Increasing the harvest for mussels *Mytilus edulis* (L.) without harming oystercatchers *Haematopus ostralegus* (L.)

Running head: Mussel fisheries and oystercatchers

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ABSTRACT: Oystercatchers *Haematopus ostralegus* (L.) arriving on their wintering grounds at the end of summer require there to be 6-8 times more mussel *Mytilus edulis* (L.) biomass available on their feeding grounds than they will consume over the winter if the birds' normal high survival rate until spring is to be maintained: that is, their 'Ecological Requirement (ER)' is considerably larger than their 'Physiological Requirement (PR)'. The ratio ER/PR was termed the 'Ecological Multiplier (EM) and has been applied to a number of shellfisheries to calculate the Total Allowable Catch (TAC). The high value of the EM, however, has meant that mussel fisheries have suffered from much reduced harvests and thus economic difficulties. This paper proposes two methods by which the TAC could be increased without any predicted impact on the birds. In the ‘roll-over’ approach, the surplus biomass remaining at the end of one month is harvested during the next. In the ‘delayed start’ approach, the EM is not set at the beginning of autumn but at the beginning of the winter, which is when birds begin to starve. The two approaches can be applied together and would enable many more mussels to be harvested than is currently allowed without reducing oystercatcher survival. In the test case presented here, the TAC over the winter could be increased from 5% to between 35% and 45% of the standing crop of mussels present in September when the birds arrive.

KEY WORDS: mussel harvesting – oystercatchers - interference competition - individual-based modelling - total allowable catch

1. INTRODUCTION

If oystercatchers *Haematopus ostralegus* (L.) that feed on intertidal cockles *Cerastoderma edule* (L.) and/or mussels *Mytilus edulis* (L.) are to survive the non-breeding season with their normally high survival rate, the food supply when they arrive in late summer must greatly exceed the population’s physiological requirements until the following spring (Goss-Custard et al. 2004). Simulations with the individual-based model *MORPH* showed that the amount of mussel biomass required to support mussel-eating oystercatchers - the ‘Ecological Requirement (ER)’ – should be 6-8 times greater than the amount they will actually consume by the end of the winter - their ‘Physiological Requirement (PR) (Goss-Custard et al. 2004, Stillman et al. 2016). The ratio ER/PR is termed the ‘Ecological Multiplier (EM). The EM is generally much smaller in oystercatchers eating cockles than in those eating mussels, the focus of this paper.

So far, three hypotheses have emerged to explain why the ER at the beginning of the non-breeding season so greatly exceeds the PR. First, foraging oystercatchers consume only a fraction of the mussels they encounter. Over the low-tide exposure period, mussels are protected by their thick and usually tightly-clamped shells. Oystercatchers that extract the flesh by hammering their bill-tips into the dorsal shell, for example, must find the occasional mussel whose shell has eroded sufficiently to enable the birds to hammer a hole without risking potentially lethal damage to their bills. Similarly, oystercatchers that attack mussels by stabbing, or forcing, their bill-tips into a gap between the two mussel valves must locate the occasional one that is temporarily gaping or that in some other way allows the bird to lever the two valves apart. Oystercatchers in winter also select mussel size-classes that maximise their intake rate (Zwarts et al. 1996). For these two reasons, the birds consume only a very small fraction of the mussels they encounter. [But despite this, and in ways not yet properly understood, oystercatchers are able to maintain their intake rate at very low mussel densities so that the asymptote of the functional response is level over a very wide range of mussel abundance (Goss-Custard et al. 2006).] The second reason that the ER is higher than the PR is the interference that occurs between foraging oystercatchers caused by dominant individuals stealing mussels from sub-dominants (Stillman *et al.* 2002). That interference is much stronger in mussel-feeders than in cockle-feeders may partially explain why the EM is higher in mussel-feeders. Oystercatchers therefore need an abundant food supply throughout the non-breeding season to allow them to find the occasional profitable and safe bivalve as well as enough space to avoid more dominant birds. The third reason for the high value of the EM is that oystercatcher intake rate depends much more on prey flesh-content than on their numerical density (Goss-Custard et al. 2006). As the flesh-content can decrease by a very large amount between September and March in both mussels and cockles, a high biomass must be present in autumn for there to be enough biomass remaining at the end. More research is required to test whether these three possible mechanisms are all necessary and sufficient to explain the high value of the EM in oystercatchers.

A ‘Bird Food Model (BFM)’ enables the value of the ecological requirement for the oystercatchers in a particular fishery in a particular year to be calculated by using average values of the EM (Stillman & Wood 2013, Stillman et al. 2016). The BFM has been used in a number of shellfisheries to calculate how much shellfish should be left over after summer harvesting for oystercatchers when they return in August and September. However, the particularly high values of the EM in mussel fisheries have meant that the Total Allowable Catch (TAC) has been so low that businesses and jobs have been threatened. A ‘fresh-eyes’ re-appraisal stimulated two new ideas that apply when mussels can be harvested through the autumn and winter: the ‘roll-over’ and ‘delayed start’ approaches. Both ideas would mean that far fewer mussels than predicted by the BFM would need to be retained to maintain the birds’ high winter survival rate so that more mussels could be harvested instead.

