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Modelling carrying capacity dynamics for the conservation and management of territorial salmonids

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ABSTRACT

Inherent in the carrying capacity notion is the basic idea of a maximum population a particular level of resources can support over a period of time. Knowledge of carrying capacity is essential for wildlife conservation since it is intrinsic in determining how much habitat must be conserved to maintain healthy populations. Further, this concept has been the cornerstone of the management of exploited animal and plant populations. Yet the question about what determines carrying capacity for territorial species and how it can be quantified has been long neglected by ecological research. We propose a novel method to model carrying capacity dynamics for territorial salmonids, which can be further applied to any territorial species as long as they are principally limited by habitat conditions. In our model, maximum abundance is limited by environmentally induced fluctuating habitat conditions and regulated through territorial behaviour. Carrying capacity is estimated as the amount of habitat available divided by the expected individual territory area for a given life stage. We tested whether the model was capable of explaining the annual fluctuations in densities of brown trout *Salmo trutta* from 12 Mediterranean populations for a 12-year study period. We observed not only that density of the different life stages tracked carrying capacity dynamics, but also that the eventual cohort performance was affected by both intercohort competition and intensity of intracohort competition experienced in the previous year. Likewise, recruitment depended on the levels of carrying capacity saturation experienced by adult stock the year before. In any case, resilience decreased with carrying capacity. Such results suggest that restoration measures attempting to increase population abundance through stocking, increased breeding dispersion or cohort survival may reduce the performance of both the enhanced and competing cohorts. Further, high exploitation rates may lead populations occurring at low carrying capacities to extinction.

1. Introduction

Carrying capacity has been defined in many different ways (e.g. see reviews by del Monte-Luna et al., 2004; Pulliam and Haddad, 1994), so that its concept has remained controversial and elusive, to the point that there is a great uncertainty about how it should be used and measured and, indeed, what information can be inferred from it for wildlife conservation and management (Goss-Custard et al., 2002). Nevertheless, inherent in the carrying capacity notion is the basic idea of a maximum population that can be supported over a period of time for a particular level of resources. But carrying capacity is not a static number. Because both available resources and the requirements of a species change over time, carrying capacity is always changing, across seasons, years and through ontogeny. Population numbers of animals are therefore never constant from year to year, but rather fluctuate around an inter-annual mean carrying capacity that reflects the average environmental conditions over the long term (Jonsson and Jonsson, 2011). However, the carrying capacity of an environment is not only determined by the abundance and distribution of limited resources but also by how individuals compete for their use. This notion is especially relevant in organisms that compete via both exploitation and interference because behavioural responses induced by aggressive interactions typically result in a much reduced exploitation of the limited resource than could be accounted for by resource depletion alone (Begon et al., 2006). In territorial species, the behavioural adjustment of the size and shape of territories has profound consequences for their population regulation, demography, and spatial ecology (Adams, 2001). Yet, surprisingly, the question about what determines the carrying capacity for territorial species has been long neglected by ecological research (López-Sepulcre and Kokko, 2005).

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The concept of carrying capacity has played an important role in the study and management of animal and plant populations, being the cornerstone of the management of exploited renewable resources (Hilborn et al., 1995). Harvest models need specific information on carrying capacity, maximum population growth rate and abundance to estimate the maximum sustainable yield (Sibly et al., 2003). When the management goal lies in the conservancy side, estimation of carrying capacity provides a basis for evaluating the conservation status of populations and for assessing the changes in population dynamics resulting from anthropogenic impacts (Ayllón et al., 2012). Regarding fish population management, carrying capacity is needed to determine the target spawning escapement (Elliott and Elliott, 2006), the size of fish passage facilities (Clay, 1995), the optimal allocation of instream flow (Cardwell et al., 1996) or the probability of population persistence (Hilderbrand, 2003), as well as to calibrate population dynamics models (e.g., Dumas and Prouzet, 2003; Sabaton et al., 1997).

Carrying capacity is therefore an essential parameter in population management and modelling, though it is rarely estimated since it is extremely difficult to quantify (Morris and Mukherjee, 2007). The traditional approach to determining carrying capacity for anadromous salmonids has been through stock-recruitment analysis (Potter et al., 2003). However, this approach has proven to be imprecise in most cases since it requires long-time data series including a wide range of run sizes, which are usually not available in the majority of salmonid populations (Cramer and Ackerman, 2009). Carrying capacity for both stream-dwelling and anadromous salmonids has also been estimated from historical maximum habitat occupancies (e.g., Capra et al., 2003; Dumas and Prouzet, 2003). This approach is also burdened with the necessity of long data series and estimates of carrying capacity may be biased by extraordinary explosions in population numbers that may not reflect a long-term sustainable level. In addition, historical values of maximum habitat occupancy in a stream reach are difficult to extrapolate to other streams or even to other reaches within the same stream. Process-based bioenergetic models have also been used to predict carrying capacity for drift-feeding salmonids (e.g., Hayes et al., 2007). Though promising, these complex models require detailed data of composition, abundance and spatial patterns of invertebrate drift as well as the development of drift-foraging models describing the feeding habits and energetics of target species, so their generalization to other species or river systems must be considered with caution.

