Spatial Patterning in Resource Exploitation and Conservation [and Discussion]

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Spatial patterning in resource exploitation and conservation

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SUMMARY

Marine and terrestrial ecosystems share the feature that resources are often patchily distributed over space or time. Thus, we must develop methods to predict how organisms will respond to pattern. One method is described and illustrated with examples of the harvesting of krill in the southern oceans and predicting the spread and intensity of pest infestations.

1. INTRODUCTION

A commonality of marine and terrestrial ecosystems is that resources are often patchily distributed over time or space. Here, I focus on a wide range of spatial scales, keeping in mind that these are determined by the organism of interest. In particular, successful management requires that we not only describe spatial pattern (see Fasham *et al.* 1978), but are able to predict how organisms will respond to it. I consider two problems in resource conservation and management: (i) harvesting and protection of southern ocean krill; and (ii) predicting the spread and intensity of an infestation of fruit flies of economic importance. One involves a marine ecosystem in which the scales of interest are of the order of kilometres and the other a terrestrial ecosystem in which the scales are of the order of metres. The commonality is the spatial structure of the resource as it affects the behaviour of the exploiter. A correct consideration of spatial structure is essential because if the size of study units is arbitrary rather than based upon a scale appropriate to the organism, problems arise (Addicott *et al.* 1987; Wiens & Milne 1989; Kareiva 1991). First, it is difficult or impossible to compare across species or systems. Second, a given patch size need not necessarily correspond to the particular ecological neighbourhood appropriate for examining a given ecological problem (Rosenheim *et al.* 1989). Third, because different processes may occur at different scales, it may not be sufficient to examine the system at a single scale.

2. KRILL CONSERVATION: 'PATCHES WITHIN PATCHES'

Krill (*Euphausia superba*) are the centre of the southern ocean food web (Miller & Hampton 1989*a*; Everson 1992). Over the past twenty years a commercial fishery developed for krill and now harvests about 400 000 metric tons per year. Many seabirds and marine mammals have krill as a main dietary source. It is clear that marine mammals and seabirds respond to krill distribution (e.g. Fraser *et al.* 1989; Hunt *et al.* 1992) and that in many cases the fishery is removing exactly the same organisms that the marine mammals or birds eat (Croxall 1987). Although in some circles the virtual destruction of the great whales is viewed as a source of a 'krill surplus', there is concern about the recovery of whale stocks, the maintenance of marine mammals and birds, and the interactions with the fishery (e.g. Yamanaka 1983). These concerns broadly involve the status of the krill stock and the spatial distribution of the catch. For example, since 1988, the vast majority of the commercial krill catch has occurred within 100 km (and often within 50 km) of major seabird colonies.

To address these kinds of concerns, Butterworth (1989) and I (Mangel 1989) developed models for the krill fisheries with a number of spatial and temporal scales (table 1). Although on short timescales there is variability in krill patterning (Everson & Goss 1991), the persistence of high density concentrations is evidenced by repeated fishing in the same spatial areas over different years (figure 1). Based on the data collected during the first and second Biomass Experiments, we constructed a model for the spatial patterning of krill in a large sector of the ocean that had individual krill aggregating into swarms and swarms into concentrations (foci for fishing). The model compared favourably with observations (Levin *et al.* 1989). We showed that a good index of abundance is catch/towtime/searchtime (Butterworth 1989; Mangel 1989). This index has a foundation in search theory (Mangel 1985) as catch/towtime is a measure of krill density within swarms and 1/searchtime is a rough measure of the abundance of swarms. One of the difficulties with constructing this measure from stan-

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Table 1. *Spatial and temporal scales of krill fisheries*

unit	spatial scale	temporal scale
individual krill	0.05 m	1–7 years
swarm of krill	1–100 m	10–70 h
patch of swarms	1000–100 000 m	days–months
concentrations of patches	> 100 000	months

dard log-book data (Mangel 1990) is that we often have no indication of the amount of searching conducted by vessels between fishing events. That is, we recognize that vessels have moved some distance in an interval of time but do not know why they moved or what they encountered during the movement. In § 5, I shall show how the methods developed here could be used to shed light on this question.

