4B. Within the size range most consumed by Oystercatchers (40–50 mm), the quadratic expression predicts values of AFDM that are as much as 20–30% higher than those predicted by the linear expression. The conclusion is that, when deriving an equation with which to predict the AFDM of prey of given lengths, one should always test whether higher-order polynomials provide a better fit to the data than a linear expression.

The second cautionary point is that, when using logs, the back-transformation procedure using the antilogarithm may distort the prediction because the effect that taking the logarithm of AFDM can have on the sample variance. Although, in our experience, the effect is usually rather small compared with the other errors discussed in this paper, this may not always be the case. The Error Mean Square back-transformation correction should therefore be made to each predicted AFDM, as follows: First, one calculates the quantity Z, the predicted and uncorrected $\log_e$AFDM of a prey of a given length:

$$Z = a + b(\log_e L) + c((\log_e L)^2) \qquad \text{eqn. 2}$$

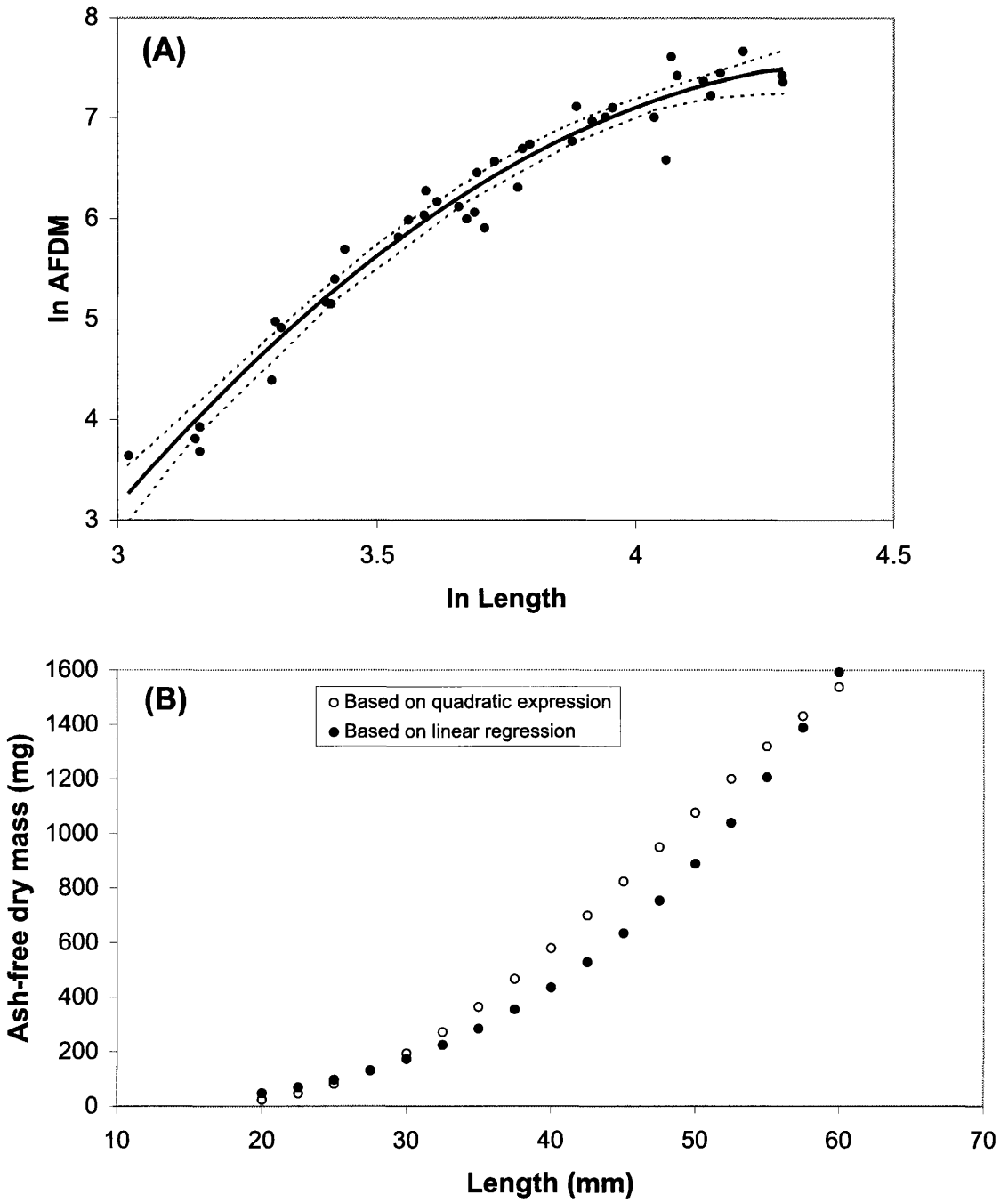

Fig. 4 (A). The relationship between the $\log_e$ ash-free dry mass (AFDM in mg) of mussels on the Exe estuary and their $\log_e$Length (mm) described by the quadratic function: $Y = -33.03 + 18.13X - 2.02X^2$; $R^2 = 96.1\%$. The fitted regression and 