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Modelling the Short-Term Movements of Grey Seals between Breeding Colonies and their Long-Term Population Consequences
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Summary
The requirement to model within-year grey seal movement between breeding colonies in a biologically realistic and computationally manageable way has led to the development of the framework presented here. We attain biological realism by modelling behavioural attributes of the animals (such as site-fidelity and philopatry) and computational expediency by solving the model at equilibrium, hence, directly obtaining a yearly, redistribution function. We present preliminary results on the long-term population consequences of this model.

Introduction
The use of mathematical models to manage risk for any ecological system presents us with two, equally important, requirements. First, we need a functionally realistic and parametrically flexible mathematical model whose deterministic and stochastic properties are well understood. Second, we need efficient methods for fitting the model to data and quantifying the uncertainty in its predictions.

Model-fitting is often a computationally intensive process, performed on a finite amount of data. This imposes the additional requirement for a model that is no more complex and parameter-rich than the limitations in computer speed and the availability of data will allow. This trade-off becomes particularly important when modelling the population dynamics of large, marine mammals. This is because the animals' complex behaviour prevents us from attaining realism with simple population models and because their long life-span and large-scale movements in an environment that is principally opaque to human observation limit the amount of data available.

In grey seals, movement of females between colonies affects the spatial distribution of "hotspots" of pup production hence increasing the need for a spatially explicit population model. Also patterns of colonization and extinction of local breeding populations may affect the rate of growth of the grey seal population as a whole.

There is general consensus that we need to be able to tease apart the effects of movement and demography on local population dynamics. However, it is also clear that a spatially explicit model of movement, nested within a model of population dynamics, may present us with a bottleneck in running speed that makes model-fitting and uncertainty estimation prohibitive.

The objective of this work is to satisfy both the requirements of speed and realism in a model of within-year movement and to investigate the behaviour of such a model in a population dynamical context. This work is still in its early stages (initiated July 2003) and no part of it is published so we indulge in slightly more detail than in other Briefing papers.

Model of movement
To achieve our target of high running speed we aimed to obtain a redistribution function as the steady state solution of a system of ordinary differential equations modelling within-year movement in a network of breeding colonies. If we assume that no mortality occurs during migration and focus on the period just before the breeding season then steady state will be achieved when the net rate of movement between colonies is zero. This involves the rather strict assumption that seals have enough time to reach an equilibrium distribution and enough knowledge about the network of colonies to allow them to make their choice. The legitimacy of this assumption in grey seals stems from the fact that the animals take approximately five years to mature reproductively and during this time they travel extensively for foraging, and aggregate annually around breeding colonies even before they breed themselves.

There are three aspects of grey seal behaviour that need to be taken into account:
1. Site fidelity: Females that have given birth in previous years display strong site-fidelity towards

the site where they first gave birth. In future versions of this framework, we can model this as a variable proportion of veteran mothers, related to external factors such as human disturbance. However, in this version, we assume that choosing a breeding colony is a life-long decision.
2. Philopatry: A newly matured seal's choice of breeding colony is strongly biased towards its natal site. The animals that stay put, as a proportion of each local population, determine the initial conditions for our model. However, each year, crowding can force females out of their natal site leading to a variable proportion of migrants. Our model operates on this pool of mobile animals. Importantly, this allows us to ignore the animals' natal site after the movement starts (this is not an individual-based simulation and such tracking would be cumbersome).
3. Flux of migrants through the colonies: The flux of animals through each colony will depend on the topology of the network of colonies and the probability that an animal will jump from one colony to another as a function of the distance between them.
4. Decision to settle at a colony: This decision is ultimately density-dependent. This can be seen as a trade-off between the benefits of being among conspecifics and the drawbacks of having to contend with too many of them. There may therefore exist an optimal density at which the probability of settling is maximized.