2. METHODS

2.1 The two approaches

The ‘roll-over’ idea can best be described by considering an hypothetical estuary with a mussel *Mytilus edulis* (L.) fishery in which, at the beginning of September, the standing crop is 5000 tonnes of mussels, measured as ash-free dry mass (AFDM) to exclude indigestible inorganic material, particularly the shells. The oystercatcher *Haematopus ostralegus* (L.) population requires an average, say, of 100 tonnes a month, and so will consume approximately 700 tonnes over the seven months of winter (1 September to 15 March). From modelling with *MORPH*, EM is estimated to be 7, so there needs to be 4900 tonnes (7x700) remaining at the end of summer harvesting. As the standing crop biomass on 1 September is

5000 tonnes, the fishery can only take 100 tonnes during autumn and winter if oystercatcher survival is to remain at its normal level.

The ‘roll-over’ idea derives from the fact that only 100 of the 700 tonnes reserved for the birds for the month of September, for example, is actually consumed by them during that month. Accordingly, 600 of the 700 tonnes allocated for September remain at the end of the month and may no longer be required. The ‘roll-over’ idea is that the surplus of 600 tonnes, which by then has served its purpose, could be harvested by the fishery in the next or later months without harming the birds’ subsequent survival.

To develop this idea further, imagine that the oystercatchers arrive on 1 October instead of 1 September. Their physiological requirement is now 600 not 700 tonnes and, with an EM of 7, the ER for the six winter months would be 4200 tonnes. Were they to arrive on 1 November, their ER would be 7x500 tonnes and on 1 December it would be 7x400 tonnes, and so on throughout the winter. The surplus of 600 tonnes from each successive month could be carried forward as ‘roll-over’ tonnage and added to the subsequent shellfishery harvest, the ‘Total Allowable Catch’ (TAC). Even though part of the surplus biomass would be removed by mortality factors, such as gales, there would be a substantial gain to the fishery without harming the birds.

The ‘delayed start’ idea is that the EM would only be applied at the time when oystercatchers begin to have difficulties in obtaining their food requirements; *i.e.* at the beginning of the ‘starvation window’. Oystercatchers’ energy demands are at their lowest and their shellfish food supplies are at their highest during autumn so that most starvation occurs subsequently during the winter (Goss-Custard et al. 1996). Accordingly, the monthly surplus biomass that is currently retained during the autumn might not be needed for birds to survive the winter. The hypothesis is that the time to ensure that enough mussel biomass remains after harvesting could be at the beginning of the winter starvation window rather than on 1 September.

2.2 Individual-based model

It was thought essential to test both ideas using a real system as the test case. This is because it is difficult to work out *a priori* how the outcome might be affected by the overwinter decrease in the flesh-content of the shellfish and their mortality due to causes other than oystercatchers and fishing. The usually very high rate of over-winter flesh-loss in mussels was thought likely to be particularly important because the intake rate of shorebirds depends largely on the average energy content of individual prey items rather than on their numerical density (Goss-Custard *et al.* 2006). The test case was the Exe estuary where about half the mussel biomass in September is lost during the winter to 'other' mortality agents and, particularly, to flesh-loss in individual mussels (Goss-Custard et al. 1993).

The Exe estuary mussel and oystercatcher populations are described in Stillman et al. (2000) which also describes the individual-based model (IBM) of the bird population that was first used to measure the EM but has since been replaced by the new IBM platform, *MORPH* (Stillman 2008). In reality, there has been little or no harvesting of the intertidal mussels of the Exe estuary for many years. Here the Exe has been used solely as a real-world system to test by modelling the potential of two new approaches to harvesting mussels which might be trialled in other locations where there is an intertidal mussel fishery. The paper concerns 'what-if', even 'theoretical', explorations with a real-world and field-validated model to avoid leaving out important natural history details whose absence could render the results irrelevant. In order to focus solely on the consequences of the two proposed approaches, it was assumed that the amounts harvested and the harvesting methods 'employed' in the simulations would have no long-term consequences for the abundance of the mussels, as discussed by Stillman et al. (2001).

MORPH represents individual birds that use optimisation decision rules to decide how to obtain most rapidly their daily energy requirements which, in the model as in reality, depend on the ambient temperature. Individuals vary in competitive ability and each bird takes into account the decisions made by competitors in deciding when (*e.g.* night or day), where (*e.g.* which shellfish bed) and on what (e.g. cockles, mussels or alternative prey species) it should feed. Because shellfish are particularly profitable for wintering oystercatchers (Zwarts et al. 1996), oystercatchers attempt first to obtain their requirements from shellfish alone but, should they fail, they eat other intertidal invertebrates or terrestrial prey, such as earthworms Lumbricidae. Once an individual has obtained its current daily energy requirements, it stores subsequent consumption as fat up to a daily limit. A bird uses its fat reserves should it ever fail to obtain its daily requirement from current foraging and starves to death if its body reserves fall to zero. A full description of *MORPH* is in Stillman (2008).

The original version of the Exe oystercatcher-mussel IBM was calibrated to predict the observed within-winter mortality rate of adults for the ‘calibration’ years 1976-80 when there were, on average, 1550 oystercatchers (Stillman et al. 2000). This model correctly predicted the increased mortality rate in adults that accompanied the increase in population size over the winters 1980-81 to 1991-92: the ‘validation years’. However, it did not accurately predict mortality rates in birds using different methods to open mussels. For this, and for several other reasons, *ExeMORPH* was developed and re-parameterised using research carried out since 2000 to up-date many parameter values, as detailed in Goss-Custard (2018). [1]https://figshare.com/articles/Goss-Custard_J_D_2018_Calibration_of_the_individual-based_model_MORPH_for_mussel-eating_oystercatchers_of_the_Exe_Estuary_/7259105

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ExeMORPH predicted that the mortality rate over the validation years would be 1.94 times the rate during the calibration years, which compared well with the observed increase of 1.88 times. This suggested that *ExeMORPH* could be used with some confidence.