95% confidence limits are shown. **(B)** The predicted relationship of AFDM against mussel length from the quadratic expression above (open circles) and the linear regression ($Y = -5.73 + 3.20X$) fitted to the same data.

where L = length (mm), and ***a***, ***b*** and ***c*** are the coefficients of the quadratic equation of $\log_e$AFDM against $\log_e$Length. The corrected $AFDM_L$ of an animal of length L is then:

$$AFDM_L = exp(Z + S^2/2) \qquad \text{eqn. 3}$$

where S^2 = Error Mean Square (sometimes called the Residual Mean Square) from the ANOVA table of the regression equation. In this example, the quadratic equation was the most appropriate one to apply to the data but the same procedure should be applied to linear regressions or even to higher-order expressions than the quadratic. Further details of this correction when back-transforming log transformations can be found in Newman (1993).

Before leaving AFDM, it is worth re-stating that AFDM has to be measured with fresh animals. Numerous papers published over the last 30 years have shown that severe loss of mass can often occur in macrobenthos preserved in either formalin or alcohol (Lasker 1966, Howmiller 1972, Lappalainen & Kangas 1975, Schram *et al.* 1981, Mills *et al.* 1982, Williams & Robins 1982, Leuven *et al.* 1985). It is therefore very important that fresh or deep-frozen animals are used. If the

