Interactions With Prey

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Overview: *The sandeel is one of the main prey species of grey seals in the North sea. In this lab, we build on the single-species system examined in Lab 5 by adding a size-structured, density dependent prey population. We introduce the concept of multispecies functional responses for generalist predators and use them to investigate the consumption of sandeels by seals. We use the prey population model and the multispecies functional response to predict the diet of seals in years of differing prey availability. We quantify the impact of consumption on the predators' demographic rates but we stop short of examining its consequences for predator dynamics. This practical builds on the information given out in Lab 5 and you will progress considerably faster if you keep handy the notes and R code you have already developed.*

1. The Study System

Sandeels are small eel-like fish that swim in large shoals. They are an abundant and important component of food webs in the North Atlantic. They also support the largest fishery in the North Sea, with annual landings in the last decade of around a million tonnes. Of the five species of sandeels inhabiting the North Sea, the lesser sandeel, *Ammodytes marinus* is the most abundant and comprises over 90% of sandeel fishery catches.

Ammodytes marinus

Native range

Sandeels have a close association with sandy substrates into which they burrow. Research by the UK Fisheries Research Services (FRS) has shown that sandeels live in specific types of sand. Tagging studies have indicated that sandeels remain in preferred sandy areas. This dependence on sandy sediments means that the distribution of juvenile and adult sandeels is restricted by the patchiness of their preferred sandy habitat.

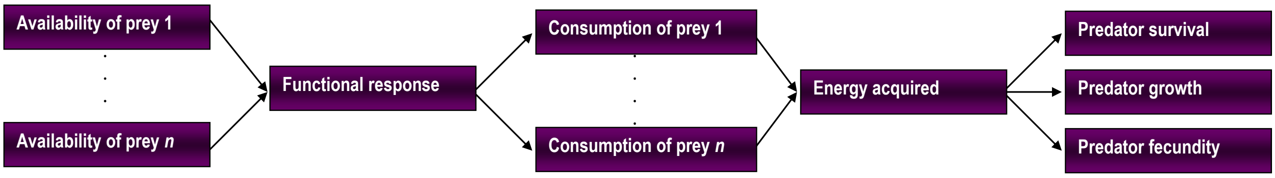
Sandeels mature between age one and three. They spawn a single batch of eggs in December-January and deposit those on the seabed. The larvae hatch after several weeks, usually in February-March, and drift in the currents for one to three months, after which they settle on the sandy seabed. Each mature female can produce up to 50 hatchlings that survive their first year. Mortality in the second year is about 90%. Annual mortality in older sandeels is about 50%. They are comparatively short-lived with a life span of less than 10 years. They settle, after their planktonic phase, at around 4-5 cm length, and may reach 5-10 cm length within three months of hatching. Sandeels off the Firth of Forth are relatively slow-growing compared to those in the main fished areas, around the Dogger and Fisher Banks. Further, whilst a significant proportion of sandeels from the Fisher, Outer Shoal and Klondyke Banks are likely to spawn at age one, many of those from the Firth of Forth do not spawn until age three. Shetland sandeels also tend to be slower growing, although they generally grow faster than Firth of Forth sandeels.

During the active feeding season (April-September) *A. marinus* tend to emerge during daylight hours to forage close to their burrows. Their main prey is calanoid copepods, but other planktonic prey, including fish larvae, are also taken. Large sandeels may also take benthic prey such as polychaete worms.

2. ecological theory

The early theory on functional responses dealt with specialist predators, i.e. those that focus and rely on a single type of prey. However, many predators are generalists. Although the dynamics of generalist predators are not tightly coupled to those of any one of their prey, such predators can have dramatic effects on prey populations. They can dampen or eliminate cyclical interactions between specialist predators and their prey, hold prey populations at low density equilibria and drive rare species to extinction.

In order to model the functional responses of generalists, we need to describe their response to changes in the abundance of all prey species, by making use of multispecies functional responses or MSFRs. An MSFR has as many response variables (consumption of each species) as explanatory variables (availability of each species) and is able to represent the relative, realised preferences of the predator for different prey (the predator's diet). The name "multispecies" can be more broadly interpreted as referring to several different components of the same prey population. For example, if it is known that a predator prefers larger individuals belonging to the same species, we might decide to treat prey of different size as different components of the predator's diet.



