Fish harvesting, marine reserves, and distribution of individuals over space

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Abstract: We analysed exploitation of populations that are partly protected in a marine harvest refuge to prevent their over-harvesting in the remaining unprotected area. We carried out our analysis by introducing the model of ideal free distribution to the population renewal process. In the model, individuals in the target population are distributed so that per capita resource availability becomes matched in the harvested and non-harvested areas. We show that the yield from the harvest effort is strongly affected by the fraction of area protected from harvesting. The harvest effort maximising the yield depends on the relative size of the protected area. Maximum yield is independent of the size of the protected area unless the fraction is > 0.56. If this value is exceeded, annual yield declines rapidly with increasing protected fraction. However, our major – and somewhat surprising – finding is that protected areas can be established without any loss to commercial harvesting if harvesting follows reproduction and population densities are balanced between harvesting seasons according to resource availability.

Key words: spatial population dynamics, habitat selection, spill-over effect, marine reserve, no-take zone, marine harvest refuge

INTRODUCTION

Worldwide depletion of many commercially exploited natural populations, especially in marine habitats (LUDWIG et al. 1993, HUTCHINGS 2000), has led managers and conservation biologists to propose new concepts for saving depleting and endangered resources. Marine reserves or marine harvest refuges are one method to protect target populations from over-exploitation (DIAMOND & MAY 1976, GAME 1980, DEMARTINI 1993, BOTSFORD et al. 1997, ROBERTS 1997a, 1998, MANGEL 1998, 2000, HASTINGS & BOTSFORD 1999, LUNDBERG & JONZÉN 1999, ACOSTA 2002, LOCKWOOD et al. 2002, LUBCHENKO et al. 2003). In this method, a certain fraction

of the distribution range of the target population is set aside from utilisation, while harvesting takes place outside this refuge. Marine reserves take an explicit spatial approach of population ecology to address the problem of population over-exploitation. Hence, it calls for a spatial ecology approach to analyse the usefulness of the concept.

The ecological basis of marine reserves and other comparable conservation areas relies on the assumption that a fraction of the target population remains out of reach of harvesting in the protected areas. One model explaining how individuals should be distributed in a habitat, where sub-areas may differ in terms of profitability, is based on the concept of ideal-free distribution, IFD (FRETWELL & LUCAS 1970, FRETWELL 1972) or the theory of resource/habitat matching (PARKER 1974, MORRIS 1994). IFD models predict that individuals should distribute themselves in a habitat so that per capita fitness will become equal regardless of the spatial unit an individual resides in. Under such circumstances accessible resources will be used so that moving elsewhere will not increase the fitness of an individual. The model is *ideal* as the distribution and value of accessible resources are common knowledge and the individuals are *free* to choose any sub-area with its resources. The resulting distribution of individuals, via a fitness-equalising process, is referred to as an ideal free distribution (FRETWELL & LUCAS 1970).

FRETWELL (1972) introduced also ideal despotic distribution, IDD, to model population distributions of territorial birds. Here, each bird arriving in an area of habitable patches differing in resource availability can assess the value of the patches but is not free to settle into those already occupied. Although despotism can be expected to be common in many natural situations, including fish (e.g., HUNTINGFORD & TURNER 1987), we do not address this model here. In its simplest form, the only prediction of IDD that is not common to IFD is that territory ownership will lead to differential success of otherwise equal competitors (TREGENZA 1995). Thus, we do not expect IDD to have crucial effect on a spatial scale of marine reserves.

Recently, LUNDBERG & JONZÉN (1999) presented a study that combined the idea of harvest-free areas with the ecological model of IFD. They divided the area occupied by a population into two sub-areas: one where the target population was subject to harvesting (harvested area) and one where harvesting was not allowed (protected area). They assumed that the driving force behind redistribution of individuals is fitness-equalisation in the protected and non-protected areas. In this scenario, IFD is reached when individuals both in the protected and harvested area have equal fitness.