Model description
Let M be the total population size in a particular year. Let $M_i(t)$ be the total number of animals in colony i. This will consist of N_i, the number of animals that decided to stay attached to their natal colony and $P_i(t)$, the number of mobile animals currently in the ith colony. We outline the structure of a functionally unspecified initial value problem and introduce some further notation. The model can be stated in terms of the state variable $P_i(t)$ and the initial conditions in terms of $M_i(0)$ and N_i.

$$\frac{dP_i}{dt} = \begin{pmatrix} \text{Animals coming} \\ \text{from other} \\ \text{colonies} \end{pmatrix} - \begin{pmatrix} \text{Animals} \\ \text{leaving} \\ \text{this colony} \end{pmatrix}$$

with (1)

$$P_i(0) = M_i(0) - N_i$$

We define the following (per-capita) functions:

Function	Interpretation
$f(M_i(0))$	Probability of leaving natal site
$h(d_{ij})$	Probability of moving from colony i to colony j as a function of their distance d_{ij}
$g(M_i(t))$	Probability of leaving current colony

The model is written

$$\frac{dP_i}{dt} = \sum_{j=1}^{m} h(d_{ji}) P_j g(N_j + P_j) - P_i g(N_i + P_i)$$

with (2)

$$P_i(0) = M_i(0) f(M_i(0)),$$
$$N_i = M_i(0)(1 - f(M_i(0))) = \text{constant}$$

Note that animals are allowed to revisit colonies at which they have been before (including their natal site).

Equilibrium solutions
We seek the equilibrium solutions $\{P_i^*\}$ of the system (2) under the constraint

$$\sum_{i=1}^{m} M_i(t) = M \qquad (3)$$

This constraint (conservation of total female numbers) prevents the system from reaching its natural steady state and therefore, system (2) is not sufficient to give us the final outcome in this model. However, it can be used as follows. First, write all but one of the equations at equilibrium

$$\sum_{j=1}^{m} h(d_{ji}) P_j^* g(N_j + P_j^*) - P_i^* g(N_i + P_i^*) = 0 \quad (4)$$

where $1 \le i \le m-1$. Define the new variable

$$x_i = P_i^* g(N_i + P_i^*), \qquad (5)$$

to get the following system of algebraic equations

$$\sum_{j=1}^{m} h(d_{ji}) x_j - x_i = 0, \quad 1 \le i \le m-1 \quad (6)$$

This has m variables and m-1 equations. It can be solved to give m-1 expressions of the type

$$x_i = H_i x_m \qquad (7)$$

where H_i is a colony "connectivity" parameter made up of the individual parameters h_{ij}. Now, assuming that (5) can be solved for P_i^* we have the following $2m$ equations in $2m$ unknowns

$$\sum_{i=1}^{m} P_i^* = M - \sum_{i=1}^{m} N_i \ , \ x_i = H_i x_m, \ P_i^* = q(x_i) \ (8)$$

This approach, entirely rests on being able to inverse-solve (5) i.e. find the function $q(x_i)$. If it is possible, the problem is reduced to finding the solution of

$$\sum_{i=1}^{m} q(H_i x_m) = M - \sum_{i=1}^{m} N_i \qquad (9)$$

Note that this is a single algebraic equation in x_m.

Example 1: Monotonic density dependence in the departure rate The probability of leaving a colony increases monotonically with density

$$g(P_i) = \frac{N_i + P_i}{(b_i + N_i + P_i)} \qquad (10)$$

The variable x_i is written

$$x_i = \frac{(N_i + P_i^*)P_i^*}{(b_i + N_i + P_i^*)} \qquad (11)$$

This has only one positive solution

$$P_i^* = \tfrac{1}{2}\left(x_i - N_i + \sqrt{(x_i + N_i)^2 + 4 b_i x_i} \right) \quad (12)$$

The problem now becomes finding a solution for the single algebraic equation

$$\sum_{i=1}^{m} \frac{H_i x_m - N_i + \sqrt{(H_i x_m + N_i)^2 + 4 b_i H_i x_m}}{2}$$
$$= M - \sum_{i=1}^{m} N_i \qquad (13)$$

There is no closed-form solution, but a numerical solution is almost instantaneous.