3. mathematical theory

The single-species functional responses proposed by Real in 1977,

$$F = \frac{aN^m}{1 + atN^m} \tag{1}$$

can be generalised to a multispecies functional response by specifying consumption and availability as vectors. For example, given the vector of densities for three prey species $\mathbf{N} = (N_1, N_2, N_3)$, a three-species functional response can be written as

$$\mathbf{F}(\mathbf{N}) = \{F_1(\mathbf{N}), F_2(\mathbf{N}), F_3(\mathbf{N})\} = \left\{ \frac{a_1 N_1^{\ m_1}}{1 + \sum a_i t_i N_i^{\ m_i}}, \frac{a_2 N_2^{\ m_2}}{1 + \sum a_i t_i N_i^{\ m_i}}, \frac{a_3 N_3^{\ m_3}}{1 + \sum a_i t_i N_i^{\ m_i}} \right\} \tag{2}$$

In this expression, $F_i(\mathbf{N})$ is the consumption of the ith prey species as a function of the densities of all prey. Once the amount of prey has been consumed, the contribution of each prey species to the predator's condition needs to be calculated. A somewhat simplistic approach converts each prey item to a common currency of energetic units and then uses energetic state as a measure of condition. The time units used by the model are very important in this calculation. If the functional response describes daily consumption then the condition of the predator at the reproductive season needs to integrate information from the whole year. If the functional response models annual consumption, this simplifies the modelling considerably but may not be very realistic biologically.

4. R ingredients

■ *Adding legents to plots*: Consider the two time series below, comprising random numbers

```
a<-rnorm(100, 100,20)
b<-rnorm(100, 140,20)
```

The following command will generate a plot for the first series and superimpose a red line plot for the second time series. The `type` option is specified to give lines (rather than e.g. a sequence of points). The `ylim` option sets the limits for the y axis, making sure that both time series are included in the plotting area.

```
plot(a, xlab="Time", ylab="Population size", type="l", ylim=c(0,200))
lines(b, col="Red")
```

A legend can be added to this plot to identify its two components:

```
legend(70,30,legend=c("Population a","Population b"), fill=c("Black","Red"))
```

Here, the first two numbers specify the position of the legend (x, y in the scale of the plot's axes), `legend` specifies the text that will appear next to each item, and `fill` specifies the colors.

4. R ingredients

5. Practical tasks

■1■ Read carefully the material in sections 1-3 above.
■2■ Read through the tasks in this section
■3■ Decide on the important and useful facts from sections 1-3 that you will need in dealing with the tasks

Model 1: Deterministic, density dependent prey model
■4■ Adapt your code for Model 2 in practical 5 to obtain a model for the sandeel population. Due to the large size of the prey population, we will ignore demographic stochasticity. Assume that sandeels mature at age 2 and that the population sex ratio is 1:1. It is therefore a good idea to model only females explicitly, within a three-stage Leslie model.
■5■ We will now assume that, within the patches of sandy sediment, the fecundity of females suffers as a result of crowding <u>by all ages and both sexes</u>. Add density dependence in prey fecundity (use eq. (4) from practical I) with the value $\beta = 100000$.
■6■ Use the following population structure as initial conditions to your simulation : $\mathbf{P}_1 = \{0,0,10\}$ (i.e. ten adult females in the 1st year).
■7■ Generate a 100-year time series plot of all three classes of prey.
■8■ Record sandeel population structure in years 5, 10, 20, 100. This should give you four, vectors, each of length three. Plot these as pie charts of prey availability.

Model 2: Functional response
■9■ Write an R function that implements a three-species functional response. The function must take as its input the abundance of the three prey and produce the consumption of each prey by the predator. Use the following parameter values $\mathbf{a} = \{10,30,40\}, \mathbf{t} = \{0.01,0.01,0.01\}, \mathbf{m} = \{1,2,2\}$.
Assume that,

- These parameters will yield annual prey consumption (in units of thousands of fish) by each seal.
- There are no differences in the functional response of different seal classes

■10■ Plot these estimates of diet as pie charts (One for each of the years 5,10, 20 & 100).

5. Practical tasks

6. Assessment

Write a report no longer than 3 pages of A4 (single-spaced, Times Roman, 12pt) containing the following:

Model 1 (50% of mark):

■1■ A mathematical and diagrammatic description of your population model.

■2■ A time series plot of total population size also showing all three components of the population in the first 100 years

■3■ A table of population structure at years 5, 10, 20 and 100.

Model 2 (40% of mark):

■4■ Pie charts of prey availability and seal diet in years 5,10, 20 and 100.

■5■ Briefly comment on how diet changes with changes in relative prey availability.

■6■ Attach your code at the end of the 3 pages as an Appendix.