LUNDBERG & JONZÉN (1999) assume that the fitness includes two components: reproduction at a certain population density and harvesting mortality in the harvested area. Fish in the protected area do not suffer from harvesting mortality. This scenario leads to a situation where the population density is lower in the harvested area: lower population density increases reproductive success, thus compensating for the decreased reproductive success due to harvesting. It is noteworthy that the density differences between the areas do not tend to decrease between harvesting seasons. This scenario embeds an important assumption: the individuals in the population are influenced by harvesting, and consequently, choose their place of residence on the basis of the density of conspecifics.

Alternatively, distribution of individuals across a landscape may be conditioned by resource availability. In the case of harvest refuge, we may argue that the target population may tend to redistribute between the harvesting seasons (after reproduction and harvesting, before the next reproductive bout) so that the population densities become equalised between the harvested and protected areas. Thus, in this case, the driving force is not in the fitness components as such (in the sense of LUNDBERG & JONZÉN 1999), but in the distribution of resources necessary for fish, such as spawning sites, food, space, etc., which are here assumed to be distributed evenly over space. The outcome, known as resource matching (PARKER 1974, MORRIS 1994), is that in the beginning of each season, distribution of individuals matches resource availability in different areas, i.e., areas with rich resources harbour more individuals than resource-lean areas. That fish may distribute according to the resource--matching model has been verified in laboratory experiments, e.g., by MILINSKI (1979, 1984), GRAND & GRANT (1994), GRAND (1997) and TYLER & GILLIAM (1995), but rarely in the field (POWER 1984).

We set out here to study the significance of the protected area when the ecological mechanism behind the dispersal of individuals is based on the concept of resource matching. As in LUNDBERG & JONZÉN (1999), we divide the distribution range of the target population into two: an area where harvesting is allowed and a protected area with no harvesting. The individuals reproduce in both areas, and are harvested only in the harvested area. However, unlike in LUNDBERG & JONZÉN (1999), the population densities will be balanced between harvesting seasons according to resource availability.

MATERIAL AND METHODS

Assume that a population that is a target of commercial harvesting occupies a distribution range A in a homogenous environment. A fraction c of that range is protected from harvesting while the fraction $(1-c)$ is accessible for harvesting. During reproduction, the population densities are updated according to Ricker dynamics:

$$
\begin{aligned}
X_R'(t) &= X_R(t)\lambda_R \, \exp\left[-a_R X_R(t)\right] \\
X_H'(t) &= X_H(t)\lambda_H \, \exp\left[-a_H X_H(t)\right] - E X_H(t) \, ,
\end{aligned}
\tag{1}
$$

where X_R and X_H are population densities in the refuge (R) and in the harvested area (H), respectively; a_R and a_H are parameters; λ_R and λ_H are the population growth rates in different areas; and E is the harvest effort (LUNDBERG & JONZÉN 1999). The corresponding population sizes are given as follows:

$$
\begin{aligned}
N_R'(t) &= cAX_R'(t) \\
N_H'(t) &= (1-c)AX_H'(t) \, .
\end{aligned}
\tag{2}
$$

We next assume that redistribution of individuals takes place after reproduction and harvesting, so that the population densities will be balanced according to

resource matching. Since in our model the resources are evenly distributed over space, at this point of time the population densities will be updated as follows:

$$X_R(t + 1) = X_H(t + 1) =$$
$$[N_R'(t) + N_N'(t)] / A =$$
$$cX_R(t)\lambda_R \exp[-a_R X_R(t)] + (1 - c)\{X_H(t)\lambda_H \exp[-a_H X_H(t)] - EX_H(t)\}.$$

(3)

Equations (1)-(3) define the temporal dynamics of the population densities from time t to $t + 1$. At equilibrium, we get

$$1 = c\lambda_1 \exp[-a_1 X] + (1 - c)\{\lambda_2 \exp[-a_2 X] - E\}.$$

(4)

Assume that $a_R = a_H = a$. We have the population density

$$X = \frac{\ln\left[\dfrac{1 + (1 - c)E}{c\lambda_R + (1 - c)\lambda_H}\right]}{-a}$$

(5)

and the yield Y is given as

$$Y = (1 - c)AEX$$

(6)

The fitness in the two areas is determined by the phase of reproduction, followed by harvesting mortality. Redistribution does not affect fitness, as neither mortality nor reproduction occurs during this phase. Thus, the fitness in the protected and harvested areas are given as

$$\lambda_R \exp(-a_R X_R)$$
$$\lambda_H \exp(-a_H X_H) - E,$$

(7)

respectively. Since in our model $X_R = X_H$ and both growth rates (λ's) and a's are equal, the fitness in the harvested area is lower than in the protected area.