When calculating the value of the EM, Goss-Custard et al. (2004) used 0.5% as the normal overwinter mortality rate of adult oystercatchers, the age-class to which population size in this species is the most sensitive (Atkinson et al. 2003). Subsequently research in the UK and The Netherlands have shown that the normal adult winter mortality rate is about 2%.[2]https://figshare.com/articles/Goss-Custard_JD_Stillman_RA_Bowgen_KM_2017_Mortality_rate_of_oystercatchers_in_winter_-_what_should_be_the_target_doc/7259057 The ER at the point at which the predicted mortality rate is 2% (2%ER) divided by the bird population's physiological requirement (PR) for the remainder of the winter gives the '2%EM'. As *ExeMORPH* only predicts the number of oystercatchers that die of starvation, and the field-measured rate of 2% includes birds that would have died from other causes, such as accidents, the 2%EM is precautionary.

2.3 Testing the roll-over idea

This idea was tested in two stages. In the first, the 2%ER on the first day of each month was determined in order to find out how much mussel biomass was required at the beginning of that month if 98% of adult oystercatchers were to survive to the end of winter. This was done by running *ExeMORPH* simulations over the period 1 October to 15 March, then 1 November to 15 March, and so on, ending with the period 1 February to 15 March, the last six weeks when birds were present. There was no harvesting or consumption by oystercatchers in these simulations so mussel biomass decreased only through flesh-loss and other mortality factors, such as gales. These simulations established for each successive starting, or arrival, date the mussel biomass – the 2%ER - that the oystercatcher population required for 98% to survive

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until mid-March. The second stage was to re-run the simulations but with oystercatchers present so that the mussel biomass was reduced by oystercatcher consumption, as would happen in a real fishery. This enabled the surplus biomass that could be rolled over at the end of a month for later harvesting to be calculated; this was the difference between the standing crop biomass remaining at the end of the month and the 2%ER on the first day of the next month.

The simulations were run as follows: The biomass of mussels 30-65mm long only was considered, these being the size-classes taken by both oystercatchers and shellfishers. The mussel biomass on all the mussel beds combined on 1 September was 126.3 tonnes AFDM; details of numerical densities and AFDM of the seven 5mm size-classes of mussels (30-35mm *etc*) on each of the mussel beds of varying surface area over the seven winters of the study are in Stillman et al. (2000). In the simulations to estimate the 2%ER, the biomass of mussels on 1 September was varied by multiplying the densities of each size class by the same factor, ranging from x2 to x0.25. Twenty simulations were run with each factor value until a smooth, quadratic function had been obtained (Fig. 1). The 2%ER on 1 September was 7.96; *i.e.* 119.53 tonnes AFDM were required on 1 September to give an over-winter survival rate of 98%.

Estimates of the over-winter mortality rate of Exe mussels not due to oystercatcher predation or harvesting are available for three winters (McGrorty et al. 1990, Nagarajan 2000) and the average of 5% was used here. Many estimates are available for the rate of winter flesh-loss of individual mussels, ranging from 30 to 60% for Exe mussels (Cayford & Goss-Custard 1990, Goss-Custard et al. 1993, Sitters 2000, Nagarajan et al. 2006) and elsewhere (Dare & Edwards 1975, Bayne & Worral 1980, Hawkins et al. 1985, Ens et al. 1996, Smaal & Vonck 1997). The typical value for the Exe of 45% was used here.

In view of the high rate of flesh-loss, the best option to maximise the TAC measured as AFDM would be to harvest each month's surplus in the following month before too much of the surplus biomass from the previous month had been eroded. However, in a real fishery, flesh-loss is an irrelevant consideration because the TAC is measured as fresh-weight, which includes the shells: flesh-loss just lowers the 'quality' of mussels. The AFDM as a proportion of fresh-weight is very low because the shells are so heavy, averaging 0.05 over 14 estimates (Rumohr et al. 1987, Zwarts et al. 1996, Ricciardi & Bourget 1998, Munch-Petersen & Kristensen 2001, Laursen et al. 2010, West & McGrorty 2015). A more realistic way of testing the efficacy of the roll-over idea is to measure the potential harvest as tonnes fresh-weight. Accordingly, all values of biomass measured as AFDM were divided by 0.05. The mussels in the model simulations still lost flesh at the overwinter rate of 45% but, by dealing in the units actually used by the fishery, this loss is not directly involved in these calculations.

The maximum harvest that can be taken during the month of September, for example, is the difference between the standing crop biomass s_n on 1 September and the 2%ER on that same day. The general formulation will be:

$$h_n^{max} = s_n - r_n e_n \qquad \text{equ. 1}$$

where h_n^{max} = the maximum biomass in tonnes fresh-weight that can be harvested in month n; r_n = the oystercatcher population's food requirements for the remainder of the winter in tonnes fresh-weight on the first day of month n, and e_n = the 2%EM on that same day: the expression $r_n e_n$ = 2%ER in tonnes fresh-weight on the first day of month n.