3. AGRICULTURAL PEST CONTROL: THE BEHAVIOURAL ECOLOGY OF TEPHRITID FRUIT FLIES

Tephritid fruit flies (Prokopy & Roitberg 1984) cause considerable damage each year (Mangel *et al.* 1986) and it has become clear that behavioural controls provide a true alternative to chemical pesticides (Roitberg & Angerilli 1986). However, we actually know remarkably little about the causes of the spread of pest infestations. We are conducting a long-term study of the host choice and patterning of egg laying in the fly *Rhagoletis basiola*, which attacks the wild roses. For this reason *R. basiola* is not an economic pest, but it is a congener of the apple maggot fly *R. pomonella* so that what we learn about the behaviour and control of this fly should be transferable to pest control.

Adults are free ranging and live for about three weeks. In southwestern British Columbia, they emerge in late July just as the fruit are ripening. The fruit are clustered, with up to seven fruit in a single cluster, but usually between two and five fruit in a cluster. Clusters are spatially aggregated. A female typically lays about ten eggs per day, usually one egg per fruit. After laying an egg, she drags her ovipositor across the fruit, marking it with a pheromone. After landing on a fruit, a female walks around it a number of times; tarsal receptors respond to marking pheromone and in this way she can determine if the fruit has been previously parasitized. On occasion, females will superparasitize and lay an egg in a previously parasitized fruit, even though only one offspring will emerge from the host. In the wild, the main sources of mortality of adult flies are strong rain storms, birds and spiders. The main source of mortality of the eggs is the parasitoid *Halticoptera rosae*, which uses *R. basiola* marking pheromone and fruit wound chemicals to find eggs (Roitberg & Lalonde 1991).

Our field work is motivated by the observation that *Rhagoletis* spp. often do not attack apparently perfectly healthy, unparasitized fruit. For example, the apple maggot fly in a semi-natural setting exploited only between 5% and 30% of the uninfested hosts (Roitberg *et al.* 1982); in 1992 we observed a similar phenomenon with flies attacking wild roses. For example, although all clusters of seven fruit had at least one egg in them, most (55%) had only one fruit of the seven attacked and 90% of the clusters had three or fewer eggs. Similar phenomena have been observed in other species (Strong 1988; Thompson 1987). Such behaviour clearly has important effects on the determination of damage caused by tephritid fruit flies and on the spread of the infestation. Although we understand why flies might accept a previously parasitized host (Mangel 1987; Roitberg & Mangel 1988), it remains enigmatic that flies should not lay eggs in perfectly fine hosts. To say they are 'spreading the risk' describes the phenomenon, but does not provide a functional explanation for their behaviour. In § 5, I will explore the possibility that it

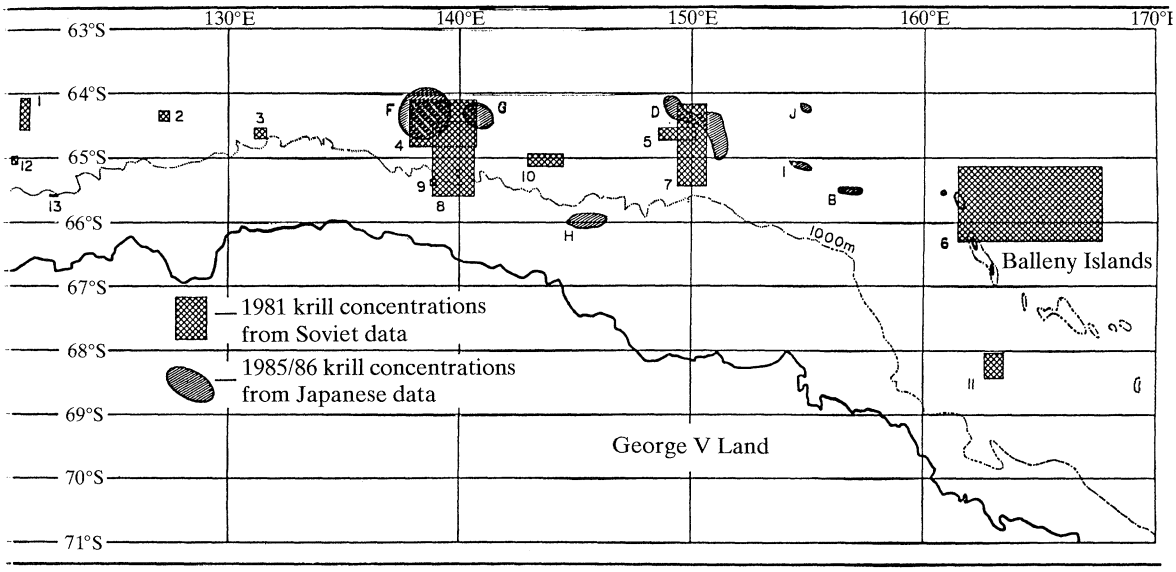

Figure 1. The evidence for the persistence of large concentrations of krill based on repeated fishing by Soviet and Japanese fleets.