RESULTS

It follows from the process of redistribution, eq. (5), that the proportion of the population in the protected area is not dependent on harvesting but is determined only by parameter c defining the protected fraction.

Population size in the two areas depends both on the size of the protected area and the harvest effort, eq. (7). When $c = 1$ (no harvesting), the population density in our example ($a_R = a_H = 0.002$, $\lambda_R = \lambda_H = 2$) is ca. 350. When only part of the area is protected ($c < 1$) the population density decreases with increasing harvest effort (Fig. 1A).
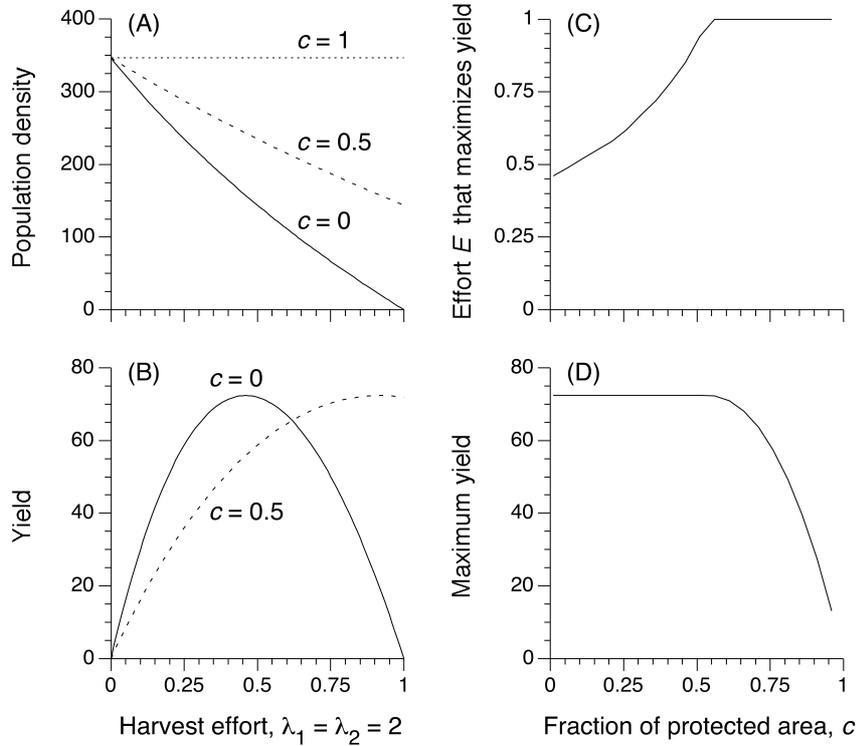
Fig. 1. (A) Population densities as a function of harvest effort, E. When the reproductive conditions in each area are homogeneous, ideal free distribution is achieved when the population densities are equal in each area and fitness is equal to one. (B) The shape of the yield curve as a function of the harvest effort depends on the size of the protected area, c. (C) The harvest effort maximising the yield depends on the size of the protected area. (D) The maximum yield is insensitive to small protection fractions but may decline rapidly for too large protected areas

The shape of the yield curve as a function of harvest effort E depends on the protected fraction of the population. For example, when there is no harvest refuge ($c = 0$) the optimal harvest effort is ≈ 0.46. Increasing the size of the reserve area allows a higher fishing effort (Fig. 1B). The proportion of the protected area determines the harvest effort that maximises the yield. As the proportion of the area where fishing is not allowed increases, also the effort giving the largest yield increases and reaches the value of 1 at a threshold value of $c \approx 0.56$ (Fig. 1C). Our results also show that the maximum yield is stable and unaffected by the protected fraction of the area for small values of c, but at values of c exceeding 0.56, the maximum achievable yield will collapse rapidly (Fig. 1D).