The standing crop on the first day of the subsequent month is:

$$s_{n+1} = s_n - c_n - m_n s_n - h_n^{max} \qquad \text{equ. 2}$$

where s_n = the initial standing crop biomass in tonnes fresh-weight on the first day of month n; c_n = the consumption by oystercatchers in tonnes fresh-weight during the month n; m_n = the proportional mortality of mussels over the month n, and h_n^{max} = the maximum biomass that can be harvested in month n.

Substituting h_n^{max} in equation 2 with $s_n - r_n e_n$ from equation 1 gives:

$$s_{n+1} = s_n - c_n - m_n s_n - (s_n - r_n e_n) = r_n e_n - c_n - m_n s_n \qquad \text{equ. 3}$$

In words, the maximum harvest in any month is the standing crop biomass on day 1 of that month less the 2%ER on that same day. The maximum harvest would therefore be the standing crop biomass that had been present on the first day of the previous month less the amount that had been removed during that month by oystercatcher consumption, mussel mortality and by the roll-over harvesting carried out during that month. We consider the maximum harvest because the aim is to find out how much extra biomass could, in principle, be harvested if the roll-over idea was applied. If the maximum was not in practice harvested in one or more months, the actual amount harvested would replace the expression $\mathrm{h_n^{max}}$. Harvesting was stopped at the end of February, the last complete month when oystercatchers were present.

2.4 Testing the delayed start idea

Model birds do not begin to starve until December, and then only in very small numbers (Fig. 2), which replicates the pattern recorded on the Exe (Stillman et al. 2000). The ‘window of starvation’ extends from about 1 December or 1 January through to mid-March when the birds emigrate. The requirement for the delayed start approach is that the mussel biomass remaining at the beginning of the starvation window is equivalent to the 2%ER appropriate for that start date, whichever date be chosen.

The idea was tested as follows: Consider the case where the start date of the starvation window is taken to be 1 December. The standing crop mussel biomass and 2%ER on 1

September are 2526 and 2391 tonnes fresh-weight respectively (see below; Table 2). The 2%ER on 1 December is 1492 tonnes fresh-weight, or 0.591 of the standing crop biomass that was present on 1 September. The question is whether the potential aggregate, three-month surplus (September, October and November) of 1034 (2526-1492) over-and-above the 2%ER on 1 December could be removed during autumn, or even earlier, without increasing the mortality rate of the birds during autumn (September, October and November) above 0%. The test was to run two sets of simulations for each of the candidate start dates of the starvation window. In one set - the 'controls' - the standing crop biomass on 1 September was the real-world value. In the second set of simulations - the 'experimentals' - the standing crop biomass on 1 September was reduced by the maximum possible amount that could be harvested without reducing the birds' subsequent survival; that is, to the equivalent of the 2%ER on day 1 of the starvation window, increased by the biomass that would have been removed by oystercatchers and other mortality agents before the first day of the starvation window. The model was then run from 1 September to the 'start date' of the current starvation window to measure the numbers of adults that starved during autumn in the control and experimental scenarios. These paired sets of simulations were repeated using 1 November, 1 December and 1 January, the most probable, alternative start dates.

2.5 Fresh-weight biomass

In most fisheries, the fresh-weight biomass of mussels in late summer/early autumn measures the standing crop from which the TAC will be taken over the whole of the subsequent shellfishing season. Fresh-weight – and not the gradually declining flesh-content - is also used to measure the allowable biomass that can be harvested during any particular part of the shellfishing season. In order for our findings to be easily transferred to real fisheries, it was therefore necessary to use fresh weight when referring to both the initial standing crop and to the allowable catch for the whole (the TAC) or particular parts of the shellfishing season. All the model simulations began on 1

September and, as in a real fishery, fresh-weight rather than AFDM was used to measure the allowable harvest over all or any part of the subsequent shellfishing season. But unless otherwise stated, individual mussels lost flesh from 1 September onwards in all of the simulations, just as they do in real fisheries. Therefore, the effect of the over-winter flesh-loss on the ability of oystercatchers to survive was automatically taken into account, whatever the period being considered, even though the metric for the harvest was fresh-weight and not AFDM, which is the quantity that is important to the birds.

3. RESULTS

3.1 Roll-over

The 2%ER decreases as the start date occurs later and later in the winter, as illustrated by the start dates 1 September and 1 December (Fig. 3). The 2%EM remained in the range of 7-9 until mid-winter but then increased (Table 1). Surplus biomass that could be rolled-over for later harvesting remained at the end of every month (Fig. 4).

The cumulative surplus of 47 tonnes AFDM at the end of the winter in Fig. 4 would have been larger if the mussels *Mytilus edulis* (L.) had not died or lost flesh over the preceding months. On the Exe, the 45% rate of flesh-loss in individual mussels was far more important than the 5% mortality rate. Simulations were run in which the mortality rate was retained at 5% and the over-winter flesh-loss was reduced by stages from 45% to 0 and these confirmed the importance of the rate of flesh-loss large in determining the value of 2%EM (Fig. 5).

