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Size-structured demographic models of coral populations

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Abstract

The demographic processes of growth, mortality, and the recruitment of young individuals, are the major organizing forces regulating communities in open systems. Here we present a size-structured (rather than age-structured) population model to examine the role of these different processes in space-limited open systems, taking coral reefs as an example. In this flux-diffusion model the growth rate of corals depends both on the available free-space (i.e. density-dependence) and on the particular size of the coral. In our analysis we progressively study several different forms of growth rate functions to disentangle the effects of free space and size-dependence on the model's stability. Unlike Roughgarden et al. [1985. Demographic theory for an open marine population space-limited recruitment. Ecology 66(1), 54–67], whose principal result is that the growth of settled organisms is destabilizing, we find that size-dependent growth rate often has the potential to endow stability. This is particularly true, if the growth rate is dependent on available free space (i.e. density dependent), but examples are given for growth rates that even lack this property. Further insights into reef system fragility are found through studying the sensitivity of the model steady state to changes in recruitment.

Keywords: Open system; Recruitment; Size structure; Coral populations

1. Introduction

The demographic processes of growth, mortality, and the recruitment of young individuals, are the major organizing forces controlling the establishment and regulation of coral reef communities. Here we present a size-structured population model to examine the role of these different processes in space-limited open systems. In particular, we pay close attention to those factors that give rise to stable population distributions. Although a number of important theoretical studies have already attempted to achieve this goal, apart from a few notable exceptions, nearly all have dealt with age-structured rather than size-structured populations. However, as we discuss below, for corals, the latter is more likely to be appropriate. Furthermore, a size-structured formulation opens the way for investigating realistic scenarios in which coral growth rates are themselves size-dependent and/or dependent on free space (i.e. density-dependent).

Our interest centers on benthic stony corals which are marine sessile organisms having a two-phase life cycle; a small larval dispersal phase and a larger adult phase. Larvae recruits settle onto unoccupied areas of the reef and begin to spread out by asexual reproduction to form colonies. Colonies begin to grow, and as sedentary adults, they occupy hard substrate of the free area in the reef. When the corals reach maturity, individuals start reproducing sexually, and disperse planktonic larvae. Larvae from different habitats are mixed in a pelagic pool that is distant and separated from the reef, and then settle back to vacant spaces in the reef. Note that recruited larvae rarely return to the same reef they originate from. Because the recruitment of new individuals derives from an external pool that is decoupled from the local population, coral reefs (similar to many marine systems) are often considered demographically open. The ability of open systems to persist in time is something of a paradox because local populations are unable to regulate themselves by their own fecundity (Caley et al., 1996), but instead rely solely on external recruits. Explaining the stability of open systems that lack intrinsic density-dependent birth–death processes

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is an area of research that is currently receiving much attention (Armsworth, 2002).

As larvae rarely settle on living colonies, recruitment depends on coral coverage and is proportional to the amount of free space available in the reef (Hughes et al., 1985; Connell et al., 1997). This has been shown in various field studies where a positive correlation between the number of new recruits and the amount of free-space available has been reported (Hughes, 1990; Connell et al., 1997; Gaines and Roughgarden, 1985). The amount of free space available to settle can often be severely limiting, and can act as a form of density-dependence. A space-limited reef that is largely occupied is unable to bring in new recruits, while a reef with a relatively large amount of free space is more accessible for new young individuals to settle. This density-dependence has led to the view that space-limited recruitment may act as a regulating process (Hughes, 1990, 1996) and has become known as the "Recruitment Limitation Hypothesis", raising debates on the role of recruitment in regulation with relation to other regulatory mechanisms (Caley et al., 1996; Chesson, 1998; Armsworth, 2002; Hixon et al., 2002).

In order to understand these processes better Roughgarden et al. (1985) introduced an age-structured demographic model suitable for open marine populations. Although intended for barnacle populations, the model is equally relevant for many single species populations of sessile marine invertebrates that have a pelagic larval phase. The model predicts the stable-age distribution of a population with age being taken as a continuous variable (i.e. in contrast to dividing the population into distinct age-classes). The three main processes in the model involve recruitment of larvae, growth after settlement and mortality of adults. The rate of recruitment was assumed to depend explicitly on the amount of unoccupied space in the local area. In simple terms, the dynamics of the model are such that larvae land on unoccupied space, grow, and, as space fills up with adults, the recruitment to the system decreases. The model exhibits two distinctive regimes. If the growth rate is sufficiently slow relative to the death rate, then space fills up with organisms to a point where recruitment balances death. This leads to a globally stable steady state with individuals having a stable age distribution. However, under other parameter ranges where the organisms grow quickly relative to the rate of renewal of space due to mortality, this growth will rapidly fill up unoccupied space, thereby interfering with recruitment. If the recruitment rate is sufficiently large, this interference can destroy the stability of the steady state. It could, for example, cause a limit cycle oscillation in the number of individuals through time or, it might cause the system to collapse.

Another very important result found by Roughgarden et al. (1985) is known as the "50% rule" which states that if free-space at steady state is larger than 50%, then this steady state must be asymptotically stable. The rule has been discussed widely in the ecological literature and has inspired a number of important mathematical analyses. Bence and Nisbet (1989), for example, have attempted to explain why the steady state can become unstable and lead to cyclic fluctuations when free space is limiting (see also Zhang et al., 1999; Inaba, 2002). Inaba (2002) has rigorously examined stability properties of an important class of related models in which mortality is a density-dependent process.

Although Roughgarden et al. (1985) incorporated space-dependency via recruitment limitation in their age-class model, they concluded that there is a need to extend this: "For many species, growth, rather than mortality, is sensitive to the amount of free space in the system. The growth may simply stop when free space is exhausted." Here we consider whether a density-dependent (i.e. free space dependent) growth rate might not affect the stability of the system. This is a line of inquiry initiated by Muko et al. (2001) and Olinky (2000) who examined a specific model and found that incorporation of density-dependent growth indeed enhances stability. We extend these works by examining the stability properties of a much larger range of models having increasing degrees of realism. In particular, growth rate functions with non-monotonic size-dependence. The model set up also permits examination of sensitivity to recruitment rates. Namely, it becomes possible to identify regimes in which small changes of recruitment can lead to relatively large variations in coral coverage.

2. A size-structured model for coral populations

Field research shows that for corals many demographic and life history processes, such as growth and death, depend on the size of individuals rather than age (Harper, 1977; Hughes and Jackson, 1980; Kojis and Quinn, 1985). Hughes (1984) suggests that: "Conventional age-related population analysis is totally unsuited to the demographic characteristics of colonies." He argues that many corals in the same size class can be of widely different ages; small corals are frequently older than large corals due to coral fragmentation. Furthermore, coral size can be a better estimator of growth than age; often smaller colonies have faster growth rates. For these reasons, there have been several attempts to construct size-structured population models relevant to coral population dynamics. Hughes and Connell (1987), Tanner (1997), Pascual and Caswell (1989) and Svensson et al. (2005) have modified Leslie matrix demographic models for this purpose and deal with the dynamics of a population divided into discrete size-classes. However, there have been few attempts to analyse continuous time size-structured models in which size is also continuous rather than divided into discrete classes, and most of these did not consider the effect of space-limitation in open systems (Sinko and Streifer, 1967; VanSickle, 1977; Murphy, 1983). As Gurney and Nisbet (1998) point out, this is no easy matter: "Continuous time models of populations composed of individuals