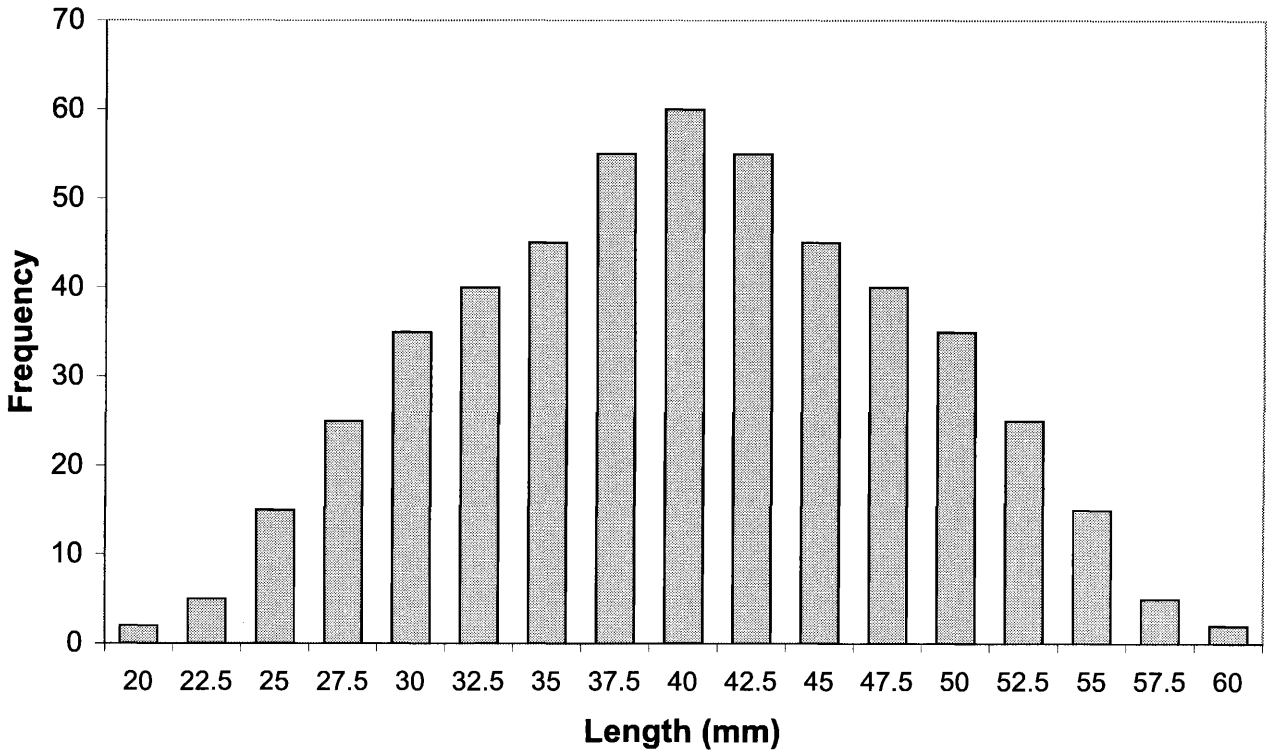

Fig. 5. The frequency distribution of prey sizes used to illustrate the effect of using the mean length to calculate the mean AFDM of the prey consumed by the birds.

animals are deep-frozen before their masses are determined, care should be taken not to lose fluid that might contain mass when the samples are being put into crucibles (Moreira & Pugh Thomas 1988); for example, the animals should be defrosted and/or opened in the crucible used for burning. Molluscs can often be frozen in groups of several animals and their flesh extracted later without loss. But this is very difficult with soft-bodied animals, such as polychaetes. These animals defrost very quickly and turn into a formless mess, which is difficult to deal with. The only way we have found to solve this problem is to deep-freeze each worm separately in its own little polythene bag. A bag is much better than a plastic bottle because the air can be expelled so that less space is used in the deep freezer. In addition, worms can freeze-dry in a jar because of the large volume of air relative to the volume of the worm. The worm can then become stuck to the bottom of the pot in their own escaped juices and difficult to extract from the pot. In contrast, all the contents of a bag can be squeezed out while the animal is still completely or partly frozen and put safely into the crucible.

Wherever possible, of course, the AFDM of molluscs should be obtained from flesh extracted from the shells because any loss from the shell on ignition can cause the ash-free mass to be over-estimated. Below 550°C, the periostracum will burn off, along with any protein in the shell. As the temperature rises above 550°C, there is first a loss of water of crystallisation from $CaCO_3$ followed at even higher temperatures by the breakdown of $CaCO_3$ to CaO and CO_2.

ESTIMATING MEAN ASH-FREE DRY MASS FROM THE MEAN LENGTH OF PREY

Occasionally the mean AFDM of the prey consumed by birds is calculated directly from the mean length of the consumed prey. That is, the mean length is calculated first and then the predicted AFDM for that length is obtained by substitution in an allometric function of AFDM on length. This can give rise to quite substantial errors in estimating mean prey mass on those occasions when the untransformed relationship between AFDM and length is non-linear. In these circumstances, a frequency histogram of prey lengths should be drawn with prey length divided into a suitable number (k) of prey size categories and the AFDM at the mid-point of each size category obtained from the AFDM-length function. The mean AFDM of the prey is then given by the expression:

$$\sum_{i=1}^{k} (F_i A_i)/N \qquad \text{eqn. 4}$$

where

F_i is the frequency of the i-th prey size category,
A_i is the AFDM of an animal at the mid-point of the i-th prey size category and
$N = \sum F_i$ is the total number of animals summed across all prey size categories.