Example 2: Allee effect in departure rate A possible formulation for the function $g(P_i)$ is

$$g(P_i) = 1 - \frac{a(N_i + P_i)}{(a + N_i + P_i)(b + N_i + P_i)} \quad (14)$$

This expresses the trade-off as a product of two models. The model $(N_i + P_i)/(b + N_i + P_i)$ describes the increase in the probability of settling as a result of the need to be near conspecifics. The model $a/(a + N_i + P_i)$ expresses the decrease in probability as a result of the detrimental effects of density on pup survival. The variable x_i is written

$$x_i = \left(1 - \frac{a(N_i + P_i)}{(a + N_i + P_i)(b + N_i + P_i)} \right) P_i^* \ (15)$$

This is a cubic with only one real solution. It is too long-winded to write here so, call it $P_i^*(x_i)$. The problem now becomes finding a solution for the single algebraic equation

$$\sum_{i=1}^{m} P_i^*(H_i x_m) = M - \sum_{i=1}^{m} N_i \qquad (16)$$

Once again, numerical methods can be used to solve this single algebraic equation. For example, using Newton's method, a solution of (16) takes marginally more time than a solution of (13).

Long-term population consequences

One of the main debates concerning grey seal population dynamics is on the relative contribution of local and global population regulation. Local regulation could come about through the effects of colony crowding on pup survival. Global regulation could arise from some resource limitation on the population as a whole. This could manifest as adult and sub-adult mortality or reduced fecundity. The principal argument against local population regulation is that, given the number of empty and potentially suitable breeding sites, there is no obvious reason why existing colonies should be crowded. The principal argument against global population regulation is that, although some colonies seem to be reaching a plateau, others are still increasing exponentially.

In order to quantify the strength and consequences of some of these arguments, we placed our movement model in a suitable demographic model (see Briefing paper by Thomas and Harwood) containing only demographic stochasticity and examined the long-term dynamics and occupancy patterns arising in a system of 20 colonies.

In each simulation, we begun by seeding one colony with the same number of adult individuals and recorded the dynamics for 500 years. The exploration of the parameter space was not systematic, we just report here on the results of four selected experiments:

1. Local population regulation, tracked by philopatry.
For this experiment, we assumed that density at the breeding colonies regulates pup survival according to a Beverton-Holt function. We also assumed that females abandon their natal colony with a probability that tracks pup mortality. In other words, there is local population regulation but mothers are efficient in overcoming their philopatry for the sake of their pups.

(a)   (b)
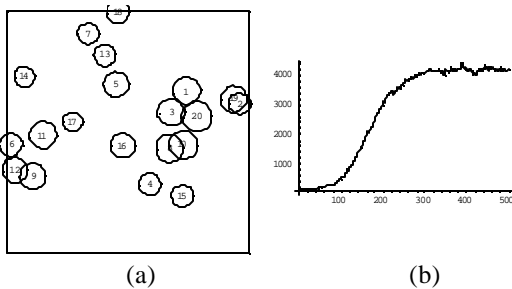
Figure 1: Typical simulation output after 500 years. a) Final distribution of animals in space, the size of the circles is proportional to the number of animals associated with each breeding colony. b) The time series of total population size.
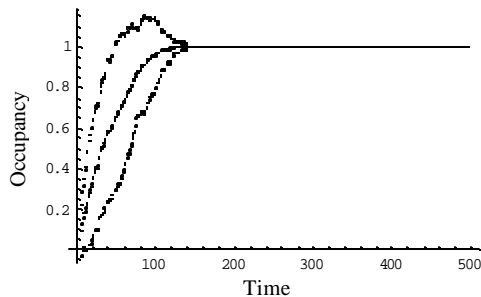

Figure 2: Proportion of occupied colonies shown against time. The central curve shows mean occupancy from 50 realisations of the process. The accompanying curves represent ± 1.98 standard deviations from the mean.

In all realizations of this process we observed logistic population growth (Fig. 1) and, spatially,

a smooth process of colonization culminating in all colonies being occupied by the end of the 500 years (Fig. 2).

2. Local population regulation, stepwise response of philopatry
In this case, we assumed that the decision of females to leave their natal site is taken on the basis of a rule of thumb on density rather than incrementally, as a function of pup survival. In practice, we did this by using a generalized Beverton-Holt function to model the decision of mothers to leave (Fig. 3).
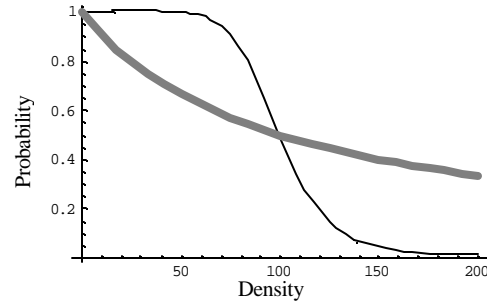

Figure 3: Pup survival probability (thick grey curve) and probability of leaving natal site (thin black curve) used for the simulations.