Measured as fresh-weight, the potential monthly harvest averaged 194 tonnes over the first five months of winter then increased sharply in February (Table 2). Over those first five months, 971 tonnes fresh-weight, or 38% of the initial stock of 2526 tonnes present on 1 September, could be harvested before the end of January without decreasing the survival of oystercatchers. If all the potential February harvest is included, the total tonnage increases to

1452, or 57% on the initial standing crop. Even if only the average harvest for the previous five months was harvested in February to conserve a recruitment stock of mussels, the total harvest over the winter would be 1164 tonnes fresh-weight, equivalent to 46% of the initial stock on 1 September.

3.2 Delayed start

With the start date of 1 November, there was no difference in mortality rate during the previous two months between experimental and control simulations: almost no adults starved in either case (Table 3): accordingly, there would have been no difference either with a start date of 1 October. A few adults starved in both control and experimental simulations during the preceding three months of autumn when the start date was 1 December, with almost significantly more doing so in the experimental runs. In fact, even with the start date of 1 January, the increase in the starvation rate during autumn in the experimental simulations was only very small and from a very low base.

4. DISCUSSION

4.1 Roll-over idea

The 2%EM on 1 September was 7.86 which means that almost 8 times the amount that oystercatchers *Haematopus ostralegus* (L.) require to meet their consumption needs over the autumn and winter must remain on the mussel beds after summer harvesting to ensure the 98% survival of oystercatchers until March. In some fisheries, this is such a huge amount that real financial pressure has been placed on the industry. This study has shown, however, that throughout the winter, there can be a gradually increasing surplus of mussels *Mytilus edulis* (L.) that would no longer be needed by oystercatchers. In round figures, perhaps 35-50% of the initial biomass fresh-weight of 2526 tonnes might be harvested: in contrast, based on the winter-long 2%EM, the harvest would have been 5%. Not considered here is the amount that must remain to ensure the long-term survival of the mussel population and the method by which they are harvested (Stillman et al. 2001, Goss-Custard et al. 2004).

The simulations also showed that the winter-long 2%EM was related to the rate of flesh-loss of mussels (Fig. 5). With no decrease at all, the 2%EM was 2.7 which we interpret as the consequence of intense interference competition between oystercatchers eating mussels (Stillman et al. 1996). The rate of flesh-loss in mussels was far more important than their mortality in determining the 2%EM because (i) it was nine times larger, and (ii) the intake rate of oystercatchers is much affected by the flesh-content of individual shellfish and rather little by their numerical density (Goss-Custard et al. 2006). The high rate of flesh-loss, probably in combination with the increasing energy demands of the birds, also explains why the 2%EM increased sharply at the end of winter. In contrast, the fresh-weight harvest was little affected by flesh-loss because of the massive contribution of the shell. It could, however, be affected by the mortality rate of mussels if it was much higher than the winter-long value of 5% on the Exe.

4.2 Delayed start

The results suggest that the start date could be delayed until the end of autumn without raising the autumn adult mortality rate above its normal value of 0%. The start date could even be set at 1 December without increasing the autumn mortality rate by more than a trivial amount: the 95% confidence limits of the almost significant increase (P=0.064) are 0.001% to 0.032%. Only when the start date was set at 1 January, well into the winter, did the autumn mortality rate increase significantly. Managing the fishery by targeting the 2%ER for 1 December rather than for 1 September does look to be an achievable goal, at least in the test case of the Exe estuary.

4.3 Combining the two approaches

The two approaches are not incompatible. With the delayed start approach, the fishery would be managed so that the 2%ER was in place at the start of the birds' starvation window rather than at the start of every month throughout the winter – a simplification that is likely to be welcomed by both fishery managers and the shellfishing industry. Then, from the start day of the starvation window, the roll-over option could be introduced.

4.4 Effect on the shellfish harvest

The gain to the shellfishery could be substantial. On the assumption that the typical rate of decrease in the biomass of mussels from September to March is 30-50%, and for the roll-over approach alone, the results suggest that oystercatchers would not be harmed if shellfisheries harvested over the winter between about a third and a half of the 2%ER mussel biomass (fresh-weight) that is present at the beginning of September.

To calculate the size of a bird-friendly harvest, however, the rates of flesh-loss and mortality in mussels need to be known, preferably for the different size-classes of mussels and at each stage of the winter**.** The former is potentially significant because of its importance for calculating the value of the 2%EM and the latter because of its potential significance to the size of the TAC. It would be beneficial to conservation and fishery authorities to make routine measurements of the rate of overwinter flesh-loss and mortality of mussels. As the shell thickness of mussels also changes through the winter (Nagarajan et al. 2006), so might the ratio fresh-weight/AFDM. Consequently, routine monitoring of this ratio through the winter of might also prove useful in refining the size of the harvest.