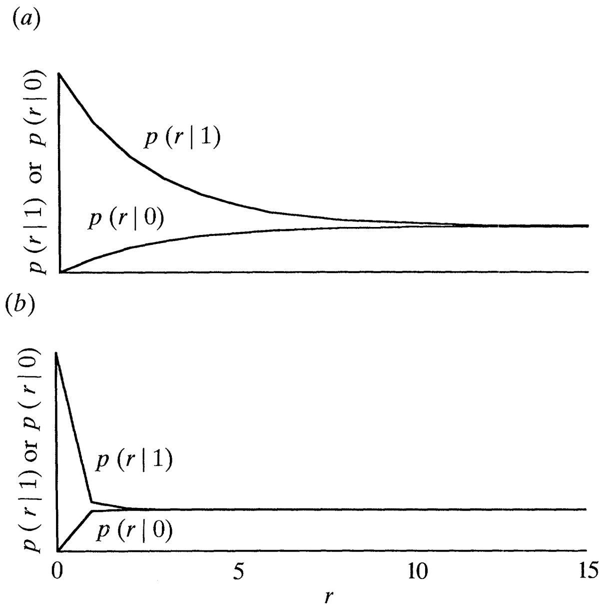

Figure 2. Structure functions generated by a one-dimensional Markov process. (*a*) $p_1=0.75$, $p_0=0.075$ so that $p_a=0.231$; (*b*) $p=0.25$, $p_0=0.02$ so that $p_a=0.211$. As described in the text, the upper limit for the ordinate is 1 and the lower limit is 0.

is the interactions with organisms at different trophic levels (hosts and parasitoids) that structure the behaviour of the fly. To do so, we must be able to describe the spatial characteristics of the fruit in a manner that allows those characteristics to interact with the behaviour of the fly.

4. THE STRUCTURE FUNCTION AS A UNIFYING CONCEPT ACROSS MARINE AND TERRESTRIAL ECOSYSTEMS

Imagine that space is divided into discrete cells. An organism foraging for spatially structured resources has global information concerning the overall density of the resource in the environment and local information concerning the likelihood that there is resource in a cell r units away, given the resource state at the current cell. This local information constitutes the structure function:

$p(r|1) = \text{Prob}\{$resource in a cell r units away, given that there is resource at the current cell$\}$,

$p(r|0) = \text{Prob}\{$resource in a cell r units away, given that there is no resource at the current cell$\}$. (1)

If p_a is the average density of resource in the environment, then

$$p_a p(r|1) + (1-p_a)p(r|0) = p_a, \tag{2}$$

so that

$$p(r|0) = \frac{p_a(1-p(r|1))}{1-p_a}. \tag{3}$$

If the spatial structure is generated by a first order Markov process,

$$p_1 = \text{Prob}\{Z(r+1)=1|Z(r)=1\},$$

$$p_0 = \text{Prob}\{Z(r+1)=1|Z(r)=0\}, \tag{4}$$

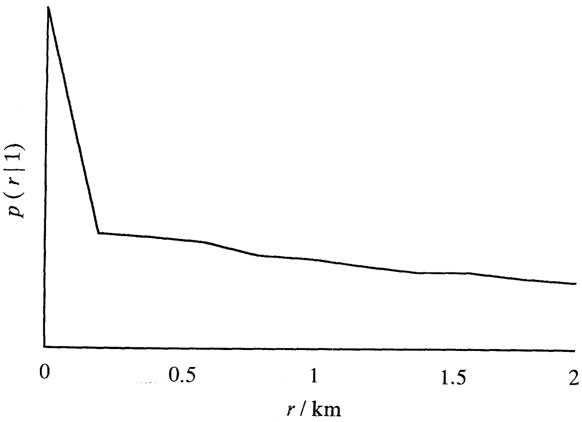

Figure 3. The structure function for krill aggregations (Miller & Hampton 1989*b*; Butterworth *et al.* 1991).

with

$$p_a p_1 + (1-p_a)p_0 = p_a, \tag{5}$$

the structure function is (Mangel & Adler 1994)

$$p(r|1) = p_a + (1-p_a)(p_1-p_0)^r. \tag{6}$$

This structure function (figure 2) these gives a hint of what will follow in the next section. An organism moving in the world characterized by figure 2*a* will most likely behave quite differently from an organism moving in the world characterized by figure 2*b*. For example, we might predict long distance moves from a cell devoid of resources if the structure function is as in figure 2*a*, but short moves if the situation is as in figure 2*b* (O'Brien *et al.* 1990).