In this work we propose a novel method to estimate the carrying capacity for territorial salmonids. In the proposed model, maximum abundance is limited by environmentally induced fluctuating habitat conditions and regulated through territorial behaviour. The quantity of suitable habitat available for fish of a given age is estimated as a function of discharge using physical habitat simulations, and the maximum number of fish that can be sustained is estimated as the area of suitable habitat divided by the expected individual territory area for the given aged cohort. We tested whether the model is capable of explaining the annual fluctuations in young-of-the-year, juvenile and adult densities in brown trout *Salmo trutta* L. populations from twelve Mediterranean rivers.

2. Materials and methods

2.1. Rationale of the model

We define carrying capacity as the maximum density of fish a river can naturally support during the period of minimum available habitat. That is, habitat quantity (the area that generates positive growth and survival for an organism across a riverscape, i.e. the usable habitat) and quality (realised growth and survival rates in different habitat types) would determine the maximum number of individuals in a stream. Since stream habitats change spatially and temporally, life histories and demographic traits of conspecific populations also vary in space and time, so that the habitat acts as a template for the ecology of salmonid species (Jonsson and Jonsson, 2011). Consequently, spatio-temporal variations in population density of salmonids are typically related to changes in habitat conditions (Klemetsen et al., 2003; Milner et al., 2003). Though physical habitat structure and prey abundance jointly determine both habitat quantity and quality (Rosenfeld and Taylor, 2009), for the purposes of modelling, we considered physical habitat the main environmental factor limiting population size. Given the territorial nature of salmonids and their energetic requirements, there is clearly a limit to the number of fish that any habitat can support (Grant and Kramer, 1990; Milner et al., 2003). Hence territory size will set the maximum number of individuals that a stream can sustain, providing the link between available habitat and carrying capacity.

The rationale of the approach is simple: at low population densities, individuals will establish large territories at habitats of the highest quality; but with increasing density, individuals will be progressively forced to defend territories of increasingly smaller size and to occupy sub-optimal habitats (Bult et al., 1999; Newman, 1993). However, there is a threshold of habitat quality in which it is not profitable in terms of energy gain to defend a territory, so that individuals will either display an alternative behaviour (non-territoriality or floating), emigrate or die (Elliott, 1994; Newman, 1993). Consequently, as the habitat becomes increasingly saturated with territories, the probability of observing density-dependent losses increases (Grant and Kramer, 1990). Yet the prior operation of density-dependence on growth would moderate the magnitude of population decline due to density-dependent mortality and emigration, so that the population would be maintained at the highest possible abundance (Keeley, 2001; Lobón-Cerviá, 2007). Although density-dependent effects on growth are generally stronger at low densities, density-dependent growth patterns actually depend on the distribution of habitat quality within the stream (Ward et al., 2007). The point when all suitable habitats are saturated with territories representing the minimum spatial requirements of individuals corresponds to the stream carrying capacity.

2.2. The model

The dynamics of stream physical habitat can be modelled by means of physical habitat simulation models. These models simulate the temporal evolution of habitat quality and quantity in relation to flow conditions. Physical habitat is characterized by means of the key habitat features limiting distribution and abundance of salmonids, which are typically considered to be depth, current velocity, substrate and cover (see review by Armstrong et al., 2003). Hydraulic conditions (depth and velocity) are simulated through hydraulic models. The suitability of channel structure (substrate and cover) and simulated hydraulic conditions for an aquatic species and its life stages is then assessed by means of habitat suitability models (the habitat suitability criteria, HSC). The HSC are commonly depicted as habitat selection curves, which represent habitat preference under the prevailing biotic and abiotic conditions in any particular stream, so that they can be seen as operational applications of the realized ecological niche (Rosenfeld, 2003). The standard output of physical habitat simulations is the curve that relates the weighted usable area (WUA; m^2 WUA ha^{-1}, an index combining quality and quantity of available habitat) with stream flow.

It is usually assumed that the niche separation of different fish sizes and salmonid species is enough to keep intercohort and interspecific competition at low levels (Milner et al., 2003).