To illustrate the effect on the estimate of the mean prey AFDM, we use the relationship $\log_e$AFDM (mg) = –5.73 + 3.20$\log_e$Length (mm), which is the relationship shown by closed symbols in Fig. 4(B). Using the approximately normally distributed frequency histogram of prey size categories shown in Fig. 5, the mean AFDM was calculated (i) using equation 4 and (ii) from the mean length of all the animals, which is 40 mm. Equation 4 gives a mean AFDM of 499 mg whereas the AFDM of an animal of mean length

is 435 mg, or 13% less. This under-estimate arises because of the non-linear relationship between untransformed AFDM (mg) and untransformed length (mm) shown in Fig. 4(B). Larger and smaller differences between the two methods of calculating the mean AFDM across a range of prey sizes would be produced with different shapes of histogram and different slopes of $\log_e$AFDM against $\log_e$Length.

The conclusion is that, when calculating the mean AFDM of the average-sized prey, one should base the calculations on a size frequency histogram, using equation 4, when the untransformed relationship of AFDM against length is non-linear. Otherwise, substantial errors may arise.

DISCUSSION

Ours is by no means an exhaustive list of possible errors that can be made when intake rates are being estimated. Others include unrepresentative sampling of birds as may arise, for example, by continually re-watching the same unknown unmarked individual. This is a problem that can really only be solved by working on individually marked birds, which is not always possible.

The four examples we have chosen are, however, errors that are made quite regularly and can easily be avoided or corrected. They can be important, as the examples given from Oystercatchers illustrate. Three of the errors ((ii)–(iv)) can also be made when estimating prey biomass density in the feeding area or the mean AFDM of the prey available to the birds.

Studies on intake rate and prey biomass are so time-consuming that it is worthwhile making sure that the least possible number of mistakes are made in making our estimates, and we hope that this article may contribute to our more frequently achieving this objective.

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REFERENCES

Cayford, J.T. 1988. A field test of the accuracy of estimating prey size-selection in Oystercatchers from recovered mussel shells. *Wader Study Group Bull.* 54: 29–32.

Cayford, J.T. & Goss-Custard, J.D. 1990. Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*: an optimality approach. *Animal Behaviour* 40: 609–624.

Goss-Custard, J.D., Cayford, J.T., Boates, J.S. & Durell, S.E.A. Le V. dit. 1987. Field tests of the accuracy of measuring prey size against bill length in oystercatchers, *Haematopus ostralegus*, eating mussels, *Mytilus edulis*. *Animal Behaviour* 35: 1078–1083.

Haccou, P. & Meelis, E. 1994. *Statistical Analysis of behavioural data: an approach based on time-structured models*. Oxford University Press, Oxford.

Howmiller, R.P. 1972. Effects of preservatives on weights of some common macrobenthic invertebrates. *Transactions of the American Fisheries Society* 4: 743–746.

Kendall, M.G. & Stuart, A. 1977. *The advanced theory of statistics*, Fourth edition, Vol 1. Griffin, London.

Lappalainen, A. & Kangas, P. 1975. Littoral benthos of the northern Baltic Sea II. Interrelationships of wet, dry and ash-free dry weights of macrofauna in the Tvarminne area. *International Revue Gesamten Hydrobiologia* 60: 297–312.

Lasker, R. 1966. Feeding, growth, respiration, and carbon utilization of a euphausid crustacean. *Journal of the Fisheries Research Board of Canada* 23: 1291–1317.

Lee, N.M. & Hockey, P.A.R. 2001. Biases in the field estimation of shorebird prey sizes. *Journal of Field Ornithology* 72: 49–61.

Leuven, R.S.E.W., Brock, T.C.M. & van Druten, H.A.M. 1985. Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macro-invertebrates. *Hydrobiologia* 127: 151–159.

Mills, E.L., Pittman, K. & Munroe, B. 1982. Effect of preservation on the weight of marine benthic invertebrates. *Canadian Journal of Fisheries and Aquatic Science* 39: 221–224.

Moreira, H.M. & Pugh Thomas, M. 1988. The effect of deep freeze storage and subsequent thawing on *Macoma balthica* and its implication for energy related ecological studies. *Journal of Environmental Biology* 9: 417–428.