The construction of structure functions from higher order processes, in two or three dimensions, or empirical data is more difficult (Mangel & Adler 1994). The structure functions for krill (figure 3) and rose hips (figure 4) give a sense of how the resources are structured on the scale appropriate to the organism exploiting the resource.

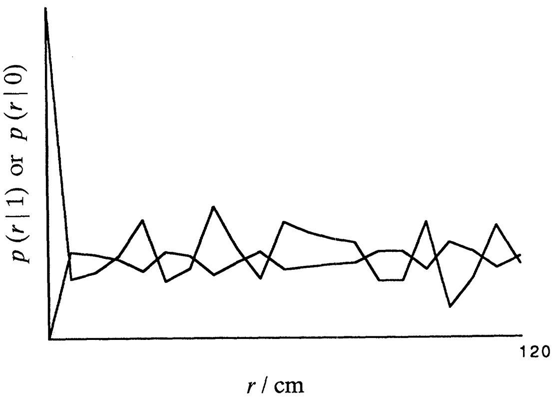

Figure 4. The structure function for clusters of rose hips on bushes in southwestern British Columbia. Note the 'peaks' and 'valleys' in the structure function; there is a refractory distance such that close to a cluster it is less likely than average to find another cluster. A structure function such as this one implicitly involves global information; the structure function summarizes global information in a local format.

5. PREDICTING SPATIAL AND TEMPORAL BEHAVIOURS

Once we have described spatial pattern, we must consider how organisms respond to it.

(*a*) *The movement of fishing vessels*

Let us begin by considering the movement between sets of vessels fishing for krill. As described above, it is difficult to reconstruct from log-book data alone the amount of search (time or distance) between fishing events. We can, however, develop a model for the movement of vessels. Suppose that the process of fishing for krill disrupts the structure of krill swarms in the vicinity of the point being fished. If $f(r)$ is the probability that krill swarms at distance r from the current fishing site are disrupted by fishing, then $p(r|1)(1-f(r))$ is the probability that there are krill at distance r from the current site and they are not disrupted. We thus predict that vessels will move the distance r^* that maximizes this product before starting to search for krill again. This information allows to understand the small scale movement of vessels (cf. Everson & Goss 1991) and estimate search distance or time between fishing events.

(*b*) *The movement and intensity of pest infestations*

To predict the spread and intensity of a pest infestation, we must link spatial pattern and behaviour. Ignoring egg complement as a state variable we still must consider search speed (v), mortality during search (m) and oviposition (m_o), and the increment in lifetime reproduction obtained by laying a clutch of size $c(R(c))$, taking density dependence due to the parasitoid into account.

The behavioural landscape (Mangel 1991; Mangel & Ludwig 1992) can be summarized by how far to move from a point devoid of resources (k_0), how far to move from a point containing resources (k_1) and the clutch to lay in a cluster (c). Lifetime reproductive success is accumulated through oviposition. Although we have ignored egg complement, spatial location is a state variable. To characterize reproductive success requires:

$F_0(t;k_0,k_1,c)$ = expected reproductive success from time t onwards, for a fly currently at a cell devoid of hosts and following $\{k_0,k_1,c\}$

$F_1(t;k_0,k_1,c)$ = expected reproductive success from time t onwards, for a fly currently at a cell containing of hosts, before it has oviposited, and following $\{k_0,k_1,c\}$.

These fitness functions satisfy iteration equations, in which fitness in one period is linked to that in the next. For a fly currently at a cell devoid of resources

$$F_0(t;k_0,k_1,c) = (1-m)^{k_0/v}\,[p(k_0|0)F_1(t+k_0/v;k_0,k_1,c) + (1-p(k_0|0))F_0(t+k_0/v;k_0,k_1,c)]. \quad (7)$$

That is, from a cell without resources, the fly either moves to one with resources, with probability $p(k_0|0)$, or to one without resources, with probability $1-p(k_0|0)$. Either of these moves takes time k_0/v, so that the fly survives the move with probability $(1-m)^{k_0/v}$. From a point with hosts, future reproductive success is $F_1(t+k_0/v;k_0,k_1,c)$ and from a point devoid of hosts, future reproductive success is $F_0(t+k_0/v;k_0,k_1,c)$.

