Dynamics of a predator–prey interaction with seasonal reproduction and continuous predation

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A B S T R A C T

Dynamics of predator–prey systems are affected by life history attributes of both predator and prey. We compare performance of several different models of one specific type of predator–prey interaction in which both predator and prey exhibit seasonal reproduction and predation is continuous. We show that use of a discrete-time model that preserves seasonal reproduction, whether stage-structured or non-stage-structured, always produces equilibria that are locally stable, whereas use of a continuous-time predator–prey model with an instantaneous approximation of seasonal reproduction can produce a limit cycle (self-sustained population fluctuations). This difference in dynamics results from the mismatch of life history properties between the mathematical model and the biological system under the continuous time model. We conclude that seasonal reproduction may be an important stabilizing factor in predator–prey interactions. Finally, with stage-structured predator–prey models, we show how life history parameters affect asymptotic dynamics of the system. Discrete-time models provide a more natural match to the biology of these systems. Our results suggest that discrete-time models have the potential for reducing the gap between theoretical models and empirical observations for these systems.

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1. Introduction

A good model should incorporate corresponding attributes of the natural system. For example, it is important to consider relative timescales of multiple events (Hanski, 1991) and incorporate them appropriately into a model in order to understand ecological systems (Hastings, 2004, 2010). For modeling predator–prey interactions, continuous-time models with ordinary differential equations (Lotka, 1925; Volterra, 1928; Holling, 1959) are most common. Although these models are suitable when predation and other life history events such as birth and death occur simultaneously in time (Pimm, 1991), they are not suitable for modeling organisms with seasonal reproduction. On the other hand, discrete time models using difference equations are more appropriate when life history events occur sequentially (Hassell, 1978; Hadeler and Gerstmann, 1990; Neubert et al., 1995). Although an alternative could be to convert a continuous-time model into a discrete-time model by analytically solving the differential equations (Nicholson and Bailey, 1935; Funasaki, 1993; Liu, 2004; Zhang, 2005), this approach is only possible with a small set of differential equations. Another alternative, called semi-discrete models, or "pulsed differential equations," also exists. These models use

differential equations to describe within-year dynamics (mortality) and difference equations as "update rules" to describe between-year dynamics (reproduction or recruitment), thus incorporating both continuous and discrete life history events (Pachepsky et al., 2008). Finally, individual based models (Petersen and DeAngelis, 1992; McCauley et al., 1993; Rose, 1999) are also available. The latter two types of models are more flexible, but they do not take full advantage of the rich analytical tools available for ODE or difference equation models.

In this study, we investigate the effect of population structures on predator–prey dynamics. In particular, we develop and analyze a set of predator–prey models for animal populations that exhibit seasonal reproduction (that occurs in one distinct season each year) and continuous predation (that is continuous throughout the year). Interacting populations with seasonal reproduction and continuous predation are common in nature, e.g., the Canadian lynx and hare system (Elton and Nicholson, 1942), wolf and moose system on Isle Royale (Vucetich and Peterson, 2009), and the piscivorous fish system in coral reefs (Connell, 1997, 1998). Recent studies have emphasized the importance of the stage structure in understanding population dynamics (e.g., Wang and Chen, 1997; Liu et al., 2002; Thornber and Gaines, 2004; Fujiwara, 2012). This becomes especially true when we are dealing with populations experiencing trophic interactions because many animal populations have abrupt shifts in habitat and diet preference accompanying ontogenetic development. For example, highly migratory fish such as