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Table 1. The 2%EM for successive months of the winter (final column). Column 1 is the date on which oystercatchers *Haematopus ostralegus* (L.) arrived on the model mussel beds. Column 2 is the 2%ER on each start date but measured in terms of the abundance and AFDM of the mussels on 1 September and so not on the start date itself. Since mussels lose flesh and die between 1 September and each of the successive start dates, the biomass in column 2 has to be reduced by the combined magnitude of these two losses to measure the 2%ER in terms of the numbers and flesh-content of the mussels present on the start date itself. Deducting column 3 from column 2 gives in column 4 the biomass required on each start date, measured in terms of the AFDM of the mussels actually present at the time. Column 5 shows how much food the population of oystercatchers requires to survive until the end of the winter (day 196) on each start date. The final column gives the ratio ER/PR, the resulting 2%EM**.**

Start date	2%ER	Biomass lost by start day	2%ER on start day	PR for rest of winter	2%EM for rest of winter
	(tonnes AFDM)	(tonnes AFDM)	(tonnes AFDM)	(tonnes AFDM)	
1 September	119.53	0	119.53	15.21	7.86
1 October	108.83	8.35	100.48	12.88	7.80
1 November	103.02	16.06	86.96	10.48	8.30
1 December	97.21	22.60	74.61	8.15	9.16
1 January	94.81	29.54	65.27	5.74	11.37
1 February	62.94	24 .58	38.36	3.42	11.23

Table 2. Parameter values (in tonnes fresh-weight) used in equations 1 to 3 to calculate the maximum permissible harvest resulting from the roll-over approach, as shown in the final column. The standing crop on 1 September was the mean value across the seven years (1976-83) of the field study (McGrorty et al. 1990, Stillman et al. 2000). ; r_n = the oystercatcher population's food requirements on the first day of month *n* for the remainder of the winter in tonnes fresh-weight; e_n = the 2%EM on that same day; m_n = the proportional mortality of mussels over the month *n*; s_n = the initial standing crop biomass in tonnes fresh-weight on the first day of month n; c_n = the consumption by oystercatchers in tonnes fresh-weight during the month *n*; h_n^{max} = maximum biomass in tonnes fresh-weight that can be harvested in month n. The expression r_ne_n = 2%ER in tonnes fresh-weight on the first day of month *n*.

Start date	2%ER	Biomass mortality	Bird consumption	Standing crop	Harvest
(symbol)	(r_ne_n)	(m_ns_n)	(c_n)	(s_n)	(h_n^{max})
	(tonnes FW)	(tonnes FW)	(tonnes FW)	(tonnes FW)	(tonnes FW)
1 September	2391	18.7	46.6	2526	135
1 October	2010	16.1	48.1	2326	316
1 November	1739	13.4	46.6	1946	207
1 December	1492	11.8	48.1	1679	187
1 January	1306	10.2	48.1	1432	126
1 February	767	5.4	43.4	1248	481

Table 3. The adult mortality rate between 1 September and the start of the starvation window (‘start date’), defined in three ways. In the ‘control’ simulations, the standing crop biomass (fresh-weight) on 1 September was the real-world value. In the ‘experimental’ simulations, the standing crop biomass (fresh-weight) on 1 September was reduced by the fraction F to reduce the initial biomass to the 2%Ecological Requirement (fresh-weight) on the start date, but with the intervening loss due to mortality and oystercatcher consumption added on to take these losses into account. The P-value of the difference between the means (highlighted in bold) is shown.

Start date	Controls			F	Experimentals			Significance of the difference
	Mortality to start date				Mortality to start date			
	Mean %	s.e.	N		Mean %	s.e.	N	P-value
1 November	0	0	60	0.726	0.005	0.002	60	ns
1 December	0.021	0.005	60	0.640	0.037	0.006	60	0.064
1 January	0.129	0.012	60	0.572	0.421	0.026	32	0.000