We can summarise our results by stating simply that harvest refuges can be established without any loss to commercial harvesting. This is, of course, valid if (1) the size of the protected area in comparison to the size of harvested area is not too large (i.e., $c < 0.56$); (2) harvesting follows reproduction; and (3) population densities are balanced between harvesting seasons according to resource availability.

DISCUSSION

We have used a new approach using resource-matching IFD to model population management where it is possible to protect a part of the population in conservation areas. It is a fair assumption (often supported with real data, e.g., MILINSKI & PARKER 1991) that competing animals can disperse in space according to resource availability. In systems where this kind of distribution is important, we may need to add ecological knowledge to our understanding of how the populations change over time. Spatial distribution of animals has been a target of research for a while (e.g., BASCOMPTE & SOLÉ 1997, TILMAN & KAREIVA 1997, BJØRNSTAD et al. 1999, DIECKMANN et al. 2000). One basic component of spatial population structure is ideal free distribution, which can largely explain the distribution patterns of animals where areas differ in profitability. We have acknowledged, however, that driving forces behind the IFD process may be different. Thus, the choice of a particular IFD model may depend on the application. It is important to understand that the choice of the IFD model may affect the qualitative conclusions to be drawn from the analysis.

The importance of the choice of the IFD model is clearly seen when we compare our results with those obtained by LUNDBERG & JONZÉN (1999). They showed that the proportion of the population in the protected area increases with increasing fishing effort. (They failed to note, however, that the population size in the protected area actually remains constant and the difference is due to the depletion of the harvested population.) They also showed that optimal harvest effort is independent of the size of the protected area relative to the harvested area. Our results are different. In particular, we have shown that the shape of the yield curve as a function of harvest effort may crucially depend on the protected fraction of the area. Thus, the harvest effort maximising the yield may also be strongly dependent on the protected fraction. This will most probably have direct effects on the maximum yield available in each setting.

A careful reading of the model of LUNDBERG & JONZÉN (1999) reveals that the fitness component in their model includes fishing mortality. While this is a profound assumption, earlier presented by KAITALA & GETZ (1995), it also implies that the movements of individuals are affected by harvesting, or there are some evolutionary mechanisms, related to fishing mortality, restricting the movements between the areas. Furthermore, we can argue that there may be alternative driving forces behind the IFD, such as redistributing according to food resources or available space, which may affect the distribution of individuals. In a homogeneous environment, the latter results in equalisation of population densities among the areas before harvest. The redistribution of individuals between protected and harvested areas could be especially likely if there is, for example, an ice cover for a certain period of time during the year, hindering the harvesting. In such a case, it seems very likely that individuals would not be affected by harvest pressure when choosing their location, but redistribute more or less evenly during the non-harvesting period.

Applying IFD models in resource management may be feasible only when there is a cost-free flow of individuals across the reserve border and when despotic territorial behaviour is not present. This so-called spill-over effect has recently received some attention (CARR & REED 1993, ROBERTS 1997b, 1998, MCCLANAHAN & KAUN-

DRA-ARARA 1996, LAUCK et al. 1998, LUNDBERG & JONZÉN 1999). Our model, with the redistribution of individuals between harvesting seasons, includes the spill-over effect as individuals spill over also in the harvested area, and do not stay in the protected area only. If the IFD assumptions used do not apply, the conclusions may change. Such a case may arise when only a fraction of the population may disperse, or when dispersal is insufficient to balance sub-populations, or when the animals behave according to an ideal despotic manner. This would, however, require a considerable spatial heterogeneity in favour of the protected area, or alternatively very poor reproduction in the protected area.

We have analysed a resource management policy that includes the spatial component in terms of conservation areas. Such a policy can be viewed as an alternative to proportional threshold harvest policies that, by definition, have a conservation aspect included in it in the form of protecting populations (e.g., KAITALA et al. 2003). Whether spatial conservation is superior to threshold conservation remains unknown, mainly due to the underdevelopment of the theory and practice of spatial conservation policy.

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