This led to markedly different results. Until density reached a critical value, very few females moved away from their natal site, hence imposing high mortality on their pups. This led to the entire population being "trapped", for long time intervals, within only a subset of the available breeding colonies (Fig. 4a). Overall, population growth was punctuated (Fig. 4b) as, for long periods of time, the population reached an apparent equilibrium until demographic stochasticity caused some females to colonise a new site and, hence, encourage further population growth.

(a)   (b)
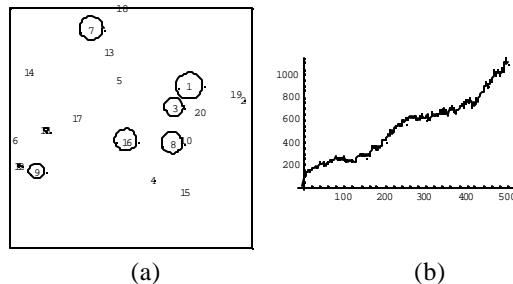
Figure 4: Typical simulation output after 500 years. a) Final distribution of animals in space, the size of the circles is proportional to the number of animals associated with each breeding colony. b) The time series of total population size.

The pattern of occupancy over 50 realisations of the process (Fig. 5) was also markedly different from that of Fig. 2. Specifically, modeling philopatry in this way not only decreased the rate of colonization (seen as the mean proportion of occupied colonies in Fig. 5), but also increased the variability around it as colonization events depended less on deterministic growth rates and more on demographic stochasticity.
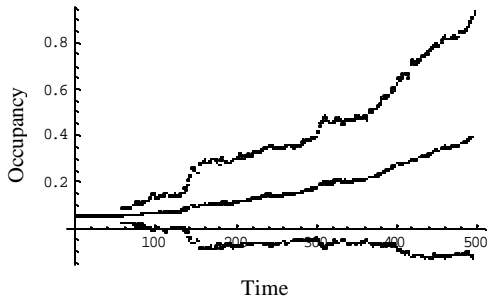
Figure 5: Proportion of occupied colonies shown against time. The central curve shows mean occupancy from 50 realisations of the process. The accompanying curves represent ± 1.98 standard deviations from the mean.
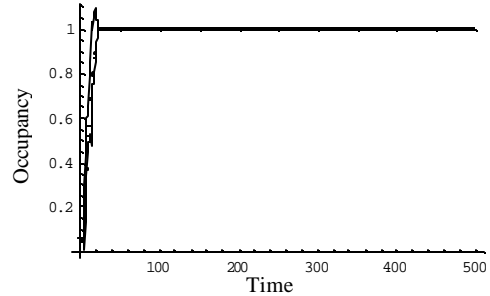
3. Global population regulation

We implemented global population regulation by making adult and juvenile survival a decreasing function of total density. The assumed proximate cause was global resource limitation. Again, we used a simple Beverton-Holt function for this. Philopatry was modeled as a simple Beverton-Holt function of local density.

(a)   (b)
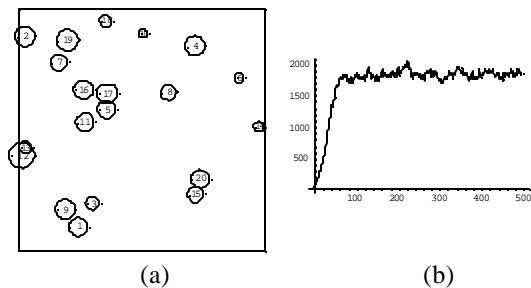
Figure 6: Typical simulation output after 500 years. a) Final distribution of animals in space, the size of the circles is proportional to the number of animals associated with each breeding colony. b) The time series of total population size.

Simulations of this system gave us logistic growth in total population numbers, with the animals being homogeneously distributed between suitable breeding sites (Fig. 6). All the breeding sites were colonised within approximately 30 years and the system maintained full occupancy from then until the end of the 500 years with no exception between different realizations of the process (Fig. 7).