Nagarajan, R. 2000. The foraging behaviour of oystercatcher (*Haematopus ostralegus*) in relation to food depletion during winter on the river Exe estuary, England. Unpubl. PhD thesis, University of Exeter.

Nagarajan, R., Goss-Custard, J.D. & Lea, S.E.G. 2002. Oystercatchers use colour preference to achieve longer term optimality. *Proceedings Royal Society* B, 269: 523–528.

Newman, M.C. 1993. Regression analysis of log transformed data: Statistical bias and its correction. *Environmental Toxicology and Chemistry* 12: 1129–1131.

Schram, M.D., Ploskey, G.R. & Schmitz, E.H. 1981. Dry weight loss in *Ceriodaphnia lacustris* (Crustacea, Cladocera) following formalin preservation. *Transactions of the American Microscopical Society* 100: 326–329.

Sitters, H.P. 2000. The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding Oystercatchers. Unpubl. D.Phil. Thesis, University of Oxford.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging Theory*. Princeton U.P., Princeton, New Jersey.

Williams, R. & Robins, D.B. 1982. Effects of preservation on wet weight, dry weight, nitrogen and carbon contents of *Calanus helgolandicus* (Crustacea: Copepoda). *Marine Biology* 71: 271–281.

Zwarts, L. & Dirksen, S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* 78: 257–278.

Zwarts, L. & Esselink, P. 1989. Versatility of male Curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availablity. *Marine Ecology Progress Series* 56: 255–269.

Appendix 1

Mathematical explanation of why using inter-catch intervals (ICI) can substantially over-estimate the average feeding rate

Let the random variable X denote the inter-catch interval (ICI) from the end of the swallowing of one prey to the end of the swallowing of the next.

Let $x_1, x_2, \ldots, x_n$ denote a sample of n (independent) observations of X.

Assume that x_i has an unknown distribution, but with Mean = μ and variance = σ^2.

The coefficient of variation of ICI is

$$CV = \sigma / \mu$$

The true (long-term) average feeding rate is $\mu_{FR} = 1/\mu$

$\bar{x} = \sum_{i=1}^{n} x_i / n$ = sample mean of the ICI observations.

Expected value of $\bar{x} = \mu$ and Variance of $x = \sigma^2 / n$

To estimate the average feeding rate,

(i) the '*individual ICI*' method uses: $\bar{y} = \sum_{i=1}^{n} y_i / n$ where $y_i = 1/x_i$

and

(ii) the '*mean ICI*' method uses: $m = 1/\bar{x}$

If R is any random variable with mean μ_R and variance σ_R^2 then, using a second order approximation derived from a Taylor expansion (Kendal & Stuart, 1977, p. 260), the expected (i.e. mean) value of $1/R$ is approximately: $E[1/R] \approx 1/\mu_R + \sigma_R^2 / \mu_R^3$

Therefore:

(i) The expected (i.e. mean) value of y_i is: $E[y_i] \approx 1/\mu + \sigma^2 / \mu^3$

Because $\bar{y}$ is just the arithmetic average of the $\{ y_i \}$, $E[\bar{y}] = E[y_i]$

Therefore $E[\bar{y}] \approx 1/\mu + \sigma^2 / \mu^3 = \mu_{FR}\{1 + CV^2\}$

(ii) The expected value of $m = 1/\bar{x}$ is: $E[m] \approx 1/\mu + \sigma^2 / n\mu^3 = \mu_{FR}\{1 + CV^2 / n\}$

Therefore both $\bar{y}$ and m overestimate μ_{FR}.

However, very importantly, the bias for estimator $\bar{y}$ is independent of the number (n) of observations of ICI, whereas, in contrast, the bias in estimator m decreases with sample size n. m is always the better estimator. For large sample sizes, the estimator m is approximately unbiased.

The over-estimate of mean FR using either estimator increases with the CV in ICI. If the ICI was constant (very unlikely in the field), then the variance, σ^2, of x_i is zero, and both $\bar{y}$ and m give the same unbiased estimate of the average feeding rate.