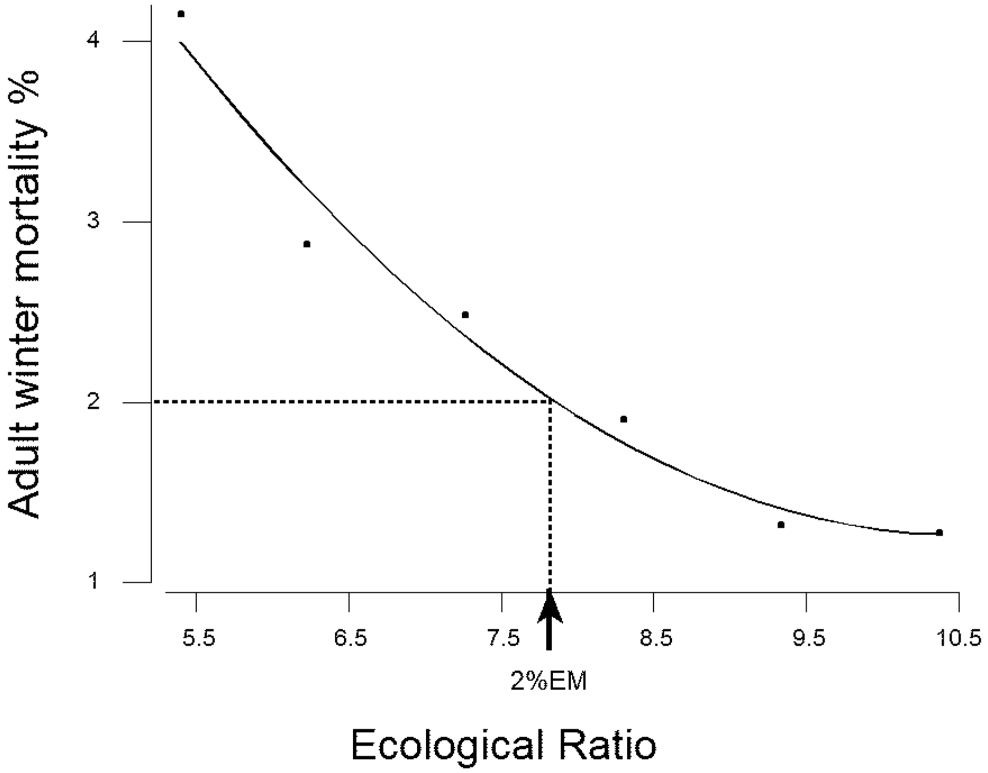

Fig. 1. How the 2%EM is calculated from simulations with *ExeMORPH*, using the bird arrival date of 1 September as the example. The ecological ratio is SC/PR, where SC = standing crop biomass of mussels on 1 September and PR = the physiological requirement, the biomass required to support the population to the end of the non-breeding season (15.21 tonnes AFDM). The 2%EM is the particular value of the ER that gives a mortality rate of 2%. Using the software www.desmos.com, the ratio where the over-winter mortality rate is 2% was obtained from the equation: $2 = 12.832 – 2.2024ER + 0.1049ER^2$, and is 7.86. Accordingly, the ecological requirement is 119.5 tonnes AFDM (7.86x15.21), equivalent to 95% of the biomass that was actually present on 1 September. Each point is the mean of 20 simulations.

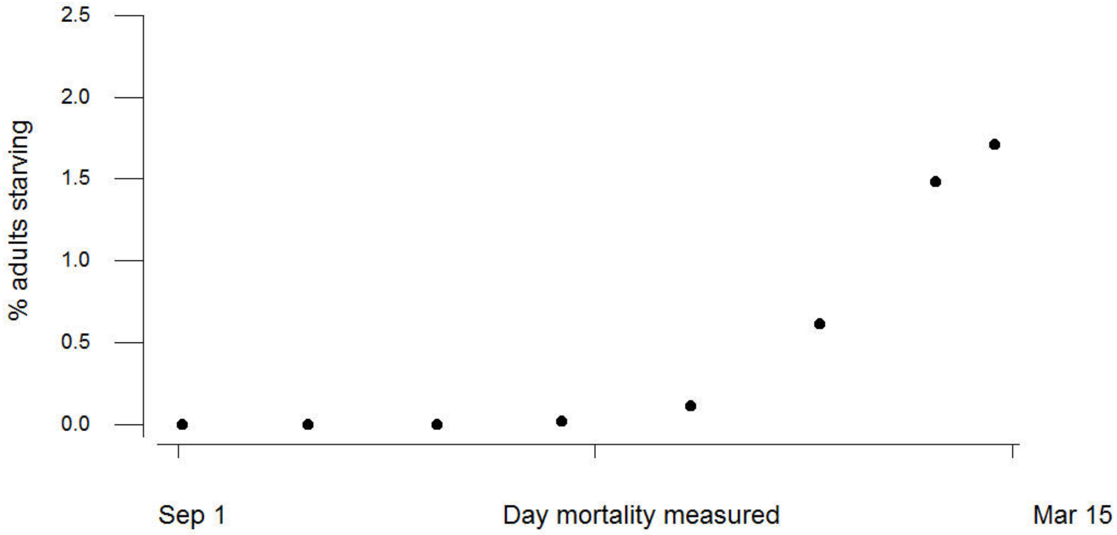

Fig. 2. The cumulative percentage of adult oystercatchers that have starved by the first day of each month during autumn and winter. Each point is the mean of 20 simulations with ExeMORPH.

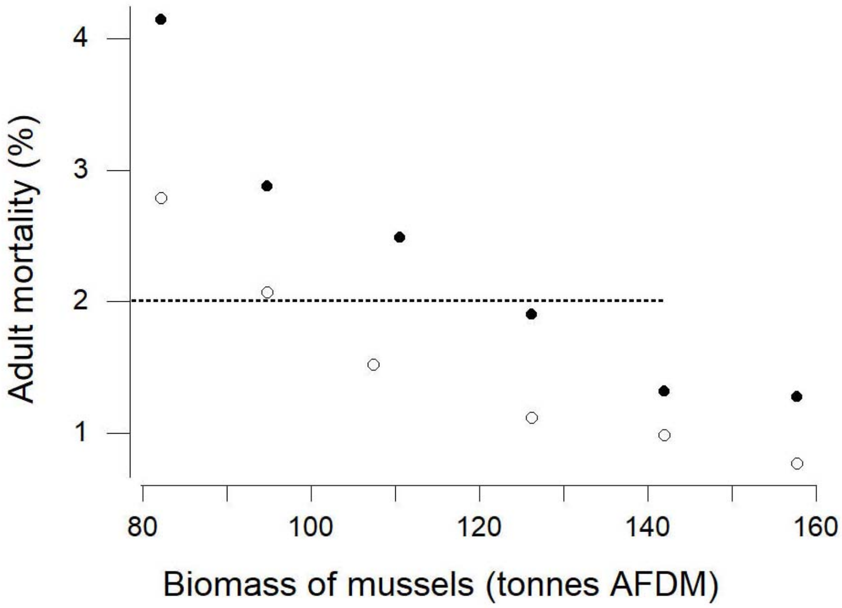

Fig. 3. Adult mortality rate in relation to the initial (1 September) biomass of mussels with two exemplary start dates. Each datum is the mean of 20 simulations. The horizontal line

shows the 2% mortality rate. From the quadratic equations for 1 September ($y = 12.8 - 0.115x + 0.000453x^2$) and 1 December ($y = 9.8 - 117x + 0.000383x^2$), the 2%ER is 119.5 tonnes on 1 September (solid circles) and 97.2 tonnes on 1 December (open circles).