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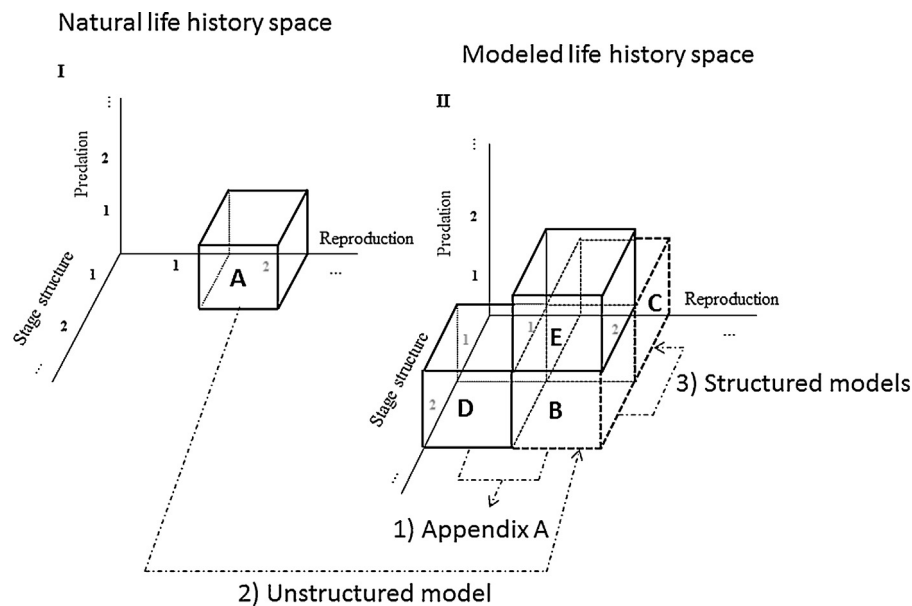
Fig. 1. Alternative methods of mapping the life history state space of a predator–prey system in which both predator and prey exhibit seasonal reproduction and predation is continuous (sector A) into modeled life history state space (sectors B–E). Here, the state space is defined by three categorical variables: reproduction (1 = continuous, 2 = discrete), predation (1 = continuous, 2 = discrete), and population stage structure (1 = structured, 2 = non-structured). Broken arrows represent the modeling processes we consider in this paper. In Appendix A, we compare the dynamics of two unstructured models (sectors B and D), and then we build an unstructured model (sector B) from a natural system (sector A). Finally, we add stage-structure to the unstructured model (sector B) to obtain the structured models (sector C). See Section 1 for details.

bluefin tuna *Thunnus thynnus* and yellowfin tuna *Thunnus albacares* show a shift in feeding preferences due to different use of habitats and food items as a function of their life stage (Graham et al., 2007; Sar and Sarà, 2007). The dynamics of those stage-structured populations are often studied within the framework of matrix population models (Lima and Páez, 1997; Jarry et al., 1998; Fujiwara and Caswell, 2001; Zabel et al., 2006; Crozier et al., 2008). Recent theoretical treatment of stage-structured interspecific interactions includes two-population, two-stage models with Ricker type (Moll and Brown, 2008) and Beverton–Holt type (Fujiwara et al., 2011) competitive interactions, and intra-guild predation with Nicholson–Bailey trophic interaction between juvenile stages (Faria et al., 2011). Ohlberger et al. (2011) used a continuous-time stage-structured consumer-resource model that was originally developed by De Roos and Roos (2007) with a type II functional response to show the biomass overcompensation of the juvenile stage in response to increased adult mortality in a wild perch population. These studies suggest the importance of distinguishing different stages within a population in inter- and intra-specific interactions in order to capture the rich dynamics exhibited by the natural systems.

Predator–prey systems with continuous predation and seasonal reproduction may be conceptualized as occupying a location in the life history state space of predator–prey systems (Fig. 1). Here, the space is defined by three categorical variables: reproduction (1 = continuous, 2 = discrete), predation (1 = continuous, 2 = discrete), and population stage structure (1 = structured, 2 = non-structured). The scope of this study is to model the predator-prey system that exhibits discrete reproduction and continuous predation (natural life history sector (A) in panel I of Fig. 1). Note that natural populations are almost always structured, e.g., by age, developmental stage, physiological state, or other characteristics (see Caswell, 2000, and references therein). The plan of this paper is as follows. First, we compare dynamics of two modeling sectors, both unstructured and showing continuous predation, but one with discrete reproduction (B) and the other with an instantaneous approximation (D) to the discrete reproductive process in Appendix A. This is to highlight the

potential problems associated with the timescale approximation process. Then, we develop an unstructured model (B) from a natural predator–prey system (A, Getz, 1984). Later, we incorporate stage structure (C) into the previous unstructured model and compare their dynamics. Yet another method of mapping the life history state space into modeled life history state space (E) represents models that exhibit complex dynamics (Neubert and Kot, 1992; Jing and Yang, 2006; Liu and Xiao, 2007). Although of mathematical interest, exploration of these models is beyond the scope of the current study. Moreover, there exist more types of mode of predation, reproduction and structure than those considered there, and these are discussed in Section 4.

2. Methods

2.1. Models

We will develop three models beginning with one in which both predator and prey populations are unstructured (sector B in Fig. 1). Next, we introduce spatial structure to the predator population. In this model, a predator can move from one location to the other unidirectionally. We envision that this type of system can be useful in investigating the possibility of biological control of pests. Finally, we develop a model for the system in which both predator and prey populations are structured into different life stages. Because the dynamics of the second model can be understood using the results from the unstructured model (first model), we describe the development of unstructured and structured predator–prey models.

2.1.1. Unstructured model

A discrete time single-stage predator–prey model can be written as

$$N_{t+1} = F[G(N_t, P_t)]N_t, \tag{1}$$

$$P_{t+1} = H(N_t, P_t)P_t, \tag{2}$$