Figure 7: Proportion of occupied colonies shown against time. The central curve shows mean occupancy from 50 realisations of the process. The accompanying curves represent ± 1.98 standard deviations from the mean.

4. Global population regulation, stepwise philopatry.

For this example we used exactly the same simulation setup as in the previous example, but replaced the philopatry model with the step-wise function of Fig. 3. This, makes the females' decision to leave their natal site, initially, unresponsive to increases in local density. As might be expected, total population numbers followed a similar trajectory (Fig. 8b) to that observed in the previous example (Fig. 6b). However, the distribution of animals was more heterogeneous (Fig. 8a, compare with Fig. 6a). This clustering was a direct result of tradition at the population level arising from philopatry and site-fidelity at the level of the individual.

(a)   (b)
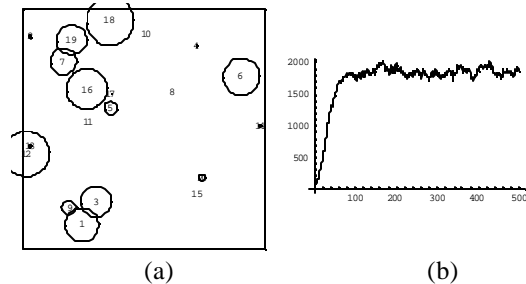
Figure 8: Typical simulation output after 500 years. a) Final distribution of animals in space, the size of the circles is proportional to the number of animals associated with each breeding colony. b) The time series of total population size.

The occupancy graph (Fig. 9) can illustrate this process more clearly. Initially (within the first 30 years or so), all sites become colonised. However, through random demographic events, some colonies manage to grow and hence, indirectly, inflict higher mortality on other colonies. This, therefore, is an example of competition between colonies for limited resources.
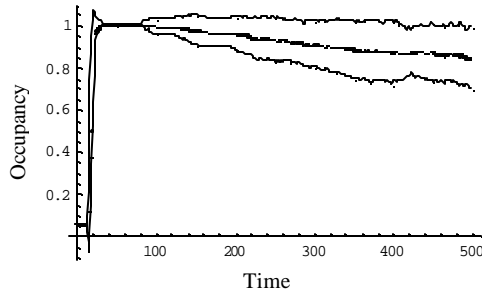
Figure 9: Proportion of occupied colonies shown against time. The central curve shows mean occupancy from 50 realisations of the process. The accompanying curves represent ± 1.98 standard deviations from the mean.

Discussion

We outlined a biologically plausible model of movement between breeding colonies for grey seals and the technique used for deriving a redistribution function on the basis of a within-year equilibrium assumption.

The computational gain in speed has allowed us to place the movement model inside an age-structured population model and investigate verbal hypotheses about population regulation in grey seals.

We focused on the dichotomy between global and local population regulation and demonstrated that, depending on the nature of the decision-making of philopatric females, it is possible to generate markedly different types of population dynamics and patterns of colonization.

Ironically, our preliminary results suggest that the principal arguments against both local and global population regulation are not necessarily valid. Hence, our first example suggests that if the population is regulated locally, all breeding sites may be colonised. In contrast, our second example shows that this is only true in the long-run as the population may, temporarily, be trapped in a subset of the available breeding sites. Similarly, our third example suggests that global population regulation can lead to local dynamics that mirror global dynamics, but our fourth example shows that clustering can produce intermittent occupancy (extinction/colonization events).

The main question now is which of these examples best approximates the truth. This can, perhaps, be resolved by fitting this version of the model to spatially disaggregated data. Whatever the answer, these examples have demonstrated how movement behaviour can affect local and global population dynamics and hence reinforced the case for continuing to develop spatially explicit models of the grey seal population.

Admittedly, spatially explicit models increase the demand for data. We hope that disaggregating already existing data sets down to the colony level may be able to satisfy at least part of these requirements.

One final comment in support of this approach is the additional predictive power that it provides us with. Understanding the animals' behaviour and its population implications can prevent us from misreading our data. A good example is provided by Fig. 4b. Misinterpreting any one of the multiple plateaus in the population time series as the environment's carrying capacity and developing a management strategy on that basis would completely miss the potential of an imminent period of further exponential growth.