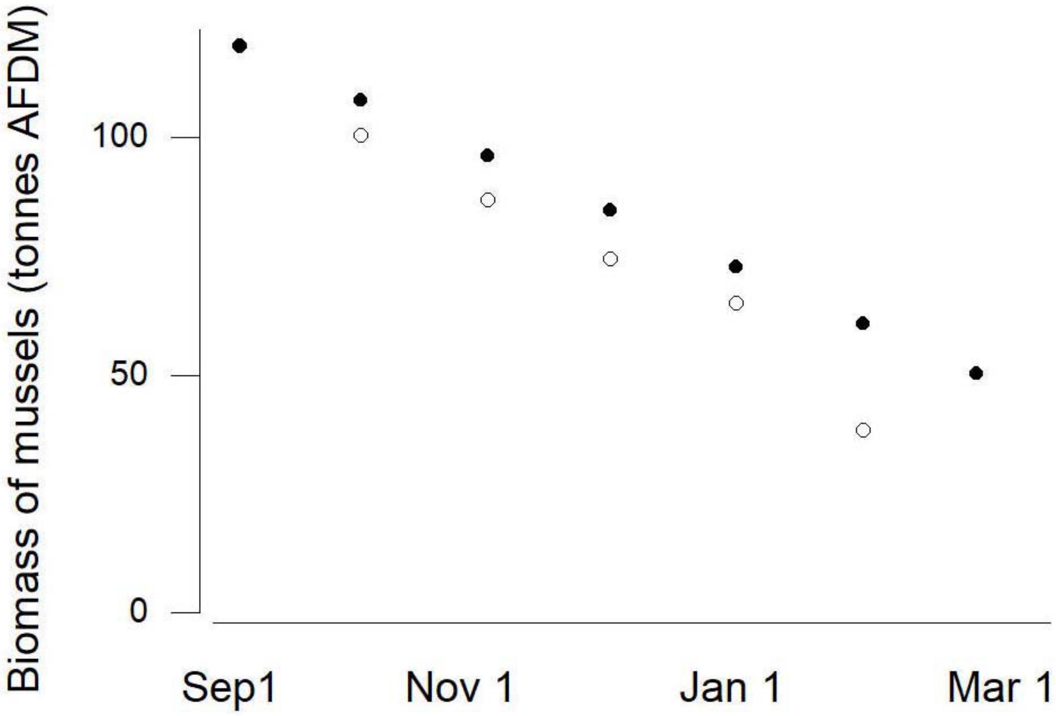

Fig. 4. The biomass oystercatchers require at the start of each month for 98% of adults to survive the remainder of the winter (open circles) and the biomass on the mussel beds at the time (closed circles).

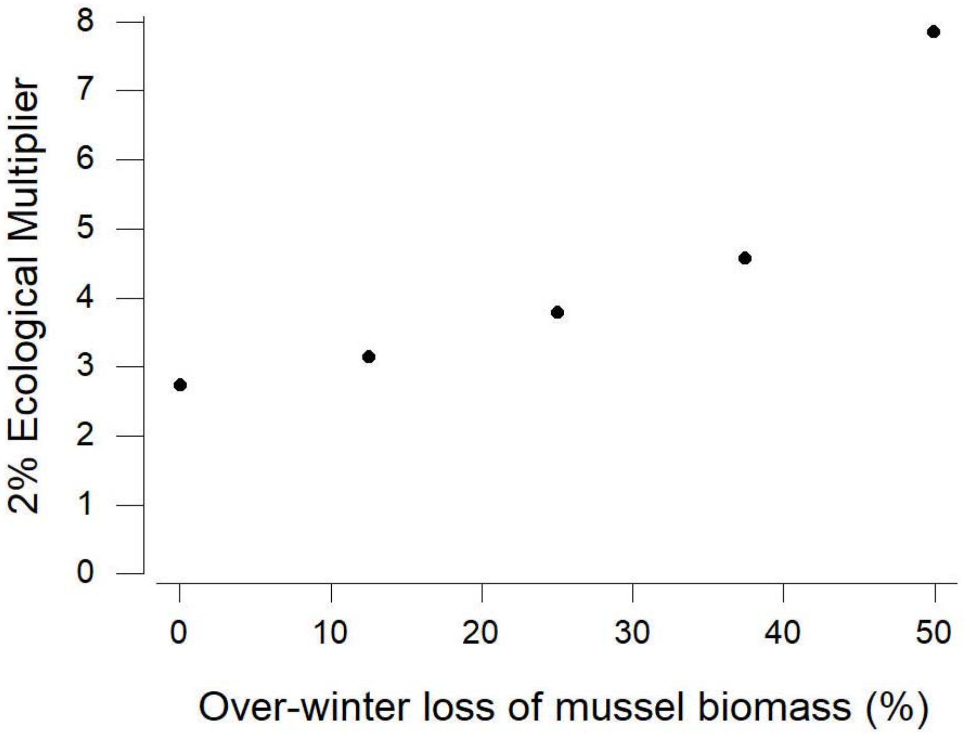

Fig. 5. The 2%EM on 1 September in relation to the over-winter rate of flesh-loss in individual mussels. The over-winter mussel mortality was 5% in all cases.