The equation characterizing the reproductive success of a fly currently at a cell with hosts must include the gain in reproductive success following oviposition and the additional possible mortality during the oviposition:

$$F_1(t;k_0,k_1,c) = R(c) + (1-m_o)(1-m)^{k_1/v}\,[p(k_1|0)F_1(t+k_1/v;k_0,k_1,c) + (1-p(k_1|0))F_1(t+k_1/v;k_0,k_2,c)]. \quad (8)$$

If the end of the reproductive interval is far away, we can consider the stationary (Mangel & Clark 1988) solutions F_{1s},F_{0s} of equations (7) and (8). The average stationary reproductive success is obtained by averaging over possible starting points.

A typical result, for a Markovian structure function is that the optimal values are $k_0{}^*=2$, $k_1{}^*=1$ and $c^*=2$. Thus a fly following the optimal behaviour will not lay eggs in all the hosts in a cluster and will move greater distances from cells devoid of hosts than from cells containing hosts. In addition, there is a very gradual decline of $F_{0s}(k_0,k_1,c)$ for $k_0>2$ but $F_{1s}(k_0,k_1,c)$ drops more sharply as k_1 increases. From this we could conclude that selection pressure on movement from cells containing hosts is stronger than the selection pressure on movement from cells devoid of hosts. Similarly, although $c^*=2$, clutches of size $c=3$ are almost nearly optimal in fitness and those of size $c=1$ or $c=4$ are only slightly less optimal; only a clutch of size 5 is highly suboptimal. These results depend upon both the spatial structure of the resource and the intensity of parasitism ($R(c)$). We can predict the movement pattern of the fly and the intensity of the pest infestation and are now in a position to manage it.

The theory developed here provides additional understanding of behavioural processes. For example, insects are often said to exhibit 'area restricted search', in which movement distances from a point devoid of resources are greater than those from a point containing resources. Viewing $F_{0s}(k_0,k_1,c)$ as a function of k_0, with k_1 and c at their optimal values, the animal will exhibit area restricted search or not according to whether the derivative of $F_{0s}(k_0,k_1,c)$ at $k_0=1$ is positive or not, because if this derivative is positive, the animal can increase its reproductive success by continuing to move.

6. CONCLUSION

A commonality of terrestrial and marine ecosystems is the principle of considering the organism in its environment at the correct spatial scale provided. It has two implications. First, the organisms living in such systems and exploiting those systems deal with resources that are spatially structured. Second, we must consider how spatial structure affects their behaviour and fitness. Descriptors such as the semivariogram are highly aggregated and summarized; they do not provide information which the organism can use at a local level to determine behaviour. Structure functions provide sufficient information about the spatial structure of the world because they link global and local information. We must develop methods for incorporating pattern into the descriptions of the behaviour of the organism of interest. Dynamic iteration methods provide a powerful tool for linking ecological and physiological or ecological and operational factors within a consistent framework. Although optimal behaviours are important, we must consider fitness surfaces. Finally, to recognize commonalities across terrestrial and marine ecosystems, we must avoid a taxonomic bias and must focus on problems. It is only by thoroughly and deeply examining problems that we shall begin to see common features that otherwise might elude us. And by seeing these features, we shall be able to forge links between apparently disparate systems.

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Discussion

J. R. Beddington (*Renewable Resources Assessment Group, Imperial College of Science, Technology and Medicine, U.K.*). In the fishery for krill, very different patterns of fishing occur. The former U.S.S.R. fleet has fished with scouting vessels which locate krill concentrations and call in additional boats to fish the concentration. The Japanese fish as individual vessels. Is it possible to assess for given krill distributions in what circumstances are these different strategies optimal?

M. Mangel. It is exactly correct that methods analogous to the ones described here can be used to determine the optimal fishing strategy, conditioned on a particular spatial distribution of krill. To do so, one needs to specify the spatial structure of the krill population by using the structure function and an optimization criterion such as maximizing expected catch or expected profit (taking movement costs into account). The optimal movement rules are then determined as described in the text. In addition, one can assess (measured, for example, in total expected catch or profit) the suboptimality of alternative strategies.